

specify a feedback coupling and determine the resulting interaction function; this has been done, for example, for coupled neural oscillators (9). In what amounts to turning the problem on its head, Kiss *et al.* proceed in the reverse direction: They specify the interaction function that they would like to have (that is, the interaction function that generates some specified behavior), and then follow an optimization procedure to determine the feedback that generates it.

The result is a systematic procedure for generating a wide variety of dynamical behaviors. One of the simplest is synchronization, where all oscillations are at the same frequency and the phase difference between each pair of oscillators is constant. By carefully choosing the target interaction function, however, the optimized feedback allows dynamics that switch between different synchronized states, each with a distinct set of phase differences. Still another choice for the target interaction function produces complete desynchronization when the feedback control is turned on. This is the goal in anti-pacemaker applications when one needs to destroy some pathological global resonance.

There is a voluminous literature on the mathematics of coupled oscillators. The

approach of Kiss *et al.* is unique in that it does not merely involve theoretical models of coupled nonlinear oscillators, or a comparison between such theoretical models and experimental results. Rather, it shows that such models can be made sufficiently accurate to provide precise control of experimental systems.

There are obvious limitations to the approach. The oscillators need to be sufficiently similar to one another, and the interactions must be independent of their spatial location—one cannot have specific arrangements in space, as for a school of fish or a flock of birds. In addition, there are cases of continuous spatiotemporal evolution, such as the Belusov-Zhabotinsky reaction, where one cannot identify specific agents and decompose the system into an array of discrete oscillators. But the method is worthy of further exploration. The ability to use a light touch is a strong plus, engineering change without altering the essential nature of the system. The possibility of doing so in the absence of detailed information about the elements of the system is another.

Ecological systems have a natural rhythm and, despite formidable obstacles, it may be tempting to look for applications in this area. The most promising applications, however, may arise in medical science and biological

systems—not by creating order, but by destroying synchronization. Parkinson's disease and epilepsy are two compelling and challenging examples. The former is already being treated with some success using deep brain stimulation (10); it is hoped that further research into both the oscillations in the brain involved in such disorders and methods of the type introduced by Kiss *et al.* will, one day, lead to new, more effective ways of alleviating such conditions.

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BEHAVIOR

A Narrow Road to Cooperation

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In every human society, from small-scale foraging bands to gigantic modern nation states, people cooperate with each other to solve collective-action problems. They share food to ensure against shortfalls, risk their lives in warfare to protect their group, work together in building canals and fortifications, and punish murderers and thieves to maintain social order. Because collective action benefits everyone in the group, whether or not they contribute, natural selection favors non-contributors. So, why do people contribute? Everyday experience suggests that people contribute to avoid being punished by others.

But this answer raises a second question: Why do people punish? From an evolutionary perspective, this question has two parts: First, how can contributors who punish avoid being replaced by “second-order” free-riders who

contribute but do not incur the cost of punishing? There has been much work on this topic lately, and plausible solutions have emerged (1–5). However, these solutions are not much good unless we can solve the second problem: How can punishment become established within populations in the first place? On page 1905 of this issue, Hauert *et al.* provide the first cogent answer to this question (6). Surprisingly, they find that punishment can become established if there are individuals who neither produce collective benefits nor consume collective benefits produced by others.

In previous models of the evolution of collective action, individuals in a group can either contribute and benefit from the public good (i.e., cooperate), or not contribute and benefit (i.e., defect). In the absence of punishment, defection wins. However, if punishment is possible and punishers are common, it does not pay to defect. But punishment is costly to impose. A rare punisher in a group of defectors suffers an enormous disadvantage from

A new model of collective action shows how socially beneficial punishment can arise and evolve.

having to punish everyone in the group. This means that in very large populations, punishment can sustain cooperation when punishment is common, but punishing strategies cannot increase in numbers when they are rare (i.e., invade a population of defectors). In a finite population, random chance affects the number of each type that reproduce, and the resulting stochastic fluctuations allow punishers to eventually invade a population of defectors, even though selection favors defectors. However, it can take a very long time for this to occur, and thus, most of the time there is no punishment and no cooperation.

Hauert *et al.* provide a way out of this dilemma. They introduce a strategy that simply opts out of collective action. These “nonparticipants” neither contribute to the collective good nor consume the benefits, but instead pursue some solitary activity. Surprisingly, this innovation allows punishment to increase when rare. To see why, consider a population of defectors. Hauert *et al.* assume that nonparticipants get a

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In or out? (Top) A group of Hadza men hunting cooperatively. Hadza hunter-gatherers living in Tanzania sometimes consume smaller kills in the bush, consistent with the Hauert *et al.* model. **(Center)** People from the village of Lamalera, Indonesia, hunt whales cooperatively. This form of cooperative hunting exhibits strong economies of scale not represented in the Hauert *et al.* model. **(Bottom)** Demonstrators in Kiev during the first anniversary of the Orange Revolution, November 2005. In the contemporary world people often participate in collective political action whose benefits are not excludable.

higher payoff than defectors who attempt to free-ride when there are no cooperators in their group. Therefore, nonparticipants invade the defectors. Now, consider a population of all nonparticipants. Hauert *et al.* assume that two contributors working together can produce a higher payoff than a nonparticipant working alone. This means that rare contributors invade nonparticipants. Once contributors are common, defectors invade, and the cycle continues. The three strategies oscillate endlessly (7).

The key contribution of the current paper is to show that punishers readily invade this oscillating mixture of cooperators, defectors, and nonparticipants, and once they do they tend to persist. The reason is that defectors are absent during part of each cycle of the oscillation, and as a result punishers are not selected against during these periods. Consequently, stochastic fluctuations in a finite population cause punishers to invade rapidly. Once common, punishers do better than other types, and it takes a long time for cooperators and then defectors to drift back in. This means that the population spends most of the time in a happy state in which cooperation and punishment of defectors predominate.

Adding nonparticipants to the standard models required Hauert *et al.* to make a number of new assumptions. Three of these are crucial; punishment cannot invade without them. There are many examples of collective action that do not conform to these assumptions, and, as a consequence, the model explains the origin of punishment for some kinds of collective action but not others.

First, the collective good must be excludable. Otherwise, abstaining from the benefits once the good is created is not an option. In human societies, collective action produces many types of goods, and not all are excludable. For instance, if warriors steal cows on a cattle raid (8) and keep the cows that they steal, the booty doesn't benefit the entire group—the good is excludable (see the figure). On the other hand, when warriors successfully defend a village from an invading army, the benefits of deterrence from future attacks and protection of land, belongings, and lives flows to everyone in the victorious group—the good is not excludable.

Second, Hauert *et al.* assume that opting out is better than mutual defection. This assumption applies when defectors experience some

opportunity cost that non-participants do not. For example, in some settings, hunters consume small kills before they return to camp (9). To share such kills, you need to leave your garden for the day and join a hunting party. But if the hunting party that you join consists of defectors who don't work hard enough to make a kill, you will be worse off than nonparticipants who stayed home and tended their gardens. However, in many small-scale societies, hunters bring their kills back to camp (10, 11), where others have a chance to scrounge some meat. Here, defectors can tend their gardens just like nonparticipants, but then scrounge. In this case, defection has at least as high a payoff as opting out.

Third, Hauert *et al.* assume that there are no economies of scale. In their model, the per capita payoff from participating in collective action does not depend on the number of contributors, only on the ratio of contributors to defectors. This means that two contributors who work together can generate the same per capita payoff as a much larger group of contributors. This assumption applies to the payoff structure of recent public goods experiments (12, 13) and approximates some real-world situations like sharing food to reduce the risk of shortfall (14). However, many collective action problems are subject to strong economies of scale. These include warfare, hunting large game (15, 16), and the construction and maintenance of capital facilities like forts, irrigation works, and roadways. These examples are important because it is the ability to mobilize sizable groups to solve such problems that distinguishes human cooperation from that of other mammals.

The model by Hauert *et al.* is an important contribution because it provides the first cogent mechanism that can jump-start the evolution of punishment. It can help us to understand the evolution of collective action in which benefits are excludable, opting out is



preferable to mutual defection, and there are no economies of scale. The challenge is now to understand how punishment can arise in the remaining cases.

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