will be challenging if they are unstable.

New functions for poly(U) are emerging. The tail can be added to mRNAs to trigger their decay. mRNAs that direct the synthesis of histones—the major protein constituents of chromatin—during the cell division cycle are rapidly degraded once DNA replication is completed or blocked. Intermediate mRNAs in this decay process often have poly(U) tails of 8 to 10 residues (*10*). Small interfering RNAs directed against two candidate PUP enzymes blocked this degradation, implying that poly(U) addition is essential for their decay. Also, in *S. pombe*, a PUP adds poly(U) to actin mRNA, though its effect on turnover is unknown (*9*).

A poly(U) tail may enhance degradation by stimulating removal of the mRNA's 5′ cap structure, a key step in mRNA turnover. Poly(U) tails enhance "decapping" in a cell-free system (*11*). Likely, the tails bind the Lsm protein complex, which associates with decapping factors (*11*, *12*). Indeed, depletion of Lsm1 inhibits histone mRNA turnover (*10*).

Addition of uridines probably has diverse consequences, including RNA stabilization (*6*); yet this modification often occurs on an RNA's road to ruin (see the figure). Aberrantly unmethylated microRNAs in the plant *Arabidopsis thaliana* are modified with oligo(U) and destroyed (*2*). Fragmentation of mRNA by microRNAs is accompanied by the addition of oligo(U) to the pieces before they disappear (*13*). The most common mRNA decay pathway involves association of the Lsm complex to the mRNA after poly(A) removal. Even this route may rely on evanescent, short oligo(U) because the Lsm complex preferentially binds 3′-terminal uridine tails.

The discovery of poly(U) tails on mRNAs opens unexplored territory in the RNA world. Dual-personality enzymes could switch an mRNA's fate from life to death simply by a change in the nucleotide they accept. Others may well wait in the wings, along with proteins that target specific RNAs, or remove the tails. Count on new roles for poly(U), an expanding list of RNAs that receive it, and more startling enzymes that put it on and take it off.

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BEHAVIOR

Punishment and Cooperation

Herbert Gintis

Data from economic games show that the effectiveness of punishment in fostering cooperation varies greatly from society to society.

Even champions of modern society agree that it involves a loss of community (based on family and ethnic ties) and an expansion of civil society, with emphasis on the more impersonal interactions among individuals with minimal social ties. For two centuries, this dichotomy has anchored our understanding of modern Western society, applauded by its defenders as the fount of freedom (*1*), yet identified as the source of inequality (*2*), the decline of community (*3*), the destruction of the environment (*4*), and the impotence of grassroots political action (*5*). On page 1362 of this issue, Herrmann *et al.* (*6*) report their discovery that university students in democratic societies with advanced market economies show different social behavior from that exhibited by students in more traditional societies based on authoritarian and parochial social institutions. Their results suggest that the success of democratic market societies may depend critically on moral virtues as well as material interests, so the depiction of civil society as the sphere of "naked self-interest" is radically incorrect.

The standard view holds that human nature has a private side in which we interact morally with a small circle of intimates and a public side in which we behave as selfish maximizers. Herrmann *et al*. suggest that most individuals have a deep reservoir of behaviors and mores that can be exhibited in the most impersonal interactions with unrelated others. This reservoir of moral predispositions is based on an innate prosociality that is a product of our evolution as a species, as well as the uniquely human capacity to internalize norms of social behavior. Both forces predispose individuals to behave morally even when this conflicts with their material interests.

These results are the latest to document a principle of reciprocity according to which people are more willing to sacrifice private gain for the public good as the cost of the sacrifice decreases and as expectations of the extent that others will sacrifice grows. In addition, individuals embrace such character virtues as honesty, trustworthiness, consideration, and loyalty (*7*). Of course, these moral predispositions moderate rather than eliminate considerations of self-interest and loyalties to kith and kin.

Suggestive evidence for the principle of reciprocity comes from daily life. For instance, political democracy has frequently been attained through popular collective action. Voting in elections is widespread despite its being personally time consuming, and the benefits are purely public (a single vote can change an electoral outcome only with infinitesimal probability). Moreover, citizens in democratic societies often vote to give substantial sums to charity, and to approve of poverty relief, although these measures increase the tax burden for the average voter.

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Experimental evidence for reciprocity comes from behavioral game theory, which uses economic games in which subjects make choices under varied social conditions. For instance, Herrmann et al. employ a public goods game in which each of four anonymous subjects is initially given 20 tokens, and each is told he can place any number of these tokens in a public account. The tokens in the account are multiplied by 1.6 and the result divided evenly among the four. At the end of the experiment, the tokens are exchanged for real money.

In this game, each individual helps the group most by placing his 20 tokens in the

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public account, and if all do so, each earns 32 tokens. However, if a single individual is selfish, he will place nothing in the public account, and his earnings will be 20 + 60(1.6)/4 = 44 tokens. But, if all four are selfish, each earns only 20 tokens. Because the four subjects are strangers, the standard view of human nature suggests that there will be zero contributions. However, in the many times this game has been played in a variety of social settings, the older view is virtually never supported, and the average contribution is about half the initial endowment (*8*).

The public game indicates that individuals generally fall halfway between selfishness (keep all 20 tokens) and public-spiritedness (place all 20 tokens in the public account). However, mean contributions to the public account generally fall over many trials, reaching a very low level after 10 repetitions. By varying the rules of the game, researchers have concluded that the principle of reciprocity is responsible for the observed decay of cooperation: Subjects who contributed more than average on one round contribute less on the following round, showing their disapproval of the unfairness of their fellow players. Indeed, a single selfish individual in the group can lead contributions to spiral down to almost zero.

An innovation of Fehr and Gächter (*9*), used by Herrmann *et al*. as well, was to add punishment after each round of play. Each player A could specify that the player B associated with a particular contribution have three tokens deducted from his payoff, for each token deducted from A's payoff. Under these new conditions, the high contributors punished the low contributors who, in succeeding rounds, increased their contributions, so that in the 10th and final round, there was almost 100% cooperation. The behavioral propensity to cooperate with others at personal cost, and to punish non-cooperators even when this is personally costly in the long run, has been called strong reciprocity. The punishment meted out is considered altruistic because it increases the payoff of group members at a personal cost to the punisher.

The natural interpretation is that low contributors are selfish types who increase their contribution after punishment in order to avoid future punishment. However, many low contributors respond almost as much to symbolic as to monetary penalties, which indicates that many punishees are not self-interested but rather are motivated to increase their offers because they feel guilty for having violated a contribution norm (*10*). However, some researchers found a curious phenomenon. A few subjects, when punished, rather than contributing more, suspected that it was the high contributors who punished them, and responded with antisocial punishment: They punished the high contributors in future rounds, leading the latter to reduce both their contribution and altruistic punishment (*11*).

Herrmann *et al*. collected data in 15 countries with widely varying levels of economic development. The subjects were university students in all societies. The authors found that antisocial punishment was rare in the most democratic societies and very common otherwise. Indexed to the World Democracy Audit (WDA) evaluation of countries' performance in political rights, civil liberties, press freedom, and corruption, the top six performers among the countries studied were also in the lowest seven for antisocial punishment. These were the United States, the United Kingdom, Germany, Denmark, Australia, and Switzerland. The seventh country in the low antisocial punishment group was China, currently among the fastest-growing market economies in the world. The countries with a high level of antisocial punishment and a low score on the WDA evaluation included Oman, Saudi Arabia, Greece, Russia, Turkey, and Belarus.

The most likely explanation is that in more traditional societies, the experimental setup represents a clash of cultures. On the one hand, high payoffs in the experiment require the modern ethic of cooperation with unrelated strangers, so subjects who are reprimanded for low contribution are likely to respond with feelings of guilt and a resolve to be more cooperative in the future. In a more traditional society, many players may hold to the ethic of altruism and sacrifice on behalf on one's family and friends, with indifference toward unrelated strangers. When punished, such subjects are likely to respond with anger rather than guilt. Punishing the high contributors is thus a means of asserting one's personal values, which take precedence over maximizing one's payoff in the game.

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OCEANS

On Phytoplankton Trends

Victor Smetacek[1] and James E. Cloern[2]

How are phytoplankton at coastal sites around the world responding to ongoing global change?

Phytoplankton—unicellular algae in the surface layer of lakes and oceans—fuel the lacustrine and marine food chains and play a key role in regulating atmospheric carbon dioxide concentrations. How will rising carbon dioxide concentrations in the air and surface ocean in turn affect phytoplankton? Answering this question is crucial for projecting future climate change. However, because phytoplankton species populations appear and disappear within weeks, assessing change requires high-resolution monitoring of annual cycles over many years. Such long-term studies at coastal sites ranging from estuaries and harbors to open coastlines and islands are yielding bewildering variability, but also fundamental insights on the driving forces that underlie phytoplankton cycles (*1*).

An example of regularity is provided by a 45-year data set from weekly phytoplankton monitoring in Lake Windermere, England, which shows that the diatom species *Asterionella formosa* dominates phytoplankton biomass from autumn to spring but is virtually absent during summer; this species drives silicon cycling in the lake (*2*). In contrast, weekly data collected in Narragansett Bay in Rhode Island since 1959 reveal that the phytoplankton react with wide fluctuations in composition and timing of the annual biomass

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