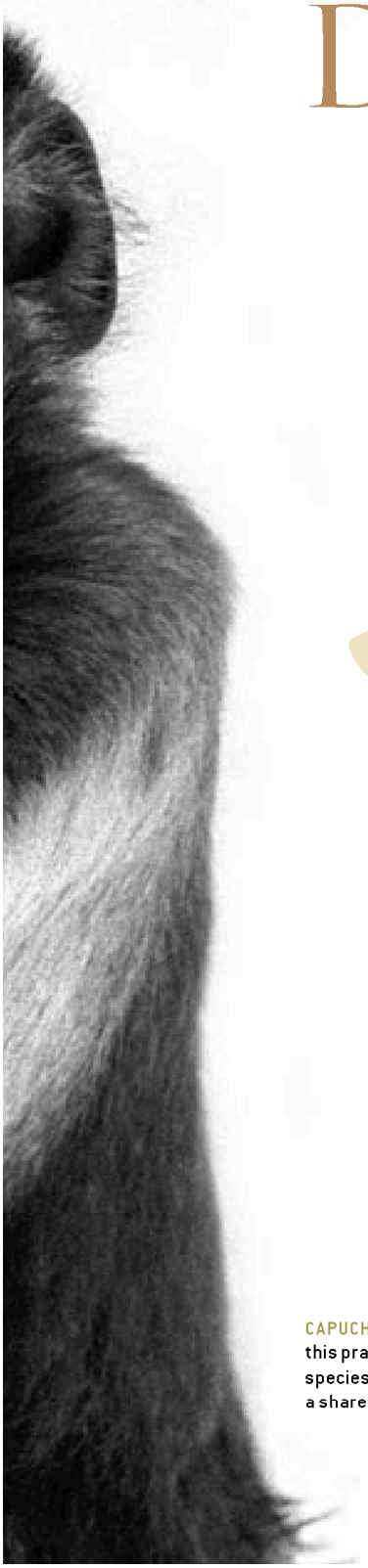
How Animals Do Business



By Frans B. M. de Waal

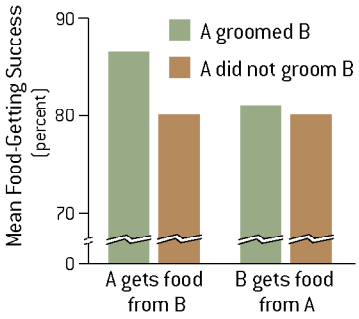
Just as my office would not stay empty for long were I to move out, nature's real estate changes hands all the time. Potential homes range from holes drilled by woodpeckers to empty shells on the beach. A typical example of what economists call a "vacancy chain" is the housing market among hermit crabs. To protect its soft abdomen, each crab carries its house around, usually an abandoned gastropod shell. The problem is that the crab grows, whereas its house does not. Hermit crabs are always on the lookout for new accommodations. The moment they upgrade to a roomier shell, other crabs line up for the vacated one.

One can easily see supply and demand at work here, but because it plays itself out on a rather impersonal level, few would view the crab version as related to human economic transactions. The crab interactions would be more interesting if the animals struck deals along the lines of "you can have my house if I can have that dead fish." Hermit crabs are not deal makers, though, and in fact have no qualms about evicting homeowners by force. Other, more social animals do negotiate, however, and their approach to the exchange of resources and services helps us understand how and why human economic behavior may have evolved.

The New Economics

CLASSICAL ECONOMICS views people as profit maximizers driven by pure selfishness. As 17th-century English philosopher Thomas Hobbes put it, "Every man is presumed to seek what is good for himselfe naturally, and what is just, only for Peaces sake, and accidentally." In this still prevailing view, sociality is but an afterthought, a "social contract" that our ancestors en-

CAPUCHIN MONKEYS share food just as chimpanzees and humans do. Rare among other primates, this practice may have evolved along with cooperative hunting, a strategy used by all three species. Without joint payoffs, there would be no joint hunting. Here a juvenile capuchin begs for a share by cupping his hand next to the food an adult male is eating.



CHIMPANZEES share food—these branches with leaves, for example—in return for favors such as grooming. This reciprocity was demonstrated experimentally by recording groomings on the mornings of days when food-sharing tests were scheduled. As the graph shows, chimp A's success in obtaining food from chimp B increased after A had groomed B, but B's success in obtaining food from A was unaffected by A's grooming. Thus, it is specifically the groomer who benefits, meaning that the rule is one of exchange of food for grooming.

tered into because of its benefits, not because they were attracted to one another. For the biologist, this imaginary history falls as wide off the mark as can be. We descend from a long line of group-living primates, meaning that we are naturally equipped with a strong desire to fit in and find partners to live and work with. This evolutionary explanation for why we interact as we do is gaining influence with the advent of a new school, known as behavioral economics, that focuses on actual human behavior rather than on the abstract forces of the marketplace as a guide for understanding economic decision making. In 2002 the school was recognized by a shared Nobel Prize for two of its founders: Daniel Kahneman and Vernon L. Smith.

Animal behavioral economics is a fledgling field that lends support to the new theories by showing that basic human economic tendencies and preoccupations—such as reciprocity, the division of rewards, and cooperation—are not limited to our species. They probably evolved in other animals for the same reasons they evolved in us—to help individuals take optimal advantage of one another without undermining the shared interests that support group life.

Take a recent incident during my research at the Yerkes National Primate Research Center in Atlanta. We had taught capuchin monkeys to reach a cup of food on a tray by pulling on a bar attached to the tray. By making the tray too heavy for a single individual, we gave the monkeys a reason to work together.

On one occasion, the pulling was to be done by two females, Bias and Sammy. Sitting in adjoining cages, they successfully brought a tray bearing two cups of food within reach. Sammy, however, was in such a hurry to collect her reward that she released the bar and grabbed her cup before Bias had a chance to get hers. The tray bounced back, out of Bias's reach. While Sammy munched away, Bias threw a tantrum. She screamed her lungs out for half a minute until Sammy approached her pull bar again. She then helped Bias bring in the tray a second time. Sammy did not do so for her own benefit, because by now the cup accessible to her was empty.

Sammy's corrective behavior appeared to be a response to Bias's protest against the loss of an anticipated reward. Such action comes much closer to human economic transactions than that of the hermit crabs, because it shows cooperation, communication and the fulfillment of an expectation, perhaps even a sense of obligation. Sammy seemed sensitive to the quid pro quo of the situation. This sensitivity is not surprising given that the group life of capuchin monkeys revolves around the same mixture of cooperation and competition that marks our own societies.

Overview/*Evolved Economics*

- The new field of behavioral economics views the way humans conduct business as an evolved heritage of our species.
- Just as tit for tat and supply and demand influence the trading of goods and services in human economies, they also affect trading activities among animals.
- Emotional reactions—such as outrage at unfair arrangements—underlie the negotiations of both animals and humans.
- This shared psychology may explain such curious behaviors as altruism—they are part of our background as cooperative primates.

The Evolution of Reciprocity

ANIMALS AND PEOPLE occasionally help one another without any obvious benefits for the helper. How could such behavior have evolved? If the aid is di-

FRANS B. M. DE WAAL (*preceding pages and this page*); ALISON KENDALL (*graph*)

rected at a family member, the question is relatively easy to answer. "Blood is thicker than water," we say, and biologists recognize genetic advantages to such assistance: if your kin survive, the odds of your genes making their way into the next generation increase. But cooperation among unrelated individuals suggests no immediate genetic advantages. Pëtr Kropotkin, a Russian prince, offered an early explanation in his book *Mutual Aid*, published in 1902. If helping is communal, he reasoned, all parties stand to gain—everyone's chances for survival go up. We had to wait until 1971, however, for Robert L. Trivers, then at Harvard University, to phrase the issue in modern evolutionary terms with his theory of reciprocal altruism.

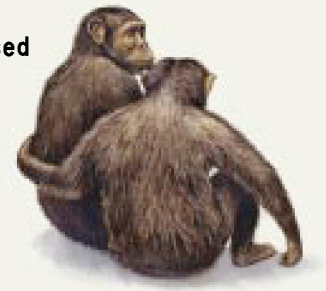
Trivers contended that making a sacrifice for another pays off if the other later returns the favor. Reciprocity boils down to "I'll scratch your back, if you scratch mine." Do animals show such tit for tat? Monkeys and apes form coalitions; two or more individuals, for example, gang up on a third. And researchers have found a positive correlation between how often A supports B and how often B supports A. But does this mean that animals actually keep track of given and received favors? They may just divide the world into "buddies," whom they prefer, and "nonbuddies," whom they care little about. If such feelings are mutual, relationships will be either mutually helpful or mutually unhelpful. Such symmetries can account for the reciprocity reported for fish, vampire bats (which regurgitate blood to their buddies), dolphins and many monkeys.

Just because these animals may not keep track of favors does not mean they lack reciprocity. The issue rather is how a favor done for another finds its way back to the original altruist. What exactly is the reciprocity mechanism? Mental record keeping is just one way of getting reciprocity to work, and whether animals do this remains to be tested. Thus far chimpanzees are the only exception. In the wild, they hunt in teams to capture colobus monkeys. One hunter usually captures the prey, after which he tears it apart and shares it. Not everyone gets a piece, though, and even the highest-ranking male, if he did not take part in the hunt, may beg in vain. This by itself suggests reciprocity: hunters seem to enjoy priority during the division of spoils.

To try to find the mechanisms at work here, we exploited the tendency of these apes to share—which they also show in captivity—by handing one of the chimpanzees in our colony a watermelon or some branches with leaves. The owner would be at the center of a sharing cluster, soon to be followed by secondary clusters around individuals who had managed to get a major share, until all the food had trickled down to everyone. Claiming another's food by force is almost unheard of among chimpanzees—a phenomenon known as "re-

What Makes Reciprocity Tick

Humans and other animals exchange benefits in several ways, known technically as reciprocity mechanisms. No matter what the mechanism, the common thread is that benefits find their way back to the original giver.

RECIPROCITY MECHANISM		KEY FEATURES
Symmetry-based "We're buddies"		Mutual affection between two parties prompts similar behavior in both directions without need to keep track of daily give-and-take, so long as the overall relationship remains satisfactory. Possibly the most common mechanism of reciprocity in nature, this kind is typical of humans and chimpanzees in close relationships. **Example:** Chimpanzee friends associate, groom together and support each other in fights.
Attitudinal "If you're nice, I'll be nice"		Parties mirror one another's attitudes, exchanging favors on the spot. Instant attitudinal reciprocity occurs among monkeys, and people often rely on it with strangers. **Example:** Capuchins share food with those who help them pull a treat-laden tray.
Calculated "What have you done for me lately?"		Individuals keep track of the benefits they exchange with particular partners, which helps them decide to whom to return favors. This mechanism is typical of chimpanzees and common among people in distant and professional relationships. **Example:** Chimpanzees can expect food in the afternoon from those they groomed in the morning.

ROBERTO OSTI

CLEANER FISH nibbles parasites in the open mouth of a large client fish. Roaming client fish rarely return to the station of a cleaner fish after they have been kept waiting (*left graph*) or cheated (*right graph*), meaning that the cleaner took a bite out of the client's healthy tissue. Cleaner fish therefore tend to treat roaming clients better than residents, who have no choice of cleaning stations.

spect of possession." Beggars hold out their hand, palm upward, much like human beggars in the street. They whimper and whine, but aggressive confrontations are rare. If these do occur, the possessor almost always initiates them to make someone leave the circle. She whacks the offenders over the head with a sizable branch or barks at them in a shrill voice until they leave her alone. Whatever their rank, possessors control the food flow.

We analyzed nearly 7,000 of these approaches, comparing the possessor's tolerance of specific beggars with previously received services. We had detailed records of grooming on the mornings of days with planned food tests. If the top male, Socko, had groomed May, for example, his chances of obtaining a few branches from her in the afternoon were much improved. This relation between past and present behavior proved general. Symmetrical connections could not explain this outcome, as the pattern varied from day to day. Ours was the first animal study to demonstrate a contingency between favors given and received. Moreover, these food-for-grooming deals were partner-specific—that is, May's tolerance benefited Socko, the one who had groomed her, but no one else.

This reciprocity mechanism requires memory of previous events as well as the coloring of memory such that it induces friendly behavior. In our own species, this coloring process is known as "gratitude," and there is no reason to call it something else in chimpanzees. Whether apes also feel obligations remains unclear, but it is interesting that the tendency to return favors is not the same for all relationships. Between individuals who associate and groom a great deal, a single grooming session carries little weight. All kinds of daily exchanges occur between them, probably without their keeping track. They seem instead to follow the buddy system discussed before. Only in the more distant relationships does grooming stand out as specifically deserving reward. Because Socko and May are not close friends, Socko's grooming was duly noticed.

A similar difference is apparent in human behavior, where we are more inclined to keep track of give-and-take with strangers and colleagues than with our friends and family. In fact, score-keeping in close relationships, such as between spouses, is a sure sign of distrust.

Biological Markets

BECAUSE RECIPROCITY requires partners, partner choice ranks as a central issue in behavioral economics. The

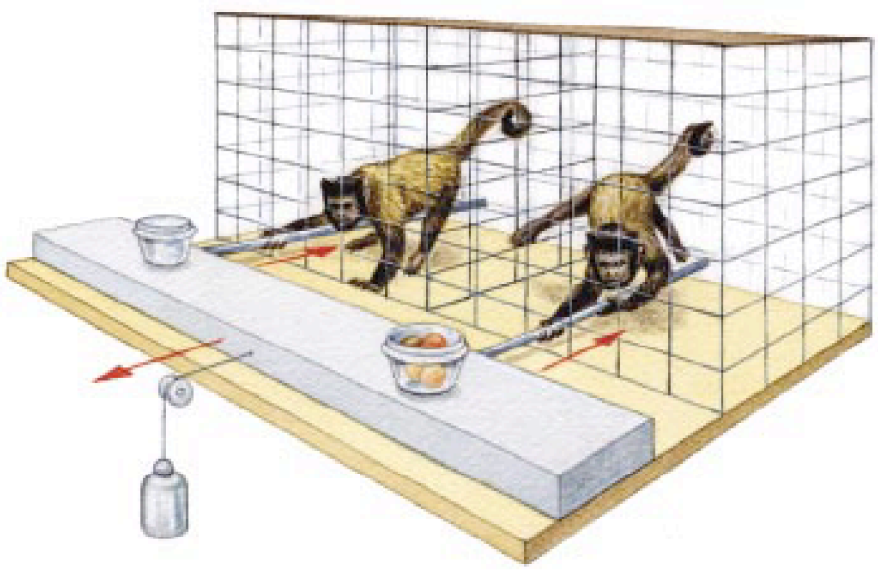
BABOON FEMALES pay a price in grooming to get a peek at a new infant; the fewer the infants, the longer the grooming time required. The value of commodities—baby baboons in this case—increases as their availability decreases.

TIM LAMAN *National Geographic Image Collection* (*top*); S. P. HENZI (*bottom*); ALISON KENDALL (*graph*)

hand-me-down housing of hermit crabs is exceedingly simple compared with the interactions among primates, which involve multiple partners exchanging multiple currencies, such as grooming, sex, support in fights, food, babysitting and so on. This "marketplace of services," as I dubbed it in *Chimpanzee Politics*, means that each individual needs to be on good terms with higher-ups, to foster grooming partnerships and—if ambitious—to strike deals with like-minded others. Chimpanzee males form coalitions to challenge the reigning ruler, a process fraught with risk. After an overthrow, the new ruler needs to keep his supporters contented: an alpha male who tries to monopolize the privileges of power, such as access to females, is unlikely to keep his position for long. And chimps do this without having read Niccolò Machiavelli.

With each individual shopping for the best partners and selling its own services, the framework for reciprocity becomes one of supply and demand, which is precisely what Ronald Noë and Peter Hammerstein, then at the Max Planck Institute for Behavioral Physiology in Seewiesen, Germany, had in mind with their biological market theory. This theory, which applies whenever trading partners can choose with whom to deal, postulates that the value of commodities and partners varies with their availability. Two studies of market forces elaborate this point: one concerns the baby market among baboons, the other the job performance of small fish called cleaner wrasses.

Like all primate females, female baboons are irresistibly attracted to infants—not only their own but also those of others. They give friendly grunts and try to touch them. Mothers are highly protective, however, and reluctant to let anyone handle their precious newborns. To get close, interested females groom the mother while peeking over her shoulder or underneath her arm at the baby. After a relaxing grooming session, a mother may give in to the groomer's desire for a closer look. The other thus buys infant time. Market theory predicts that the value of babies should go up if there are fewer around. In a study of wild chacma baboons in South Africa, Louise Barrett of the University of Liverpool and Peter Henzi of the University of Central Lancashire, both in England, found that, indeed, mothers of rare infants were able to extract a higher price (longer grooming) than mothers in a troop full of babies.



TRAY-PULLING EXPERIMENT demonstrates that capuchin monkeys are more likely to share food with cooperative partners than with those who are not helpful. The test chamber houses two capuchins, separated by mesh. To reach their treat cups, they must use a bar to pull a counterweighted tray; the tray is too heavy for one monkey to handle alone. The "laborer" (*on left*), whose transparent cup is obviously empty, works for the "winner," who has food in its cup. The winner generally shares food with the laborer through the mesh. Failing to do so will cause the laborer to lose interest in the task.

Cleaner wrasses (*Labroides dimidiatus*) are small marine fish that feed on the external parasites of larger fish. Each cleaner owns a "station" on a reef where clientele come to spread their pectoral fins and adopt postures that offer the cleaner a chance to do its job. The exchange exemplifies a perfect mutualism.

The cleaner nibbles the parasites off the client's body surface, gills and even the inside of its mouth. Sometimes the cleaner is so busy that clients have to wait in line. Client fish come in two varieties: residents and roamers. Residents belong to species with small territories; they have no choice but to go to their local cleaner. Roamers, on the other hand, either hold large territories or travel widely, which means that they have several cleaning stations to choose from. They want short waiting times, excellent service and no cheating. Cheating occurs when a cleaner fish takes a bite out of its client, feeding on healthy mucus. This makes clients jolt and swim away.

Research on cleaner wrasses by Redouan Bshary of the Max Planck institute in Seewiesen consists mainly of observations on the reef but also includes ingenious experiments in the laboratory. His papers read much like a manual for good business practice. Roamers are more likely to change stations if a cleaner has ignored them for too long or cheated them. Cleaners seem to know this and treat roamers better than they do residents. If a roamer and a resident arrive at the same time, the cleaner almost always services the roamer first. Residents

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have nowhere else to go, and so they can be kept waiting. The only category of fish that cleaners never cheat are predators, who possess a radical counterstrategy, which is to swallow the cleaner. With predators, cleaner fish wisely adopt, in Bshary's words, an "unconditionally cooperative strategy."

Biological market theory offers an elegant solution to the problem of freeloaders, which has occupied biologists for a long time because reciprocity systems are obviously vulnerable to those who take rather than give. Theorists often assume that offenders must be punished, although this has yet to be demonstrated for animals. Instead cheaters can be taken care of in a much simpler way. If there is a choice of partners, animals can simply abandon unsatisfactory relationships and replace them with those offering more benefits. Market mechanisms are all that is needed to sideline profiteers. In our own societies, too, we neither like nor trust those who take more than they give, and we tend to stay away from them.

Fair Is Fair

TO REAP THE BENEFITS of cooperation, an individual must monitor its efforts relative to others and compare its rewards with the effort put in. To explore whether animals actually carry out such monitoring, we turned again to our capuchin monkeys, testing them in a miniature labor market inspired by field observations of capuchins attacking giant squirrels. Squirrel hunting is a group effort, but one in which all rewards end up in the hands of a single individual: the captor. If captors were to keep the prey solely for themselves, one can imagine that others would lose interest in joining them in the future. Capuchins share meat for the same reason chimpanzees (and people) do: there can be no joint hunting without joint payoffs.

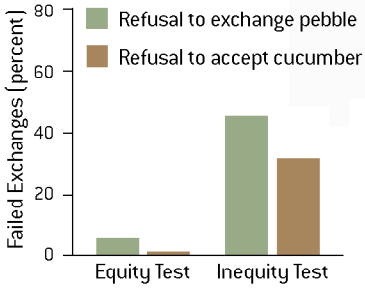
We mimicked this situation in the laboratory by making certain that only one monkey (whom we called the winner) of a tray-pulling pair received a cup with apple pieces. Its partner (the laborer) had no food in its cup, which was obvious from the outset because the cups were transparent. Hence, the laborer pulled for the winner's benefit. The monkeys sat side by side, separated by mesh. From previous tests we knew that food possessors might bring food to the partition and permit their neighbor to reach for it through the mesh. On rare occasions, they push pieces to the other.

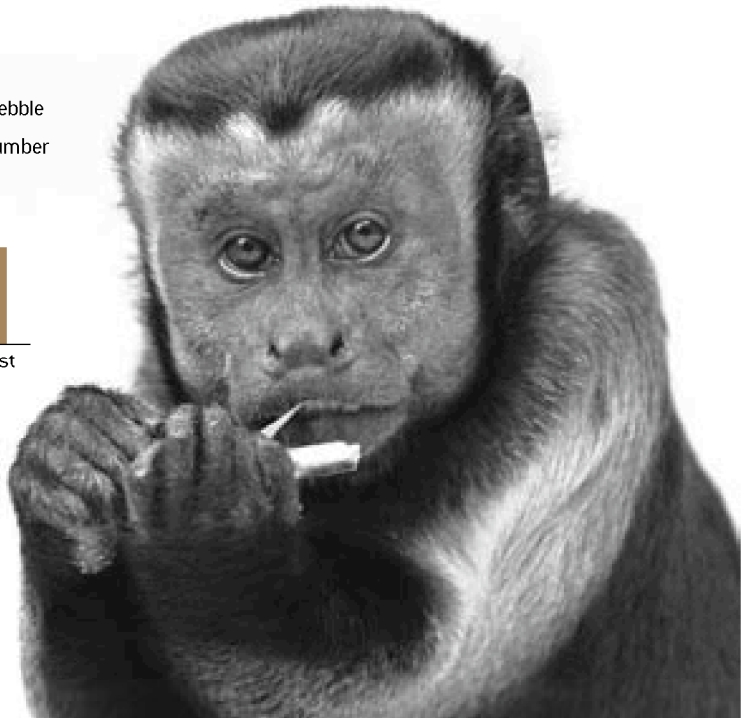
We contrasted collective pulls with solo pulls. In one condition, both animals had a pull bar and the tray was heavy; in the other, the partner lacked a bar and the winner handled a lighter tray on its own. We counted more acts of food sharing after collective than solo pulls: winners were in effect compensating their partners for the assistance they had received. We also confirmed that sharing affects future cooperation. Because a pair's success rate would drop if the winner failed to share, payment of the laborer was a smart strategy.

Sarah F. Brosnan, one of my colleagues at Yerkes, went further in exploring reactions to the way rewards are divided. She would offer a capuchin monkey a small pebble, then hold up a slice of cucumber as enticement for returning the pebble. The monkeys quickly grasped the principle of exchange. Placed side by side, two monkeys would gladly exchange pebbles for cucumber with the researcher. If one of them got grapes, however, whereas the other stayed on cucumber, things took an unexpected turn. Grapes are much preferred. Monkeys who had been perfectly willing to work for cucumber suddenly went on strike. Not only did they perform reluctantly seeing that the other was getting a better deal, but they became agitated, hurling the pebbles out of the test chamber and sometimes even the cucumber slices. A food normally never refused had become less than desirable.

To reject unequal pay—which people do as well—goes against the assump-

FRANS B. M. DE WAAL; ALISON KENDALL (*graph*)





CAPUCHIN MONKEYS have definite preferences when it comes to food. They will, for example, choose fruit over vegetables, such as the celery this capuchin is thoughtfully consuming. Trained to exchange a pebble for a slice of cucumber, they happily did so as long as the monkey in the adjoining test chamber also received cucumber (*Equity Test on graph*). But when the monkey next door was given a grape while they continued to receive cucumber (*Inequity Test*), they balked at "unfair pay." They either refused to accept the cucumber, sometimes even throwing it out of the cage, or refused to return the pebble.

How Humans Do Business

The emotions that Frans de Waal describes in the economic exchanges of social animals have parallels in our own transactions. Such similarities suggest that human economic interactions are controlled at least in part by ancient tendencies and emotions. Indeed, the animal work supports a burgeoning school of research known as behavioral economics. This new discipline is challenging and modifying the "standard model" of economic research, which maintains that humans base economic decisions on rational thought processes. For example, people reject offers that strike them as unfair, whereas classical economics predicts that people take anything they can get. In 2002 the Nobel Prize in Economics went to two pioneers of the field: Daniel Kahneman, a psychologist at Princeton University, and Vernon L. Smith, an economist at George Mason University.

Kahneman, with his colleague Amos Tversky, who died in 1996 and thus was not eligible for the prize, analyzed how humans make decisions when confronted by uncertainty and risk. Classical economists had thought of human decisions in terms of expected utility—the sum of the gains people think they will get from some future event multiplied by its probability of occurring. But Kahneman and Tversky demonstrated that people are much more frightened of losses than they are encouraged by potential gains and that people follow the herd. The bursting of the stock-market bubble in 2000 provides a potent example: the desire to stay with the herd may have led people to shell out far more for shares than any purely rational investor would have paid.

IRRATIONAL EXUBERANCE can grip the floor of a stock exchange.

Smith's work demonstrated that laboratory experiments would function in economics, which had traditionally been considered a nonexperimental science that relied solely on observation. Among his findings in the lab: emotional decisions are not necessarily unwise. *—The Editors*

tions of traditional economics. If maximizing benefits were all that mattered, one should take what one can get and never let resentment or envy interfere. Behavioral economists, on the other hand, assume evolution has led to emotions that preserve the spirit of cooperation and that such emotions powerfully influence behavior. In the short run, caring about what others get may seem irrational, but in the long run it keeps one from being taken advantage of. Discouraging exploitation is critical for continued cooperation.

It is a lot of trouble, though, to always keep a watchful eye on the flow of benefits and favors. This is why humans protect themselves against freeloading and exploitation by forming buddy relationships with partners—such as spouses and good friends—who have withstood the test of time. Once we have determined whom to trust, we relax the rules. Only with more distant partners do we keep mental records and react strongly to imbalances, calling them "unfair."

We found indications for the same effect of social distance in chimpanzees. Straight tit for tat, as we have seen, is rare among friends who routinely do favors for one another. These relationships also seem relatively immune to inequity. Brosnan conducted her exchange task using grapes and cucumbers with chimpanzees as well as capuchins. The strongest reaction among chimpanzees concerned those who had known one another for a relatively short time, whereas the members of a colony that had lived together for more than 30 years hardly reacted at all. Possibly, the greater their familiarity, the longer the time frame over which chimpanzees evaluate their relationships. Only distant relations are sensitive to day-to-day fluctuations.

All economic agents, whether human or animal, need to come to grips with the freeloader problem and the way yields are divided after joint efforts. They do so by sharing most with those who help them most and by displaying strong emotional reactions to violated expectations. A truly evolutionary discipline of economics recognizes this shared psychology and considers the possibility that we embrace the golden rule not accidentally, as Hobbes thought, but as part of our background as cooperative primates. SA

MORE TO EXPLORE

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Living Links Center site: **www.emory.edu/LIVING_LINKS/**

Classic cooperation experiment with chimpanzees: **www.emory.edu/LIVING_LINKS/crawfordvideo.html**

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