The psychology of reciprocal altruism

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Synonyms
Reciprocity

Definition
Different forms of reciprocal altruism—taking turns offering altruistic help—require different psychological building blocks.

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Introduction

A pair of pied flycatchers busily snatch insects to bring back to their nest and feed to their young. Suddenly, an owl appears close to the nest, posing a serious predation threat to their offspring. The pair fly straight to the owl, shrieking and dive bombing it to chase it away. A nearby pair of flycatchers detects the ruckus and also arrives to attack the predator. Another nearby pair, however, fails to help. An hour later, two owls appear, one at each of the neighboring nests. What should the original pair do? Krams, Krama, Igaune, and Mänd (2008) conducted this experiment and found that, out of 32 pairs of flycatchers, 2 stayed at the nest, 30 attacked the owl near the pair who helped them previously, and none attacked the owl near the pair who did not help them before. This willingness to pay a cost to cooperate or help another who has helped you before is called *reciprocal altruism* or *reciprocity*.

Natural selection favors genes that benefit the individual relative to others in the population. At first glance, it is unclear how altruistic cooperation could evolve since it benefits another individual at a cost to oneself. Hamilton (1964) proposed that costly acts could provide inclusive fitness benefits by helping individuals who share a proportion of your genes. Trivers (1971) removed the need for shared genes with reciprocal altruism. Trivers catalyzed the study of reciprocal altruism in his classic paper that formalized the concept, described its evolutionary preconditions, provided illustrative examples, and outlined the relevant psychological components. He proposed how natural selection could favor behavioral interactions in non-kin that yield overall net fitness benefits even if they produced immediate fitness costs. Reciprocal altruism recoups the immediate costs of altruism by emphasizing the long-term benefits of interacting repeatedly—you scratch my back, I'll scratch yours.

Trivers proposed evolutionary conditions needed for reciprocal altruism to evolve. First, the fitness benefits to the recipient of help must outweigh the costs to the cooperator. That is, after reversing roles once, helping has to result in a net fitness increase. Second, the probability of reciprocation must be high. Several factors may increase the probability of reciprocation, including (1) many opportunities for future altruistic situations, (2) repeated interactions with the same individuals, and (3) symmetrical exchanges in which the roles of donor and recipient reverse frequently enough to result in roughly equal experiences at both roles.

Researchers have proposed a number of cases of reciprocal altruism across a broad range of species, from hermaphroditic worms to humans (Dugatkin, 1997). Much of the data on reciprocal altruism involves correlations of altruistic behaviors between individuals. For example, vervet monkeys (*Chlorocebus pygerythrus*) are more likely to come to the aid of an individual who has previously groomed them (Seyfarth & Cheney, 1984). There are, however, multiple types of reciprocal altruism. *Calculated reciprocity* involves tracking the precise actions of specific partners, along with the costs and benefits of those actions. Calculated reciprocity uses scorekeeping to ensure exact reciprocation, and this concept most closely matches the intuition behind "you scratch my back, I'll scratch yours". The first formal model of reciprocal altruism—tit-for-tat—is a strategy that exemplifies calculated reciprocity because cooperation is contingent on the partner's cooperation in the last interaction (Axelrod & Hamilton, 1981). Tit-for-tat strategists copy their partner's last action: cooperate or defect (not cooperate).

Other, less precise mechanisms can also generate observed reciprocal correlations. *Attitudinal reciprocity* (Brosnan & de Waal, 2002) and the similar notion of *emotional bookkeeping* (Schino & Aureli, 2010) refer to situations in which altruism from a partner invokes positive attitudes/emotions toward that partner, which results in reciprocated altruism. Instead of precisely keeping track of previous actions, individuals an overall emotional reaction to a partner. *Symmetry-based reciprocity* refers to reciprocal patterns of altruism that occur because of some symmetry in the relationship between two individuals (de Waal & Luttrell, 1988). For example, if individual A and B often associate with one another but A and C rarely associate, A and B may be more likely to help each other due to their higher likely of interacting, whereas A and C will be less likely to help each other because they are rarely in contact. In symmetry-based reciprocity therefore, reciprocal altruism is a by-product of some other symmetrical relationship, such as spatial proximity.

Researchers typically refer to these aforementioned types of reciprocity as cases of direct reciprocity, in which the reciprocal exchange occurs between two individuals. Other forms of reciprocity, however, involve more than just a pair of individuals. *Indirect reciprocity* refers to situations in which a third party tracks interactions between other individuals (Nowak & Sigmund, 1998). If, for example, individual C observes that individual A helps individual B, then C would help A in a future interaction. Indirect reciprocity, therefore, uses third-party reputation rather than direct experience to reciprocate help. *Generalized reciprocity*, in contrast, does not track actions of specific partners. Donors help when they were helped in the previous interaction, irrespective of who helped them, thereby "paying it forward". Thus, this form of reciprocity tracks only the actions of the last interaction regardless of partner (Pfeiffer, Rutte, Killingback, Taborsky, & Bonhoeffer, 2005).

These forms of reciprocal altruism have different psychological building blocks that are needed to implement reciprocal behaviors. For example, to use tit-for-tat, an individual must be able to recognize partners and remember their previous behavior, which require the building blocks of individual recognition and accurate memory. Understanding both cognitive and emotional building blocks is critical to the evolution of reciprocal altruism because the degree to which these building blocks are present can constrain what types of reciprocal altruism can evolve. Symmetry-based reciprocity may not require sophisticated psychological building blocks, because the reciprocity is a by-product of other features of the relationship. Calculated reciprocity, in contrast, may require a number of building blocks to maintain the precise scorekeeping. Further, other psychological building blocks may not be required for reciprocity but greatly facilitate its use.

Cognitive building blocks

Cognition refers to information processing, and cognitive building blocks are core cognitive abilities that process information. Though not all cognitive building blocks are required for reciprocal altruism, several may be key, especially for calculated reciprocity.

Partner identification

Reciprocal altruism involves reversing roles as donor and recipient with partners. Some mechanisms underlying reciprocity may require being able to identify partners. Both direct and indirect reciprocity, for example, require partner identification, though generalized reciprocity does not.

Individual recognition

One cognitive building block that allows partner identification is individual recognition. Though humans take for granted the ability to recognize different individuals, other species may not be able to distinguish specific individuals from others. This may be especially true in species that do not have individually based repeated interactions, such as large swarms of invertebrates. Nevertheless, many species do recognize specific individuals. Social wasps, in particular, show remarkable abilities to use visual cues to recognize individuals, with species showing complex social interactions demonstrating highly identifiable features (Tibbetts & Dale, 2007). Thus, the evolutionary pressures of social interactions may shape the degree of individual recognition that evolves.

Individual recognition may not be strictly required for all reciprocal interactions. Other cues such as location may act as a proxy for identity. Cleaner fish clients, for example, may return to the specific location to be serviced by the same cleaner fish (Trivers, 1971). In this case, the clients do not have to recognize specific cleaners but simply remember a location.

Attributes of payoffs

Though the ultimate currency of fitness is measured in terms of genes, animals make decisions about fitness proxies such as food, mates, predation risk, and habitat quality. Characteristics of these fitness payoffs have critical implications for processing information about them. For some payoffs, animals must be able to compare the quality of various options, or inhibit the impulse to choose an immediately available, yet sub-optimal choice. Thus, certain cognitive building blocks are necessary to properly assess and decide between payoffs.

Quantification

Altruism involves a cost, which may require comparing two tangible fitness payoffs. These comparisons can be difficult since, across a wide range of species, large quantities are more difficult to discriminate than small quantities (Feigenson, Dehaene, & Spelke, 2004). In cooperative games, for example, Furlong and Opfer (2009) found that people cooperated more when the payoffs were described in U.S. cents (e.g., 300¢ vs. 500¢) compared to U.S. dollars (e.g., $3 vs. $5), even though the values were the same. When the values were larger and less discriminable, people cooperated more because it seemed less costly. Thus, the ability to quantify and compare the payoffs of various options can influence cooperation.

Inhibitory control

After discriminating between fitness payoffs, individuals must choose between them. Since altruistic cooperation involves a cost and results in smaller payoffs compared to defecting, to cooperate, individuals must chose a smaller payoff over a larger one. Children and other species, however, have difficulty inhibiting a strong preference for larger rewards.

In the reverse-reward contingency task, individuals select between a small and large reward, but they must choose the smaller to receive the larger (Boysen & Berntson, 1995). Young children and numerous species of primates fail at this task (Shifferman, 2009), and special training is needed for them to override the strong preference for the larger payoff. Yet, the ability to forgo larger payoffs for smaller ones is exactly what altruism requires when given the choice between acting altruistically (and suffering a loss) or acting selfishly. Inhibitory control, an animal's ability to inhibit an immediately desirable response, can therefore facilitate reciprocal altruism. When fitness payoffs are presented sequentially instead of simultaneously, inhibitory control may not pose a problem for altruism.

Time lag

By definition, reciprocal altruism involves a reversal of roles where an individual sometimes gives help and at other times receives help. In most cases of reciprocal altruism, a time lag exists between giving and receiving help. This time lag is important because donors must wait before their help is reciprocated (Trivers, 1971), and this has critical implications for cognition because individuals may forget and have difficulty waiting for delayed payoffs.

Memory for actions

Tracking the behavior of partners involves remembering either specific previous actions or overall summaries of actions for individuals. Tit-for-tat, for instance, requires remembering only the last action for a specific partner (Axelrod & Hamilton, 1981). Though this is a rather simple memory problem for computers to solve, memory in humans and other species does not work like computer memory. Instead, natural memory systems are subject to error. Namely, they fall prey to two forms of interference: proactive and retroactive.

Proactive interference occurs when information already in memory interferes with the recall of new information. This is relevant for tit-for-tat because it requires recall of only of the last interaction with a partner. But it is possible that earlier interactions with that individual interfere with accurately recalling the most recent interaction, thus leading to an error in remembering what the individual's partner last did. Retroactive interference occurs when new information interferes with the retrieval of older information. This is where the time lag between interactions becomes important, because often individuals have a number of social partners with whom they interact. Individuals likely interact with other partners between interactions with any particular partner. Therefore, these intervening interactions can interfere with accurately remembering the previous actions of any particular partner.

In a study of cooperative memory, Stevens, Volstorf, Schooler, and Rieskamp (2011) tested the impact of these two forms of interference on human memory. Though proactive interference did not impact memory, retroactive interference greatly reduced memory accuracy of previous partner actions. Increasing both the overall number of partners as well as the number of intervening partner interactions degraded memory. Further, evolutionary simulations suggested that tit-for-tat and related strategies would have difficulty evolving with the memory errors rates demonstrated in the experiment. Thus, tit-for-tat's memory requirement of accurately recalling a

partner's most recent action does not seem to match how human memory systems work. Importantly, other forms of reciprocal altruism are less subject to such memory constraints. Generalized reciprocity, for example, does not necessitate remembering what specific individuals do.

Memory for individuals

Though calculated reciprocity requires tracking individual actions, other forms of reciprocal altruism do not. Attitudinal reciprocity and emotional bookkeeping require generating an overall impression of a partner and deciding to help based on that. Thus, rather than remembering individual actions, these forms of reciprocal altruism track a general impression of a partner, which seems much more amenable to actual memory systems (Bell & Buchner, 2012).

One of the simplest forms of memory is recognition. Rather than remembering any content about an individual, recognition simply tracks whether the individual has been encountered previously. Aktipis (2006) demonstrated in a simulation that relatively simple memory strategies that simply recognized cooperators and only cooperated with individuals they recognized could maintain cooperation. So, simple recognition memory alone may allow cooperation to evolve.

In addition to recognition, individuals may remember an overall impression of a partner as a cooperator or defector. Cosmides and Tooby (1989) proposed that the costs of falling prey to defectors (cheaters) is so great that natural selection should favor individuals who can detect cheaters. Following this logic, researchers have tested whether people are better at remembering cheaters compared to cooperators, since, in general, missing out on the benefits of cooperation is not as costly as being cheated. In fact, evidence suggests that people do have better memory for cheaters when the cheaters' misdeeds are described verbally, and this memory effect seems to be moderated by negative emotions associated with threatening information about the cheater (Bell & Buchner, 2012).

In playing cooperative games against cooperators and cheaters, however, there does not seem to be a preference for remembering cheaters. Instead, people show a preference for remembering the rare type in the population (Barclay, 2008). If there are many cheaters in the population, for example, remembering the cooperators provides a memory shortcut.

Patience

Another difficulty with time lags is that humans and other animals do not like to wait for delayed payoffs. Altruism requires forgoing larger, immediate payoffs, and reciprocity requires waiting to recoup the larger payoffs after a time delay. Reciprocal altruists, therefore, must be patient enough to wait for the reciprocated benefits. Waiting can be costly, however, because the future is uncertain—there is a risk that the partner might not reciprocate. This risk increases with the time delay for two reasons. First, the longer the delay, the more likely it is that something interrupts the partner, preventing him/her from reciprocating (e.g., death). Second, the longer the delay, the more likely it is that the partner will forget to cooperate in return (see Memory for actions). Therefore, the increased risk with time makes impatience evolutionarily rational as time delays increase.

When given choices between smaller, sooner and larger, later food options, nonhuman animals wait on the order of seconds or minutes for the delayed options, which is shorter than expected if they are maximizing the long-term rate of food intake per unit time (Hayden, 2015). Humans also make short-sighted choices, preferring smaller, sooner options over larger, later ones, even when waiting provides better long-term payoffs, such as investing money in retirement funds (Frederick, Loewenstein, & O'Donoghue, 2002). Thus, humans and other animals have a difficult time waiting, which could constrain reciprocal strategies when long time intervals are involved.

Researchers have investigated this relationship between patience and cooperation by measuring both in the same individuals and correlating their responses. Human participants who can wait for delayed rewards also are more cooperative (Harris & Madden, 2002), suggesting that patience is required for cooperation. To more directly test the effect of patience on cooperation, Stephens, McLinn, and Stevens (2002) directly manipulated patience in

blue jays (*Cyanocitta cristata*) when playing a cooperative game. When the jays were experimentally induced to be more patient, they also cooperated reliably when paired with a reciprocating partner. Patience, therefore, is a key building block for reciprocal altruism.

Language
To avoid memory problems associated with the time lags inherent to reciprocal altruism, humans have evolved the ability to offload these transactions from memory onto physical objects via recordkeeping. In fact, archaeologists propose that the earliest instances of symbolic writings are records of economic transactions rather than written transcriptions of language (Nissen, Damerow, & Englund, 1993). Basu, Dickhaut, Hecht, Towry, and Waymire (2009) explored the effects of recordkeeping on individual economic behavior by demonstrating that allowing recordkeeping increases cooperative choices, reduces risky investments, and facilitates the formation of reputation in cooperative games. Thus, humans have evolved a workaround for the constraints of memory, and tracking cooperative interactions may have driven the evolution of written language.

Spoken language, though not a requirement, may greatly facilitate reciprocal altruism in a number of ways. First, it increases the precision of the altruistic exchange. In many cases, the fitness benefit and/or the time frame of a reciprocal exchange are rather abstract. Language allows more concrete exchanges because individuals can enumerate and describe benefits that may not be present at the time—for example, exchanging one goat now for 10 bushels of wheat after the harvest. It can also allow discussion of a future time frame, which is difficult to represent, otherwise. By specifying abstract concepts, language opens the possibility for formal contracts.

Language also provides a very flexible means to attempt to change the behavior of social partners through bargaining and coercion. Rather than requiring fixed exchanges, social partners can negotiate with language, describing multiple possible outcomes before settling on one. Moreover, a potential recipient can attempt to induce helping by imploring a potential donor with promises of future reciprocation or by cajoling the donor with warnings of withholding future help. The potential donor can, in turn, threaten the potential recipient with sanctions if the aid is not reciprocated. Language can allow for ‘cheap talk’, though; and enforcing the promises and threats can be difficult.

Language’s most powerful influence on reciprocal altruism is probably through indirect rather than direct reciprocity. Observing social interactions between others is a faster way to gain information about social partners than direct experience alone. Hearing about interactions that one did not directly observe opens the door to even more information about behaviors of social partners not witnessed by the focal individual. Thus, language greatly enhances the ability to track partner actions via gossip (Sommerfeld, Krambeck, Semmann, & Milinski, 2007). In modern day social interactions, ratings provide an indispensable way for online sellers and buyers to trade goods for currency. With publicly visible ratings of their trustworthiness, sellers are forced to make good on their contract to provide good and services to buyers. For humans, language is an essential cognitive building block for multiple forms of reciprocal altruism.

Emotional building blocks
Emotional processes can also be important psychological building blocks for reciprocal altruism (Fessler & Haley, 2003; Trivers, 1971). In fact, attitudinal reciprocity and emotional bookkeeping critically depend on emotional building blocks. Though the emotional components are not well described for these forms of reciprocal altruism, they generally refer to a positive or negative affect directed toward individuals (Schino & Aureli, 2010). These general emotional reactions are akin to liking and disliking, and they facilitate the development of social bonds and friendships. Trivers (1971) suggested that, in humans, specific emotions may have evolved to facilitate reciprocal altruism, with different emotions associated with donating or receiving altruistic help.

Donor emotions
Emotions experienced by donors help them detect a need for altruistic help in others and respond to instances of cheating.

Sympathy and empathy
The first step a donor faces in an altruistic situation is to determine the degree to which a partner needs help. Sympathy and empathy are emotions that facilitate detecting partner need by attempting to understand others' needs. Trivers (1971) suggested that these emotions motivate altruistic behavior based on need; the greater the need, the greater the sympathy or empathy. This emotional response may be necessary to overcome the cognitive impediments associated with strong preferences for maximizing current fitness payoffs for self (inhibitory control problems and impatience).

Trust and betrayal
Donating help in a reciprocal way involves uncertainty since the partner may not reciprocate. This can occur in the time-dependent manner described previously (see Patience and risk tolerance) or simply because the partner will choose not to reciprocate. Trust helps overcome an initial aversion to risk caused by the uncertainty associated with future reciprocation. When trust is validated by reciprocation, the level of trust will increase, and donors may be willing to accept greater altruistic costs. When trust is violated by cheating, donors experience the emotions associated with betrayal and withhold future altruism. Shackelford and Buss (1996) propose that the emotion of trust betrayal serves two functions. First, betrayal motivates the donor to communicate the breach of trust to the partner, which may deter future cheating. Second, betrayal may prompt the donor to sever the relationship with the partner, preventing future exploitation. Betrayal can feed into the cognitive components of reciprocal altruism by highly weighting memories for cheating by partners. Combined, trust and betrayal induce a donor to take a risk and help a partner—potentially reinforcing a strong positive relationship with that partner—but also track a partner's lack of reciprocation to minimize future cheating.

Anger and moralistic aggression
Though betrayal can motivate the rather mild response of communicating a breach of trust with a partner, it can also induce a stronger negative response by instigating anger or moralistic aggression. Trivers (1971) suggested that moralistic aggression protects against cheaters by (1) overriding positive emotions leading to continued altruism with that partner, (2) frightening the cheater into reciprocating, and (3) directly reducing the fitness of the cheater by injuring, exiling, or even killing him/her.

Anger can act as an honest signal of intention to punish and do harm. Sometimes the aggressive acts caused by anger seem out of proportion with the costs of cheating. If, however, there are many opportunities for future interactions, the benefits of inducing future cooperation may outweigh the costs of aggressive punishment (Trivers 1971). Moreover, anger can have strong reputational effects, such that third parties are induced to cooperate after observing or hearing about aggressive acts, even without direct experience with the angry donor. Thus, anger deters cheating in both direct and indirect reciprocity situations.

Recipient emotions
Recipients have also evolved emotions associated with reciprocity, primarily to induce reciprocation.

Gratitude
Gratitude is appreciation for an altruistic act that serves three functions relevant to altruism (McCullough, Kilpatrick, Emmons, & Larson, 2001). First, it detects that a donor has provided a benefit to the recipient. This helps recipients track altruistic acts. Second, it motivates the recipient to pay back the altruistic debt in the future. Third, expressing gratitude toward a donor reinforces that donor's actions, potentially increasing the likelihood of future altruistic behavior on his/her part. Trivers (1971) suggested that gratitude scales to the costs and benefits of altruism—the greater the costs and benefits, the greater the gratitude. This increases the motivation to reciprocate when the donor has accepted substantial costs or donated substantial benefits. Moreover, gratitude can overcome disliking individuals who have previously failed to reciprocate but have made amends (Trivers 1971). Gratitude, therefore, greatly facilitates reciprocal altruism by ensuring appropriately scaled reciprocation, inducing future altruism, and repairing damaged relationships.

Guilt

Guilt is the negative emotion that occurs when one has violated a moral or social standard (Kugler & Jones, 1992). For reciprocal altruism, this occurs when a recipient has or is contemplating cheating rather than reciprocating. Following cheating, guilt may function to induce a cheater to correct the wrong either by immediately reciprocating or by compensating the donor in other ways (Trivers 1971). This allows the cheater to repair the relationship and avoid the long-term costs of never receiving altruistic support from the donor in the future. Anticipating the guilt associated with intended cheating also can motivate reciprocation. Guilt identifies, prevents, and repairs damage done to social partners, even if the damage was unintentional (Fessler & Haley, 2003).

Conclusion

Psychology constrains the types of reciprocal altruism that can evolve, and models of reciprocal altruism without psychological constraints provide little predictive power. Species vary in what building blocks they possess, and, therefore, measuring these building blocks can focus attention on relevant types of reciprocal altruism. We cannot understand the evolution of reciprocal altruism without understanding the psychology underlying it.

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