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Evolution

Why humans reciprocate but animals usually do not

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Reciprocal cooperation can be advantageous, but why it is more common in humans than in other social animals is a puzzle. A modelling and experimental study pinpoints the conditions needed for reciprocity to evolve.

Reciprocity is so intuitive to humans that its evolutionary logic can seem self-evident. If there is a high chance that individuals will interact again, it pays to be nice to those who might return the favour. A rich body of theoretical work¹ has confirmed this idea, showing that – as long as there is a high probability of interacting with the same person again, and individuals preferentially help those who have previously helped them – reciprocal cooperation is advantageous despite its short-term cost. However, writing in *Nature*, Efferson *et al.*² report evidence suggesting that the evolutionary path to reciprocity is treacherous at best, and impossible at worst – unless natural selection favours not only individuals, but also groups, that cooperate more.

As counterintuitive as the finding might be, it could clarify a key paradox about reciprocity theory. Despite the long-term gains that reciprocal cooperation offers, most animals do not cooperate with individuals that are not related to them, even when they have many opportunities for future interactions³. By contrast, humans exchange a wide variety of goods and services with unrelated individuals during daily life (Fig. 1) in a manner that is consistent with reciprocity theory⁴. A satisfactory theory should explain not just why humans cooperate, but also why other animals do not when the conditions for cooperation to evolve seem to be met.

Despite theoretical shortcomings in explaining why most animals do not behave reciprocally, researchers continue to ascribe cooperation in repeated interactions to reciprocity, and have turned their gaze to a more unusual phenomenon – cooperation in one-off interactions. In a conspicuous deviation from reciprocal cooperation, humans help strangers, even in transient interactions.

If the recipient cannot return the favour later, then how does the helper recoup the cost of helping? Some think that cooperation in such one-off interactions is a ‘mis-firing’ in modern settings, resulting from a reciprocity-driven psychology that evolved when humans lived in smaller groups in which interactions between individuals were almost always repeated⁵. Others think that such cooperation arises through group selection, in which competition between groups of people with different cooperative behaviours and norms favours those with high levels of in-group cooperation, including in one-off interactions⁶. Teasing apart which of these explanations is correct is difficult,

fuelling a debate over the roots of our altruistic disposition^{5,7}.

To try to settle this argument, Efferson *et al.* developed a model that simulates which cooperation strategies evolve in populations over time when interactions are repeated and when group selection occurs, to derive precise predictions of the scenarios that give rise to one-off cooperation. Contrary to both sides of the debate, neither repeated interactions nor group selection consistently produced one-off cooperation. More surprisingly, repeated interactions did not yield the most obvious outcome, reciprocal cooperation. These results emerged because the model was constructed in a way that did not make standard simplifying assumptions, thus ensuring that it did not sidestep certain realities of the natural world that have profound effects.

First, rather than having the model consider cooperation and non-cooperation as two discrete options, individuals could cooperate to any extent along a continuous scale. Second, any conceivable cooperation strategy could arise through chance and compete with existing strategies in the population. In standard models, the strategies that can arise are predetermined to make the model more straightforward, so existing strategies in the population are artificially protected from their full range of competing strategies. These two decisions exposed a fundamental weakness of repeated interactions as a mechanism by which cooperation can evolve – when



Figure 1 | Hair braiding in Namibia. Efferson *et al.*² shed light on how reciprocal behaviour (such as this type of cooperative activity) might have evolved in human societies.

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cooperative reciprocity gains a foothold, it opens the door for less-cooperative strategies in which individuals reciprocate by giving a little less than they receive. Over time, cooperation slides down to negligible levels.

With reciprocal cooperation on a slippery slope, why didn't group selection claim victory instead? To encompass a wide range of realistic scenarios in their model, Efferson *et al.* varied the timing of when cooperation events take place relative to when individuals disperse from their original group, which affects whom individuals will cooperate with, as well as whom they will compete with for resources. In the majority of the resulting scenarios, the advantage that cooperators get by being around other cooperators, is cancelled out by cooperators competing with other cooperators for resources. Researchers have long known how this 'cancellation effect' plays out at the individual level⁸, but only in the past four years has its detrimental effects been described at the group level⁹. Efferson and colleagues' study assessed the cancellation effect at both the individual and group level.

Remarkably, although neither repeated interactions nor group selection work in isolation, they almost always generate reciprocal cooperation when they act in concert. Moreover, the resulting cooperation is much bigger than the sum of what either reciprocity or group selection can generate alone, which the authors refer to as super-additive cooperation.

To test the theoretical findings, the authors then conducted a social-dilemma experiment with participants from the Ngenika and Perepka groups in Papua New Guinea. The influence of state institutions at the location of these groups is weak, so it is easier to observe how individual social strategies influence cooperation.

In the experiment, individuals could transfer any amount of their endowed cash to their partner, who then received double the amount transferred. When paired with an in-group

member, first-movers transferred high amounts and second-movers reciprocated more than they received; when paired with an out-group partner, first-movers made low transfers, and second-movers reciprocated less than they received. This pattern of escalating and de-escalating reciprocity in in-group and out-group interactions respectively, was observed in the theoretical model only when repeated interactions and group selection operate simultaneously.

The finding that repeated interaction needs group selection to yield super-additive reciprocal cooperation could be the long-awaited answer to why reciprocity is pervasive in humans and includes high-stakes interactions (such as proactive sharing of food), but is rare in other social animals and usually restricted to low-stakes interactions (such as tolerating an individual at a feeding site). Repeated interaction needs group selection to yield reciprocal cooperation, but the conditions for group selection to occur are nearly universally absent in the natural world, because there is insufficient genetic variation between groups. However, cultural characteristics, which influence human behaviour, do differ between groups¹⁰. Therefore, groups can differ in their success when competing with other groups, making group-level selection an important force in shaping the evolution of human societies.

Having gained a finer awareness of the limitations of the prevailing theories, we can now ask new questions. Given that reciprocity models produce qualitatively different results when traits are modelled as continuous versus discrete characteristics, are there other theories based on models of discrete traits that should be re-examined? For instance, researchers have shown that the intuitive idea that arbitrary conventions can persist owing to the social pressure to do what others do, which applies to discrete norms (such as which side of the road to drive on), does not hold up for continuous norms (for example, how much to

tip at a restaurant)¹¹.

Another intriguing question is whether cultural norms can mitigate the cancellation effect by manipulating the social scale at which people cooperate and compete. For example, norms can dissuade people from waging war with culturally similar groups, but not from going to war with culturally dissimilar people¹⁰. Perhaps such norms reoccur in different societies because they expand and redraw group boundaries in ways that dampen the effect of cancellation.

What other combinations of mechanisms can yield super-additive cooperation? Will the reciprocation strategies observed in the Ngenika and Perepka extend to other cultural contexts? Evidently, the case regarding cooperation isn't closed, but we can undoubtedly make faster progress if we stop assuming reciprocity to be the baseline from which deviations in cooperation are assessed – because reciprocity in theory, as in real life, cannot be taken for granted.

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The author declares no competing interests.