

## HUMAN BEHAVIOUR

# Simple moral code supports cooperation

The evolution of cooperation is a frequently debated topic. A study assessing scenarios in which people judge each other shows that a simple moral rule suffices to drive the evolution of cooperation. [SEE LETTER P.242](#)

CHARLES EFFERSON & ERNST FEHR

The evolution of cooperation hinges on the benefits of cooperation being shared among those who cooperate<sup>1</sup>. On page 242, Santos *et al.*<sup>2</sup> investigate the evolution of cooperation using computer-based modelling analyses, and they identify a rule for moral judgements that provides an especially powerful system to drive cooperation.

Cooperation can be defined as a behaviour that is costly to the individual providing help, but which provides a greater overall societal benefit. For example, if Angela has a sandwich that is of greater value to Emmanuel than to her, Angela can increase total societal welfare by giving her sandwich to Emmanuel. This requires sacrifice on her part if she likes sandwiches. Reciprocity offers a way for benefactors to avoid helping uncooperative individuals in such situations. If Angela knows Emmanuel is cooperative because she and Emmanuel have interacted before, her reciprocity is direct. If she has heard from others that Emmanuel is a cooperative person, her reciprocity is indirect — a mechanism of particular relevance to human societies<sup>3</sup>.

A strategy is a rule that a donor uses to decide whether or not to cooperate, and the evolution of reciprocal strategies that support cooperation depends crucially on the amount of information that individuals process. Santos and colleagues develop a model to assess the evolution of cooperation through indirect reciprocity. The individuals in their model can consider a relatively large amount of information compared with that used in previous studies.

This increased amount of information is essential for at least two reasons. First, models of direct reciprocity show that having more information allows for many possible strategies, which can paradoxically reduce cooperation<sup>4</sup>. Does something similar happen for indirect reciprocity? Second, indirect reciprocity requires individuals to assess and disseminate reliable information about each other. In a real-world context, this mechanism is most convincing if the amount of information being processed is not excessive. These two considerations suggest that the most compelling models of indirect reciprocity should be simple and should support cooperation in settings in which many alternative possibilities exist.

In Santos and colleagues' set-up, social

prediction that hydrogen ionizes to produce free-moving protons and electrons in such a high-pressure environment. These particles generate strong drag forces that suppress winds flowing in opposite directions<sup>7</sup>.

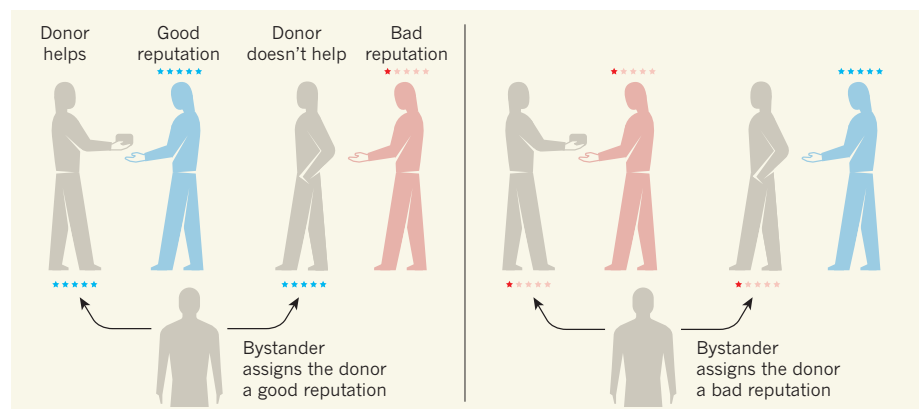
The three studies confirm previous suggestions that high-precision measurements of a planet's gravitational field can be used to answer questions of deep planetary dynamics<sup>8,9</sup>. In terms of future work, scientists could use the Juno spacecraft to measure the depths of storms on Jupiter such as the Great Red Spot, or to observe the planet's response to tides raised by its large moons. Such analyses would provide a further window into Jupiter's interior.

The work demonstrated here is extremely robust, perhaps unlike other inferences made using data from Juno, including the mass and density of Jupiter's primordial core<sup>10</sup>, that are somewhat model-dependent and rely on our imperfect understanding of the physics of hydrogen under extreme pressure. I do not foresee another leap in knowledge on Jupiter's interior after the Juno mission ends unless astronomers are able to study the planet's internal oscillations<sup>11</sup>, as has been done for the Sun<sup>12</sup>.

Given the inherent complexity of planets, comparative planetary science has become an essential framework through which to study these astrophysical objects. Thankfully, Jupiter has a sibling, the gas-giant planet Saturn. NASA's Cassini mission to Saturn, which ended in 2017, provided a Juno-like data set for Saturn's gravitational field that is now being analysed<sup>13</sup>. Because Saturn has a lower internal pressure than has Jupiter, its atmospheric winds should be able to extend much deeper into its interior before hydrogen ionization and the associated drag forces take control. If a consistent physical picture could be put together for the two gas giants of the Solar System, it would go a long way towards solidifying our understanding of the internal dynamics of this class of astrophysical object. ■

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**Figure 1 | The stern-judging rule.** Santos *et al.*<sup>2</sup> used a computer-modelling approach to investigate how cooperation might evolve. They investigated scenarios in which a donor can give or refuse help to a recipient depending on the strategy that the donor uses. The donor's action is judged by a bystander who uses a rule (termed a norm) to judge the donor's action and assigns a reputation to the donor that the bystander reports to other members of the society. The authors used this system to test 65,536 different norms in terms of each norm's ability to support the evolution of cooperative strategies. The norm that stood out as being both low complexity and also highly likely to drive the evolution of cooperation is one known as stern judging. This figure shows how the stern-judging norm is used by a bystander to assess a donor's action and thereby assign the donor a good or bad reputation.

interactions involve three individuals: a donor, a recipient and a bystander. The donor uses a strategy to decide whether or not to cooperate and pay a cost that produces a benefit for the recipient. The bystander witnesses this and, using a rule termed a norm, assigns a reputation to the donor that is communicated to others in the population. In future social interactions, this reputation affects whether the donor receives the benefits of cooperation when taking on the role of a recipient.

One version of this interaction is known as a first-order system. In this scenario, two strategies exist. The donor can cooperate or not cooperate (defect). The bystander considers the donor's cooperation or defection when using a norm to assign a good or bad reputation.

Yet even in this simple system, four possible norms exist for the bystander: always assign a good reputation; always assign a bad reputation; assign a good reputation if the donor cooperates and a bad reputation if the donor defects; or assign a bad reputation if the donor cooperates and a good reputation if the donor defects. These norms vary in complexity. The first two are independent of the donor's action and the complexity is low. The latter two norms are dependent on the donor's action and the complexity is relatively high.

This reflects a general pattern. Give a bystander some information, and the level of complexity can vary between the possible norms. Moreover, the complexity of the most-complex norms increases with the information available, and the scope for increasing complexity is striking. In a second-order system, another component is added to the interaction. For example, both the donor and the bystander consider the reputation of the recipient. This allows 4 possible strategies and 16 possible norms. A third-order system could also include the donor's reputation, yielding 16 possible strategies and 256 possible norms<sup>5</sup>.

Santos and colleagues' fourth-order system additionally allows individuals to consider information about the past reputation of either the recipient or the donor. By incorporating the past, a donor's reputation is not dependent on a single point in time. In this scenario, 256 strategies and a staggering 65,536 norms are possible.

With ample scope for complexity in place, Santos and colleagues then examined each norm separately, and allowed the strategies used to evolve (the frequency of use of each strategy could change over time). The strategies that prevail, given a particular norm, affect the amount of cooperation that occurs. One norm, termed stern judging, stands out from the glut of conceivable norms as a relatively low-complexity norm that is highly likely to promote the evolution of cooperation.

The essence of stern judging is to assign a good reputation to a donor who cooperates

with a good recipient or who defects with a bad recipient, and assign a bad reputation to a donor who defects with a good recipient or who cooperates with a bad recipient (Fig. 1). This is a simple second-order norm that supports the evolution of simple and highly cooperative strategies, and it does so even when tested in higher-order systems. From the profusion of feasible norms, more-complex norms do not improve the evolution of cooperation, at least up to the fourth-order system studied by the authors. This suggests that a relatively simple norm, with its correspondingly simple requirements in terms of processing and disseminating information, can suffice to drive indirect reciprocity.

This finding also raises a question for the future. Given so many conceivable norms, why use stern judging? In Santos and colleagues' system, strategies evolve, but norms do not. In reality, strategies and norms evolve together<sup>6</sup>. Both the way people behave (strategies) and the way they evaluate behaviour (norms) change over time, and this process almost certainly involves both genetic and cultural components<sup>7</sup>. Examining the co-evolution of strategies and norms with culture in the mix would be challenging in a fourth-order system, but it would increase our understanding of whether and when we might expect to observe people using reciprocity norms effectively to support cooperation.

In addition, in Santos and colleagues' work, every bystander in a given simulated population uses the same norm. However, in many social settings, there can be variation in the level of subtlety with which different people evaluate social situations. This kind of variation, which could result in bystanders using

norms of different levels of complexity, may or may not<sup>8</sup> result in disagreements between individuals about how to assign reputations. If disagreements occur, how much disagreement can indirect reciprocity tolerate before cooperation breaks down?

Finally, large-scale cooperation occurs in human societies<sup>9</sup>, and efforts to explain how this evolved have generated controversy, possibly because mutually compatible mechanisms are sometimes treated as strict alternatives. Perhaps the next step needed to address this will be to systematically combine multiple mechanisms<sup>4</sup>, including indirect reciprocity, and to test whether specific combinations of mechanisms are especially potent at promoting the evolution of cooperation. ■

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## STRUCTURAL BIOLOGY

# A new era of rationally designed antipsychotics

The ideal drugs for treating schizophrenia are postulated to selectively block the D2 dopamine receptor with optimum binding kinetics. The structure of D2 bound to an antipsychotic sheds light on how to design such drugs. [SEE LETTER P.269](#)

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Schizophrenia is a disorder that involves hallucinations, delusions and cognitive impairment, and that affects nearly 1% of the global population<sup>1</sup>. The mainstays of therapy have been drugs that block the activity of the D2 dopamine receptor (D2R), a member of the large G-protein-coupled receptor (GPCR) superfamily of membrane proteins. Unfortunately, most of these antipsychotic

drugs come with a plethora of debilitating side effects, many of which are due to off-target interactions with other GPCRs. On page 269, Wang *et al.*<sup>2</sup> now report the crystal structure of D2R in complex with the antipsychotic drug risperidone. The structure reveals features that might be useful for the design or discovery of drugs that have greater selectivity for D2R than existing therapeutics, and consequently have fewer side effects.

The naturally occurring ligand for D2R is