comment

Insights into human cooperation from comparative economics

Many species face the problems of how, when and with whom to cooperate. Comparing responses across species can reveal the evolutionary trajectory of these decisions, including in humans. Using nearly identical economic game methods to compare species could identify the evolutionary constraints and catalysts to cooperation.

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Fig. 1 | An advantage of games derived from experimental economics is the ability to test different decision-making situations identically across species. a–d, To determine whether context influences decision-making, in our studies both humans (**a**,**c**) and non-human primates (represented by capuchin monkeys; **b**,**d**) decide which of two strategies to play on each trial by either selecting the token representing that strategy (**a**,**b**) or by using a joystick to select the icon representing the strategy on a computer screen (**c**,**d**; humans and monkeys are playing the same game with different screen resolutions). Credit: (**a** and **c**): Bart Wilson (Chapman University)

How do we find solutions for the social dilemmas that we face in our everyday lives? Other primates are quite sophisticated in dealing with this problem. For example, chimpanzees in some populations coordinate on hunts for colobus monkeys, with different individuals taking different roles in the hunt. The successful hunters then share the spoils more equitably than do chimpanzees from other regions that do not coordinate on hunts, a difference that is presumably due to ecological differences between those regions. Laboratory experiments indicate that primates understand at least some of the contingencies of cooperation. Chimpanzees not only work together to achieve outcomes, but actively solicit partners who are more tolerant[1]. Capuchin monkeys seem to be cognizant of the necessity of their partners, show evidence of behaviourally coordinating to acquire resources and cease working with partners who do not share outcomes.

These experiments have also uncovered the limits to other species' collaborative abilities. Humans excel at collective action problems, working together to maintain access to resources that would otherwise be depleted if one individual dominated them (for example, the tragedy of the commons)[2]. Children as young as three share more equally in collaborative action problems than other joint action problems, but while chimpanzees do help one another and work together on cooperative problems, they may share irrespective of whether they previously collaborated[3]. In addition, when given a choice, chimpanzees prefer to work on their own rather than collaborate with a partner.

Such experiments have also shown how cooperative abilities compare among species. For instance, similar experiments show that, contrary to hypotheses about the role of domestication in cooperation and tolerance, pack-living wolves are much better at coordinating actions than are pack-living domestic dogs, reiterating the importance of socioecology in determining cooperation[4]. This comparative approach is key for understanding the evolution of cooperation; by studying closely related species, we can triangulate in on how a common ancestor may have behaved. If we understand how cooperation evolved, including the conditions that favoured it, we can potentially learn both the constraints under which cooperation operates as well as the conditions in which it is most likely to succeed.

While the aforementioned studies have been invaluable in helping us to better understand primate cooperation, one limitation has been that experimental procedures often differ, making truly direct comparisons difficult. A promising new approach addresses this specific challenge by using games derived from experimental economics. By using identical procedures, we can more directly compare across species and contexts, which provides a firmer foundation for drawing conclusions and the potential to better understand underlying mechanisms. Much like experimental economics, this does not replace the previous approach, but adds to it, providing a framework for interpreting the more ecologically and species-focused studies and designing new studies to expand our understanding of the roles of the social and ecological contexts.

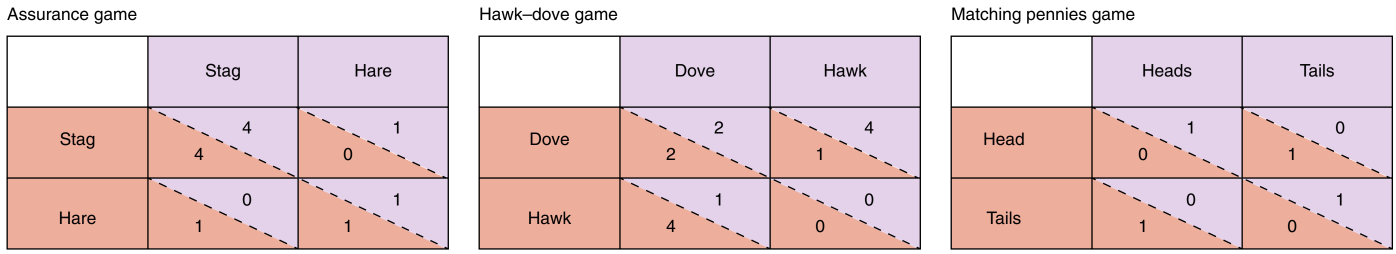

Fig. 2 | Three common games used in comparative experimental economics research include the assurance game, the hawk–dove game and the matching pennies game. Participants are rewarded dependent on both their and their partner's choices (indicated by the different colours). The assurance game is a coordination game in which the best-paying (payoff dominant) Nash equilibrium is to coordinate on 'stag', whereas the least risky strategy is to play 'hare', because you get a reward no matter what your partner chooses; coordinating on 'hare' is also a Nash equilibrium. The hawk–dove game is an anti-coordination game in which there are two Nash equilibriums, 'hawk'/'dove' and 'dove'/'hawk'. The best strategy is to alternate Nash equilibrium, which averages more rewards per trial than coordinating on 'dove'. The matching pennies game is a zero-sum game that rewards the matcher if the subjects make the same choice and the mismatcher if they do not; there is no outcome that benefits both simultaneously. The solution is to choose each option with equal probability (that is, to play at random, a mixed-strategy Nash equilibrium).

Experimental economics

For comparative work, the key to games derived from experimental economics is their simplicity. In these games, complex decision scenarios, such as whether to cooperate, are distilled down to very simple, often dichotomous, choices. Choices can be represented in a variety of ways, which allows us to 'ask' other species what they prefer without the use of traditional language-based paradigms. Subjects can choose one of two targets on a computer screen or one of two tokens to be returned to the experimenter (Fig. 1). Subsequent payoffs are based on both players' choices. These designs can explore a variety of decisions, including whether individuals coordinate and, if so, whether they coordinate on a better-paying, but riskier, option (the assurance, or stag hunt, game; Fig. 2) and how individuals negotiate anti-coordination (the hawk–dove, or chicken, game and the snowdrift game) or direct competition (the matching pennies game).

Another key difference with human work is that we cannot give animals verbal instructions or pre-tests. This limits what experiments can be done; however, the lack of instruction also means that we are measuring how individuals figure out the rules of the game, without inadvertently biasing the subjects towards our intended understanding (although inopportune pre-training can introduce similar biases). While this is done to standardize procedures across species, it also provides benefits for understanding how individuals learn the 'rules of the game' in situations in which payoffs are not known. While it is sometimes useful to provide extensive information before experiments, not explaining the game in detail can be extremely helpful for understanding more amorphous interactions in day-to-day life. As in real life, we may know at least general parameters in many cases, but there are plenty of contexts in which we make decisions about whether to participate without even knowing what 'game' we are playing, much less what the actual payoffs will be (for instance, is this collaboration going to be collaborative or competitive, and will there be a big enough payoff to be worth fighting over?). By allowing participants to choose their strategy based on their explorations of the game space, we can identify features of human decision-making that complement the data drawn from more traditional game situations.

My lab has used this approach with four species; humans, chimpanzees, rhesus monkeys and capuchin monkeys, and found both similarities and differences among the species. For instance, all four species managed to coordinate on the highest-paying solution in the assurance game (Fig. 2) in at least some contexts[5,6] (this solution was also a Nash equilibrium, meaning that it is an outcome for which there is no better option given the strategy used by the partner). However, while outcomes are similar, the ways in which the subjects reach those outcomes differ. We have little evidence that either monkey species was doing more than matching their partner's play (capuchin monkeys) or developing a preference for one of the tokens (rhesus monkeys). While these were effective strategies, they are limited in flexibility and likely constrain the monkeys' decision-making.

Chimpanzees, in contrast, formed strategies. Once they learned to coordinate on the best-paying strategy, they were able to rapidly apply their strategy to novel situations with the same payoffs. Chimpanzees showed a strong experience effect; those with a long history of participating in cognitive tasks outperformed those who had less experience, despite otherwise similar backgrounds. Other labs' research has found that chimpanzees are influenced by the social partner, apparently making different decisions depending on the identity of their partner, and are flexible, employing a leader–follower dynamic, in which one individual follows what their partner does[7].

Humans showed a curious response; while some pairs found the higher-paying coordinated outcome, others played the lower-paying one. This was where our alternative procedure identified an interesting quirk; lacking instruction, many humans apparently stopped exploring the parameter space as soon as they found an option for which both were rewarded. Indeed, not a single one of these pairs ever experienced the higher-paying option. This was unlike the primates, who explored extensively before settling on a pattern of play. In a condition in which humans spoke to one another, those who chose to talk about the game found the payoff-dominant coordinated outcome, which we believe indicates that humans are using language to explore the decision space[8].

Other interesting differences emerged in competitive situations. In the hawk–dove anti-coordination game (Fig. 2), both of our monkey species found a Nash equilibrium; however, only humans were able to find the much more difficult alternating Nash equilibrium that maximized the pair's payoffs[9]. This was true even in cases in which they could not speak to one another, emphasizing that humans excel even when they are not able to use language. Notably, alternating essentially turns a competitive game in to a more cooperative one, perhaps revealing something about humans' goals when playing these games[2].

However, humans may not always have the advantage. In the zero-sum, competitive matching pennies game, one subject is rewarded for matching their partner (matcher) while the other is rewarded for not matching (mismatcher; Fig. 2). The Nash equilibrium is to play randomly, which chimpanzees are much better at than humans[10]. Interestingly, matchers make their responses more rapidly than mismatchers, which may indicate that matching is either a cognitively simpler task than anti-matching or that anti-matching requires overriding an automatic motor response. Considering the implications for other games, while monkeys can 'anti-match' in the hawk–dove game, just as they matched in the assurance game, this may put additional limitations on decisions that involve anti-matching.

Back to socioecology

Once these economic approaches have provided a better understanding of how different species are solving these dilemmas, the next step is to go back to more species-specific paradigms to test the hypotheses that have emerged from this model system. Ideally we will be able to use identical paradigms across species, but even where we cannot, having the framework in place allows us to more clearly interpret the comparative results by relating them to differences in outcome and mechanism that we know exist in these games. For example, one notable finding of experimental economics is that in situations without explicit instruction, humans appear to be less exploratory than other species. Why is this? Perhaps humans have become secondarily less exploratory due to their increasing reliance on social information through language, or perhaps there was increased pressure on some primates to become more exploratory to find solutions to problems, social or other. A second step is to determine the degree to which these results generalize to more naturalistic contexts. Most studies, including those of humans, are limited to dyads or small groups interacting in limited or contrived ways. There are very good reasons for this; it is nearly impossible to do controlled experimental studies in freely interacting large groups, not to mention interpret the ensuing results, but with an understanding derived from these more tightly controlled situations, we can interpret results from larger and more freely interacting groups more accurately and thereby gain a more realistic understanding of decision-making at the group level. Ultimately, we hope to use these model games as part of a programme to understand decision-making to the point that we can provide experimentally tested solutions to some of the most contentious dilemmas that face humans today. ❐

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Competing interests

The author declares no competing interests.