Update

Forum

The social side of *Homo economicus*

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Many recent experiments in the field of behavioural economics appear to demonstrate a willingness of humans to behave altruistically, even when it is not in their interest to do so. This has led to the assertion that humans have evolved a special predisposition towards altruism. Recent studies have questioned this, and demonstrated that selfless cooperation does not hold up in controlled experiments. As I discuss here, this calls for more economic 'field experiments' and highlights the need for greater integration of the evolutionary and economic sciences.

> Kto nekradne, okráda svoju rodinu
> (He who does not steal, steals from his family)
> Slovak Saying

The apparent puzzle of human cooperation

Humans live in complex societies. Our entire society is built upon cooperation, and our economy depends on countless acts of cooperation, most of which one would call trade. Although cooperation, in the broadest sense, is common, there has been much debate across disciplines about the nature and causes of human altruism [1,2]. Biologically speaking, altruism is defined as any act that confers a benefit to another individual at a net life-time fitness cost to the acting individual [3]. Thus, acts that are reciprocated ('I scratch your back if you scratch mine'), or where there is mutual benefit to be gained (as in the case of trade) do not fall into this definition, as the net cost to the actor is regained within their lifetime [3].

One of the main assumptions in economics is the idea of *Homo economicus*, which assumes a rational, self-interested human who acts to maximise their own utility [4]. Although utility is often assumed to be monetary, it can encompass more motives than maximising one's own material gain, and can often be seen as a set of preferences that can range from preferring a flat in the city over a house in the suburbs, to a preference for coffee over tea. Thus, the idea of 'rational man' can be applied to many problems, which are not necessarily related to money, such as avoiding traffic jams or even decisions of when and whom to marry. Despite facing criticism from within both evolutionary biology (e.g. [2,5]) and economics (e.g. [6,7]), many behavioural economists have taken to the idea that humans behave altruistically, and have built up a field based on these assumptions [1,8–11]. Drawing on games that often involve anonymous one-shot interactions, the researchers find that individuals tend to behave more cooperatively than traditional economic theory would predict [1,11].

Are humans especially cooperative?

Cooperation in public goods games is unstable and most players quickly realise that not contributing maximises their profit (see Figure 1 for an explanation of public goods games). Despite this, the public goods game frequently results in higher levels of contribution than one would expect if individuals were selfishly rational and ~10% of participants contribute in the long run [1,12]. This has led to the conclusion that humans have a special degree of cooperation, or 'other regarding preferences', that cannot be explained from a purely selfish perspective and that has been used as evidence that humans behave more cooperatively than theory would predict [1,12].

Studies that claim to demonstrate higher levels of cooperation generally look at the case where it is not in the interest of players to cooperate. However, such studies rarely include a control situation, where it is entirely in the interest of players to cooperate, to determine whether the cooperation observed is statistically significant [5]. One recent study, by Kümmerli *et al.* [5], challenged the notion that humans display especially cooperative behaviours in public goods games. To examine whether the results of such studies really show an innate predisposition to cooperation, the authors used several controls under which the 'selfish' strategy was to cooperate [5]. This was compared with the results of a standard public goods game, where it was in everyone's interest not to cooperate. To do this, they repressed competition by changing the scale of competition within the group, to create incentives to contribute to the common pot (Figure 1). In the standard public goods game, cooperation decreased after several rounds, but cooperation did not disappear entirely. However, in the treatments where it was in all individuals' interest to cooperate, full cooperation was never achieved. The fact that, regardless of the situation, not all individuals acted completely rationally discredits the idea that individuals have innately altruistic (or even selfish) preferences [5]. To examine the reasons for this, the authors gave out questionnaires to estimate how players perceive their group mates and found that participants still perceived each other as competitors, even when competition was fully repressed [5]. This suggests that some participants make mistakes regarding when and how they perceive their group mates as collaborators.

This interpretation fits well into the established idea of 'bounded rationality', where the rationality of individuals is limited by cognitive limitations or the amount of time or

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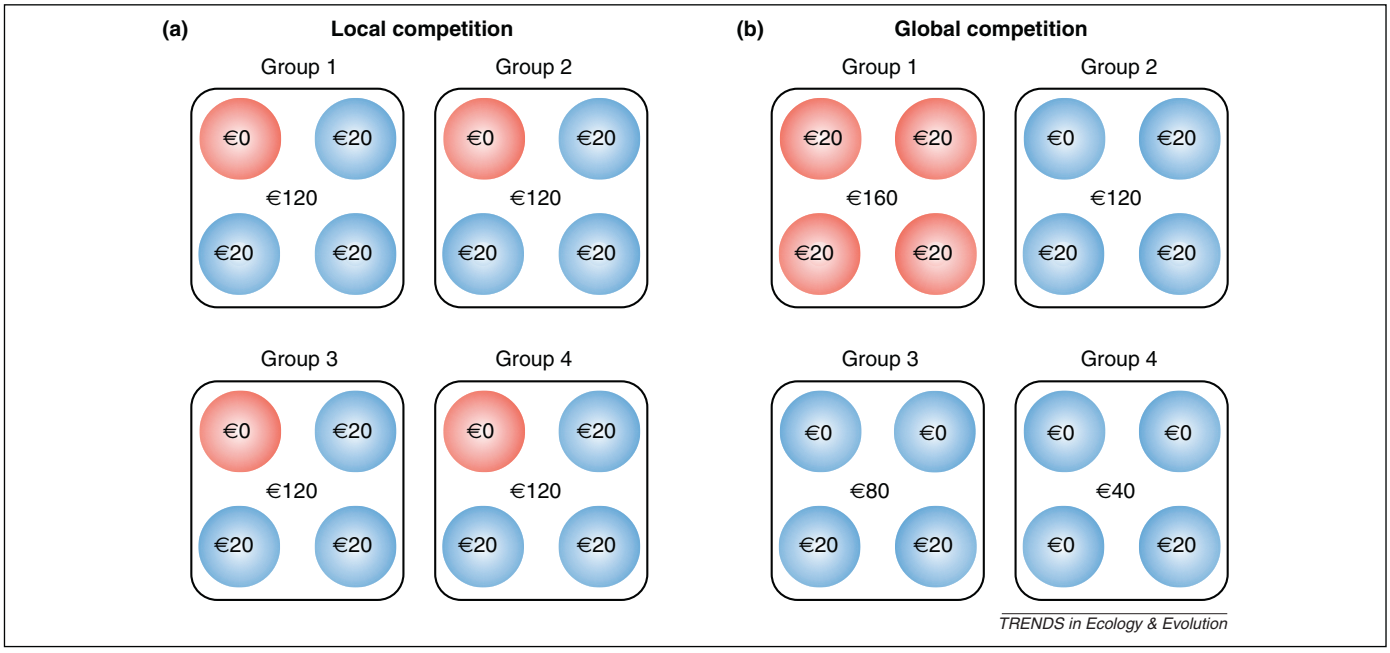

Figure 1. Example of the standard public goods game, with local **(a)** and global **(b)** competition. Participants are given a set amount of money and can contribute a certain amount of this to a common pot (the group total is given in bold). All contributions (shown in circles) are then multiplied by a factor b and then redistributed among all n participants, meaning that, as long as $n > b$, it is in each player's best interest to never contribute to the common pot. For example, if four participants each contribute €20 and this sum is doubled (i.e. $b = 2$), each receives €40 in return, yielding a profit of €20 each. However, if only three contribute €20, and one contributes nothing, each receives €30, meaning the non-contributing player has a total of €50 (i.e. the original €20, plus the €30 they receive from the common pot). The study of Kümmerli *et al.* [5] manipulated the scale of competition. In **(a)**, competition is global (i.e. among the individuals within each group). Here, it is best not to contribute as only the top-scoring individuals in each group (in red; i.e. those that do not contribute) will receive a high payout [5]. In **(b)**, competition is local (i.e. competition takes place among groups). Here, it is best to contribute as only the members of the top-scoring group (in red; i.e. those that contribute) will receive a high payout [5]. Other treatments can create situations in which it is in the participant's interest to cooperate, such as using $b = 5$ as the multiplier (i.e. multiplying the contribution by 5: if there are four participants, this will return 1.25 credits for each credit contributed), and this can also promote group cohesion [5].

information they have to make decisions [13]. Acknowledging mistakes in studies of social behaviour helps to link evolutionary biology and the study of human cooperation to mainstream economics: one could argue that humans do indeed behave rationally, but they are constrained both by the mistakes they make, or the limited information available to them.

The need for field experiments to study social evolution

It is hard to draw evolutionary implications from simple economic games. Economic experiments can generally only inform us of the proximate reasons why humans cooperate, but cannot tell us the evolutionary mechanisms that have led to such behaviour (Box 1). Additionally, laboratory experiments can only tell us how humans behave in the constrained environment of the laboratory. Participants in experiments often come from a biased pool, sometimes even taken from students in the department where the experiment is taking place. It has been argued that the volunteers who agree to participate in experiments are also the ones who are prepared to give up their time in the interest of science (and a small fee), and are thus more cooperative [14]. Additionally, participants are always observed by an experimenter and observation

Box 1. Ultimate and proximate mechanisms promoting human cooperation

The evolutionary literature is rife with studies trying to explain human cooperation and many studies commonly confuse proximate explanations with ultimate explanations. Proximate explanations for behaviours refer to questions regarding the mechanisms or stimuli that trigger a behaviour, whereas ultimate explanations for behaviours refer to questions regarding the evolutionary factors that caused such a behaviour to evolve. Some of the most pervasive mechanisms promoting cooperation among strangers are with regard to direct benefits, in terms of mutual interests, and reputation. One well-invoked mechanism is indirect reciprocity: helping individuals who have previously been observed to help others [15,16]. However, caution is required here as reputation could be regarded either as an ultimate or a proximate explanation for cooperative behaviours. An ultimate explanation for indirect reciprocity would be that humans could have directly evolved to cooperate in response to an evolutionary pressure created by the effects of reputation. In this case, individuals who help would receive greater benefits and, thus, have a higher fitness. Therefore, cooperation would be hard wired into the brains of those individuals.

Indirect reciprocity could also be regarded as a proximate mechanism driving cooperation. If a species has sufficient abilities to recognise individuals and process information about what those individuals have done, cooperation could arise through proximate mechanisms. In this case, cooperation simply occurs as a response to being observed by others. The evolutionary roots for such behaviours must therefore lie in other phenomenon, such as the ability to recognise other members of the population. Here, cooperation itself has not been selected for, but the cognitive abilities that can lead to cooperation (i.e. recognition and the ability to remember who did what to whom) have evolved and the emergence of cooperation occurs as a result of this, and is not selected for. All that is needed is a selfish, rational-thinking, individual who realises that they can benefit from being seen to help others. Field studies demonstrate that humans adjust their level of cooperation according to whether they are observed [14,16], suggesting that indirect reciprocity could be seen as a proximate, rather than ultimate, driver of cooperation. This highlights the need for experiments with proper controls (e.g. [5]), as well as field experiments (e.g. [6]), to help disentangle the proximate and ultimate causes of human sociality.

itself might alter their behaviour from what it would be in a real-world setting. The knowledge that being observed increases cooperation is well established in the evolutionary literature [15,16]. This has led to calls for more economic 'field experiments', and the results of these suggest that participants tend to behave more selfishly in real life than experiments would suggest [6]. For example, a study of baseball card collectors and traders showed that traders offered a fair price to collectors in a controlled experimental setting [14]. When actors were asked to go into a wider baseball-card convention and buy cards as a collector, the price they paid was significantly higher than the value of the cards they received in return [14]. This shows that, in studies of human sociality, humans behave more selfishly in natural settings than when they are being observed in the laboratory.

Studies of human behaviour in which economic experiments are conducted often take their cue from experimental economics. Although conducting experiments in the laboratory is a useful way of obtaining real-world confirmations of theoretical models (e.g. [15]), it is limited in what it can tell us about human social behaviour. Field experiments should be conducted to compliment laboratory experiments with clear controls. To do this, studies of human behaviour should draw from fields such as social psychology and study human behaviour by manipulating real-world settings. As evolutionary ecologists, we are acutely aware that the behaviour of our organisms can differ substantially in the laboratory, compared to when we study them in the real world.

Conclusion

Despite much overlap, economics and evolution have remained very separate fields. Experimental economics has made much progress regarding our understanding of human social interactions, but the interpretation of the results in the context of evolution has often been misguided [2]. Recent studies on the subject [5,14,17] provide new insight, and help to highlight the limited conclusions that can be drawn from such experiments into human social evolution. Both *Homo economicus* and inclusive fitness theory view the individual as a maximising agent, and the two approaches are in no way contradictory. It is clear that humans do not only act to maximise their own utility, but also to maximise the utility of other family members. *Homo economicus* clearly does have a social side, but it is unlikely to be as social as some researchers might hope.

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