What behaviour in economic games tells us about the evolution of non-human species' economic decision-making behaviour

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In the past decade, there has been a surge of interest in using games derived from experimental economics to test decision-making behaviour across species. In most cases, researchers are using the games as a tool, for instance, to understand what factors influence decision-making, how decision-making differs across species or contexts, or to ask broader questions about species' propensities to cooperate or compete. These games have been quite successful in this regard. To what degree, however, do these games tap into species' economic decision-making? For the purpose of understanding the evolution of economic systems in humans, this is the key question. To study this, we can break economic decision-making down into smaller components, each of which is a potential step in the evolution of human economic behaviour. We can then use data from economic games, which are simplified, highly structured models of decision-making and therefore ideal for the comparative approach, to directly compare these components across species and contexts, as well as in relation to more naturalistic behaviours, to better understand the evolution of economic behaviour and the social and ecological contexts that influenced it. The comparative approach has successfully informed us about the evolution of other complex traits, such as language and morality, and should help us more deeply understand why and how human economic systems evolved.

This article is part of the theme issue 'Existence and prevalence of economic behaviours among non-human primates'.

1. Introduction

A key question when discussing any quintessential human behaviour is to understand how the behaviour evolved. This tells us not only the trajectory the behaviour took, but also potentially something about the ecological and social environments that provided selective pressure for it, and ultimately, to help us understand, and address, quirks. For instance, one potential reason that humans are so poor at taking long-term benefits into account (steep discounting, for instance hyperbolic or exponential discounting) is that in our past, less certainty and shorter lifespans may have reduced the potential benefits of planning too far (i.e. years) in advance [1]. Of course, we can't go back to study our ancestors *in situ*, so we have to explore these questions in other ways. One such approach is the comparative method, in which we study other species to make predictions about how and why such traits evolved. This can either be done by exploring our closest phylogenetic relatives, the other primates, or by looking at species that share key features in common, such as large brains for their body size or fission–fusion social systems. The comparative approach has been very fruitful in helping us to understand traits such as language [2], complex culture [3], morality [4–6] and, more recently, economic decision-making [7].

Although there are a variety of ways economic decision-making can be studied, as outlined by the different papers in this special issue, I focus on using games derived from experimental economics to test decision-making behaviour across species. Economic games are highly structured decision tasks in which subjects' outcomes are dependent upon their choices and, typically, those of a partner or partners. In most cases, scientists are using the games as a tool, for instance, to understand what factors influence decision-making, to determine how decision-making differs across species or contexts, or to ask broader questions about species' propensities to cooperate, compete and so forth. They can, however, also help us explore potential precursors to human economic systems. To do this, we need to break down economic systems into a series of different components, each of which may exist, separately or in concert with others, in other species, and finally explore to what degree other species share behavioural outcomes. If they are shared, there are two additional considerations: whether (or not) they are underpinned by shared mechanisms and to what degree human-specific characteristics, such as language, shape human decision-making in unique ways, or mask our ability to see shared underlying behaviours. Economic games are a particularly good tool for this, as they are both simple and highly structured, allowing them to (relatively) easily be compared across species and contexts. Of course, these games are a model system that lacks ecological validity, so once these games have been used to develop hypotheses about the similarities and differences across species, we must then test these hypotheses using more species-specific approaches that may help us better understand the impact of ecology and social system and the unique selective pressures of each species [8]. In this way, we may better understand the evolutionary trajectory of economics, as well as the social and ecological contexts that influenced it.

2. The evolution of economics

Economic systems can be defined as 'a culturally-established structure through which exchanges or other joint activities can take place for the general benefit. [… A] modern human economic system is an institution that is agreed upon among participants, at some level of awareness and explicit representation, and that offers solutions to various survival or welfare-increasing problems arising in a shared natural and social environment' [7, p.1]. Although other species do not have economic systems in the same way that humans do, we can explore whether the roots of our economic systems are present in other species by considering what behaviours other species show that can be informative about economic behaviour. I refer to these as 'precursor' traits, following chemistry, where a precursor is a molecule that can form into something different under the right conditions [9].

One such precursor is how individuals achieve mutual benefit in social contexts. We know that species are very good at maximizing their benefits in other contexts (i.e. foraging), so this just assumes that this maximization extends to taking into account the results of others' actions. Note that animals may functionally achieve this without any need for conscious recognition that they are doing so; it may be that initially there was selective pressure to work together for mutual benefit and only later did recognition of this evolve,

potentially after the necessary cognitive abilities were selected for other reasons. We can also explore how individuals adjust their strategies around their partner, such as recognizing complimentary roles and changing one's behaviour based on a partner's outcomes. This can involve more complex cognition, such as theory of mind, to explicitly represent one's own and one's partner's roles. Although similarities across species are obviously informative, differences also provide insights into what cognitive abilities were involved in the rapid growth of human economic systems.

There are some important caveats when considering precursors to complex behaviours, such as language, morality or economics. First, just because behaviours look superficially similar does not mean that they are the same. In particular, one must be careful to keep function and mechanism separate. An evolutionary function is the reason why a trait evolved, or its evolutionary history, whereas the proximate mechanism is how the trait instantiates in an organism, including factors such as genetics, development, neural and hormonal pathways, and individual and social learning. Traits can have similar functions without sharing an underlying mechanism (think of the wings of birds, bats and bumblebees, which differ substantially in form but share the same function), or can have a similar mechanism that results in a different outcome (penguins use their wings to 'fly' through the water to swim). Failing to account for the first of these can lead to an over attribution of shared mechanisms, whereas failing to account for the second risks missing shared traits that are there.

Second, comparisons are inherently tricky, whether across species, across cultures or across contexts. In human work, responses to experimental games are influenced by the way in which the task is presented or the cultural interpretation (i.e. sharing money in economic games can be perceived as generous, an effort to put the recipient in one's debt or highly frowned upon and punished; see, for example, [10,11]). Similarly, comparisons across species must be carefully done to avoid either giving a species a task that is not appropriate, such as using the wrong sensory modality for a cognitive task or incorrectly assuming that the animal understands the experimental set-up in the same way that humans do [12–13]. This problem will be exacerbated for species that neither share a body plan nor interact with the world in similar ways, and is particularly challenging when comparing humans with other species. People are interacting with conspecific (same species) experimenters, rather than heterospecifics, often can interact more directly with the experimenter (rather than across a barrier of some sort) and can be given verbal instruction. This inherently favours the humans. Of course, it is also possible to simplify the task for the non-human species to the degree that it is either made easier for them or isn't even testing the same question. Thus, comparisons require extreme care and preferably should be tested using multiple modalities [8].

3. Using economic games to study the precursors to economic decision-making

(a) Economic games
One approach to studying decision-making that has recently gained traction in comparative work is games derived from

experimental economics. Economic games emerged from von Neumann's work ([14]; originally published in 1944) and were developed relatively simultaneously in the fields of experimental economics [15] and evolutionary biology [16]. They have been used to great effect to explore how individuals make decisions and how these decisions are influenced by the social and environmental context [17]. The games are very structured tasks in which subjects are given two (or more) options and the outcomes are dependent upon what both they and their partner(s) choose. This simplicity allows us to study complex decisions using very simple, often dichotomous choices, which makes them particularly amenable to comparative work. There are recent review papers that cover their use in other species in depth [18–21], so I will only summarize these games and the findings here as they are relevant to understanding the evolution of economic systems.

One of the challenges of studying these games in other species is that the lack of language means that we cannot use the typical human procedure of explaining the payoffs nor give pre-tests to ensure that subjects understand.[1] There are two different approaches that have been used with non-human species, each of which answers a different question. In the first, subjects learn the payoffs as they go, and the question of interest is how their strategy develops and what strategy (if any) they finally settle on [21]. In the second, subjects are given experience with the different payoff outcomes first, and what is of interest is which they choose to use. Each approach has different benefits and limitations; in the first, if subjects fail to develop a consistent pattern of play, it is difficult to know if they did not understand the task, or if they understood but were unable to find a stable pattern of play. However, it allows us to see how decisions develop with experience and minimizes the risk of inadvertent pre-training. In the second, it is very difficult to avoid the training biasing the subjects' eventual choices (i.e. if they are aware that there is an option that sometimes results in a preferred outcome, they may be more predisposed to play it irrespective of their cooperation preferences), but there is more confidence that they understand their different options, which can give more certainty when exploring how their choices are impacted by changing contexts.

In either case, one indication that they understand the task is if they find the Nash equilibrium (NE), which is the option that maximizes a subjects' benefit given the choice the partner is making.[2] This will, of course, sound familiar to anyone studying animal behaviour as it is reminiscent of the cost–benefit approach used in ethology. Indeed, there is no *a priori* reason why animals should not be able to maximize in these situations, nor does the mere fact of doing so suggest that they recognize that they are interacting with a partner. For instance, in coordination games the subjects' best options are aligned, so finding the NE does not require understanding their partner's role. However, we can look at features such as order of play, or whether they play differently with different partners, to begin to address this issue. Importantly, when I discuss results I am always discussing *functional* outcomes and making no assumptions about the underlying cognitive mechanisms, including the degree to which the subjects understand the task in the same way that we do.

One often used approach is to study the same game using different modalities to see if the results converge. For instance, these games can be run on a computerized interface, in which subjects must select their choice from among icons on a screen. Computerized games allow for more control (Do the subjects see each other's choices? Does one subject get to choose first?) while minimizing the potential for unintentional cuing (there is no human in the room, and computers' timing is more standardized than human experimenters'). However, computer tasks may also not provide the intuitive understanding present in manual tasks, in which subjects may return tokens to a human experimenter at the same time as a partner, or move from one area of the enclosure to the other at the same time as a partner; such behavioural synchrony may provide additional cues to the animal that their outcomes are tied to that partner's choices as well as their own [22]. Thus, whenever possible, it is best to use multiple approaches to maximize the chances that we will correctly identify the animals' abilities and preferences.

(b) Finding mutual benefit

The most straightforward task is mutually beneficial coordination when outcomes are the same, such as the Assurance, or Stag Hunt, game (figure 1a). In this game, subjects choose between two outcomes, Stag and Hare. Coordination on either results in mutual benefit, with the highest benefit for all if both coordinate on Stag. However, Hare is risk dominant, in that this choice is rewarded no matter what the partner chooses. No matter the choice, however, subjects' goals are aligned, and this does not differ depending on whether the participants play only once (one-shot) or repeatedly; since both individuals gain equally, mutual coordination is the best option for both (i.e. the NE). Likely because of this, these games have been given little attention in humans; if we use the typical human procedure, where the participants are given an explanation of the game and a payoff matrix to explain what their potential outcomes are, not to mention a possible pre-test to ensure that they understand it, coordination on the higher-paying equilibrium point is by far the most common response. However, some have argued that despite this (potentially misleading) laboratory consistency, this game is quite important. Not only are many very interesting human decisions often best described by coordination, but in the real world, with imperfect information, coordination faces many barriers [27]. Indeed, while both coordination points are Nash equilibria, the lower-payoff NE is, in fact, relatively *more* attractive when one doubts one's opponent's ability to find or interest in choosing the higher-paying equilibrium point. This makes this a much less straightforward, and much more interesting and relevant, game in real life. These characteristics hold for other species as well. In addition, there is a practical reason to use it: if individuals understand the laboratory task, they should always coordinate, making it a good test of whether other species understand the procedure before moving to more complex games, where they may not choose to play the NE even though they understand the procedure and their options.

Most of the primates tested thus far have found the NE in the Assurance game. Tellingly, the species that struggled the most to find this outcome is squirrel monkeys, which coordinate very rarely in the wild [28]. Even among the species that do coordinate, however, they appear to reach the coordinated outcome in different ways. Capuchin monkeys match the choice of their partner, and are unable to maintain the coordinated outcome when they can't see what their partner

(a) Assurance game

	Stag	Hare
Stag	4 / 4	1 / 0
Hare	0 / 1	1 / 1

(c) matching pennies

	heads	tails
heads	1 / 0	0 / 1
tails	0 / 1	1 / 0

(b) Hawk Dove game

	Hawk	Dove
Hawk	0 / 0	1 / 4
Dove	4 / 1	2 / 2

(d) Prisoner's dilemma

	coop	defect
coop	3 / 3	4 / 0
defect	0 / 4	1 / 1

Figure 1. The payoff matrices for the various games discussed in this chapter (**Player 1** is indicated in **bold/italics** and Player 2 in normal font). For the matching pennies game, **Player 1** is the matcher and Player 2 is the mis-matcher. Note that payoffs vary across studies; these are those used by Brosnan *et al.* [23–25] and Martin *et al.* [26].

chose, suggesting matching [23,24]. However, when they can see one another's choices, all pairs tested ended up coordinating on the highest-paying outcome, suggesting that this matching was accomplished with a bias towards the option that (sometimes) paid the best. Rhesus monkeys (also called rhesus macaques) coordinated on the best-paying outcome whether or not they saw their partner's choice [24]. However, subsequent work suggests that they simply developed a preference for this (sometimes) better-paying option and stuck with it. To explore this, we had rhesus monkey subjects play a simulation that varied in the frequency of playing the highest-paying option. They showed little flexibility, choosing Stag—which paid best on average across most of the simulations—no matter what the simulation 'played', suggesting that they were insensitive to their partners' choices [29].

Chimpanzees showed the most evidence of understanding their choice as part of a strategy, with some chimpanzees quickly adjusting to novel options with the same payoff structure (i.e. tokens of different colours). However, this was experience-dependent; subjects that had daily experience with cognitive testing for their entire lives were likely to coordinate on the highest-paying option, whereas those with very little experience with cognitive testing settled for the still good, but not maximizing, option of matching their partner, or even no strategy ([23,30]; note that subjects received at least one reward on most trials, and such a high level of reward by chance can result in low levels of learning; [31]). Indeed, mirroring the partner's choice may in the long run be a good strategy, as it is safer if individuals do not know what their partner will choose.

One key issue is the degree to which the subjects understood that this was a coordination task, rather than simply a reward maximization task (which would not even require that they understand that the actions of the individual next to them matter). It is difficult to make this assessment with the monkeys' data. However, the chimpanzees' ability to extrapolate rapidly to novel tokens suggests that they understood their choice as part of a strategy. Additional evidence comes from a different study using the same payoff structure but an intuitive foraging-based task design in which, rather than returning tokens that represented different choices, chimpanzees had to move together between two different food sources. The researchers found that subjects used a leader–follower dynamic, in which

one chimpanzee followed what the other did, suggesting that they understood that they were working together [32]. Such kinesthetic feedback may support their ability to understand a coordination task [22]. We do note one potentially informative anecdote: among the chimpanzees tested at Georgia State, when we first introduced a barrier that blocked visual access to the partner's choice, on the initial trial our best pair of subjects seemed agitated and made repeated attempts to see their partner's choice (SF Brosnan and MJ Beran 2011, personal observation). Once both subjects returned the maximizing token, they immediately returned to their rapid choice of that token on subsequent trials.

As a whole, these data suggest that chimpanzees, at least, have some understanding that they are playing a partner and are actively adjusting their decisions around the partner's choices. Indeed, I would speculate that we will find this is the case for all highly social species with some minimal level of social awareness who engage in contexts in which their outcomes are tied to their social partners' actions. These results also, however, highlight the challenges of trying to determine what the subjects understand about their actions. The most suggestive data, despite appearing in the context of controlled experimental studies, are anecdotal, and motivations remain elusive. In the aforementioned Brosnan and Beran observation, the chimpanzees hesitated only once. Is this because after they ascertained that their partners would coordinate on Stag, they assumed consistency in their partners' future choices? We don't know. It is relatively straightforward to determine what individuals of other species *do*, even if it can be challenging to design experiments to ask every question we may have, but it is much more difficult to figure out why they do it.

(c) Adjust your strategies around your partner
(i) What if it's not a mutually beneficial game?
In the above game, a subject can maximize their benefit with no understanding that another is involved. However, what happens when one must pay attention to others' actions to maximize one's own benefit? In anti-coordination games, such as the Hawk Dove game (figure 1b; also the Chicken or Snowdrift games), chimpanzees [30] and squirrel monkeys [28] rarely settle on a consistent pattern of play. Capuchin and rhesus monkeys are able to find the NE, but only when they can see their partners' choices [25,33]. One important

caveat is that we suspect that the capuchins' and rhesus' superior performance was owing to these particular populations being far more experienced with cognitive tasks than either the chimpanzee or squirrel monkey populations, a situation that improves performance in cognition studies [23,34]. Nonetheless, even the capuchin and rhesus monkeys had more difficulty than on the coordination game, suggesting that anti-coordination is more difficult than coordination. Similarly, work with chimpanzees using the matching pennies game (figure 1c), in which one subject 'wins' if they match their partner and the other wins if they do not match, finds that they make decisions faster when they are the matcher, suggesting that it is the easier role for apes [26]. Intriguingly, for theories of the role of dominance in the Hawk Dove game, in the capuchins' case dominance did not determine who played Hawk [25], perhaps suggesting that in these game contexts in which otherwise irrelevant cues (i.e. coloured tokens) are assigned specific meanings by the experimenter, which monkeys settle on which outcomes may be based more on stochastic factors (such as who played it first) than factors intrinsic to the monkeys (such as dominance).

Work has also been done with the prisoner's dilemma (figure 1d), a game in which there is a temptation to defect for short-term maximization. This game is particularly interesting because the best choice depends on whether it is a one-shot interaction, in which case the best outcome is to defect, or repeated, in which case cooperation dominates. In our results, capuchins' responses differ across pairs, with some tending to the one-shot NE of mutual defection and others to the mutually cooperative outcome, which maximizes benefit in the long term within stable, mutually cooperative relationships, which these highly social monkeys exhibit[3] [33]. Moreover, subjects seem to be sensitive to previous outcomes. Capuchins were both more likely to defect after mutual defection and, in at least some cases, more likely to cooperate after mutual cooperation. Another study using a different procedure found that rhesus monkeys typically defected, but were also more likely to cooperate on trials following a cooperative outcome [36]. Intriguingly, rhesus cooperated less often when subjects were not sitting side by side, suggesting that orientation impacts the perception of working together (side-by-side versus face-to-face orientation may impact chimpanzees' responses as well; [37]). Notably, the prisoner's dilemma is the only economic game studied to date in other species that shows such variability, suggesting that it may be a particularly good option for future studies looking at the role of social context in decision-making. The variability across pairs suggests that it captures differences in relationship quality, while the variability across trials within in the same pair suggests that it is also sensitive enough to capture short-term fluctuations in the relationship or context.

(d) Adjust to your partner's strategies

Subjects may also adjust to their partner's strategies. Again there is particularly strong evidence for this in chimpanzees. For instance, in the abovementioned coordination game by Bullinger et al. [32], chimpanzees adjusted their choices to the actions of their partner, suggesting that they understood the need to coordinate. In addition, chimpanzees adjusted their behaviour flexibly in the matching pennies game [26]. It is important to note, however, that while data such as

these are certainly suggestive of active adjustment, brains are not required [38,39]; plants can adapt their support of rhizomes to match those rhizomes' nitrogen fixation [40].

Similar evidence emerges from cooperative tasks in which subjects perform complementary actions to complete the task. Either behavioural synchrony or social facilitation may be able to explain at least some instances of coordination (i.e. one individual is primed to pull on a rope when they see a partner doing the same thing), but when the actions are highly dissimilar it is more suggestive of at least some understanding of the partner's necessity. In one study, capuchin monkeys learned a two-step task that required both pulling and pushing, and then learned that if they had access to only half of the testing area, they could not complete both actions. When the monkeys were then placed in half of the testing area with another capuchin from their group in the other half, they spontaneously worked with their partner, each completing one action, suggesting that they understood that both actions were required and that their partner could play the other role [41].

This raises the question of whether they are aware that they are playing with another individual. While many of these results suggest that they are, we lack conclusive evidence that this is the case. Outside of economic games, however, there is evidence that rhesus macaques use strategic thinking. In a zero sum competitive 'soccer' game in which one player 'kicked' a 'ball' on a computer screen and the other player (the goalie) attempted to intercept it, rhesus monkeys and humans used similarly complex strategies in both roles, suggesting that the monkeys were aware that they were playing against another agent [42]. This task, too, required individuals to make decisions for which payoffs varied depending on the partner's choices, suggesting that such awareness could also be present in economic game decision-making.

Adjusting to one's partner's strategies also suggests some attention to one's partners' outcomes, which also could help in making better decisions in social tasks. Indeed, many primates, and in particular those that cooperate routinely, react when they receive less than another [43], which may help them determine whether to continue in a cooperative relationship. Moreover, chimpanzees apparently noted when they were *advantaged* compared with a partner, refusing a preferred reward more frequently if others were getting a less preferred one than when both got the preferred one (although they refused far more often when they were the disadvantaged chimpanzee! [39]). This attention to their partner's outcomes may help them maximize their own benefits. Indeed, in a different study, chimpanzees seemed to recognize when their partner accrued a cost to assist them and were more likely to choose an outcome that benefits both, despite the cost, in such a case [44].

(e) How do humans differ from other primates in these games?

Comparing humans and other primates is challenging; although humans show much more sophisticated strategic ability than other species, these are typically not fair comparisons [8]. When humans are given one of these games using the same method as the other primates, with no verbal instruction, payoff matrices, previous experience or pre-tests, they may actually do *worse*. For instance, in one Assurance game (coordination) study, nearly 40% (10/26) of the human pairs settled on the lower-paying coordinated outcome rather than

the higher-paying one. However, none of these pairs ever experienced the higher-paying outcome, and debriefing suggested that they thought that they had found the best solution [23]. We suspect that this is, in part, owing to the fact that humans typically use language to explore the parameter space; indeed, on a different version of the task, pairs that discussed the game eventually found the higher-paying coordinated outcome, whereas those that did not discuss it settled on the lower-paying outcome [24]. Chimpanzees also outperformed humans on the matching pennies game, making choices that conformed more closely to game theoretic predictions and making their choices in a third less time, on average [26]. The authors propose that this was, in part, owing to experienced chimpanzees' good working memory, and suggest that they adjusted to changes in their opponents' patterns of play and incentive structures more rapidly.

Of course, humans use language and are accustomed to instruction, so is it fair to give them a task that essentially handicaps them? In addition, humans are typically far less experienced with the tasks used in these studies compared with the non-human primates, which also disadvantages them [45]. And indeed, on other similar tasks, humans do outperform other primates. For example, in the anti-coordination game, both rhesus and capuchin monkeys typically played the uncoordinated NE, in which one subject got substantially more than the partner did when they could see what their partner played (and they chose at random when they could not see their partner's choices: [25]). However, more than a third of human subjects across two studies (9/26 and 11/27) found the mutually beneficial alternating NE, in which subjects alternate between the two asymmetric NE so that both subjects benefit half of the time. Again, the humans got no instruction, so how did they do this, and why were so many successful here when they were so bad at finding the higher-paying equilibrium in the Assurance game? One possible answer to the second question is that the complexity of this game—and the lack of a sub-par but nonetheless mutually beneficial outcome—encouraged humans to explore the parameter space to a greater degree than in the Assurance game, and to a greater degree than the monkeys did. This suggests that an answer to the first question is that one area of humans' advantage is a greater ability and/or motivation to discern more complex strategies and figure out how to use them. Then again, monkeys appear to be quite sophisticated in other contexts [42], and humans may struggle (i.e. the Assurance game), suggesting that the relatively artificial interaction space of these games, while beneficial for comparative work, may inhibit full expression of abilities in both humans and other species. This reiterates the need to test the same questions using multiple studies across multiple modalities.

4. What can we say about the evolution of economic systems?

Economic games are a model system that allows for close comparisons across contexts and species [46]. However, they are not intended to be natural situations, thus the data generated are best used to test hypotheses generated from observational or experimental work and generate new hypotheses that may be tested with more species-specific and/or naturalistic approaches [8]. While this can be done in diverse ways, there are two literatures that obviously

connect to the existing data on experimental economics, that on cooperation and that on trade. Both literatures are extensive enough for entire reviews on their own, but I briefly discuss them as they tie into the main points raised above.

The assurance game highlights the fact that not all species coordinate, and even among those that do, coordination may be achieved by different underlying mechanisms. This reflects their behaviour in natural contexts as well. For instance, in capuchins, group territorial defence (i.e. [47]) and coordinated defence against predators (i.e. snake mobbing: [48]) are typically done among individuals with a clear view of one another and in situations in which all individuals are performing similar actions. This is reminiscent of capuchins' behaviour in the Assurance game, in which they appeared to coordinate by matching their partners, and only achieved coordination when they could see the other's outcomes. This suggests that behaviour matching is a key mechanism for coordination in capuchins, possibly facilitated by behavioural synchrony and/or social facilitation. Indeed, although capuchins in experimental contexts can solve coordination tasks that require different actions (i.e. [41]), this was a rather simple case in which individuals could see one another and performed actions that they previously learned individually as a sequence.

On the other hand, chimpanzees show more complex coordinated behaviour, such as the coordinated hunting in which different individuals take on different roles, seen in some populations [49], which presumably requires an ability to understand the larger picture. This, too, matches their behaviour in the economic games, in which at least some chimpanzees (those with extensive experience with cognitive tasks) extrapolated to novel options in coordination games, suggesting that they understood their choice as part of a larger strategy. In some experimental contexts, too, chimpanzees show evidence of understanding the bigger picture, for instance choosing to benefit, at a cost to themselves, a chimpanzee that previously paid a cost to make that choice available [44]. Such specificity in how they make decisions suggests that they see their choice within a broader framework.

This synchrony between the outcomes of the highly structured economic games and these primates' natural behaviours suggests that the games are indeed useful models. They allow for studying mechanisms that may be impossible to study in more natural situations and for comparison across populations or species, and may be particularly helpful if differences in body form or ecology make it impossible to compare in more naturalistic contexts. Within the same population or species, these games can also be used to generate new hypotheses regarding behaviour, and the mechanisms underlying it, in more naturalistic contexts. Future work using more naturalistic experimental tasks, like the cooperative barpull (reviewed in [50]), or field-based experiments (as has been done in social learning research; [51]) that combine the naturalistic contexts of the observational work with the structured methodology of the economic games will help determine the limits and flexibility of the different species' coordination ability and the cognitive mechanisms that underlie them.

We can similarly learn from how primates trade goods and services. Primates' ability to find the NE in economic games suggests that they should be able to maximize their outcomes in barter, too. Indeed, in natural contexts, primates do trade, although typically this involves services (grooming, support in conflicts, and mating opportunities) rather than

goods (there are exceptions; for instance, chimpanzees trade meat for mating opportunities and support; [52]). There are several possible reasons for this; objects are zero sum commodities, and few items in primates' natural lives are worth trading, as most are either easy to acquire or cannot be stored for future trades [5]. This does suggest, however, that they should trade objects when it is worth doing so, and indeed, in experimental tasks, primates trade tokens with experimenters (or, sometimes, other primates) in order to obtain different food rewards (see Addessi *et al.* [53] and Beran & Parrish [54]). Some macaques have even spontaneously developed exchange systems with humans in free-ranging contexts [55].

What is notably absent, however, is the transfer of these barter relationships with humans to trade with one another. We tested this among three highly trained chimpanzees at Georgia State's Language Research Center (the same chimpanzees that showed evidence of strategy use in the Assurance game). These chimpanzees had been taught a symbol language that allowed us to communicate with more specificity than is typically possible [56]. We made tokens representing specific foods (labelled by their symbol) that they could exchange back to an experimenter for food if—and only if—that food was present in their personal bin. In a series of tasks, we then explored whether the chimpanzees would learn to trade tokens that were of no value to them (because the food was not in their bin) to a partner to whom the tokens were valuable (because the food was in the partner's bin) so as to maximize both chimpanzees' benefits [57].

To cut a long story short, the chimpanzees learned to do so effectively as long as a human experimenter mediated the interactions such that neither chimpanzee could exchange a token with the experimenter for food until they had reciprocated any trades from the partner (we did not restrict which token they had to trade to a partner, just that they traded something). Despite having previously maximized their rewards, within one session of us removing experimenter-mediated quid pro quo, the chimpanzees ceased trading any tokens with their partners. Since they demonstrated all of the necessary cognitive abilities to understand trade, we hypothesized that the issue holding them back was an inability to trust their partners and a lack of third party enforcement mechanisms to make doing so worthwhile [57].

In concert with the results from experimental games, this suggests that at least some primates have the cognitive ability to understand these strategies and maximize their outcomes, which may be evident in service markets, but lack the enforcement mechanisms that lead to beneficial trade of goods. This is important for two reasons. First, it suggests that even these very structured, artificial laboratory situations are indeed useful for understanding the true scope of primates' abilities, by removing factors that may inhibit expression. Second, this suggests that primates have a more developed set of abilities related to economic behaviour than is necessarily indicated in their natural behaviour. This not only guides future research aimed at understanding economic behaviour in natural contexts, but suggests that humans' abilities are not as separate from the other primates' as we might think. Indeed, this isn't the only context in which experimental tasks have revealed such similarities; primates also share psychological adaptations related to economic

decision-making, such as the endowment effect [58] and framing effects [59,60]. Increasing evidence suggests that other species have the cognitive toolkit for economic behaviour and simply lack the opportunity to use it.

If this is the case, our next step is twofold. First, we must explore the range of economic behaviours in other species, ideally with the goal of delineating possible underlying cognitive mechanisms, and determine the contexts in which animals show these behaviours and how they are influenced by changes in social and ecological context. This will require creative experimental studies (both in the laboratory and, hopefully, in the field) to unpack what underlying abilities are present and when they manifest, as well as observational research to determine if related behaviours are seen in more natural contexts [61]. Indeed, further work in this area will also help to clarify the degree to which these abilities were selected specifically for this context versus others. Second, to more fully understand the cognitive precursors to economic behaviour, we also need to look beyond the primates. Although there has been work in this direction already, with studies of economic game behaviour in species as diverse as birds [62], rodents [63] and fish [64,65], even in those cases the focus has been on one or a few species. A more diverse approach is important for understanding how economic behaviour evolved; species vary in their needs, so a broad exploration will inform our understanding of the contexts, environments and pressures that selected for different economic behaviours. Ultimately, this will clarify how these abilities expanded so greatly in humans to result in the complex economic systems we enjoy today.

Endnotes

[1]However, this can also be an advantage since we do not inadvertently train them or base our conclusions on what they *say* rather than what they *do*.
[2]In most cases with animals, this equilibrium is based on repeated games, in which subjects play the same individual sequentially, although the maximizing outcome may differ for a one-shot game, in which individuals meet only once. Many human experiments involve one-shot games with anonymous partners, typically in double-blind conditions, in order to determine what humans do in the absence of any social pressures. This is obviously impossible in other species and means that care must be taken when comparing human results with those of other species unless researchers explicitly use the same procedures.
[3]Not only do capuchins have complex social relationships [35], but all of the capuchins in our studies are group housed in large, mixed sex social groups. The vast majority of females have been housed with the same individuals since birth and live with matrilineal kin, as is true in the wild, so they have the opportunity for the same sorts of strong social relationships as their wild-living peers. They are tested with other monkeys from their social groups.

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