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# Comparative economics: how studying other primates helps us better understand the evolution of our own economic decision making

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The origins of evolutionary games are rooted in both economics and animal behaviour, but economics has, until recently, focused primarily on humans. Although historically, specific games were used in targeted circumstances with non-human species (i.e. the Prisoner's Dilemma), experimental economics has been increasingly recognized as a valuable method for directly comparing both the outcomes of economic decisions and their underlying mechanisms across species, particularly in comparison with humans, thanks to the structured procedures that allow for them to be instantiated across a variety of animals. So far, results in non-human primates suggest that even when outcomes are shared, underlying proximate mechanisms can vary substantially. Intriguingly, in some contexts non-human primates more easily find a Nash equilibrium than do humans, possibly owing to their greater willingness to explore the parameter space, but humans excel at more complex outcomes, such as alternating between two Nash equilibria, even when deprived of language or instruction, suggesting potential mechanisms that humans have evolved to allow us to solve complex social problems. We consider what these results suggest about the evolution of economic decision-making and suggest future directions, in particular the need to expand taxonomic diversity, to expand this promising approach.

This article is part of the theme issue 'Half a century of evolutionary games: a synthesis of theory, application and future directions'.

## 1. Introduction

Game theory swept through the social and biological sciences in the latter half of the twentieth century following the publication of John von Neumann and Oskar Morgenstern's book *Theory of Games and Economic Behaviour* in 1944, and John Nash's famous proof in 1951 that under many conditions, an equilibrium exists for *n*-player, non-zero sum non-cooperative games [1,2]. It took less than a decade for Reinhard Selten, Sidney Siegel, and Lawrence Fouraker to begin putting game theoretic predictions to the human test with renumerated experiments [3–5]. However, it was not until the method of experimental economics took off in the 1980s and became firmly established in the 1990s that game theory experiments with humans became a staple of economic science [6,7]. Although during this time there was some notable work in economics with other species (i.e. [8]), this was the exception more than the rule.

In the meantime, in the 1970s and 1980s John Maynard Smith and George Price left an indelible mark on evolutionary theory by formalizing the central concept of an evolutionarily stable strategy, in general, and the Hawk–Dove game of conspecific conflict, in particular [9]. Such models enjoyed a marked surge of attention in animal behaviour, with perhaps no game receiving more than the Prisoner's Dilemma (PD), particularly the repeated, or iterated, version. After Axelrod and Hamilton's famous tournament showing that a tit-for-tat (TfT) reciprocity was the most effective solution to the iterated Prisoner's Dilemma (iPD; [10]), a cottage industry arose to find examples of TfT in animals [11–15]. Calculated TfT reciprocity, however, proved remarkably difficult to find (although see [16–18]). Nonetheless, there are certainly some reciprocally patterned behaviours, and while more recent work has moved somewhat away from the early focus on TfT and focused on what other mechanisms might account for this pattern of responses [19–25], research in this area continues (e.g. [18])

Our interest in economic games is somewhat different. Rather than trying to find examples of behaviour that fit the predictions of the games, we use the games as a model system that can be instantiated in the same format across multiple species to better understand commonalities and differences across taxa. We design the games to work across species, taking advantage of a highly simplified, structured presentation of the problem that allows us (i) to compare decisions in as identical of a context as is possible across species, and (ii) to look for commonalities and differences. We then use the pattern of results across species to make specific predictions for each species that can be further tested. This latter component may often not involve games, as the focus is on testing a predicted outcome in a species-typical context.

Games derived from experimental economics are ideal for this comparative approach [26,27]. Importantly, economic games are highly structured and standardized, making them suitable to compare across species and contexts. Of course, we do not know that just because the game is played in the same way means that every species (or individual) experiences it similarly, but it is a better chance than when each task is adapted to the species, which opens the door for tasks that are difficult for some species or, in an effort to avoid that problem, overly simplified for another [28]. Moreover, the simplicity of these games lends itself well to being adapted to contexts without instruction or verbal interaction. While some games can be quite involved, many well-studied games, such as the PD, are modelled as a dichotomous choice, which can be instantiated in a variety of ways (i.e. the participants can choose one of two tokens, one of two icons on a computer screen, etc.). Indeed, the lack of verbal instruction is a key component of our games.

In this review we focus primarily on games that have been repeated in nearly identical form across multiple species, including humans, allowing us to use the comparative approach to gain some insight into how decision-making evolved. This approach has been remarkably effective in other fields attempting to explore the evolution of human behaviour, such as imitation and social learning [29], metacognition [30] and prosocial behaviour [31], to name a few. We do in some cases discuss games that do not meet this criterion when they add to our understanding and refer the reader to the above literature for a more in depth consideration of the previous work. Finally, we note that most of our discussion focuses on non-human primates (hereafter, primates), owing to the simple fact that this is the taxon on which the majority of the work has focused so far. That said, the absence of other species is a serious lacuna. It is critically important to study other taxa to gain a fuller understanding of the evolution of economic decision-making.

To date, the majority of games studied in non-human species fall into three general categories; coordination, anti-coordination, and cooperation with an incentive to defect. We briefly consider each of these below, with a focus on what the use of games and the comparative perspective adds. For more details on the procedures and additional results, we refer the reader to the original research papers, cited below.

## 2. Comparative economics

How did the human socioeconomic system come into being? This is a key question to which we do not have a good answer. On the one hand, it is obviously multi-factorial, influenced by the culture in which the system is emmeshed and a variety of learning mechanisms that are particularly well developed in humans (not the least of which is language and writing, which gives us the ability to formulate economic rules and to keep track of accounting; [32]). On the other hand, other species also show a variety of behaviours that appear to be the same as or precursors to human economic decision-making (cf., [8,33–38]), and several researchers have argued that the evolutionary roots of human socioeconomic systems are present in other species [39,40]. One challenge to demonstrating this is that many of these studies use very different methodologies, making it difficult or impossible to fairly compare outcomes and their underlying mechanisms across species [41]. This can be particularly true when humans are involved, as humans often receive additional (language-based) instruction, pre-tests to ensure that they understand, and the benefit of working with a conspecific partner, all of which change the interaction, as compared to other species, and may advantage them. One key goal of comparative economics is to use identical contexts across species to facilitate these direct comparisons. With these data we can begin to understand where there truly are commonalities and differences that are not the result of experimental differences.

A second goal derives directly from the first. In order to understand what social, ecological, and contextual factors influenced the evolution of a behaviour, we need to know how it is distributed taxonomically. Although very familiar in biology and, more recently, psychology, the comparative approach is less widely used in other disciplines. In this approach, species are compared across specific parameters relevant to the hypotheses being tested to answer one of several questions. The two most common focus on when in the evolutionary lineage a trait arose and what characteristics were related to the selective pressure for a specific trait. The first of these focuses on homologies, testing species within the same taxon, or phylogenetic lineage, with the assumption that species which share a trait through common descent will all show the trait in question. For instance, if a trait, such as large brain-to-body ratios, is shared by all five great ape species (humans, chimpanzees, bonobos, gorillas, and orangutans), but is absent to the same degree in the other catarrhine primates (macaques, baboons, etc.), then we can develop hypotheses about what selective pressure led to its emergence in great apes and consider what factors tied to the evolution of apes may have selected for it, as well as pinpointing when it emerged, which can be useful for tying the emergence of a trait to known time periods (for instance, geological or climate change events).

The second approach focuses on convergences among species that share a trait, with the logic that if species share several traits in common in addition to the trait of interest, they may be linked. For example, the great apes are not the only primates with particularly large brain-to-body ratios; one group of platyrrhines, the capuchin monkeys (Cebus and Sapajus), also have ratios on par with chimpanzees [42], and an enduring question is why, and whether some shared trait between capuchins and great apes, such as increased cooperation or tool use, is related to this expansion. As this example may suggest, the comparative approach can be used to look for shared traits in the social realm, shared cognitive factors, or shared ecological factors.

Once we have hypotheses about which factors are linked to a trait in question, this also gives us a set of hypotheses about which traits are currently linked to it. To give an example of how this works, one purported explanation for humans and other species' response to inequitable outcomes is that it evolved because it allowed individuals to identify when they were being disadvantaged in a cooperative partnership, which would give them a cue that it was time to seek out other partners [43]. This would balance out their benefits relative to others, as relative outcomes are the most important in natural selection. In this case, it turns out that not only did the comparative approach suggest this, with species that routinely cooperate showing a greater tendency to respond to inequity than those that do not [35,44], but within cooperative interactions, individuals prefer partners who are more tolerant around rewards [45], avoid situations in which one individual can dominate rewards [46], and will even quit cooperating with partners who have treated them inequitably in situations in which inequality is impossible [47], suggesting that they are responding to the partner's behaviour, not the immediate distribution.

One final related point is that when we talk about comparative approaches or evolution, there are two different ways to think about a behaviour (or any trait), its function and the underlying mechanisms [48]. A trait's function is its evolutionary history/trajectory and the selective pressures that led to it. A trait's mechanisms are the myriad factors that cause it to manifest in the individual, including development, hormonal/genetic/neural/etc. factors, and the underlying cognitive factors, including whether and how it was learned. Traits can share a similar function but differ in mechanism, or the other way around, and one cannot be assumed from the other. When discussing cognitive mechanisms underlying decision-making, we cannot assume outcome from mechanism or the reverse; that is, just because two traits share a similar outcome does not mean that they share a mechanism in common, and even if two species are known to both have a similar cognitive ability, we cannot assume that they are using it in the same contexts.

## 3. Our approach

Coordination is deceptively simple. Present two individuals with a pair of options, one of which rewards both of them better than either could get any other way, and the choice seems clear—mutual cooperation. However, there are a slew of assumptions hidden in this straightforward presentation. Do both parties know what their options are, what their partner's options are, and how the task generates rewards? Do the parties share a common idea of what is a pay-off maximizing outcome? Are both parties paying attention and making deliberate decisions? If so, coordination is easy, but without such assurances, it becomes significantly more challenging to interpret the results. While simple 2 x 2 coordination games are not often explored among humans (if you fully explain the tasks, it appears there is no strategic tension), others have argued that this is not how coordination works in the naturally occurring world [49]. We rarely go into a situation knowing precisely what the parameters will be—if it is even possible to know them—or everything about our partner's knowledge, but it is probably the case that even many games that are not initially coordination games can be *turned into* such.

More than a decade ago, when we began our inquiry with the Assurance game, or Stag Hunt game, a coordination game, the typical approach in experimental economics was to either tell individuals the contingencies and administer pre-tests, to ensure they understood the task, or to train them on those contingencies (for non-human subjects who could not be given a pay-off matrix). The dependent variable was what option they chose given their knowledge of the contingencies. Instead, our participants (both human and non-human primate) were given no instruction and we watched what outcomes endogenously emerged as they played the game [50]. We took this approach for two reasons. First, it is ecologically natural. Individuals in the wild do not get a playbook that tells them what comes next; they have to figure out what their options are and what to do with them. In some cases, this is probably true for humans. Whereas we typically have more information available, we also have a greater variety of options and outcomes than for monkeys, who have a more constrained set of social decisions owing to a smaller, less complex social environment with, typically (but not always), fewer overlapping social networks. Indeed, one might make the case that in humans, nearly any situation *could* become a coordination game if it is recognized as such, making it even more difficult to know the options (which are changing) and outcomes.

Second, training monkeys on the specific contingencies before the test raised the very real possibility that they would develop consistent preferences for an option that paid well during training and then fail to adjust to the changing contingencies in the game, even if those choices did not reflect their actual preferences in the game [50]. Once individuals are trained, behaviours take time to extinguish, particularly if they are intermittently reinforced. Thus, we might get an inaccurate reflection of what their preferences in the *social* context are because of carryover from their preferences during learning. Of course, for some questions it is useful to train the animals and see what decisions they then choose to make, and indeed, this has been done quite effectively in some cases with economic games [51,52], but it needs to be clear that this is the goal of the study.

One challenge of testing other species is ensuring that the subjects understand what they are doing in the way that the experimenters intended [53,54]. After all, we cannot ask them what they thought they did. A good approach is to begin with a task with a clear predicted outcome so that you have more confidence that the animal understands it. One reason that we began with coordination tasks is that there is a straightforward pay-off maximizing equilibrium that benefits both individuals equally—coordinating on the highest value outcome—making it easy to determine if the individuals actually understood how to maximize their outcomes in the game; once we know that they can do this, then it is safer to interpret results in games for which there is no straightforward way to maximize one's pay-off in equilibrium[1].

Another challenge to comparative work is that even when tasks are identical, they may not be experienced identically across species. Participants may be more familiar with one format of testing than another, so requiring them to participate in a less familiar format may artificially reduce their performance. This is relevant here because most primate testing is done with manual tasks (i.e. the subject interacts with the experimenter), but human testing is typically done in a computerized modality, which is also a common way in which we interact with the world. An advantage of computerized testing is that there are a number of features that should enhance learning; the contingency between choice and reward can be much faster than a human experimenter's reaction time (as in manual testing), trials are faster because they require less set-up, which allows for a greater number of trials in a shorter period, and the behaviour of the icons is far more consistent than even the most experienced human could do, which minimizes extraneous cues and makes it easier to learn the task [41]. While we are lucky enough to have access to a population of primates with extensive computer testing experience, there are also drawbacks. Most animals are not computer trained, and it is a rather artificial context for primates, which could suggest that the manual task is more likely to generate meaningful data. The manual condition, however, is tricky for comparison with humans as it can be a rather socially awkward situation. When possible, we test our subjects in both a manual version of the task, in which they choose from physical tokens that are returned to the experimenter to indicate their choice and a computerized task, in which they use a joystick to select an icon on a computer monitor.

In addition, our primary goal was to compare across species, using the games as identical methodologies, but we also planned to compare across games (both within and, potentially, across species). For this, we need our pay-offs to be comparable. All of our pay-off matrices ranged between a maximum outcome of four rewards and a minimum of zero (we had no negative rewards as we give our rewards on a trial-by-trial basis to enhance learning, so taking away rewards is not possible). Of course, the Nash equilibria and pay-off maximizing outcomes varied across games, but at least they were constrained within the same set of values.

One of the most important components of comparative economics is to include humans in the testing when feasible [41]. This is needed for several reasons. First, most of the paradigms that are used in comparative economics, including those we discuss below, are directly adapted from human tasks. The challenge with adaptations, however, is that with changes it can be impossible to identify whether differences are owing to differences between species or to procedures, or whether similarities reflect a true underlying similarity in species or an unintentional bias in the adaptation that made the task easier for one species than the other. This latter point is particularly challenging. On the one hand, much as it would not be scientifically interesting to present a task in Brunei using American English, it is not scientifically interesting to present a human task without scaling it appropriately and considering any species-specific constraints (i.e. a species that interacts with the world primarily through the auditory or olfactory modalities should not be given a task that is based in the visual realm). Thus, whenever possible, adapted tasks should be 'back tested' to see how the humans respond to them. In fact, even if humans do not respond as expected based on the typical task, the data are important as it still allows direct comparison and potentially highlight the impact of whatever factors were changed on the decision-making process, even in humans. Of course there are exceptions, for instance if the modality of the task changed owing to differences in sensory systems across species, but even small procedural changes, such as in reward value or how a choice is made, may influence responses (i.e. [55,56]). Finally, since the goal is not to understand humans, broadly, but to compare the results to previous ones, which typically used college students as the sample, it is usually reasonable to use college students. However, we do not generally recommend using children, as the other species are almost always fully developed adults, and so should be compared to fully developed adult humans.

Ultimately, then, for comparative experimental economics we develop tasks, typically adapted from traditional tasks in human experimental economics so that they are possible with minimal training and no instruction or pre-testing (or very minimal pre-testing) and use them on as wide a variety of species as possible. In most cases, subjects are presented with two options and choose one; their rewards are based on a pay-off matrix that is contingent upon both what they and their partner chose [57,58]. The results from these comparative game theory approaches can then be used to develop species-specific hypotheses to predict how animals will respond in more species-typical social and ecological contexts. If our predictions are not met, we can then refine the hypothesis and try again [26]. Although clearly no one paper, or even dissertation, could possible include each of these components, over time this approach allows us to fully incorporate social, ecological, cognitive, and evolutionary factors shaping decision-making.

## 4. What decisions do animals make?

Comparative economic approaches have been very useful in understanding how decision-making compares across species. Much work has explored coordination, possibly because it is relatively straightforward. We and our collaborators, for instance, originally explored coordination using the Assurance, or Stag Hunt, game across platyrrhines (or neotropical primates), catarrhines, non-human great apes, and, for comparison, humans. Of course, one species cannot represent an entire order, but we intentionally chose chimpanzees (the great ape) and capuchins (the platyrrhine) as species with particularly enhanced brain-to-body ratios [42] who also routinely cooperate across a variety of contexts (hunting, coalitions and alliances, defence, etc; see [59,60] for reviews of these species' behaviour), as well as rhesus macaques (the catarrhine monkey); no catarrhine monkey is known to have the significantly enlarged brain to body ratio, but rhesus do cooperate extensively in the context of coalitions and alliances (i.e. [61]). We tested the capuchins, who are trained to use a joystick to control a cursor on a computer screen, and humans on both computerized and manual token trading versions of the task to compare how the different modalities influenced responses (rhesus experienced only the computerized task and chimpanzees only the token trading version). In our version of the task, the *stag-stag* pay-out was four rewards (pieces of fruit, pellets, or quarters) each, *hare* always paid one, and the uncoordinated outcome rewarded the *stag* player with nothing (see figure 1 for the complete pay-off matrix). In both cases, subjects chose from between two icons (computerized) or tokens (manual); in the

Assurance game

| | stag | hare |
|---|---|---|
| stag | 4, 4 | 0, 1 |
| hare | 1, 0 | 1, 1 |

Prisoner's Dilemma game

| | coop | defect |
|---|---|---|
| coop | 3, 3 | 0, 4 |
| defect | 4, 0 | 1, 1 |

Hawk–Dove game

| | dove | hawk |
|---|---|---|
| dove | 2, 2 | 1, 4 |
| hawk | 4, 1 | 0, 0 |

Matching Pennies game

| | heads | tails |
|---|---|---|
| heads | 0, 1 | 1, 0 |
| tails | 1, 0 | 0, 1 |

**Figure 1.** The pay-off matrices for the four primary games discussed in this paper, the Assurance game (a coordination game), the Hawk–Dove and Matching Pennies games (anti-coordination games), and the Prisoner's Dilemma (a cooperation game with a temptation to defect). In all cases the pay-offs are bounded between zero and four to facilitate comparisons among the different contexts. (Online version in colour.)

computerized task the rewards were distributed automatically by a dispenser based on participants' choices, whereas in the manual task, the token was chosen by the participant and returned to the experimenter, who then gave the participants the appropriate reward based on both participants' choices.

In general, all four species found *stag-stag*, which was the pay-off dominant coordinated outcome, but how they did so varied [57,58,62]. Capuchins originally struggled to find any consistent outcome on the manual task, but every pair did so on the computerized version. As mentioned earlier, the computerized version differs by having more trials per session, less time between trials, and a shorter delay between choice and reward, all of which promote learning, which may account for the difference (anecdotally, the capuchins' performance improved when we increased the trial count of sessions, although this was confounded with experience; [58,62]). However, in later versions of the task, capuchins did equally well on the manual version [55], suggesting that with experience there is little difference between the two modalities and, even initially, there is no difference in choices among those who did learn the contingencies.

Perhaps more importantly, capuchins could not find the pay-off dominant outcome (*stag-stag*) without seeing what their partner played. Subjects were always offered their choices at the same time, but we had two versions of the task, a 'functionally simultaneous' version, in which they only saw their partner's choice after both of them had made the decision, and a 'sequential' version, in which they could see their partner's choice as they made it. However, there were no constraints on play in the sequential version, so we did not determine who played first or any time out period after a choice, therefore the results could have been functionally simultaneous. Nonetheless, capuchins were only able to coordinate on mutual *stag* play when they could see what their partners were playing. From an ecological perspective, this may make sense; capuchins live in relatively small social groups of 15–30 individuals and are generally in view of one another, therefore there may be no reason for them to remember interactions when they cannot see the other's actions.

Rhesus monkeys did extremely well at coordinating on *stag* whether or not they could see their partner's decisions. Indeed, they coordinated at the same high rates as humans typically do. To begin to explore the underlying proximate mechanisms, we had both rhesus and humans play against simulated partners that sequentially played a variety of different strategies [63]. We wanted the rhesus to know that they were playing a simulation, not a real partner, but of course we could not actually tell them this (and deception is not allowed in economic experiments, so we needed the humans to have the same experience as the monkeys). Thus, to 'tell' the players that they were in a simulation we put them in the familiar paired set-up room, but they were the only individual there. Although we could not debrief the monkeys, humans, who had previously played as part of a pair, reported that they assumed they were playing against the computer when alone in the room. In this set-up, however, while the human and rhesus' outcomes were highly similar, the underlying mechanisms diverged; the humans showed probability matching, playing *stag* at roughly the same rate as their simulated partners, albeit with a slight bias towards *stag*. Rhesus, however, while showing a significant, albeit small, change in *stag* play across the different simulations, showed an overwhelming bias towards playing *stag*, suggesting that the proximate mechanism they may be using is a preference for *stag*, presumably because it is (sometimes) the highest paying of the options. The interesting thing is that in other contexts, rhesus do probability match [64], so they did not use this option despite having the ability, reinforcing our earlier point that the underlying mechanism cannot be assumed just because two species share it in common.

Not surprisingly, given their large brains and advanced cognitive abilities, chimpanzees exhibited some of the most sophisticated behaviour. Chimpanzees not only coordinated on the pay-off dominant outcome but appeared to understand that there was a strategy to follow. The chimpanzees at Georgia State (GSU), who had participated in extensive cognitive training and testing since they were very young, did quite well, including apparently extrapolating to novel tokens, for which they rapidly found the same strategy, suggesting that they understood that they needed to find the *stag* token. Intriguingly, however, chimpanzees were also the most variable. Contrasting the GSU chimpanzees, those at two other facilities (the National Center for Chimpanzee Care at MD Anderson in Bastrop, TX, and the Emory National Primate Center in Atlanta, GA) did not [65]. Although chimpanzees at both facilities had some experience with cognitive and behavioural testing, it was nowhere close to as extensive as that of the GSU chimpanzees, and they tended to show far less strong preferences, if a preference at all (the chimpanzees in Texas tended to match their partner on either *stag* or *hare*, which works especially well if you are not sure what your partner is planning to do). One possible explanation is that they simply did not understand that they could receive more rewards by always choosing the *stag* token, although chimpanzees tend to maximize their outcomes in other contexts [66]. Another possibility is that they did not care; chimpanzees at all three facilities (as well as the capuchins and rhesus) only participate in voluntary, non-invasive cognitive and behavioural testing and were (and are) never deprived of food or treats to motivate testing, suggesting that the difference between four treats and one treat may not have been sufficient to motivate them, especially when there were so many trials back-to-back (meaning that they got quite a lot of food rewards). One could make the case that this is smart behaviour. Why work hard for something that is neither rare nor limited?

The humans were tested primarily to see how the modified game compared to the more typical testing approaches used in human studies, but the results were fascinating. In a typical economic experiment participants are given instructions, shown a pay-off matrix, and/or given pre-tests to ensure that they understand the instructions. Here they received nothing of the sort. They were introduced and trained in the task as the non-humans were and had to discover the different pay-off combinations as they played. The humans' game was functionally simultaneous in that neither choice was displayed on screen (or by the experimenter) until both participants had made their decision (although in the manual task, they could see each other's choices and could have deduced what their partner chose). Without any instructions, many human participants coordinated on *stag*, but even more coordinated on *hare*. Importantly, *hare-hare* pairs did not fully explore the parameter space, and so never experienced the coordinated *stag-stag* outcome, suggesting that they coordinated on *hare* because they thought it was the best they could do and that there was no other reason from the environment to deviate from the fast and frugal rule (à la [67]). Even more importantly, in the computerized version of the task, all pairs spoke to one another (they could have in the manual trade-based version, but many did not, probably because an experimenter was in the room with them). Those pairs that spoke about the game found the coordinated *stag* outcome, whereas those that did not generally coordinated on *hare*, suggesting that humans are using language to coordinate. In other words, the humans may have been using language to plan their moves, turning a simultaneous game into one in which outcomes are known (if you trust your partner to do as they said). Thus, adding to other reasons that humans may make suboptimal decisions is the possibility that when we do not have language available to explore the parameter space (think of people using social media to inquire about the best place to get a haircut or board a dog), we may not be as good as other species at doing so, possibly because we are so accustomed to this shortcut that we are unused to doing so in other ways.

Of course, coordination is not the only way individuals interact; another possibility is anti-coordination, such as when individuals must decide whether to fight or flee as in John Maynard Smith's Hawk–Dove game. This has also been explored in several ways. One advantage to games from experimental economics is that they are extremely flexible and allow direct comparisons both across species, as discussed above, and across different contexts, by changing the pay-off structure. Thus, we were able to compare primates' responses in a version of the Assurance game, a coordination task, to a version of the Hawk–Dove game, an anti-coordination task [68,69]. We again constrained responses between zero (very aversive for primates) and four (the highest possible individual pay-off), but in this case, the Nash equilibria were the two anti-coordination points, where one individual played *hawk* and one played *dove* (see figure 1). In that case, the individual who played *hawk* received four units of a reward while the *dove* player received one. Mutual *hawk* resulted in no rewards for either player, making *hawk* risky, whereas mutual *dove* resulted in two rewards for both, which is less good than alternating play of both Nash equilibria, which resulted in an average of 2.5 rewards per subject per trial. We used the same format of play, but different icons/tokens.

Capuchin monkeys showed a similar strategy as with the Assurance game in that they found a consistent pattern of play, but only if they could see their partner's choice [68,69]. They settled on a Nash equilibrium, with one monkey typically playing *hawk* and the other *dove*, and which monkey played which option appeared to be stochastic. We hypothesize that it was based on who first chose *hawk*. That player would have initially received four rewards, predisposing them to continue selecting the *hawk* icon/token, whereas the other player, when they played *hawk*, would more likely have received zero (because of mutual *hawk* play), predisposing them to switch to *dove*, which at least gave them something. Rhesus monkeys also played a Nash equilibrium, but unlike in the Assurance game, in which they found a Nash equilibrium in both the synchronous and asynchronous tasks, in the Hawk–Dove game they only found a Nash equilibrium when they could see their partner's choice (the functionally asynchronous version), suggesting that this task was more challenging for them. This was also the task on which humans showed a significant advantage. Many human pairs played an alternating Nash equilibrium strategy despite not being able to speak to one another. Of course, humans are able to make this calculation, but this suggests that whereas humans in the simple coordination game did not explore the parameter space (presumably because they assumed that they had solved the task), in the more complex game, they were perhaps more likely to consider it, thereby showing the advantage of the more advanced cognitive capacity.

Unfortunately, we were unable to test the chimpanzees at GSU, who showed such complex strategy, on the Hawk–Dove game, and as with the coordination games, the other chimpanzees we tested showed less robust patterns [65]. However, others have tested chimpanzees on different anti-matching games, giving us insight into their behaviour.

Chimpanzees are able to solve the Matching Pennies game (figure 1), and were slightly faster when they were the matcher than the anti-matcher, suggesting that this is an easier strategy to follow; perhaps this is why even our monkeys appear to be better at coordination than anti-coordination [70].

As discussed above, perhaps the most popular game over the last several decades has been the PD game, a cooperation game with a temptation to defect. In this game, the Nash equilibrium of a 'one-shot' game (played a single time) is to defect, as that will yield a higher pay-off no matter what the partner does, but for a repeated (iterated) game with the same partner, virtually any strategy profile can be supported as a Nash equilibrium, including *cooperate-cooperate* [71]. Thus far we have tested only the capuchins and chimpanzees on the iPD using the same format as in our earlier games. As before, individuals were presented with choices simultaneously, but their choices were displayed as they made them, so they could choose to wait and see their partner's choice if they wished, or not. Also as before, we constrained the pay-offs between zero (the sucker's pay-off for cooperating when the partner defects) and four (the pay-off for defecting on a cooperating partner), with mutual defection resulting in one reward for each and mutual cooperation in three rewards for each. As with the other games, the chimpanzees at Emory and in Texas showed little variability in behaviour [65], however the capuchins' pattern of play was intriguing.

Unlike in the previous two games, in which the capuchins' choices were highly consistent across pairs, in this case we saw substantial variability, with some pairs primarily defecting, some cooperating, and some showing no strategy discernable from random (no pairs showed a consistent preference for either of the uncoordinated outcomes; [69]). Thus far the game has been played across three different studies (each study consisted of 10 sessions of 40 trials each), and partners stayed the same across all 30 sessions. It took most pairs more than 10 sessions (i.e. 400 trials) to develop a relatively consistent pattern of play, and this pattern shifted somewhat over time (i.e. the next two sets of 10 sessions). However, the situation in which they experienced the game in these subsequent studies also changed, making it difficult to know if the change was owing to experience with the task or the surrounding context. Nevertheless, the consistent variation among pairs in their behaviour, with some pairs consistently tending to cooperate, others consistently tending to defect, and still others showing no pattern, suggests that this is an excellent game for use in exploring individual differences or the role of social context or relationship in influencing decision-making. The capuchins' behaviour also showed evidence of contingency, with monkeys more likely to defect following mutual defection and, often, cooperate after mutual cooperation. Although the rhesus monkeys that have been tested predominately defected, they, too, showed this contingency [72]. This differs from work on birds, which largely suggests that they do not typically cooperate in the task [73], although this may be owing to cognitive limitations, such as their high levels of temporal discounting [14]. Others argue, however, that such direct reciprocity is under-recognized in the literature [74].

One of the key benefits of these games is that once they are established, they can be used to explore the impact of other factors on behaviour. For instance, as mentioned earlier, they are straightforward to compare across species to test specific hypotheses. We recently tested the hypothesis that species which were reported to cooperate more frequently in the wild would also coordinate more often in the Assurance game by testing squirrel monkeys, a platyrrhine primate that is sympatric and confamilial with capuchins, as well as highly social, but shows far less evidence of cooperation. Nonetheless, they showed relatively similar rates of coordination in the manual Assurance game as compared to the capuchins (at least on the capuchins' first exposure to the task; [75]). One possible explanation is that they were simply treating the task as a reward maximization task. The squirrel monkeys did not show any evidence of changing their behaviour contingent upon their partner's previous choice, nor did they show any evidence of playing a Nash equilibrium in either the Hawk–Dove game or the PD game [75]. More intriguingly, however, it was the female pairs who showed the tendency to coordinate. This corresponds with evidence from the field, suggesting that cooperation primarily occurs in female Bolivian squirrel monkeys (i.e. [76]) and with other data from the laboratory suggesting that behaviours related to cooperation are more likely in females (i.e. responses to inequity; [77]). Thus, while the sample size means that these data are far from conclusive, there is some evidence from the comparative data that we should be looking at demographics on a finer scale than species when making these comparisons.

Another key advantage of these games is that they are remarkably flexible, so we can adjust pay-offs to test different questions while holding most variables constant. For instance, researchers used the Snowdrift game to show that chimpanzees continue to coordinate despite a temptation to freeload, even at high costs [78]. We became curious how inequity would impact coordination in capuchins, who are known to respond negatively to receiving a less valuable reward than a partner [79], particularly in the context of cooperation [46,47]. To do so, we used the manual token trading version of the Assurance game, with the exception that we altered it to be an explicitly sequential task (one player was always given their choice first), and changed the pay-offs slightly so that one player received a lower pay-off (two rewards) for coordinating on *stag* than the other (who still received four; [55]). When the rewards were a highly preferred food, the level of coordination stayed the same, but when we switched to a less preferred reward, the rate of *stag* choices dropped off, with both the first and, in particular, the second mover more often choosing *hare*. However, we had a second problem that highlights a challenge to comparative work. The monkeys declined to work for the less good rewards and most failed to complete even half of the sessions, meaning that we did not have a complete dataset. It is important to recognize that for many of the reported studies (including all of the studies on which we are authors), the subjects are never deprived of food, water, treats or anything else to compel motivation to participate in testing, which means that they may simply not be interested in playing if the rewards are not good enough! Given that reward value [55,56] and even feeding regimen [80] affects choices, this becomes a significant influence on our results.

We can also explore how other factors change relative to these games. For example, we have studied whether giving exogenous inhaled oxytocin, a neuropeptide hormone linked to changes in social behaviour in some contexts in both humans and other species, would change capuchins' or chimpanzees' behaviour in the economic games and found that it did not [65,69]. However, while there is evidence that endogenous oxytocin is linked to chimpanzees' social decision making [81–83] and that endogenously raising oxytocin increases affiliative behaviour in capuchins [84], there is little evidence that exogenously administered oxytocin changes these species' behaviour [85–87], suggesting that we may need to look at how behaviour correlates with their natural levels instead. It would also be interesting to look at how hormones linked to stress responses, such as cortisol, are related to economic decisions, to see how monkeys' cortisol profiles, which presumably correlate with long- or short-term stress responses, are impacting decision-making [88].

This research also has connections to other lines of research in behavioural economics and psychology with the same goal of understanding the origins of human decision-making. For instance, as mentioned above, paradigms similar to the Ultimatum game have been used to study inequity in non-human species, showing that, as predicted for humans [43], inequity responses are more common in species that routinely cooperate [35]. Other work has explored whether chimpanzees, like humans, will punish those who do not give them a high enough pay-off in the Ultimatum game and found that while punishment is absent [89,90], possibly owing to the fact that these games are played with a known social partner and therefore there is recourse other than refusing the offer [91], both chimpanzees and children interacting with other students from their daycare class are more likely to choose an equitable offer in a limited form Ultimatum game than a limited form Dictator game, suggesting that they are sensitive to the possibility of their partner refusing their offer [92]. Other species also show similar biases as humans, for instance loss aversion [36], framing effects [93,94] or the sunk cost effect [95,96], while they are less susceptible to other biases, such as the cognitive set bias [97]. Aside from simply demonstrating a bias in other species, and therefore suggesting an evolutionary trajectory, in some cases we can formulate or test hypotheses by looking at other species. For instance, several non-human species show the endowment effect [98], which has been argued to be linked to evolutionarily salience [99,100]. When chimpanzees were tested to see if they showed the effect for tools that could obtain foods when the food was present, visible but not obtainable, or absent, they showed the effect only when food was present and obtainable, suggesting that salience plays a key role in chimpanzees' expression of this bias [58,62]. For more discussion of research on the evolution of decision-making, see reviews by [101–103]

## 5. What have we learned from comparative experimental economics?

Experimental economics has advanced our understanding of human decision-making in the fields of economics and psychology, and adding a comparative component to better understand the evolution of our decision-making behaviour promises further advances. Indeed, this has happened with only a few years' worth of study. For instance, as is now clear, just because all species reach the same outcomes does not mean that they do so in the same way, as is evidenced by our Assurance game data. These data also reinforce existing hypotheses, for instance about the important role of language in human decision-making and the benefits of humans' advanced cognitive capacities. Importantly, though, these games allow us to be more specific about what those advantages are, such as humans' use of language to explore the parameter space and turn a simultaneous game into a sequential one and our ability to implement an alternating Nash equilibrium strategy in the Hawk–Dove game.

Overall, these games have been very successful at finding species differences in decision-making. Such variation may help us understand how socio-ecology impacts the evolution of these behaviours in ways that cannot be done by studying a single species, such as humans. While ideally we would have a sample size encompassing dozens of species within and across taxa, even with a few species we can begin to make predictions about the ways that these differences can be linked to differences in ecology, social organization and cognition. For example, capuchin monkeys, who coordinate using matching in the Assurance game, live in relatively small social groups and are generally in fairly close proximity to one another, perhaps suggesting that they do not need to evolve a mechanism for remembering interactions beyond what they can see at the time. In addition, while their brain to body ratio is as large as that of chimpanzees [42], their absolute brain size is modest, owing to their small bodies, suggesting that there may be other cognitive factors limiting their response that we did not check [104]. Rhesus monkeys, who live in groups that can be an order of magnitude larger, formed a preference for the *stag* strategy, but did not probability match, despite the fact that these monkeys do so in other circumstances. Rhesus also were unable to anti-match in the synchronous game (but did so in the asynchronous one), which, in concert with the chimpanzee Matching Pennies data discussed above, suggests that anti-matching is cognitively more challenging than matching. Chimpanzees, which live in fission-fusion societies, as well as having the largest and most complex brains, were the only species that showed robust evidence of following a strategy, although only the chimpanzees with significant experience with cognitive testing did so, suggesting the importance of experience. Intriguingly, these apes also showed increased levels of individual variation compared to other primates.

One surprise has been the lack of individual variability in these games across most of the non-human primate species, except among the chimpanzees, for whom the experienced GSU chimpanzees were better at finding a strategy than the less experienced chimpanzees, who settled for a 'good enough' outcome, and the capuchins, who showed variation between partnerships on the PD game. It may be that these games were too simple to generate much variability, but as they are social, we nonetheless expected impacts of factors such as age, rank, sex, and relationship quality. Future research could focus on these situations in which we do see individual differences to help identify what factors are driving decisions and whether the lack of variability in other contexts is owing to a lack of reasonable options, a true lack of variability, or a failure of the monkeys to see it as a social task.

Although the games used in experimental economics are outstanding for direct comparative work, they are model systems that are simplified, structured versions of reality that have been stripped down to focus on the key features of the decision, such as the behaviour or identity of the partner or the pay-offs for different types of interactions. They are not meant to exactly mirror a natural situation any more than any other model, but to provide data to build hypotheses that can then be tested in more naturalistic contexts. A fully developed programme of comparative experimental economics requires using models to develop hypotheses about how species will behave in different contexts, and how this will differ across species, and then testing these hypotheses directly using more naturalistic contexts and species specific paradigms that, while they may not directly translate across species, will allow us to verify our hypotheses and, if they are not verified, to refine our models and try again [28].

In the future, researchers will need to focus on a broader set of contexts as well as a broader variety of species. This will help us identify the contexts and conditions that led to the evolution of specific behaviours. Most obviously is to include more naturalistic social contexts, such as group-level testing [105,106], but ideally these projects will also move to free living individuals in the field when possible, to explore the role of ecology (see [107] for a different approach to studying the role of ecology). Testing with the entire social group present will also help with a second major question, which is the role of social context, including relationships, dominance, and power, in shaping decisions. This is difficult to study in dyadic situations, particularly when participation in testing is voluntary (so only individuals with good relationships are separating together to participate in the first place; [85,86]), but in group situations, a wider variety of pairs may participate, particularly in natural or naturalistic social groups, so we can begin to answer this question. A completely untapped area of experimental economics research is comparing how different species adopt stable rules as opposed to settling on equilibrium actions [108].

Although the focus of comparative experimental economics is non-human species, and understanding the evolution of these behaviours, we have learned quite a lot about humans as well. For instance, humans' behaviour in our coordination task looked quite different from behaviour in the typical task, presumably because we did not give them instruction or show them the pay-off matrix prior to making their choices but required them to learn the contingencies as they played. This was a decision we made to equalize the humans' experience with that of the other species, but we learned something valuable. At least in these studies, humans acted as if they were used to being given information and were not terribly inclined to seek it out. This will be quite important if it remains true in other contexts. In the naturally occurring world, information is often not readily available, may change, or may be unknown, or unknowable (the latter, for instance, if it is based upon another individual's decision). Thus, while coordination may be straightforward, identifying situations in which coordination will be useful to take advantage of may be substantially more challenging.

We also discovered that as pay-off structures become even moderately more complex to maximize rewards, such as the alternating between Nash equilibria in an anti-coordination game, humans' greater cognitive ability gives us a significant advantage over other species even when we do not provide instruction or pre-training. A key difference between our coordination game and the anti-coordination game is that one strategy in the Assurance game (*hare*) always yielded the same pay-off, whereas both strategies in the Hawk–Dove game yielded a different pay-off conditional on the token the other person played. Humans appear to respond to obvious differences as opposed to randomly testing their environment to find them as the non-humans regularly do. Such passive behaviour has also been observed in another economics experiment that required human pairs to explore the action space of their environment without explicit instructions to do so [109]. An open question is why. What does seem clear in these non-human-inspired experiments, and observed regularly elsewhere, is that humans whose clear impulse is to engage their fellow participant(s) socially with language tend to persuade each other to find pay-off improving/maximizing solutions to their tasks (see also [110–116]).

Experimental economists spend considerable time writing and critiquing the detailed instructions they write for their experimental tasks [117–121]. They wish their human subjects to see the theoretical problem as they understand it to be. Non-human primatologists cannot assume as much about the subjects in their tasks. Moreover, the first inclination of non-human primatologists is not to remove or control natural communication between their subjects in social tasks. In experimental economics, however, natural language communication is currently a secondary consideration, something to be *added* to the experimental procedures, perhaps as another treatment condition (down the line). The pure stylized form of the economic problem is assumed to be language free. Conducting non-human experiments with human participants reveals that the question may be not whether humans coordinate/cooperate in a stylized form of the problem and by how much and how well. The question may be, how do people persuade each other to work together for a common end with a common benefit? In humans the heavy lifting of such persuasion is done with language. Non-human primates coordinate and cooperate, but (marvelously) without symbolic communication and the idea of a joint common end with a joint common benefit. That human pairs fail to coordinate and cooperate for joint common ends with natural language makes it that much more interesting to understand how and why others succeed.

Data accessibility. This article has no additional data.

Authors' contributions. S.F.B.: conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, writing—original draft, writing—review and editing; B.J.W.: conceptualization, funding acquisition, investigation, methodology, project administration, resources, software, supervision, writing—review and editing.

Both authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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## Endnote

[1]While we can verify that the monkeys understand how to play, we can never know for sure whether they understand the game as we understand the game. As we will discuss below there are various outcomes that can suggest understanding of their partner's role, or that they have developed a strategy, but in every situation we are inferring this understanding is based on their behavioural outcomes. Arguably this is the case in human research as well, but it is more evident in studies with non-human species, whom we cannot ask about their decisions.

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