

Are the roots of human economic systems shared with non-human primates?

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Highlights

- We review work in experimental economics, field primatology and neuroscience to assess the extent of economic abilities in non-human primates.
- We argue in favour of evolutionary precursors of complex human economic abilities present among non-human primates.
- Some of the symbolic activities performed by non-human primates show the capacity to barter and even proto-monetary behavior.
- We spell out our definitional criteria for what can count as economic behaviour beyond mere application of economic models to animal behaviour.

Abstract

We review and analyze evidence for an evolutionary rooting of human economic behaviors and organization in non-human primates. Rather than focusing on the direct application of economic models that a priori account for animal decision behavior, we adopt an inductive definition of economic behavior in terms of the contribution of individual cognitive capacities to the provision of resources within an exchange structure. We spell out to what extent non-human primates' individual and strategic decision behaviors are shared with humans. We focus on the ability to trade, through barter or token-mediated exchanges, as a landmark of an economic system among members of the same species. It is an open question why only humans have reached a high level of economic sophistication. While primates have many of the necessary cognitive abilities (symbolic and computational) in isolation, one plausible issue we identify is the limits in exerting cognitive control to combine several sources of information. The difference between human and non-human primates' economies might well then be in degree rather than kind.

Keywords

Economic behavior; Non-human primate economics; Economic games; Behavioral economics; Token-mediated exchange; Barter; Proto-monetary behavior; Value representation; Self-control; Delay of gratification; Numerosity; Risk proneness

1. Introduction

An economic system can be tentatively defined as a culturally-established structure through which exchanges or other joint activities driven by self-interest can take place for the general benefit, when this system is efficient, which of course is rarely the case as social organizations may reflect unequal allocations of resources. However, we argue that 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. How much of our human ability to perform complex economic activities and to implement individual and collective behaviors through recognizable economic structures is present in non-human primates?

Even in human economies, the level of awareness and explicit representation by agents of economic mechanisms is rarely, if ever, complete. Economies are described *as if* their agents were aware of their functioning, but it is rarely considered a cognitive prerequisite (Berg and Gigerenzer, 2010). This definition of an economic system can in principle extend beyond human boundaries. Economic systems thereby presuppose that different roles can be taken by individuals for the exchange or joint activities, and that what one individual can do is potentially different from what another can provide in order for the exchange between them to be mutually beneficial. Economic systems also suppose some shared representation about the framework and how these exchanges can take place. Economic activities recruit complex cognitive abilities and learning mechanisms involving individual special skills and commonly evolved cognitive capacities to process relevant social and expected reward information.

The degree of development of any established economic systems among humans, contrasted with the possible identification of economic activities in non-human primates, does not strongly argue for other species displaying substantial economic behavior or abilities. Our aforementioned defining features of economic systems have no apparent match in culturally constructed institutions in any other species. We acknowledge that this is a striking difference, and yet we are hesitant to claim this is a discontinuity. It is true that human economic systems, even in their most primitive forms, exceed anything seen in other species, but the question is whether human economic systems are an extension of foundational capacities seen in other species or are of a unique kind. The “products” of human economies (e.g., international commerce and trade; transgenerational cooperative agreements; transfer of symbolically represented wealth) certainly are unique, but they may all be reducible to “core” cognitive mechanisms that are engaged at scales and time periods that afford unique products. We will review the literature to determine to what extent humans’ highly complex economic system and cognitive ability to act optimally (with some limitations) and represent values correctly (to some degree), are shared with non-human primates (see Lea, 1994 and Robson, 2001, for an earlier discussion in this direction). We will also evaluate whether those behaviors are sufficient building blocks for the emergence of sophisticated economic systems. To reach our goal, we will address three distinct issues pertaining to economic systems, representations, and behaviors.

In Section 1.1, we recall past attempts to analyze animal behavior in economic terms. It is noteworthy that, as useful as these research endeavors are, the applicability of economic analysis to animal behavior is not sufficient to yield a definitive answer to our overarching question as to whether non-human primates show economic behavior. Neoclassical economists¹ might be satisfied with the application of game-theoretical² or competitive market paradigms to animal interactions, as it means that animals behave *as if* they were complying with the terms of these models. However, our present objective goes

beyond an *as if* characterization; it clearly resorts to the field of behavioral economics, and its possible extension beyond the human realm. In behavioral economics, not only do we enrich normative models³ with descriptive⁴ features relating to the actual cognitive capacities of the modelled agents, but we also aim to increase the predictive power of the models in question. Several successful attempts to extend human behavioral economics models to the analysis of non-human animal behavior exist in the literature. One common feature of these models is the recognition that living organisms more or less optimally adapt to their environment with limited cognitive abilities. This is known as the “bounded rationality” hypothesis which allows us to distinguish and compare several dimensions of boundedness among different species (Simon, 1972; Gigerenzer and Selten, 2002).

The second departure from a strictly model-dependent analysis of non-human primate economic behavior stems from the fact that (behavioral) economists rarely explain what they mean by “economic behavior.” By using an approach that is not strictly model-dependent, we seek to show that it is not sufficient to infer a theoretical correspondence between an economic model and a behavioral pattern to characterize the type of behavior as “economic” in the sense we mean in this review. Section 1.2 elaborates on this key point. It is based on observational criteria and suggests an inductive rather than a deductive approach to behavioral economics. Economic behaviors are present when we can observe individual or collective solutions in response to some supply and demand problems under scarcity of resources. The implementation of such solutions presupposes a set of cognitive abilities and social processes that are the prerequisites of economic behaviors. A first step is to analyze to what extent these cognitive and social foundations are shared among human and non-human primates and can serve as building blocks of economic behaviors. Sections 2.1 and 2.2 probe this issue in the context of stylized experimental settings involving respectively individual decision-making and strategic game-theoretical tasks. Individual decision-making processes underlying seemingly economic behaviors in several non-human primate taxa appears to be well accounted for by Prospect Theory⁵. Indeed, the choices made by captive non-human primates over risky, valenced (i.e., losses or gains according to a reference point) prospects tend to follow the descriptive aspects of that general model of human decision-making. This indicates a common way of dealing with rewards and probabilities among human and non-human primates. The lesson that can be drawn from game-theoretical tasks is more nuanced. This line of research shows that Pareto-optimal (i.e., mutually beneficial) cooperative behavior is not systematic across individuals and taxa. It is an interesting lesson, as it points to the limits of lab studies and their external validity.

Sections 3.1 and 3.2 focus on non-human primates’ abilities to adopt or invent such efficient behaviors or to use available devices added to their environment in order to maximize their individual or collective utility⁶. Section 3.1 focuses on token-mediated exchanges in laboratory settings, where several non-human primate species can return non-edible items or low-preferred food items to humans in exchange for edible rewards or high-preferred food items. Although tokens share several features with human money, their resemblance to the human monetary system is somewhat limited, possibly because of constraints imposed by the laboratory environment. In a recent effort to circumvent these limitations, more ecologically valid models of token-mediated exchanges have been proposed, such as the spontaneously expressed and culturally maintained bartering interactions in a free-ranging population of Balinese long-tailed macaques (*Macaca fascicularis*), described in Section 3.2.

We offer a two-tiered conclusion. Section 4.1 summarizes and discusses elements of our conclusions about some of the cognitive and social prerequisites underlying the plausible emergence of economic behaviors. Section 4.2 opens up the discussion to further questions and comments.

2. Past and extant economic approaches to animal behavior

Economics and animal behavior have a long history of interacting. The field of animal behavior has often borrowed methods from economics in order to better understand animal decision-making pertaining to three foci: behavioral ecology, social interactions, and individual decision rules.

The first approach consisted of incorporating the models of Game Theory into animal behavior, with payoffs translated into fitness, as Evolutionarily Stable Strategies. This was spearheaded by John Maynard Smith (1982), and utilized Game Theory methods to explore animal contests, animal communication, sex ratios, and cooperation. Game Theory arguably made a stronger impact on biology than economics, or at least a broader one. The creation of ecological models of animal foraging, specifically Optimal Foraging Theory, is another example of the intertwining between economics and animal behavior. First proposed by MacArthur and Pianka (1966), Optimal Foraging Theory states that, in order to maximize fitness, animals adopt a foraging strategy that maximizes their net energy gain. Game Theory and Optimal Foraging Theory share a focus on maximizing benefits in the context of a species' ecology and have been applied across various animal taxa.

The second application of economic rules to the study of animal behavior concerned the analysis of social dynamics. Noë and Hammerstein (1994) first called 'Biological Markets' those interactions between individuals in which it is possible to identify different classes of traders that exchange goods and services with reciprocal benefit. Biological Market models emphasize the quantitative aspects of such transactions, with the bartering value of the exchanged commodities being determined by the economic law of supply and demand. Markets are characterized by competition within trader classes (that can reduce the value of a commodity), conflicts over the exchange value of different commodities, and partner choice. Biological Markets have traditionally been the subject of multidisciplinary investigation in the context of sexual selection, cooperation among conspecifics, and heterospecific mutualism. The application of this approach is widespread within the animal kingdom, ranging from insects to fish to non-human primates (Dunayer and Berman, 2016). Among the latter, Barrett and Henzi (2006) pioneered the Biological Markets approach to the study of the exchange of grooming interactions with other commodities (e.g., tolerance for food, infant handling or agonistic support). As useful and intuitively appealing as the Biological Markets approach is, the number and complexity of the variables involved in these interactions make it challenging to explore empirically and requires further investigation in non-human primates (Sánchez-Amaro and Amici, 2015, 2016; but see Kaburu and Newton-Fisher, 2016).

A third approach has focused on whether individual decision rules are the same in human and non-human animals. Kagel et al. (1995) tested how the principles of microeconomic theory account for the behavior of rats and pigeons, but there has been little development in this area since that time. This may be due to the challenges of testing complex human theories in the absence of language-based explicit instructions, or to the lack of familiarity of animal behavior researchers with economic theories (or both). The experimental investigation of decision-making in humans generally relies on two types of paradigms that are either description-based or experience-based (Hertwig and Erev, 2009). In description-based paradigms, decision parameters are explicitly communicated to the subjects by means of symbols. If this was the only measure of economic behavior, it would presuppose that symbolic abilities were present in the tested subjects, thereby ruling out the majority of other species. In experience-based protocols, variables are learned through repeated trials. Experiments of this type test learning rather than symbolic abilities, and are therefore easier to instantiate in non-human species. In principle, description-based approaches can be applied to non-human species, whereas in practice, experienced-based approaches

are more commonly used. This disconnect makes comparisons between human and non-human animals more challenging, but not impossible.

Another approach that explored the similarities and differences in economic decision-making processes between humans and other species employs the methods of behavioral and experimental economics (Beran et al., 2016a, 2016b; Brosnan et al., 2006; Chen et al., 2006; De Petrillo et al., 2019). This line of research assesses whether human and non-human species exhibit similar economic behaviors under similar contexts, and more recent work is delving into the underlying mechanisms. Within this framework, following the recent developments of descriptive economic models, an emerging body of animal research has been devoted to the study of economic decision biases² that are typical of human decision-making (Bateson, 2010; Santos and Chen, 2009). Approximately in the same years, neuroeconomics integrated ideas and empirical evidence from different fields. Behavioral economists and cognitive psychologists employed neuroscientific methods to find alternatives to neoclassical economic theories, whereas physiologists and cognitive neuroscientists applied economic theory to the development of models of the neural underpinning of choice behavior (Glimcher et al., 2009). Since the inception of neuroeconomics, non-human primates, and especially rhesus macaques, have been largely used as experimental models to investigate the neural correlates of economic behavior, especially when employing techniques (such as lesion studies, or electrophysiological recordings) that, for ethical reasons, cannot be used with human subjects (Kalenscher and van Wingerden, 2011).

Despite this long history of parallel development between human and animal economics, the question of whether non-human species are actually able to engage in economic behavior has only been hinted at, with the notable exception of previous work tackling why economic behavior has evolved in humans (Lea, 1994) and whether the biological basis of human economic behavior can be traced back in non-human animals (Robson, 2001). As Adam Smith wrote back in 1776, “the propensity to truck, barter, and exchange one thing for another...is common to all men, and to be found in no other race of animals... (Smith and Stewart, 1963, p. 8)”. But is this indeed a matter of fact more than two hundred years later? Even though the tools of economics have been undeniably useful in helping us to understand animal behavior, they might be unable to tell us anything important about ourselves as economic agents, and the evolution of our economic behavior. Nonetheless, we suggest that one can find the foundations of human economic systems in the behavior of non-human animals. Although we expect to find these roots in a range of animal taxa, we focus here on non-human primates because humans are primates, and we are interested in their evolutionary history. However, we note that much of this work has involved non-primate species, and understanding how these behaviors may converge across different taxa will be key to fully grasping the origin of economics. Finally, even though our main approach is grounded in phylogenetics, and thus genetic evolution, some of the most relevant discussions of the evolutionary origins of economic behavior have been in the context of the gene-culture co-evolutionary theory (Gintis, 2011).

3. A definition of “economic behaviors”

In order to probe whether these different economic approaches or models to animal behavioral patterns can actually receive the label of “economic behavior,” a working definition of this phrase is welcome. The economic literature, including its behavioral branch, rarely reflects on its object of study (i.e., “economic behavior”), how it is different from other types of (social or political) behavior, or whether economic behavior should be defined at the individual or collective level (but see Lea et al., 1987; Lea, 1994; Webley et al., 2002). Moreover, most often economic behavior is recognized because it is accountable in relation to some theoretical model, rarely because a behavioral pattern is analysed in itself as a unique process.

Unlike “social behavior” which can be inductively defined on the basis of the observation of individuals engaging in partnership, communication, and reciprocity, or “political behavior,” possibly associated with the identification of hierarchies and power relations, without any much resort to theoretical models in those cases, the identification of economic behavior appears to require a more theory-laden approach. This difference could explain the tendency to apply various economic paradigms to animal behavior, such as those discussed in the previous section, and to avoid the discussion about what it would mean to characterize a behavioral pattern as being economic, on the basis of observation only.

We would rather adopt a more bottom-up and inductive approach and define a provisional set of “proto-economic behaviors” that could be subsumed under economic concepts with a sufficient degree of specificity, with respect to other types of behaviors and economic models. We can define this inductive approach in the following way. The first step is to isolate and probe decisional abilities in non-human primates, through experimental decision paradigms, such as typical probabilistic choices tasks over lotteries, intertemporal choices, or reinforcement learning. We can compare the performances of human and non-human primates on these tasks, as well as investigating potential common neural correlates. When performing this comparison, some models can be instrumentally relevant to assess the degree of similarity of behavioral patterns and their neurobiological underpinnings under humans and other primates. The tendency to label such behavior “economic” in humans is then tentatively carried over to other primates that present sufficiently similar behavior. We follow this approach in sections 2.1 and 2.2.

But that still begs the question as to what can be, in a sufficiently model-free fashion, labelled *a priori* as an “economic behavior.” A second line of evidence is provided by the human and non-human primate ability to perform relatively complex behaviors, such as trading or cooperation. Reciprocity, prosociality and the evolution of cooperative societies, although hardly or too artificially isolable as merely “economic behaviors” by contrast with broadly “social behaviors,” can be considered the social basis for the emergence of an economic system. The latter would consist in repeated and stable patterns of trading goods and services, which we report can be the case for non-human primates in laboratory and field environments (section 3.1 and 3.2).

However, besides a purely evidential and inductive basis in the view to elaborate a relatively model-free notion of economic behavior, we can also resort to various theoretical constructs and criteria, to the extent that we make a critical and heuristic use of them. In this vein, a typical first possible definitional candidate could be the generic notion of rational⁸ maximization of one’s utility under scarce resources (Backhouse and Medema, 2009; Robbins, 2007). It would encompass proto-economic behaviors such as foraging, hoarding, diversifying or specializing in some productive activities (e.g., hunting, gathering, building), and engaging in cooperation or competition. Humans and other species have developed this repertoire of behaviors that are sufficient to meet most natural needs. Economic behaviors are thus not incompatible with ecologically adaptive mechanisms. They require an active decision to use those mechanisms in a purposeful and problem-solving way. The literature tends to merge these considerations and view proto-economic abilities in animals exclusively in ecological terms. If by “rational” we mean “adaptive” (Gigerenzer and Selten, 2002), and if we substitute fitness for utility, we can indeed describe the behaviors of any living organism in its own environment as maximizing one’s utility under scarce resources.

Further analysis of the key terms associated with this traditional definition of economic behavior might help to gain in specificity and technicality. *Scarcity* defines a commodity space over which competition and cooperation can take place. These two notions are well defined by game-theoretical or other microeconomic models and can be applied to animal and even plant behavior. A plant with an artificially

split root over two sources of nutrients is faced with a choice between constant and variable resource supply, and can make a rational decision for the option that maximizes fitness (Schmid, 2016). Thus, scarcity still says little about whether what is described by such economic models is an “economic behavior” outside of the scope of these models (see Lea, 1994, for a similar conclusion). Yet, inductively, the fact that there are desirable commodities and agents who struggle to acquire them, while minimally organizing themselves to solve the coordination and competition problems that this struggle entails, is a good starting point, because it shows that agents have developed particular mechanisms to solve this friction problem.

We indeed argue that an economic behavior begins when those behavioral mechanisms become adaptive responses to a shock or a new friction in the environment. In economics, a “friction” (*sensu* Mortensen, 2011), is a technical term indicating that the match between a need and its fulfillment is not immediate, and requires the intervention of a novel mechanism or the readaptation of an extant mechanism to reach it. Therefore, we can seek a definition of economic behavior that reflects an adaptive process to a type of environment, but goes beyond sheer descriptions in ecological terms. Thus, we advocate for a definition of economic behavior that distances itself from the automaticity or spontaneity inherent to the notion of adaptiveness. Instead, we require that a definition of economic behavior acknowledges relevant cognitive mechanisms, and especially the information-processing aspects of cognition.

The main tenet of our definition of economic behavior therefore assigns to individuals a set of cognitive prerequisites. Individuals who engage in economic behavior must in principle be able to be described as representing value, foreseeing how value can change over time (e.g., by anticipating the evolution of supply), remembering the goal of choice behavior (e.g., via intentions to maximize), and then planning for present and perhaps future behavior accordingly. Other important prerequisites of such economic behavior include appreciation of the passage of time, some representation of relative quantity information, some understanding of probability (or at least, a sense of certainty or uncertainty about different outcomes in the future), and the capacity to represent simple forms of symbolizing (see also Section 4.1). A creature that can engage these mechanisms toward the goal of maximizing gains while minimizing costs is a close approximation of an economic agent. Put simply, economic agents act in changing environments, with trial-unique opportunities to gain or lose resources. They use long-term evolved adaptive heuristics⁹ that can fail to be optimal in some cases. Errors and biases are phenomena that we can use to paradoxically assess the adaptiveness of some cognitive mechanisms to decision environments. They point, indeed, towards the idea that when responding to environmental constraints individuals do not have systematic optimal solutions. This leads us to envision the connection between our attempted characterization of economic behavior and the parallel definition of a decision-environment evolving as an economic system.

An economy can be defined as a relatively closed system and an economic behavior as a subset of behavioral patterns that are embedded into that system and essential to its maintenance and the survival of its participants. When nature exogenously provides the resources, like manna from the heavens, an economic system is unlikely to emerge, no matter how socially sophisticated the community living in this natural environment can be. Therefore, we cannot define an economic behavior as the mere embedding of role-based behavioral patterns within a complex social system that has emerged in nature. A major difference between an ecological system and an economic system is that the latter has acquired a certain degree of autonomy with respect to the natural environment in which it is embedded (see also Lea, 1994, for a distinction between economics and ecology). An economy is a relatively closed system (not completely closed because human economies continue to depend on natural resources) in the sense that a number of two-way flows have been internalized within that system (e.g., between resources

production and consumption) and different ways of organizing these flows can be envisioned, corresponding for instance to different degrees of centralization or decentralization (central authority, or local and markets) and ways of allocating resources.

At this point, however, we may have leaned towards a too restricted definition of economic behavior, one that can apply only to human economies, because of the dual requisite of division of labor (between and within subjects) and of regular exchanges (see also Lea, 1994, for a discussion). However, we can sufficiently relax that definition to appeal to comparative analysis and an evolutionary perspective on economic behavior, if we allow that division of labor to be primarily about coordination of behavior between two or more actors toward gain for one or both of them.

An economic system therefore emerges as a series of solutions to supply and demand problems (i.e., internalized flows of resources) and we call economic behaviors the way agents, more or less reflexively, implement solutions to these frictions. As noted above, this means that economic behaviors emerge to engage trial-unique opportunities for potential gain. As those opportunities increased within species that survived to make repeated choices, some formalized structures could emerge through engagement of cognitive mechanisms for memory, quantity representation, and symbolization. Money has thus emerged as a good answer to the most typical trade friction: the absence of double coincidence of wants (when one of two traders does not hold the good the other is ready to accept in exchange of her own), trust, storage costs, etc. (Kiyotaki and Wright, 1993; Menger, 1892).

We do not require that the same solutions be found across species when it comes to using money (or even within species, given that many human societies do not use money; see also Lea, 1994). We do not require either that there is a clear mental representation of the solutions by the agents, but there must be choices based on even these imperfect mental representations. Again, humans using money sometimes fail to clearly understand what money is and we can show that its emergence can rely on very basic cognitive abilities (Lefebvre et al., 2018). The compatibility between an economic structure and a cognitive system can be minimal in the sense of requiring only partial representations of the purpose and nature of the solution and yet the economic behavior be correctly performed in relation to that solution (Aoki, 2011).

Our inductive approach does not discredit the role of fitting game-theoretical and other economic models over observed non-human primate behaviors, because according to the definition we have progressively envisioned, an economic behavior will be a behavioral pattern that does not automatically fit with their theoretical predictions but that will not be trivialized either into an alternative adaptive process. Moreover, the degree of discrepancy between human and non-human behavior in the light of these models can provide an indication (relative to the terms of the concerned models only) of their plausible continuity or common ground across human and non-human primates as well as other taxa.

Our working definition of economic behavior therefore concerns observed behavioral patterns showing in part non-automatic responses to natural or experimentally stylized environments. Economic behavior requires, under this definition, a character of flexibility and inventiveness that goes beyond the expectation of usual adaptive responses that are present in what we have labeled above as “proto-economic behaviors” (e.g., foraging, hoarding, reciprocating). It is the possibility to integrate cognitive and behavioral mechanisms, individually or collectively (in that latter case we obtain economic behaviors and an economy based on these behaviors) in the face of environmental changes (e.g., shortage, changes in resources expectation, demographic pressure) that lead to the emergence of new individual or collective responses. In that sense, we can associate economic behaviors with the capacity to design a new

mechanism, whether in the form of an individual or a collective rule, in order to maximize one's or the group's utility, in contexts of environmental changes. The fact that an animal is capable of such cognitive and behavioral flexibility can be studied either by experimentally manipulating its decision or its environment, or by observing, in the field, novel and adaptive responses pointing to the emergence of an economy.

4. Decision tasks as building blocks of economic behaviors

Individual decision-making focuses on obtaining rewards under different modalities. In human economics, the Expected Utility Theory, a main model of rational decision-making (see Introduction), stipulates that individuals maximize their expected utility. This should be understood properly as an "as if" description of the behavior of humans themselves. What this formulation of rationality means is that if we can observe some regular patterns on choices, in particular their transitivity among a series of comparable options, then we can describe the choice behavior in terms of expected utility maximization in the sense that the individual behaves as if an optimal option was attainable. In spite of the reformulation of this often overinterpreted tenet of rationality, it is not always clear that we can observe rational behavior in this sense. The sample of observed choices is often too restricted to infer transitivity or intransitivity (Tversky, 1969); moreover, to interpret behavior in a substantive way we are left to formulate psychological hypotheses that make the notion of choice more complex than picking up one item for consumption. This is where behavioral decision-theoretical models become relevant. They assume that individuals do not always maximize their expected utility due to some cognitive biases that affect them. These are not necessarily adaptive or locally optimal, but such cognitive biases can be understood as revealing an interface between the inner psychological dispositions of a subject and some features of the context in which the decision is made.

We should, moreover, distinguish between what is cognitively involved in individual decision-making and in strategic interactions. Whereas in theoretical economics the same principles of utility maximization generically apply, it is clear that the real world offers very different decision contexts. We first address the typical ways of modelling and understanding individual decision-making behavior. By focusing on psychological abilities and typical contexts, we increase the chances of making relevant comparisons between human and non-human primates' behavior and draw potential conclusions about a possible evolutionary continuity between the two. The context under which the decision can be performed can involve several types and degrees of risk and supposes an ability to process probability as well as reward. The subjective value of the reward is then considered with respect to the chance of obtaining it, which is called its expected utility. One main point of comparison is then the ability to combine information about the reward per se and its probability. Many experiments and comparisons have been run on this central issue.

Studies of decision-making under risk in nonhuman primates have shown that their responses are influenced by cognitive biases characteristic of irrational human economic behaviors, like gambling. Contrary to the predictions generated from the optimal foraging theory (Pyke et al., 1977), monkeys and great apes are, just like humans, susceptible to making suboptimal choices. When confronted with risky decision contexts, they are subject to similar psychological dysfunctions exhibited by pathological human gamblers, such as increased impulsivity, disadvantageous cost/benefit decision-making, and non-optimal cognitive biases (Chen et al., 2006; Paglieri et al., 2014; Proctor, 2012; Proctor et al., 2014). More specifically, several primate species are prone to choosing low-probability/high-payoff rewards (i.e., gambling-like situations) over high-probability/low-payoff rewards (i.e., non-risky alternatives), even when this strategy is costly in the long run (De Petrillo et al., 2015; Paglieri et al., 2014). Several primate

species (rhesus macaques, *Macaca mulatta* (Blanchard et al., 2014), long-tailed macaques, capuchin monkeys, *Sapajus* spp., orang-utans, *Pongo abelii* (Pelé et al., 2014) are also subject to the “hot-hand gambling fallacy,” whereby the unfounded belief in winning and losing streaks results in persevering with the selection of previously rewarded targets, a penchant difficult to override, even in situations when the rewards are chosen at random. Similar to other reward-driven activities, decision-making under risk in nonhuman primates is motivationally engaging and emotionally charged. In capuchin monkeys, researchers found evidence for behavioral correlates of conflicting motivational and emotional states (e.g., uncertainty-related anxiety, regret-like emotions) before and after probabilistic/decision making (De Petrillo et al., 2017). Importantly, the neurobiological substrates of economic decision-making in nonhuman primates are consistent with the neuronal circuits known to sustain context-dependent choices under uncertainty and risk in humans (Chen and Stuphorn, 2018).

Several studies report that, when given the choice between two options offering the same overall payoffs, namely risky/uncertain gambles and riskless/alternating rewards, rhesus macaques show a strong preference for the former (McCoy and Platt, 2005; O’Neill and Schultz, 2010). This suggests that, at least in this paradigm, uncertainty itself is attractive for these monkeys, and contributes to motivating their choice for risky options (Hayden et al., 2008). In signalled-outcome procedures, the motivational effect of win-signals could drive them to seek out these “good news” outcomes, even when risky choices are irrational (Smith et al., 2017). However, these results are contradicted by other studies that report risk aversion for gains, a behavior closer to what humans do in the face of risky prospects (Eisenreich et al., 2019; Yamada et al., 2013). The comparison of genetically closely related species with different feeding ecologies, as with chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) further suggests that the availability of resources in the environment in which a species evolved shaped its risk preferences. Chimpanzees, which live in variable environments, are more risk prone than bonobos, which live in more stable environments (Heilbronner et al., 2008; Rosati and Hare, 2011). However, there are inconsistencies in risk preferences even within these species, suggesting that there are additional factors that we are not accounting for that influence decisions. Thus, a better account of contextual factors can precisely help to resolve such ambiguous results (Heilbronner and Hayden, 2013). The repetition of the experiment, the number of rewards available for trials, and the exact characterization of the risk context may all trigger risk attitudes in different directions. These factors may also induce a meta-preference for behavioral diversification rather than the repetition of the similar behavior across dozens of trials. Whereas the above studies concern individually-tested subjects, the social context is another factor potentially affecting non-human primates’ attitudes towards risk. When involved in social interactions with a human experimenter, chimpanzees and bonobos are more risk prone in a competitive context than in a neutral context (Rosati and Hare, 2012). In contrast, capuchin monkeys tested with a familiar conspecific are less risk prone compared to solo testing (Zoratto et al., 2018).

A further critical point for interpretation is that the above studies do not implement the contrast between gains and losses. Monkeys are offered gains of variable sizes but no losses because of the impracticality of removing rewards that have been given to them. Instead, losses are achieved by setting an expectation, either by making an apparent offer or establishing a recurrent reference point, and then violating it. There is evidence that other species respond negatively to these changes in expectation (Tinklepaugh, 1932; Brosnan and de Waal, 2014, McGetrick et al., 2019), and that at least children show similar negative reactions to expectations set up in the same way (i.e, McAuliffe, Blake, Kim, Wrangham, & Warneken, 2013; reviewed in Brosnan, in press). So while this does differ from typical human trials, it does establish an expectation, and a change relative to the reference point is the crucial point in the study of Prospect Theory (Kahneman and Tversky, 1979; Tversky and Kahneman, 1992). A few notable exceptions have provided a fuller picture of attitudes towards risk (Chen et al., 2006; Santos and Chen, 2009; Nioche et al.,

2019) and have managed to document loss aversion in capuchin monkeys. This asymmetry of losses and gains is the core ingredient of an understanding of choice under risk and uncertainty in behavioral economics and appears likely to elicit tractable inter-species comparisons by providing a general and psychologically-oriented theoretical framework.

In this respect, Prospect Theory predicts aversion to risk in gains and proneness to risk in losses (see Introduction). This prediction is directly linked to the extent to which subjects maximize the utility of their expected gains and minimize the utility of their expected losses, and as such it directly connects with utility theory rather than just providing *ad hoc* psychological features. It is therefore consistent with optimal behavioral patterns. An experiment with capuchin monkeys showed that non-human primate decision-making under risk fits with this model (Lakshminarayanan et al., 2011). Capuchin subjects exhibit the “reflection effect,” a gambling-typical cognitive bias defined by the tendency to be risk-seeking in making choices framed as prospective losses (e.g., trading with a “risky” experimenter), but risk-averse in making choices framed as prospective gains (e.g., trading with a “safe” experimenter), even if the expected values of each of these two choices are identical (Lakshminarayanan et al., 2011; but see Farashahi et al., 2018 for contrasting findings in rhesus macaques).

Another central element of Prospect Theory is that subjects do not process probabilistic information in a linear way. For this reason, anticipated utility cannot just be the product of the perceived value of the consumption of a reward and the objective chance of obtaining it. In the same way, subjects ponder and discount utility across time or in relation to a reference point beyond which the subjective value of the reward marginally decreases, they do not give equal weights to probabilities whether the latter correspond to small or large chances and whether they apply to increments of reward in a context of scarcity, satisfaction, or abundance. Reward value processing and probability information processing are not fully separated as standard expected utility theory models stipulate that they should. This interaction between rewards and probability, if similar between human and non-human primates, provides a good basis to compare joint deviations from economic rationality assumptions and point towards the comparative and evolutionary relevance of the Prospect Theory. Two recent studies have investigated probability distortion in rhesus macaques (Farashahi et al., 2018; Stauffer et al., 2015a, 2015b). However, the first one involved choices in the gain domain only, whereas the second one used the same fitting parameters for probability distortion in gains and losses, assuming behavioral homogeneity across these domains. Further research is needed to precisely investigate the mechanisms, as well as the similarities and differences that lead non-human primates, as humans seem to do, to combine reward and probability information in their choice behavior.

Prospect Theory is not the only model upon which an overall comparison between human and non-human primate decision-making behavior can be based. Prospect Theory supposes that decisions are taken in a deterministic way. Even though the decision parameters can be subject to bias, an option is chosen if it stochastically dominates another one. But one could object that actual behavior is not deterministic and is prone to errors and indeterminations rather than just being biased. A general question is to know whether biases, such as an asymmetrical processing of gains or losses, or partially randomly selected responses to decision environments, are the most adaptive behaviors. It could be the case that this depends on the regularities a particular mind, human or non-human, actually expects to meet in its natural environment, an issue that cannot be fully treated in a laboratory experiment that implements artificial forms of reward and chances regularities.

Much research in economic behavior focuses on violations, because by studying where decision-making is non-optimal we can more easily learn about the underlying rules. However, this is not the full picture.

For instance, sometimes animals behave more rationally than humans; some primates are far less likely than humans to show cognitive set, in which individuals have difficulty finding a short cut once they have learned a rule (Watzek, Pope & Brosnan, 2019). Moreover, as discussed previously, just because a decision is “irrational” by the standard of optimising outcomes does not make it a bad decision. In many cases, these apparently irrational tendencies are hypothesized to have evolved because they were adapted to a particular context (Houston & McNamara, 1999; Kacelnik, 2006) or because, on average, following a rule of thumb left the individual decision-maker no worse off and reduced the cognitive load required for each individual decision (i.e., see Simon, 1972; Gigerenzer & Goldstein, 1996; see also Section 1.2). Indeed, in some cases the payoffs between the rational and “irrational” decisions may be statistically indistinguishable (Watzek & Brosnan, 2018).

The issue of detecting common decisional patterns under risk and uncertainty in human and non-human primates brings about the question of the relative importance of possibly shared cognitive decisional aptitudes and tendencies as sufficient and necessary building blocks for economic behavior in non-individual contexts, in which we can speak of economic behavior in a richer and perhaps more appropriate sense.

5. From individual to dyadic decision-making

Beyond individual economic decisions related to social cognition and strategic abilities, another building block of complex economic behavior is how subjects behave in exchange with peers. Indeed, an entire field of economics, experimental economics, is devoted to exploring how (human) subjects make decisions when their outcomes are dependent upon both what they and their partner(s) choose. A key methodology of experimental economics is experimental games, in which complex decision scenarios are distilled to very simple, often dichotomous, choices, and subjects’ payouts are dependent upon what both they and their partner choose (Smith, 1987). This simplicity makes them an excellent candidate for comparative work, across contexts, situations, or species, making them a powerful way to understand the factors influencing economic decision-making (Brosnan, 2018a, b).

Work in non-human primates is already beginning to uncover some of these factors. For instance, in coordination games, all species tested to date have shown at least some evidence of finding coordinated outcomes (Brosnan et al., 2011, 2012; Bullinger et al., 2011; Duguid et al., 2014; Smith et al., 2019; Vale et al., 2019), but they do so to varying degrees and in very different ways (Parrish et al., 2014a). For instance, both humans and rhesus macaques use a strategy called probability matching in other contexts, but only humans use it as a mechanism to solve coordination games (Parrish et al., 2014a). There are also similarities; several species appear to use a “leader-follower” dynamic, in which the mechanism by which coordination occurs is one subject following the other’s lead (Bullinger et al., 2011; Smith et al., 2019; Vale et al., 2019). This suggests that these decisions are not a monolithic ability that subjects either have or lack, but instead are based on a diversity of mechanisms that allow subjects to reach ecologically relevant outcomes, and understanding these may help us recognize key ecological and social differences that selected for humans’ different abilities.

When games are more complex, we find evidence for a human advantage. In anti-coordination games, several (but not all) primate species tested have been able to find the Nash Equilibrium (NE, or the outcome for which the subject can do no better given their partner’s choice), but only humans find the payoff maximizing alternating NE (Brosnan et al., 2017; Hall et al., 2019; Vale et al., 2019). Importantly, some human pairs are able to find the NE even when they cannot use language, suggesting that even if

language is important in shaping our concepts, it is not always required to find the solution in any given encounter (see also Lea, 1994 on the role of language in the emergence of human economic behavior). Understanding how humans do this will be critical in understanding how humans' abilities so far outstripped those of other species.

While these economic games are important as model systems that translate across contexts and species, they are limited by their simplicity and often lack ecological validity (cf. Section 3.2.), supporting the need for complementary species-specific approaches (Smith et al., 2018). This has been done effectively in the realm of cooperation, using several intuitive paradigms. In some cases, this has been done by adapting the structure of the game, as in a modified version of the Stag Hunt game that first suggested the leader-follower dynamic (Bullinger et al., 2011). More broadly, there is a large literature on cooperation in primates, mostly using a "cooperative barpull" in which subjects work together to pull in a counterweighted tray (Crawford, 1937; de Waal and Berger, 2000) or pull on a string at the same time to bring in food rewards (Hirata and Fuwa, 2007), both intuitive tasks for primates (Brosnan and de Waal, 2002). These experiments show that chimpanzees and capuchins, both species that routinely cooperate in the field (Crofoot et al., 2011; Perry et al., 2003), understand the contingencies of cooperation, cooperating best when they can actively coordinate (Mendres and de Waal, 2000) and actively choosing partners who are tolerant. In addition, these species are very sensitive to inequity (Brosnan and de Waal, 2014), and fail to cooperate when rewards are unequal or their partners are not sharing the more beneficial outcome (Brosnan et al., 2006; de Waal and Davis, 2003). Inequity responses are hypothesized to be a mechanism by which subjects judge the value of their cooperative partners (Fehr and Schmidt, 1999), suggesting similar underpinnings between humans and other species (Brosnan, 2006; Brosnan and de Waal, 2014).

Related to this, primates also show evidence of reciprocity in ecologically relevant contexts. For instance, chimpanzees show reciprocal distributions of goods (i.e., food) and services (i.e., grooming and sex) over time scales of weeks or months in the wild (Gomes & Boesch, 2009). In experimental studies, several primates reciprocally share food (i.e., de Waal and Berger, 2000; Suchak & de Waal, 2012) or trade grooming for food (de Waal, 1997). However, despite this, there is very little evidence of explicit contingency. In these studies, subjects are given the option to reciprocally benefit one another in order to increase their benefit, and rarely do so (Brosnan et al., 2009; Melis et al., 2008; Tanaka and Yamamoto, 2009). One likely explanation is that much reciprocity can be explained by the outcome of recent interactions with one another (attitudinal reciprocity; Brosnan and de Waal, 2002) or a long term emotional appraisal of one another (i.e., emotionally mediated reciprocity; Aureli et al., 2019; Schino & Aureli, 2009). This lack of explicit contingency suggests that reciprocity as studied thus far is of limited relevance for understanding economic behavior. However, recent work demonstrating explicit contingency (de Waal, 1997; Schmelz et al., 2017) suggests that this a more important topic for future work.

Finally, we still need a better understanding of how social context influences these responses. Although most economic models tested on non-human primates concern either individual decision-making abilities or dyads (but see Burkart and van Schaik, 2013), cooperation and economic decision-making take place in a larger social milieu that may change costs and benefits for the same interaction across different contexts, and decisions can be constrained or promoted by various socio-cultural factors (e.g., dominance-based competition, inequity aversion, social facilitation, conformity, and prestige-biased learning; see Brosnan and de Waal, 2003, 2004a; Hopper et al., 2011, 2013, 2014; Horner et al., 2010) and conspecifics' emotional expressions (Morimoto and Fujita, 2012). The tradeoff with more naturalistic studies, however, is a loss of control and more challenging interpretation. Indeed, there are similar issues even in dyads: in

any social testing we cannot easily (or at all, in some cases) control the choices of the individuals, making it difficult to test specific hypotheses, particularly about rare outcomes. A better understanding of context will provide more insight into the ways in which human economic decision-making differs, or not, from that of non-human primates.

6. Exchange, trade, and proto-monetary behaviors

Although non-human animals do not have monetary systems comparable to ours, as discussed in Section 2.1, plenty of studies have reported that, in captive settings, several non-human primate species spontaneously return non-edible items to humans and, even when they do not perform this behavior without training, they can easily learn to exchange non-edible items for consumable rewards or tools to be used to obtain preferred rewards (Addessi et al., 2007, 2008a, 2008b; Brosnan and de Waal, 2004b, 2005; Westergaard et al., 1998) or less-preferred food items for more preferred ones (Beran et al., 2016a, 2016b; Brosnan et al., 2008; Chalmeau and Peignot, 1998; Drapier et al., 2005; Ramseyer et al., 2005). These observations led, over the past two decades, to numerous experimental studies involving token-mediated exchanges in several non-human primate species, primarily including capuchin monkeys, macaques, and great apes. This work revived and extended early pioneering contributions on the use of tokens as secondary reinforcers in chimpanzees (Cowles, 1937; Wolfe, 1936).

The token exchange paradigm is an appealing system to assess the existence of economic behavior in non-human primates because of the physical resemblance between tokens and human coins and the similarity between the act of trading tokens and that of exchanging money for other goods. Furthermore, the exchange of tokens between non-human subjects and human experimenters has attracted the interest of various scholars because the intentional giving of objects is an aspect of complex human socio-cognitive abilities, which made it possible for exchanges based on reciprocity to emerge (Mauss, 1950).

But do the non-human primate token exchange systems indeed share some features with human monetary exchanges? On the one hand, within an experimental psychology perspective, tokens are regarded as conditioned reinforcers, whose function is established through the relation to food rewards; thus, they are not so different from other conditioned stimulus-responses associations that are easily acquired by many non-human animal species much more distantly related to humans. On the other hand, in an economic framework, tokens may be considered a type of currency that is earned and exchanged for other commodities and, like human money, they are fungible (i.e., mutually interchangeable; Hackenberg, 2009). According to Sousa and Matsuzawa (2001), a token has several properties in common with human money: it can be exchanged for different kinds of items, it can be handled and transported, it can be accumulated, and it can be used within a hierarchical system (in that tokens of different values can exist, and these can be inter-converted).

An increasing number of reports show that, for non-human primates, tokens have all the above-mentioned properties. Capuchin monkeys and chimpanzees remembered the association between various types of tokens and different quantities and kinds of food rewards and they performed flexible computations on token quantities in relative judgments, maximizing their qualitative and quantitative food payoff (Addessi et al., 2007, 2008a, 2008b; Beran et al., 2011; Evans et al., 2010). In chimpanzees, tokens were almost as effective as food rewards both in maintaining a high level of accuracy when performing an already acquired discrimination task and when learning a novel discrimination (Sousa and Matsuzawa, 2001; see also Cowles, 1937; Wolfe, 1936 for the use of tokens as rewards in different tasks). Various non-human primate species showed the ability to delay gratification, although to different

extents, in token-food, food-food, token-token and food-token exchange paradigms (Beran and Evans, 2012; Beran et al., 2016a, 2016b; De Petrillo et al., 2019; Dufour et al., 2007; Judge and Essler, 2013; Pelé et al., 2009; Ramseyer et al., 2005), even when the possibility of exchanging tokens was deferred by a few minutes (Beran and Evans, 2012). Remarkably, some individual chimpanzees could be trained to save tokens (Cowles, 1937) and, in a more recent study, other chimpanzees showed spontaneous instances of token savings (Sousa and Matsuzawa, 2001). Furthermore, capuchin monkeys quickly appreciated what relevant characteristics tokens should have to be exchanged successfully (De Petrillo et al., 2019), as shown in humans with coins (Tallon-Baudry et al., 2011), and they readily learned to exchange novel tokens to a similar extent as familiar ones. This suggests an understanding that all non-edible items with token-like appearance may have token-like properties, which may be a prerequisite for the appreciation of money fungibility. Capuchins also spontaneously engaged in advantageous food-token exchanges, such as inhibiting the consumption of a low-preferred food to instead exchange it with the experimenter for a high-preferred token. An exchange involving a primary reinforcer that temporarily becomes a secondary reinforcer, as in food-token exchanges, is a prerequisite for the emergence of commodity money, in which the transition from primary to secondary reinforcers occurred. Finally, capuchin monkeys preferred a token associated with a variety of low-preferred foods rather than a token associated with either one or multiple units of a high-preferred food (Addessi et al., 2010). This variety-seeking in token preference can be considered a prerequisite for the use of tokens as generalized reinforcers, which is one of the most prominent features of money, at least in the view that human attraction to money developed through the principles of conditioning and that money is a generalized token reinforcer whose incentive power derived from the association with the goods and services it can be exchanged for (Skinner, 1953, as reported in Lea and Webley, 2006).

Moreover, just like money in humans can be conceptualized motivationally as a multipurpose tool and an addictive drug (i.e., an object with strong incentive properties; Lea and Webley, 2006), the use of tokens displayed by non-human primates may be underlain by powerful tool-like and drug-like motivators. After the associative learning phase, tokens may become more than instrumentally relevant objects for these animal subjects; they could also acquire an intangible toy-like value through intrinsically self-rewarding object-directed activities, such as token proffering and object play (Lea and Webley, 2006; de Waal et al., 2008). In line with this view, the “Affordance Learning” theory holds that the combination of visual and tactile perception of an object’s physical and action-relevant properties, together with pressure-free and pleasurable opportunities for exploratory activity, such as those enabled by object play, contribute to determining this object’s potential use for the goal-oriented actions required for tool use (Lockman, 2000).

Nonetheless, non-human primates’ token exchange behavior also presents critical limitations in its resemblance to human monetary behavior. For instance, in token preference tasks capuchin monkeys and chimpanzees correctly preferred a high-value token over a low-value token, but they failed to return the token corresponding to the food proffered by the experimenter and either consistently returned the high-value token or did not show a preference between the two (Brosnan and de Waal, 2004a, 2004b, 2005). Although this still allowed them to maximize their receipt of the more preferred food, they did not maximize their overall intake. In another token exchange paradigm, Tonkean macaques (*Macaca tonkeana*), capuchin monkeys, and chimpanzees showed very limited planning skills when they were required to collect and transport tokens at specific times in order to exchange them for food with the experimenter after a time delay, although bonobos and orangutans were more successful (Bourjade et al., 2012, 2014; Dufour and Sterck, 2008; Osvath and Persson, 2013). In addition, when capuchins and macaques were tested in an experiment aiming to model human economic transactions and were required to “invest” part of their food budget in exchanges with two experimenters providing different

food amounts in return, virtually all subjects consistently failed to adjust the invested number of food items to the potential food amount offered by each experimenter, thus not maximizing their payoff (Steelandt et al., 2011). Furthermore, in relative quantity and quality judgments comparing food and token conditions, capuchin monkeys performed better with food than with tokens (Addessi et al., 2008a, b). There is also limited evidence that non-human primates spontaneously exchange tokens with conspecifics, which is another crucial characteristic of human monetary transactions. Indeed, intraspecific exchanges do occur, but they seem highly dependent on training, on the presence of human experimenters, or are limited to a few partner pairings (Brosnan and Beran, 2009; Dufour et al., 2009; Parrish et al., 2013; Pelé et al., 2009; Tanaka and Yamamoto, 2009).

Overall, the above findings suggest that the non-human primate species tested so far in token exchange paradigms show several important prerequisites of human money use, but they do not represent tokens in a comparably flexible way as humans can do with money. It needs to be determined whether these limitations are due to small sample sizes and/or rearing experiences, whether captive non-human primates are not motivated to maximize their outcomes because, in most cases, they can still get quite a lot of food without paying careful attention to the tokens' values and contingencies (these subjects have invariably come from groups that are never food deprived, so they may lack strong motivation to maximize total outcome rather than simply acquiring some preferred foods), or rather reflect true cognitive constraints of our primate relatives as compared to us.

7. An emerging autonomous economic system in free-ranging monkeys?

Token exchange paradigms have shown that some species of monkeys and great apes can use objects as symbols to request specific food rewards. This line of research provided vital insights into the psychobiological underpinnings of economic behavior in non-human primates. However, it is noteworthy that most of these experimental procedures involve human-induced exchanges with relatively small samples of individually trained, laboratory-bred subjects. During the experiments, these subjects (1) were typically placed in isolation from their conspecifics and their other daily activities, (2) exchanged in constrained environments characterized by a lack of alternative response options, and (3) received small rewards for the correct actions (Addessi et al., 2007; Beran et al., 2016a, 2016b; Brosnan and de Waal, 2004a; Chen et al., 2006; but see Addessi et al., 2011a, 2011b; Hopper et al., 2015, for examples of studies considering the influence of the social context on the expression of token-directed behavior in captive capuchin monkeys and chimpanzees, respectively, tested in a group setting). These conditions are in striking contrast with real-world human economic behaviors that offer many different formats and variants, often occur over extended periods of time, are spontaneously engaged in by a very heterogeneous population, employ the use of symbolic currencies (e.g., tokens, cash, virtual money), are heavily influenced by a rich social context (e.g., witnessing other individuals being rewarded in a deal or at the stock market), and whose rewarding consequences can be exponentially large (Lea and Webley, 2006).

In this respect, the external and ecological validity of the currently available token exchange paradigm could be put into question. This is not to say that the results obtained from the current studies suffer from a complete lack of validity, or that the results may not be informative about some contexts. However, the actual impact of conducting these experiments in these artificial conditions is unknown, and needs to be investigated. One way to do that is to study more externally and ecologically valid systems of economic behaviors in non-human primates, and then critically examine the generalizability of findings from laboratory models. This approach should provide a more solid platform for conducting comparative economics research, and shed light on the evolution of human monetary systems.

A free-ranging population of long-tailed macaques living around the Uluwatu Temple, in southern Bali, Indonesia, spontaneously and routinely engage in what resembles a complex form of token-mediated bartering interactions with humans. This occurs in two steps: after taking inedible objects (e.g., glasses, hats, jewels) from humans, the macaques appear to use them as tokens, by returning them to humans in exchange for food (Brotcorne et al., 2017a). More specifically, there is a sequence of appropriate conditions leading to a successful object/food bartering outcome: the monkey (1) targets a suitable token, that is a human-valued object which is likely to be exchanged for food (e.g., eyeglasses and sunglasses), as opposed to other objects that are less valuable for humans and typically not claimed (e.g., old hats, hair clips); (2) displays the ability to stay put and wait for an accustomed human barterer (i.e., one of the temple staff members), instead of fleeing with an object that only acquires a value for the monkey during the bartering process; (3) exerts self-control while engaging in bartering interactions, which may involve accumulating several food rewards before returning the token, or even discarding a non-preferred food item in anticipation of receiving a preferred food reward; and (4) returns the token in good condition, because if it is damaged, the bartering process may not occur.

These spontaneously expressed (i.e., monkey-driven) object/food bartering interactions can be viewed as a culturally maintained tradition in these macaques. Indeed, this behavioral practice is population-specific, highly prevalent (observed in 70 % of the 400 population members, across all age/sex classes), persistent across generations of monkeys for at least 30 years, and dependent on social means (e.g., observational learning, response facilitation) for its transmission and maintenance (Brotcorne et al., 2017b, in review). However, before considering this cultural behavior “economic”, as defined in this paper, caution is required and further control over psychological, behavioral, and environmental variables are necessary. To address this question and assess economic decision-making in these macaques, experimentally-induced bartering interactions are underway, including tasks that mirror those implemented in captive settings. We are using this established population-level bartering system as a unique opportunity to study bartering interactions in the field and assess the suitability of exploring macroeconomic phenomena in non-human primates (e.g., introducing new valuable items, testing sensitivity to inflation by augmenting or decreasing the value equivalence between exchanged items). This effort will make future cross-species comparisons of economic decision-making more relevant from an evolutionary perspective, and may ultimately lead to a better understanding of the origins of autonomous monetary systems in humans (De Petrillo et al., 2019).

8. Conclusion: do non-human primates have the cognitive prerequisites for economic behavior?

We return now to the aforementioned quote by Adam Smith arguing that animals do not engage in economic behavior. We ask whether there are cognitive prerequisites for engaging in economic behavior that are sufficiently lacking in the behavior of non-human primates to justify such a claim by Smith and others. Although Adam Smith was right in asserting that non-human animals are far from having developed fully-fledged economic systems, we conclude that there are not. We take a psychological perspective on the core cognitive faculties that we argue underlie economic behavior, and which ultimately reflect the necessary psychological profiles of those individuals who engage in economic behavior. Economic behavior, in its most basic form, relies on accurate calculation of subjective and objective value, accurate memory for past events that pertain to present choices, properly calculated anticipation of future outcomes (i.e., prospection), and inhibitory control. To calculate subjective and objective value requires the ability to accurately perceive quantity or quality of a commodity, typically food for non-human primates. We know that many primate species (as well as many non-primate and non-mammal animals) can represent, combine, contrast, and remember quantitative information such as how much food is in a given choice option, how many conspecifics are in a group, and how much time has

passed (Beran, 2017; Beran et al., 2015). These magnitudes are represented inexactly, but in a way that aligns with Weber's Law (Gallistel and Gelman, 2000). As amounts or numbers of things get larger, they are represented more inexactly; in fact, this approximate number system, or analog magnitude estimation system, is also present in adult humans, when they are prevented from engaging in formal counting mechanisms (Beran, 2017; Brannon and Roitman, 2003). This means within-species and between-species interactions involving the exchange of effort, time, and amounts of reward, are likely to occur where all parties represent the true world equivalently, and fairly accurately. This allows for a shared frame of reference on magnitude of commodities. The approximate nature of this system helps us understand why exchanges of small quantities often rely on exact offer values (e.g., someone may trade you two small apples for one banana, but not three small apples) but larger quantity exchanges can have more variability in their acceptable range (e.g., for 100 bananas, someone would likely exchange anywhere from 175 to 225 small apples, thereby showing faithfulness to Weber's law). Thus, non-human primates can accurately represent the "terms" of a proposed economic engagement, at least with regard to magnitude information.

As for past memories of engagements with others (e.g., exchange opportunities, cooperative behavior), it is clear that non-human primates remember their past encounters and can behave as if those encounters are contributing to present behavioral choices (Kohler, 1925; Tinklepaugh, 1932). Research has shown that non-human primates show aspects of what-where-when memory that would be integral to the idea of sustained economic behavior with repeated interactions among potential partners (Hampton et al., 2005; Hoffman et al., 2009). Remembering who did what, and what was gained (or lost) through such past interactions is a fundamental requirement of economic behavior. We contend that at least some studies with non-human primates appear to show a form of episodic remembering (Lewis et al., 2017; Martin-Ordas et al., 2013; Menzel, 1999) although this is a matter of continuing debate (Eichenbaum et al., 2005; Griffiths et al., 1999; Templer and Hampton, 2013; Zentall, 2006). We acknowledge that such episodic remembering would be highly valuable to economic behavior (e.g., remembering that last time you traded with partner A, she wanted more from you than you wanted to give relative to what she offered). However, remembering the event details themselves (e.g., what was offered/gained) without the sense of mental time travel (i.e., "re-seeing" the episode) is still sufficient to engage in economic behavior with others.

Anticipation of the future is an important part of economic behavior. To take and transport tokens, or to grow crops for later sale, rely on the capacity to anticipate what you will do in the future, and what is needed in the future. Chimpanzees and monkeys engage in prospective memory, remembering what needs to be done in the future (Beran et al., 2012a, 2012b; Evans et al., 2014; Murray and Gaffan, 2006; Perdue et al., 2014). They anticipate what will come next in previously viewed scenes (Kano and Hirata, 2015). They anticipate their own future needs and prepare for those needs (Mulcahy and Call, 2006; Osvath, 2009), and they plan future travel routes (Ban et al., 2014; Janmaat et al., 2014; Janson, 2007). In many of these cases, present behavior is only explained on the basis of how future behavior will benefit from present efforts. Still, in some token tasks, non-human primates fail to structure behavior in a way that is optimal. This might reflect a failure to anticipate future needs (Suddendorf and Corballis, 2007). However, there is sufficient evidence of prospection to support the idea that non-human primates have the minimal cognitive abilities needed to engage in economic behavior.

To barter, exchange, and cooperate requires in many cases disengaging from more immediately-possible behaviors or inhibiting more immediately-rewarding behaviors to generate other behaviors that could secure a better, but more delayed reward. To trade food with others requires not eating it now. To earn money to buy a preferred commodity requires engaging in effortful work for that money, rather than

relaxing now. To cooperate with a partner to obtain a goal requires inhibiting the act of starting on your own and waiting for the partner to engage, as in the case of the cooperative bar pull tasks and similar tasks described above. In these cases, there must be a degree of monitoring the environment to assess what is presently available, what is possible in the near future, and what behaviors are optimal for longer-term benefits. At the same time, there are competing urges to act now, and the successful economic player often must inhibit those urges. We know that non-human primates can engage in acts of self-control where they choose to save rewards and wait to obtain better rewards (Addessi et al., 2011a, 2011b; Anderson et al., 2010; Beran, 2002; Perdue et al., 2015; Stevens et al., 2005, 2011) including in contexts in which such self-control is required to optimally use tokens (Addessi et al., 2014; Beran, 2018; Beran and Evans, 2012; Evans et al., 2012; Judge and Essler, 2013; Parrish et al., 2014b). We know that they can engage in exchange behavior, to obtain larger or better, but also more delayed, rewards (Beran et al., 2016a, 2016b; Bourjade et al., 2012; Brosnan and Beran, 2009; Dufour et al., 2007; Osvath and Persson, 2013; Pelé et al., 2010, 2011). We know that they can even engage in forms of anticipatory collection of items for later use, rather than use items now (Mulcahy and Call, 2006; Osvath, 2009). Thus, this prerequisite clearly is in place. However, once again, we see limitations. For example, some perceptual experiences lead to consistent and broad failures of inhibitory control. The so-called reverse-reward contingency task demonstrates this very well (Boysen and Berntson, 1995). Non-human primates struggle to learn these kinds of contingencies, despite being good at some of the presumed component aspects of mastering this task (Beran et al., 2016a, 2016b; see Shiffman, 2009). However, in some cases, the use of tokens or other symbolic stimuli aid their performance, suggesting that secondary reinforcers operate to increase more rational choices (Addessi and Rossi, 2010; Boysen and Berntson, 1995). Some species also struggle to sustain choices to engage self-control (capuchin monkeys, Paglieri et al., 2013), in essence showing that intentions cannot align with performances, although in other cases choices to engage in self-control are seen to be aligned with self-control abilities (chimpanzees, Beran et al., 2014) and even seem to be related to general intelligence of chimpanzees (Beran and Hopkins, 2018).

One final issue that merits discussion is the question of cognitive control in non-human primates. Cognitive control is a collection of mechanisms engaged during situations in which stimuli and choice options are complex. These mechanisms include inhibitory control, as just described, but also monitoring stimulus properties, and control over the processing of conflicting information so that the nature of complex choices is accurately represented. Humans have the ability to focus on all aspects of a problem, or choice options, and to weigh numerous properties at the same time. For example, we can consider present and future interest rates when evaluating loan options, while also anticipating future revenue or income streams, and simultaneously considering the present value of the loan monies relative to the future cost of carried debt. We can recognize that a smaller number of a more valuable thing would require an offer of a larger number of less valuable things to find the point of equivalent subjective utility when we offer a barter. Bananas may be better than apples, but more apples may be better than fewer bananas. From this basic idea come many more combinatorial applications, all of which we can accommodate, at least in principle (and, in reality, we can apply formal mathematics to aid in these calculations as in the case of actuarial science). Add to this the need to formally represent (and understand) probabilistic information (e.g., the odds of a calculated risk working in our favor), and it becomes clear that cognitive control would be very important in understanding the full implication of choice options and offered barter. Non-human primates can understand some aspect of probabilistic environments and choices options, but they appear to struggle in cases where combining types of relevant information are necessary (e.g., Beran et al., 2005; Stauffer et al., 2015a, 2015b; Tecwyn et al., 2017). This could explain the extant differences in the widespread presence of economic systems in humans and lack thereof in other animals.

We also think it is important to consider what cognitive capacities are not necessary to engage in economic behavior. As noted above, the ability to perfectly represent quantities such as time or amount is not needed for basic economic behavior (although more complicated mathematics are required for complex economies). Inferential reasoning is not required (in fact, we would argue that having to infer possible outcomes from engaging in economic behavior is not likely to promote such behavior in its earliest forms because uncertainty is not conducive to exchange or bartering actions). Theory of mind (i.e., the ability to represent that someone else has a unique mind that may have different goals, desires, and knowledge states) is not a prerequisite capacity (but see Robson, 2001 for a discussion on the importance of theory of mind for game theory). Although it certainly aids efforts to engage in trade and cooperation, an individual does not have to take into account the differing perspective of a trading partner or a cooperative player to successfully engage in trading or cooperation. If the cognitive capacities outlined above are present and engaged by individuals, there is no need to know that those who are part of exchange or cooperative behavior want something different because they have different minds and therefore different thoughts about the nature of present economic engagement. Of course, this can aid in smoother transactions, and perhaps is necessary for some of the most complex forms of economic behavior, such as multi-party cooperative agreements in which many co-occurring agreements are negotiated on the basis of also considering third- (and fourth-, and beyond) party positions on the nature of agreements that will impact the entire group of participants. But, at its most basic level, economic behavior requires only that one can consistently and rationally calculate value for effort expended or for commodities possessed and desired, and then assess the relative value of barter, exchange, or cooperative engagement.

8.1. Open questions

We have given an overall positive answer to the plausibility of economic behaviors among non-human primates. They perform similarly to humans on either individual (Section 2.1) or dyadic (Section 2.2) laboratory decision tasks. They also display some ability to trade efficiently using intermediary medium for exchanges (Section 3.1) and even seem to have developed, in some natural settings, spontaneous bartering interactions with humans (Section 3.2). They meet an array of cognitive prerequisites that make plausible the extension and generalization to some extent of such economic behaviors (Section 4.1). We also consider that their economic behavior is both sufficiently large and relevant to envision some common ground between human and non-human primates with respect to the ability to develop economic abilities and structures. However, further phylogenetic analyses of economic behavior are needed to reconstruct scenarios for the evolutionary history of economic behavioral traits, which do not leave consistent fossil traces. These analyses could be used to decide whether similar economic behavioral patterns are due to common ancestry or the result of independent adaptations to similar environmental pressures.

We have presented a framework in which we argue that nonhuman primates demonstrate the prerequisite cognitive capacities for economic behavior. But, this claim must reconcile the fact that other primate species *do not, in fact, show economies that even approach any part of the scale of such economies in Homo sapiens*. There are a number of possible reasons for this (see below), but from the empirical perspective we must acknowledge some limitations in the data we have highlighted. First, the number of individuals assessed within some species is fairly small, certainly in relation to studies of human economic behavior where subjects are plentiful. Second, the number of species assessed is small, relative to how many primate species exist. A stronger argument for the psychological continuities across species for economic behavior would require more subjects and more species. We are encouraged that this will be the trend, given that primatology has consistently showed a commitment to testing more primates of

more species for exactly this reason (e.g., the recent ManyPrimates movement; Many Primates et al., 2019). Third, even with more subjects, it is important to note that many studies have required extensive training, and this may affect the final consideration of capacities for economic behavior in these subjects. That said, we would suggest that *Homo sapiens* also have an extended period of learning about many aspects of economic behavior, and so we are agnostic as to whether the nonhuman primates truly enjoy a “training privilege” with regard to this issue. The final point is that we have discussed areas in which positive evidence of capacities have been reported, to reflect the range of what has been seen in other species. This does not mean that some of these areas (e.g., comparative levels of risk tolerance) will not have to be reconsidered as new evidence is collected. That may change some aspects of the perspective we have offered.

Another open question is what made human economic abilities and systems rise to a level of sophistication that is not shared by other primates (see also Lea, 1994). Many hypothetical candidates can come to mind that specific studies should permit to rule out or confirm on the basis of data that we currently lack. Is it human linguistic ability, division of labor, or some specific computational capacities? We underlined (in Section 2.2) that coordination could take place in strategic games without linguistic communication. Many alternative signals can provide coordination devices and lead to efficient cooperation. The main purpose of language might be to provide a means for saying novel things in changing circumstances (Blume, 2000). Relatively stable environments do not promote the use of language as common knowledge structures are prevailing and are sufficient to provide required coordination among individuals. Yet, it is difficult to assess whether linguistic abilities or changing decision environments were the primary cause of economic sophistication in humans. Along these lines, Lea (1994) noticed that, across human history, people not having a common language were able to carry out successful trades and argued that language does not seem to be a necessary condition for the emergence of trade, but possibly trade itself was one of the forces driving the emergence of language. It may also be that even without a shared language, there are required levels of symbolic representation that allow for accurate comparisons of commodities involved in a trade or barter. This includes representing quantity (“how many”), unit type (“of what”), unit value (“how good”), and then the comparison of what is given versus what is gained. This level of symbolic representation and computation may be too difficult for nonhuman primates.

Lea (1994) proposed that the origins of human economic behavior lie in the fact that humans are tool-using, cooperative hunting, and socially complex primates. However, because several other primate species share these characteristics with us but obviously lack economic institutions, we argue that tool use, cooperative hunting behavior, and social complexity might not be sufficient ingredients for the emergence of sophisticated economic behavior.

Division of labor, and more generally social organization, can provide another source of explanation of the different degrees of development of human and non-human primate economies. Kaplan et al. (2009) have listed a series of remarkable characteristics differentiating, in their view, human foraging systems from non-human ones: i) a longer lifespan; ii) a larger brain relative to body size; iii) an extended period of juvenile dependence; iv) transgenerational solidarity and support of reproduction by post-reproductive individuals; v) complementary roles of females and males in providing resources, in particular to offspring; and vi) significant cooperation and food-sharing between kin and non-kin. Points iv)-v)-vi) directly relate to division of labor, which is the source of economic efficiency and development, by introducing the gains and comparative advantages of specialization. Kaplan and his colleagues look at a basic differentiation of roles in primitive foraging niches. These roles could be considered the basis over which further specialization among individuals might have evolved. It is then an open question to further qualify, at the

basic level of points iv)-v)-vi), differences in social organization and cooperation between human and non-human primates.

The issue of cognitive skills is, like linguistic abilities, difficult to assess in terms of their actual contribution to the implementation of competent and efficient decisions in economic environments and to the emergence of these environments themselves. In particular, what role does the ability to formally count and engage in arithmetic operations with exact outcomes play in economic behavior? Can true economies only emerge when the players have more sophisticated mathematical abilities? We provided evidence that powerful and sophisticated numerical cognition was not necessary to develop apt behavior in token exchanges. But, of course, it would be hard to deny that higher cognitive abilities do not, in principle, contribute to the transformation of simple bartering/economic systems into more complex ones. This point is open to discussion and relates to one of the central messages we have wished to convey. Humans can function in complex economic systems without having to understand how these systems work. The aggregation of very basic cognitive abilities is sufficient to produce a complex decision world. We have therefore tended to downplay the criteria of awareness and cognitive penetration of one's environment as a prerequisite for economic competence. Moreover, we have noted similar biases (e.g., in processing value and risk information) among human and non-human primates. These cognitive similarities play in favor of our general statement of a common ground for economic behavior, but the issue of the role of higher cognitive abilities in producing actual complex economic environments - and not only the ability to adapt to them - remains an open one.

Finally, are economic behaviors essentially different from other types of social behavior? Are economic systems essentially different from political organization and hierarchies - the latter having been documented among non-human primates? This question may look purely terminological, but we think it is not. In our leading definition, we have strived to provide conceptual and empirical demarcations between various types of behavior. Stricter or looser criteria could, of course, change the nature of our qualified positive conclusion. We focused on the optimal articulation of individual decision styles and performances and the emergence of trading patterns, as a central locus for the qualification of economic behavior. Our approach was inductive. Alternatively, starting with an open methodological structure, such as the one offered by behavioral economics and, considering this encompassing discipline as the application of cognitive and social psychology to the context of cooperation and utility maximization, could have led to a different evaluation of the array of behavioral data reported in this article. However, our aim was not to extend behavioral economics to non-human behaviors, but to critically examine a potential evolutionary grounding of human economic behaviors and organization in other primates' proper capacities.

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