Variation in primate decision-making under uncertainty and the roots of human economic behaviour

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Abstract

Uncertainty is a ubiquitous component of human economic behaviour, yet people can vary in their preferences for risk across populations, individuals, and different points in time. As uncertainty also characterizes many aspects of animal decision-making, comparative research can help evaluate different potential mechanisms that generates this variation, including the role of biological differences or maturational change versus cultural learning, as well as identify human-unique components of economic decision-making. Here we examine decision-making under risk across primates, our closest relatives. We first review theoretical approaches and current methods for understanding decision-making in animals. We then assess current evidence for variation in animal preferences between species and populations; between individuals based on personality, sex, and age; and finally, between different contexts and individual states. We then use this primate data to evaluate the processes that can shape human decision-making strategies and identify the primate foundations of human economic behaviour.

Key words: non-human primates; risk; economic behaviour; individual variation; cooperation

1. Introduction

Decisions about uncertainty are central to many aspects of human economic behaviour, from choices between assets with different levels of risk in financial markets, to choices about investment of energy and time in foraging versus hunting activities in subsistence societies. Yet humans also show great variation in their responses to risk across groups, individuals, and contexts. For example, there are differences in typical risk propensities across different nations [1-2] and small-scale societies [3-5]. Within populations, there can be stable inter-individual differences that vary by gender [6-7], personality [8-9] or stage in the life-course [9-13]. Finally, individuals can also flexibly shift strategies across time, showing different preferences for risk in different contexts [14-15] or depending on their own internal states [16-19]. Understanding the causal mechanisms generating this variation, as well the downstream consequences of different decision-strategies, is therefore a crucial issue in economics, psychology, and biology.

How and why do individuals make different kinds of choices? Studies of human decision-making first indicate that some variation in strategies can stem from an individual's (or population's) particular cultural or environmental experiences—and may even constitute adaptive, learned responses to local environments [5,12,20]. For example, various proposals highlight how market experiences [5], familiarity with particular cultural norms [1,21], or socialization practices [6,21] may drive differences in decision-making across groups or individuals. Alternatively, other processes that are not experience-dependent may also underpin aspects of this variation, such as genetic differences between individuals [22-24], hormonal status of men versus women [18-19] or the maturation of neural systems recruited in decision-making over development [25-28]. Finally, studies of economic outcomes show how variation in strategies can have profound effects on people's economic success, and consequently, on macroeconomic dynamics [2,9,13]. For example, more risk-averse individuals are less likely to engage in entrepreneurial activities and invest in stocks, and countries with higher aggregate risk aversion have lower productivity [9,13].

Yet this work also highlights how it can be difficult to parse out the causes and consequences of different strategies, because human economic behaviour is shaped by a complex interplay of both biological influences that are shared with other species, and cultural norms and institutions that are unique to humans [29]. Since other animals must also make assessments of value and cost-benefit trade-offs concerning rewards like food or mates, but are not embedded in rich cultural contexts like humans, comparative research can help adjudicate different proposals for why humans show different preferences across populations, individuals, and contexts. This can help disentangle shared biological contributions from cultural or human-specific features of decision-making, as well as provide a crucial line of insight into not just the economic consequences of different decision strategies (such as in foraging contexts), but also pinpoint the specific evolutionary contexts that promote different kinds of strategies.

Here, we examine the evolutionary roots of human economic behaviour by examining shared core features of decision-making under uncertainty across primates. While uncertainty broadly encompasses both risk (or probabilistic variation in outcomes) and ambiguity (or lack of knowledge in the associated probabilities) [30], we focus primarily on risky choice, given it has been a greater focus of comparative research to date. We focus on primates as they are our closest evolutionary relatives, and further exhibit several relevant parallels in their cognition and neurobiology [31-32], social behaviour [33], sex differentiation [34], and development [35-36]—yet also lack human-specific forms of culture and economic markets. We first provide an overview of theoretical frameworks for decision-making under risk from economics, psychology, and biology. Then, we synthesize empirical methods for measuring animal decision-making. We then focus on variation in primate choices (1) across species and populations; (2) across individual according to personality traits, sex, and developmental stage; and finally (3) within individuals according to internal states and external contexts. We use this empirical evidence to identify which features of human decision-making are more widely shared with other primates, versus which are novel and thus potentially culturally-malleable. Finally, we highlight new directions for future waves of comparative research that can help us evaluate current hypotheses for the origins of human economic behaviour.

2. Modelling decision-making under risk

Predicting how humans and nonhuman animals make decisions under risk is a major question in economics, psychology and biology. Although classical economic theories suggest that decision makers should focus on the average expected value provided by different options, people often exhibit a strong aversion to risk [37,38]. For example, when presented with choices between a certain option with a reliable outcome (such as getting $10) and a risky option that can vary (such as a 50% chance of winning $20), people overall prefer the certain option—even though both provide the same average payoff [38]. One model aiming to explain such examples of risk aversion is *expected utility theory* [38]. Here, rational actors should prefer options that offer the highest subjective utility (which may not align exactly with external markers of value), weighted by the probability to obtain that outcome [38]. While this is a straightforward and testable idea, it turns out that people rarely confirm to its predictions. *Prospect theory* therefore aimed to better capture this type of real-world behaviour, by distinguishing how people assign subjective value to options from how they judge probabilities [37,38]. Here, preferences for options depend on whether they are perceived as gains or losses [37]. Since people dislike negative changes in the status quo (losses) more than they like an equivalent increase (gains), this model accounts for several observed biases in choice, such as framing effects where people are risk-seeking for losses but risk-averse for gains [37].

In contrast to these approaches from economics, biologists have developed models that share many of the same features with a key difference: biologists assume decision-makers act to maximize their biological fitness [39-40]. These models generally formalize foraging decisions in which animals make choices about different foods, and consider how different patterns of food intake may affect fitness. A dominant model is *risk sensitivity theory*, which highlights that the relationship between calories and fitness outcomes is not one-to-one—paralleling ideas from prospect theory about the non-linear relationships of money and utility. Here, an animal's optimal responses to variance in foraging payoffs depends on their resource budget [40-41]: pursuing a predictable outcome may be advantageous for a small animal in a positive energetic state (e.g., when there is a concave relationship between the energy gain and fitness), but risk-seeking is better for the same animal in a negative energetic state (when there is a convex relationship) as this may be the only pathway to survival [41]. This provides a biological explanation of how reference points—here rooted in an animal's energetic state—may affect risky choice [42-43].

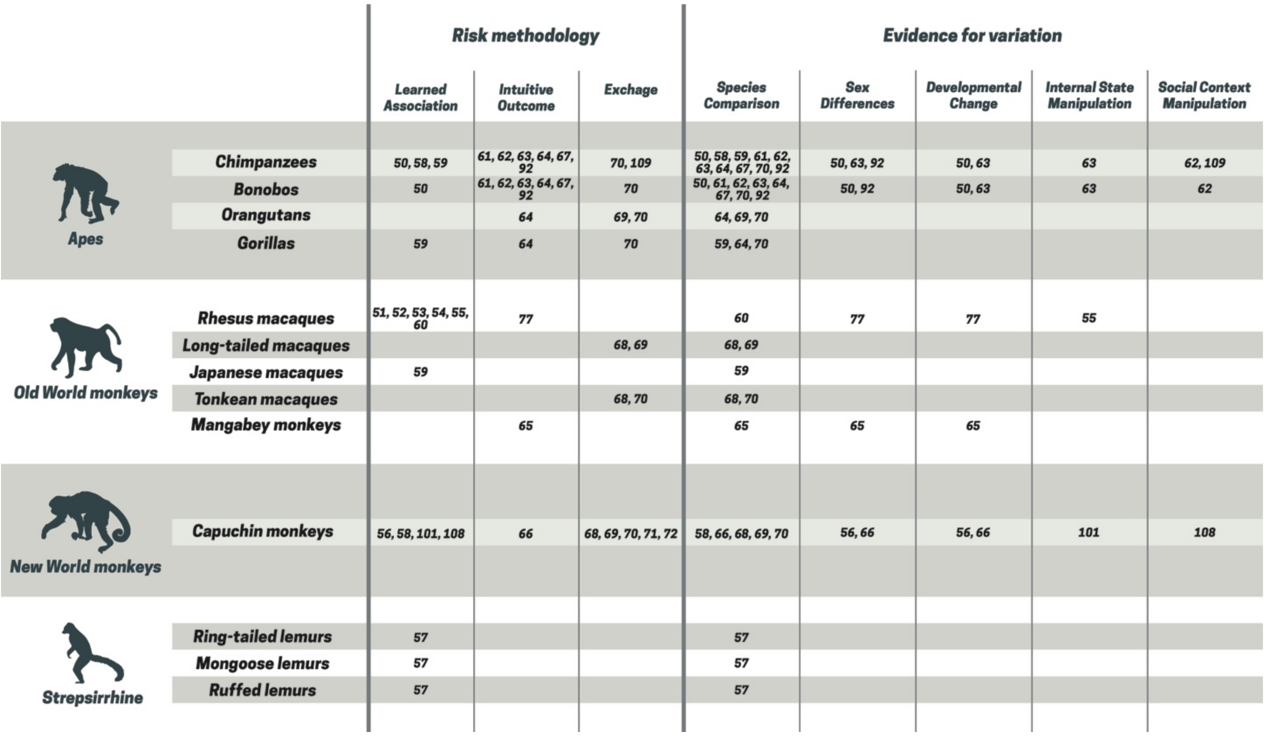
However, it is important to note that all of these approaches struggle to account for some salient aspects of variation in decision preferences seen in humans and animals. While both economic and biological theories may address how context [37, 43], including the type of goods at stake [44], impacts individuals' risk propensity, there is still no framework for understanding the origin of inter-individual or population-level differences in choice strategies—such as why there may be stable risk-seeking phenotypes displayed by some individuals but not others [32]. Similarly, humans and nonhumans sometimes behave accordingly to the predictions of risk sensitivity theory [41,45], yet this view is also not always successful at predicting individuals' risky choices [41]. For example, in larger-bodied animals—where short-term energetic requirements do not represent a significant threat to survival—risk-seeking behaviors may emerge more often when individuals are in a positive energetic state [46]. Understanding the cause of such variation across populations and individuals is therefore a crucial step for building more predictive theoretical models.

3. Measuring animal decision-making

Given that nonhumans cannot talk, read, or use money, a key issue in comparative decision-making is how to measure animal preferences. Human preferences can be measured in experiments involving choices between different options, often involving monetary rewards [47], or by looking at a person's 'revealed preferences' by observing their real-life consumer actions [48]. Most animal studies, in contrast, use a series of experiential foraging decisions about consumable rewards such as food to infer preferences [49]. Within this general methodological approach, several different kinds of tasks have been developed to probe primate responses to risk (see Figure 1 and ESM). This variation in tasks is important for then interpreting different patterns of variation across studies using different methodological approaches.

One common setup involves *learned associations* where animals are trained to understand different payoffs associated with a 'safe' option yielding a constant food reward, and a 'risky' option yielding a reward that varies probabilistically around the mean. For example, individuals might learn that a cue like the colour or location of a container (or similar cues on a computer) signals different reward distributions. Animals can then choose between two options, often involving the same average payoff, to assess if they are sensitive to risk. For example, they may choose between a safe option that always provides 3 pieces of food, and a risky option that offers 1 or 5 pieces with 50% likelihood. Thus, a preference for the safe option indicates risk aversion, a preference for the risky option indicates risk-seeking, an indifference indicates risk neutrality [49]. In other cases, the payoff contingencies may be adjusted across trials to test how animals modulate their choices when expected values shift. In many studies, animals first gain experience with reward contingencies in a learning phase to examine stabilized choice patterns [50-57], whereas other studies focus on how animals learn about the value and variance of different outcomes [58-59]. This basic kind of paradigm has been used with multiple primate species, including chimpanzees (*Pan troglodytes*) [50,58-59], bonobos (*Pan paniscus*) [50], gorilla (*Gorilla gorilla*) [59], rhesus macaques (*Macaca mulatta*) [51-55], Japanese macaques (*Macaca fuscata*) [59], capuchin monkeys (*Sapajus apella*) [56,58], and several lemur species (*Lemur catta, Eulemur mongoz, Varecia rubra*) [57], in some cases with comparisons to humans [58, 60].

A second methodology focuses on *intuitive outcomes*, examining how animals respond more spontaneously to different situations that simulate risky outcomes without explicit training on cues signalling reward distributions. For example, one reward may be hidden under one of several containers out of the animals' view, such that the number of possible containers indicates the probability that the reward is under any particular cup. This risk option can then be contrasted with a safe or known alternative to assess animals' responses to risk when both the amount of the reward and the probability of obtaining it vary [61-66]. Another intuitive task involves decisions about quality or type of food rewards [61-63]: an intermediately preferred food type is placed in one container, whereas either a high-value or low-value type of food (e.g. a banana versus a cucumber) is hidden in another out of the animal's view, to assess if they gamble on possibly receiving a preferred food type. To date, this basic kind of paradigm has been used to test chimpanzees [61-64], bonobos [61-64], orangutans (*Pongo abelii*) [64], gorillas [64], mangabeys (*Cercocebus torquatus torquatus*) [65] and capuchins [66], with comparisons to humans [67].



		Risk methodology			Evidence for variation				
		Learned Association	Intuitive Outcome	Exchage	Species Comparison	Sex Differences	Developmental Change	Internal State Manipulation	Social Context Manipulation
Apes	Chimpanzees	50, 58, 59	61, 62, 63, 64, 67, 92	70, 109	50, 58, 59, 61, 62, 63, 64, 67, 70, 92	50, 63, 92	50, 63	63	62, 109
	Bonobos	50	61, 62, 63, 64, 67, 92	70	50, 61, 62, 63, 64, 67, 70, 92	50, 92	50, 63	63	62
	Orangutans		64	69, 70	64, 69, 70				
	Gorillas	59	64	70	59, 64, 70				
Old World monkeys	Rhesus macaques	51, 52, 53, 54, 55, 60	77		60	77	77	55	
	Long-tailed macaques			68, 69	68, 69				
	Japanese macaques	59			59				
	Tonkean macaques			68, 70	68, 70				
	Mangabey monkeys		65		65	65	65		
New World monkeys	Capuchin monkeys	56, 58, 101, 108	66	68, 69, 70, 71, 72	58, 66, 68, 69, 70	56, 66	56, 66	101	108
Strepsirrhine	Ring-tailed lemurs	57			57				
	Mongoose lemurs	57			57				
	Ruffed lemurs	57			57				

Figure 1. Empirical data on primate decision-making under risk. Phylogenetic distribution of current primate data across species indicating types of tasks, comparisons across species and individual variation between sexes and by age; and finally state and context manipulations; note that there is a lack of comparisons across populations or by personality traits in studies of primate risk preferences. We report the references for studies in each category (see ESM Table S1 for full breakdown of results by study).

A final approach uses *exchange* tasks where animals to learn to exchange tokens or food with a human. For example, animals may be initially provided with a food item, and then can exchange it for the opportunity to win a larger, equal, or smaller food reward seen in one of several containers [68-70]. If the animal chooses to exchange, the content of one container is randomly selected to simulate risk (similar to the intuitive tasks described above). Other tasks involve the exchange of tokens for food rewards to simulate a primate 'market economy' [71-72]. In particular, primates are given a budget of allotted tokens they can distribute across experimenters with different exchange rates. Exchange paradigms involving either token or food trading has been used to test the four great apes [69-70], Tonkean macaques (*Macaca tonkeana*) [68, 70], long-tailed macaques [68, 69] and capuchins [68-72].

4. Variation in animal decision strategies

Human risk propensity is characterized by wide variation at both population and individual level, including differences across cultures [1-5], genders [6-7], ages [9-13] and contexts [14-19]. To understand this variation, we review empirical studies of non-human primates' and discuss how they inform the origins of human economic preferences.

4.1 Variation across species

Human populations can exhibit differences in risk propensity, so some proposals have highlighted that different strategies may be favoured in different kinds of environments. For example, some work highlights that experience with markets may promote risk-seeking responses [3,5], whereas other work argues that subsistence populations are actually relatively risk-seeking [4]. More generally, this work shows how human cultural groups may innovate different kinds of decision-making strategies to navigate their local environment. Comparisons of different animal species can provide a complimentary test of these adaptive explanations. The comparative method is a powerful tool for understating the evolutionary history of different traits by comparing species with different socio-ecological characteristics [73], so testing different species on closely-matched decision-making tasks can assess how dietary ecology or social systems may promote more risk-seeking versus risk-avoidant strategies.

Current evidence indicates that some primate species are more risk-averse or more risk-seeking than others when tested on matched tasks (see Figure 1 and ESM), even when sharing similar foundational cognitive skills for understanding numerosity [74] and probability [75-77]. For example, bonobos are relatively more risk-averse than chimpanzees in the same context [50, 61-63]. Feeding ecology may ultimately explain this variation: chimpanzees and bonobos are sister species, but show key differences in their ecological niche. Whereas chimpanzees exploit more seasonally-variable and widely-distributed fruit resources and exhibit higher rates of risky hunting, bonobos have more access to terrestrial herbaceous vegetation, an abundant and reliable food source—differences in natural history that predict a higher tolerance for risk in chimpanzees than bonobos [78]. A comparison of all the four great ape species aligns with this view: chimpanzees and orangutans were both relatively risk-seeking, whereas bonobos and gorillas were relatively risk-averse [64]. While orangutans feed on highly seasonal fruits and engage in costly extractive foraging behaviors, more like chimpanzees [79-80], gorillas rely on consistent leaves and roots food resources and do not use tools in the wild [81], more like bonobos.

Further evidence that natural history can shape decision-making strategies comes from instances of evolutionary convergence, where distantly-related species that face similar ecological problems evolve similar traits. For example, capuchin monkeys extensively use tools, hunt a variety of prey (including some which can be dangerous), and feed on variable food resources [80,82]—more like the socioecological features seen in chimpanzees. Comparisons of capuchin and ape decision-making in matched contexts found that capuchins and chimpanzees are both more risk-seeking than their closer relatives [82]. Indeed, this pattern of convergence may hold across other aspects of decision-making, as chimpanzees and capuchins monkeys also exhibit a greater preference for larger, delayed rewards in inter-temporal choice tasks compared to their closer relatives [82]. From an evolutionary perspective, future rewards are generally inherently uncertain [49], such that species that consume foods that entail long delays (such as search times) while foraging in nature may also need to tolerate the risk intrinsic to these situations.

Overall, these findings show that matched comparisons can hone in on a biological ‘signature’ of species-specific cognitive adaptations for decision-making, and identify the evolutionary contexts that promote different strategies [78,82]. Variation in animal decision-making strategies across populations provides complimentary evidence to studies of human populations [3,5,12] finding that differences in population-level risk propensity can represent adaptive response to the challenge pose by their natural environment. While that line of work has often focused on how decision depends on culture or market-integration [3-5], comparative studies further identify specific relevant characteristics of the ecological world that promotes different responses to risk: animals living in more seasonally-variable environments, and who feed on more temporally and spatially heterogenous food resources, show a greater preference for risk [78].

4.2 Variation across populations within a species

A related question is whether primates exhibit population-level differences due to experiences in their own lifetime, rather than due to species-typical traits. This kind of experience-based proposal is an important explanation for human population-level variation [5,20] that intersects with ideas about how culture shapes risk propensity [3-5]. Importantly, comparisons of different species living in similar environments, such as in zoos or sanctuaries, often equate the experiences of different species, thus minimizing the possibility that detected species differences are a direct response to their experienced habitats as might be the case in the wild. Yet a growing body of evidence also documents marked geographic variation within a given species in some kinds of behaviours, such as for tool use in wild chimpanzees, orangutans and capuchins. This variation may reflect social learning, but also may reflect individual problem-solving in response to local environmental challenges such as food scarcity or availability of relevant materials [80]. This suggests there may also be population-level differences in underlying decision-making preferences, given the important role of such preferences in foraging behaviours.

To date there have been no comparisons of whether primate populations differ in risk preferences. Some data does suggest that divergent risk preferences between chimpanzees and bonobos is detectable across different populations (e.g., zoos versus sanctuaries) tested with different methodologies [50, 61-64], suggesting this is relatively stable difference. Yet other preferences can differ across populations. For example, capuchins from an Atlanta laboratory were markedly more patient in a delay of gratification task than those from a Rome laboratory [83], raising the possibility that differences in their experiences might shape preferences. Along these lines, one relevant question is whether primate populations that have been trained to use tokens [71-72, 84] exhibit different risk preferences than those who have not. Such comparisons can test hypothesis on the drivers of human economic preferences, since degree of market integration is proposed to influence human populations [5, 20]. Thus, within-species population comparisons using the same methods are an important issue for future work on animal decision-making.

4.3 Trait differences across individuals

Human preferences also vary across individuals within the same population: some individuals are more risk-seeking, whereas others are consistently risk averse. An individual's willingness to take risks can predict decisions about the labour market, investments, and even migration [13], so personality and genetic factors that shape risk-seeking or risk-averse profiles are an important focus of research. In humans, some personality traits do appear to be related to risk propensity [8-9, 85-86]: sensation-seeking [85], impulsivity [86], and extraversion [8] are all associated with greater risk-seeking, while conscientiousness [8] and neuroticism [8] are associated with risk-aversion. These propensities may stem from heritable genetic variation, as monozygotic twins show more similar responses to risk than do dizygotic twins [22,23], and genetic variants in the serotoninergic and dopaminergic neurotransmitter pathways predict individual preferences [24]. This work therefore has highlighted the specific psychological and neurobiological mechanisms that shape risk responses across individuals.

Unfortunately, few studies have directly addressed whether primates show comparable individual variation. A key issue is that many relevant nonhuman populations (where controlled experiments are possible) are fairly small. However, some work does hint at shared neurobiological mechanisms with humans: genetic variants in the dopamine transporter predict individual differences in intertemporal choice in capuchins [87], and reducing serotonin levels via tryptophan depletion increased risk preference in rhesus macaques [53]. A crucial next step will then be characterising individual variation in risk propensity in larger samples. For example, a study of 37 chimpanzees and bonobos [63] comparing these species also found a fair amount of interindividual variation in risk propensity, as individual bonobos chose the risky option between 6% to 67% of trials, and chimpanzees between 11% to 100%. Other studies have successfully tested larger samples of a single species on decision-making tasks [88]. By relating this kind of variation in risk propensity to individuals' specific personality traits or genetics, it will be possible to assess the degree to which humans and other primates share these mechanisms for risky choice.

4.4 Sex differences

Humans also exhibit variation in risky decision-making by gender: women are less willing to take risks than men across several contexts [6-7]. This has implications for real-world economic behaviour, as women are less likely to work under variable-payment schemes in the labour market and make safer investments [7-9]. Some proposals ascribe this difference to cultural learning about gender roles [6], whereas other explanations emphasize that neurobiological differences in brain regions associated with decision-making [27-28] or variation in hormones like testosterone [19] can also drive gender differences. Since other primates lack human-like gender socialization, but exhibit strong parallels in terms of sexual differentiation in the brain and body [36], they can help distinguish between these mechanistic explanations.

Primates do show several well-characterised sex differences in behaviour that reflect females' and males' optimal behavioural strategies—and are plausibly related to risk attitudes. For example, female chimpanzees tend to be less gregarious and engage in more extractive foraging than males, reflecting the greater impact of food competition on female reproductive success, whereas male chimpanzees engage in more risky aggression and hunting than females [89-90]. Along the same lines, male capuchins spend more time on the ground foraging for exposed large invertebrates and small vertebrates, whereas females remain a few meters above ground searching for embedded invertebrates [91]. More generally, females may be more sensitive to maintaining a consistent energetic state due to the costs of pregnancy and lactation [34]. This line of reasoning suggests that males would exhibit a greater tolerance for economic risk than females.

Yet several studies have compared risk preferences across male and female primates, and consistently failed to find any appreciable sex differences (see Figure 1 and ESM). This includes studies of chimpanzees [50,63], bonobos [50], capuchins [56,66] and mangabeys [65]. While this may be in part due small sample sizes, other studies did detect sex differences in decision-making in comparable samples. For example, a study of 40 apes found that males were more susceptible to a framing manipulation than females [92]. Similarly, a study of 16 capuchins found that females could delay gratification more than males [93]. Then, current evidence suggests that there may be at best subtle sex differences in *psychological* risk propensity in primates, despite stark differences in some forms of behavioural risk-taking. This accords with a broader set of findings indicating that primates only sometimes exhibit sex differences in cognition paralleling those in humans [33, 94-95]. Overall, this evidence suggests that gender differences in risky choice observed in humans may be primarily due to socialization experiences, not to biological differences that are shared with other species, given the weak to absent evidence for parallel effects in nonhuman primates.

4.5 Developmental change over the life course

Human risk preferences can also change over the lifespan: adolescents tend to be more risk-prone than either children or adults [25-26], and older adults show a mixed pattern of increasing risk-aversion or preservation of risk attitudes depending on task demands [9-13]. These developmental shifts in risk preference have important macroeconomic consequences: aging societies invest less in risky stocks and entrepreneurial activities, and show higher support for conservative savings and investment strategies that impact societal productivity [9,13]. Several proposals argue that age-related changes in the neural circuits underlying decision-making drive these shifts bother during maturation in adolescence [25-26] and during aging [96]. Yet generational effects, such as differences in educational attainment or experience of historical events like the Great Depression, may also underlie some apparent age differences [97-98].

Other primates also exhibit relatively slow life histories like humans [99], and studies of comparative cognitive development indicates that animals can exhibit developmental change in spatial memory [100] and gaze-following [33] that mirror those in humans. However, most studies of primate risk preferences to date have not found major age-related changes (see Figure 1 and ESM). This is the case for chimpanzees [50,63], bonobos [50,63], mangabeys [65] and capuchins [56,66]. As with sex differences, it is important to note that this work has generally involved small sample sizes with limited age ranges, so a crucial step is to examine populations with greater age variation. Moreover, given that adolescence and old age are points in the life-course that show major shifts in humans, these periods warrant special attention in nonhumans. For example, a study examining probability inference in 80 rhesus monkeys ranging from juvenility to old age found that all age groups distinguished statistically unlikely from statistically likely outcomes [77], suggesting that older macaques do not show the same declines in probabilistic inference seen in older humans [96]. Thus, current work suggests that nonhumans may not show all the same age-related changes seen in humans, but are also fairly limited in scope.

4.6 State-dependent choice

Individuals can show different responses to risk across situations: the same person's choices may depend on their internal energetic state, transitory fluctuations in hormones, or their emotional state at the moment of the decision. For example, people may change their responses to risk depending on whether they are hungry [45]. Differences in levels of hormones like testosterone and cortisol can also impact risk propensity: whereas increasing cortisol drives greater risk-aversion [18] testosterone increases risk-seeking [19]. Finally, even transient emotional states affect risk propensity: while more positive emotions can increase risk-taking, negative states such as sadness or decrease people's preference for risk [16-17].

Recent work suggests that some of these processes are shared between humans and other primates. First, chimpanzees, bonobos, and capuchins show several features of human-like emotional responses to risky decision-making [63,101] (see Figure 1 and ESM). In particular, they show more indicators of negative emotional states—such as negative vocalizations, scratching, or throwing a tantrum—when they gambled and lost compared to when they gambled and won or played it safe. In addition, apes and capuchins spontaneously attempted to 'switch' their initial choices after gambling and loosing—that is, they attempt to revise their choice and select the forgone option, a response they rarely showed in response to other outcomes. In this way, choice switching might be a behavioural indicator of 'regret' [16].

In contrast, studies examining the influence of hormonal state on primate economic decision-making are scant, which is surprising given the evidence that cortisol and testosterone shape many aspects of primate behaviour [102]. Direct manipulations of primates' internal states to test causal relationships are also lacking, which is also surprising given the great theoretical attention devoted to the impact of energy budget on risk propensity [41]. To date, only one study has conducted an energy manipulation in primates, and found that rhesus macaques become more risk-seeking when their energy level is higher [55]—paralleling wild observations that larger-bodied primates engage in more risk-prone hunting in times of resource plenty, the opposite of the pattern seen in small animals [46]. Overall then, while there have not been many investigations into the impact of internal state on primate risk choice, current data does suggest some potential shared psychological or physiological mechanisms with humans.

4.6. Context-dependent variation

Decision preferences can also be affected by external factors. Several aspects of context can shape human choice, including the specific currency of the reward at stake [67,103] and the larger social context. Importantly, these processes intersect with the state-dependent effects described in the prior section: social context or reward currency may affect risk propensity by impacting internal emotional or hormonal states. That is, differences in internal states may in fact stem from cues in the external environmental context.

Here we focus primarily on social context, as this is a crucial evolutionarily-relevant context. In particular, humans exhibit both extensive and flexible cooperation compared to other primates [104], and this dependence on social exchange strategies may have shaped our responses to risk. In fact, people do tend to be more risk-seeking when other people are present than when alone [14] or in competitive contexts [15]. This may in part reflect a fundamental distinction concerning how humans respond to social versus non-social risk: people are less willing to gamble on the trustworthiness of another person compared to an identical non-social risk, a phenomenon called betrayal aversion [105]. This increased sensitivity to *social* risks may arise from uniquely-human emotions and motivations used in cooperative contexts, such as reciprocity or theory of mind skills [106]. Indeed, hunter-gatherers, who are an important model of how humans have lived for most of our species existence, appear to buffer the high risks associated with a diet focused on high-value but difficult to obtain foods by engaging in extensive food sharing [107]. Thus, studies of nonhuman primates can help disentangle how human-specific patterns of decision-making facilitate human cooperative economic behaviours like exchange, trade and investment.

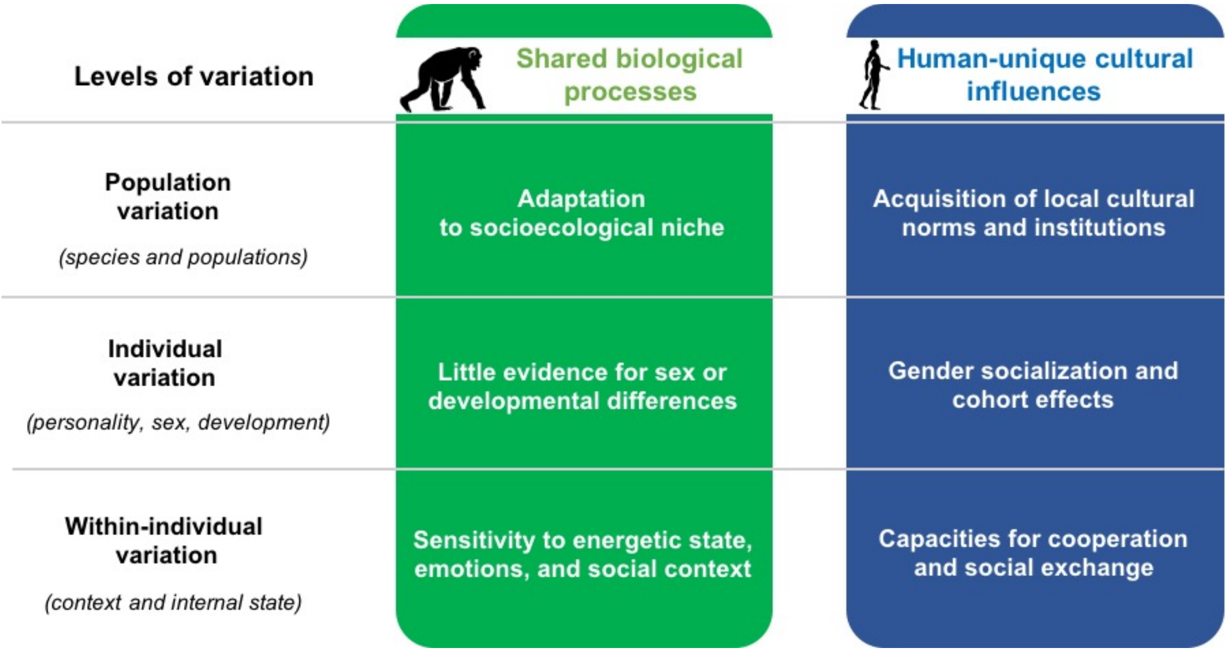
While other primates do not engage in exchange or food sharing to the extent that humans do, they are also highly social and must constantly make decisions about whether to cooperate or compete with others. These situations inherently pose problems involving risk because decision-makers must choose between courses of action where another individual's behaviour creates variability in payoffs. Accordingly, there is some evidence that social context may impact nonhuman risk choices too (see Figure 1 and ESM). For example, both chimpanzees and bonobos are more risk-seeking following a competitive interaction, compared to a neutral or a playful one [62]. Conversely, capuchins become more risk-averse in the presence of a conspecific than when alone [108]. Finally, chimpanzees were more averse to uncertainty stemming from another individual who can choose to reciprocate, versus a non-social probabilistic device [109].

More generally, several studies have adapted human economic games for use with primates, including the ultimatum game [110], the stag-hunt game [111], and the trust game [112-113]. In the modified trust game, chimpanzees could choose between obtaining a small but safe reward, or sending a larger reward to a partner who could then either reciprocate and send back a higher value reward or not. Chimpanzees will accept the social risk associated with trusting their partner [112]—especially when the partner is a close friend [113]. This suggests that a basic sensitivity towards degrees of social uncertainty may be shared with other primates. Yet a key question is therefore whether humans have special abilities to monitor social risk to thereby protect against free riders, given the greater scope of cooperation and reciprocity seen in humans [104, 114] and the importance of social risk-taking in human economic systems [115]. For example, other primates may not be as proficient at dealing with risk imposed by exchanges, because they cannot make formal agreements or enforce reciprocation. This highlights how both novel cognitive capacities (for engaging in cooperation) as well as human-specific cultural norms for these interactions may re-shape human social risk preferences compared to other species.

5- Conclusions: primate decision-making and human economic origins

Humans exhibit great variation in responses to risk across populations, individuals, and contexts, so understanding the origins of this variation is crucial to explaining patterns of human economic behaviour. We have argued that comparative studies of decision-making can disentangle the mechanisms and the function of this variation to address questions about both the proximate mechanisms and the ultimate consequences of these decision-making patterns. As such, nonhuman primates provide a complimentary line of evidence to test hypotheses about the origins of human economic behaviours (see Figure 2).

We found that nonhumans sometimes show patterns of variation like humans. For example, emotional states, social context, and some neurotransmitter systems can modulate risk preferences in primates like in humans. This suggest that at least some of the proximate psychological mechanisms driving human economic behaviour build upon cognitive, emotional, and neurobiological substrates that are shared with other primates Yet other mechanisms may be more specific to humans: while humans show robust gender differences in risk preferences as well as developmental change over the life-course, there is limited evidence for parallel shifts in nonhuman risky choice. This suggests that this variation may stem more from human-specific mechanisms, such as cultural learning and socialization. Given that culturally-based traits are more malleable and thus more amenable to interventions, this provides new clues for promoting optimal economic behaviour in humans.



Levels of variation	Shared biological processes	Human-unique cultural influences
Population variation *(species and populations)*	Adaptation to socioecological niche	Acquisition of local cultural norms and institutions
Individual variation *(personality, sex, development)*	Little evidence for sex or developmental differences	Gender socialization and cohort effects
Within-individual variation *(context and internal state)*	Sensitivity to energetic state, emotions, and social context	Capacities for cooperation and social exchange

Figure 2. The origins of human variation in human economic behaviour. Comparative studies of other primates can help disentangle the relative role of shared biological processes versus human-unique cultural influences on risk preferences. Current evidence for variation across populations, individuals, and contexts in primates suggests some processes are shared with humans whereas others are human-unique.

A second question concerns the ultimate consequences of variation in risk preferences. Here, comparative work can provide an important line of evidence for test the adaptive consequences of different strategies. For example, there are robust species differences in responses to risk indicating that species which typically feed on more variable, heterogenous resources are relatively more risk-seeking. Yet there are also crucial differences in human and animal patterns that may stem from human's novel socioecological niche. Human hunter-gatherer lifestyles are characterized by a dependence on high-value and high-risk foods that may have required new social mechanisms to cope with a greater variability in both foraging, such as food sharing and resource redistribution [107,116]. As a consequence, humans might have evolved new cognitive abilities and innovated new cultural practices to deal with the social risks presented by exchanges.

Yet there is still much work to be done. First, different species and questions have sometimes been tested using different tasks (see Figure 1), limiting some inferences across studies. In addition, primate studies in general are often limited by small sample sizes, especially with respect to questions of intra-individual variation. As such, comparisons of decision-making using standardized methods in larger populations with wider variation in sex, ages, or particular life experiences are crucial to test these ideas. Finally, animal choice typically involves biologically-relevant rewards, but there is increasing evidence that people can be more risk-seeking when making 'foraging' decisions about food than in equivalent decisions involving money [67,103]. Given that humans engage in evolutionarily-novel forms of economic exchange involving abstract currencies, but other primates can be trained to use and exchange token in specific contexts [84], animals thus present untapped opportunities to test how experience with markets impacts economic decision-making. More generally, comparative research is well-positioned to advance our understanding of human economic behaviour by pinpointing the necessary cognitive and experiential prerequisites that enable different aspects of decision-making and exchange.

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Author contributions

FDP and AGR wrote the paper together.

Conflict of interest

The authors declare that they have no conflict of interest.

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Electronic Supplementary Materials

Variation in primate decision-making under uncertainty and the roots of human economic behaviour

F. De Petrillo & A.G. Rosati

Table S1: Studies examining decision-making under risk in nonhuman primates. Each study is categorized in terms of the focus species; the basic type of task used (learned association; intuitive outcomes, or exchange; see main manuscript for information about categorizations); the study's overall sample size; whether there was a species comparison (if so, the other species and relevant study is listed for each of the species tested); whether there are relevant studies with a within-species population contrast; whether the study reported analyses examining individuals differences by age or sex; and whether the study design included either an internal state manipulation or a social context manipulation. For studies that report sex, age, or relevant condition comparisons we indicate the directionality of risk preferences. *Indicates data that was republished as part of a new comparison.

Taxonomic group	**Species**	**Study**	**Task type**	**Sample size**	**Species comparison**	**Sex difference**	**Developmental change**	**Internal state manipulation**	**Social context manipulation**
Apes	Chimpanzees *(Pan troglodytes)*	Heilbronner et al. 2008	Learned association	N = 5	Bonobos	No effect	No effect		
		Rosati & Hare, 2011	Intuitive outcome	N =16	Bonobos				
		Rosati & Hare, 2012	Intuitive outcome	N = 20	Bonobos				More risk-seeking in comparative than neutral context; no effect of play context
		Rosati & Hare, 2013, 2016*	Intuitive outcome	N = 24	Bonobos, humans (adults)	No effect	No effect	More emotional responses to negative than positive outcomes	
		Haun et al., 2011	Intuitive outcome	N = 8	Bonobos, orangutans, gorillas				
		Proctor et al., 2014	Learned association	N = 9	Humans (adults), capuchins				
		Krupenye et al., 2015	Intuitive outcome	N = 23	Bonobos	Males more sensitive to			

						framing than females			
		Calcutt et al., 2018	Exchange	N = 8		All females			More risk-seeking for non-social than social risks
		Broihanne et al., 2019	Exchange	N = 12	Bonobos, orangutans, gorillas, capuchin monkeys, Tonkean macaques				
		Leinwand et al. 2020	Learned association	N = 4	Gorilla, Japanese macaques				
	Bonobos *(Pan paniscus)*	Heilbronner et al. 2008	Learned association	N = 5	Chimpanzees	No effect	No effect		
		Rosati & Hare, 2011	Intuitive outcome	N =14	Chimpanzees				
		Rosati & Hare, 2012	Intuitive outcome	N = 16	Chimpanzees		No effect		More risk-seeking in comparative than neutral context; no effect of play context
		Rosati & Hare, 2013, 2016*	Intuitive outcome	N = 13	Chimpanzees, humans (adults)	No effect	No effect	More emotional responses to negative than positive outcomes	
		Haun et al., 2011	Intuitive outcome	N = 5	Chimpanzees, orangutans, gorillas				
		Krupenye et al., 2015	Intuitive outcome	N= 17	Chimpanzees	Males more susceptible to framing than females			
		Broihanne et al., 2019	Exchange	N = 6	Chimpanzees, orangutans, gorillas, capuchins,				

					Tonkean macaques				
	Orangutans (*Pongo abelii*; *Pongo pygmaeus*)	Haun et al., 2011	Intuitive outcome	N = 6	Chimpanzees, bonobos, gorillas				
		Pelè et al., 2014	Exchange	N = 4	Long-tailed macaques, capuchins	All females			
		Broihanne et al., 2019	Exchange	N = 6	Bonobos, chimpanzees, gorillas, capuchins, Tonkean macaques				
	Gorillas (*Gorilla gorilla*)	Haun et al., 2011	Intuitive outcome	N = 3	Chimpanzees, bonobos, orangutans				
		Broihanne et al., 2019	Exchange	N = 7	Bonobos, chimpanzees, orangutans, capuchins, Tonkean macaques				
		Leinwand et al. 2020	Learned association	N = 4	Chimpanzees, Japanese macaques				
Old World monkeys	Rhesus macaques (*Macaca mulatta*)	McCoy & Platt, 2005; Hayden & Platt, 2009*	Learned association	N = 2	Humans (adults)	All males			
		Hayden & Platt, 2007	Learned association	N = 2		All males			
		Long et al., 2009	Learned association	N = 3		All males			
		Hayden et al., 2010	Learned association	N = 4		All males			
		Yamada et al., 2013	Learned association	N = 2				More risk-seeking with high than low-energy budget	

		Xu & Kralik, 2014	Learned association	N = 2		All males			
		Smith et al., 2017	Learned association	N = 7		All males			
		De Petrillo & Rosati, 2019	Intuitive outcome	N = 160		No effect	No effect		
	Long-tailed macaques (*Macaca fascicularis*)	Steelandt et al., 2011	Exchange	N = 6	Capuchins, Tonkean macaques	All males			
		Pelè et al., 2014	Exchange	N = 5	Capuchins, orangutans	All males			
	Japanese macaque (*Macaca fuscata*)	Leinwand et al. 2020	Learned association	N = 6	Chimpanzees, gorilla				
	Tonkean macaques (*Macaca tonkeana*)	Steelandt et al., 2011	Exchange	N = 6	Capuchins, long-tailed macaques				
		Broihanne et al., 2019	Exchange	N = 5	Bonobos, chimpanzees, orangutans, gorillas, capuchins				
	Mangabeys (*Cercocebus torquatus torquatus*)	Rivière et al., 2018	Intuitive outcome	N= 17	Humans (children)	No effect	No effect		
New World monkeys	Capuchins (*Sapajus apella*)	Chen et al., 2006	Exchange	N = 6					
		Steelandt et al., 2011	Exchange	N = 9	Long-tailed macaques, Tonkean macaques				
		Lakshminarayanan et al., 2011	Exchange	N = 5					

		Proctor et al., 2014	Learned association	N = 8	Humans (adults), chimpanzees				
		Pelè et al., 2014	Exchange	N = 8	Orangutans, Tonkean macaques				
		De Petrillo et al., 2015	Learned association	N = 10		No effect	No effect		
		De Petrillo et al., 2017	Learned association	N = 10		No effect	No effect	More emotional responses to negative than positive outcomes	
		Zoratto et al., 2018	Learned association	N = 10					More risk-seeking alone than in social context
		Rivière et al., 2019	Intuitive outcome	N= 8	Humans (children), mangabeys	No effect	No effect		
		Broihanne et al., 2019	Exchange	N = 6	Bonobos, chimpanzees, orangutans, gorillas, Tonkean macaques				
Lemurs	Ring-tailed lemurs (*Lemur catta*)	MacLean et al., 2012	Learned association	N = 2	Ruffed lemurs, mongoose lemurs	All males			
	Mongoose lemurs (*Eulemur mongoz*)	MacLean et al., 2012	Learned association	N = 2	Ring-tailed lemurs, mongoose lemurs	All males			
	Ruffed lemurs (*Varecia rubra*)	MacLean et al., 2012	Learned association	N = 1	Ring-tailed lemurs, mongoose lemurs	All males			

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