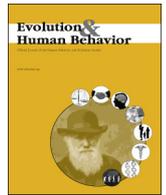




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## Original Article

## Reward currency modulates human risk preferences

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## ABSTRACT

Monetary and biological rewards differ in many ways. Yet studies of human decision-making typically involve money, whereas nonhuman studies involve food. We therefore examined how context shifts human risk preferences to illuminate the evolution of decision-making. First, we assessed peoples' risk preferences across food, prizes, and money in a task where individuals received real rewards and learned about payoffs through experience. We found that people were relatively more risk-seeking for both food and prizes compared to money—indicating that people may treat abstract reward markers differently from concrete rewards. Second, we compared human risk preferences for food with that of our closest phylogenetic relatives, chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), in order to illuminate the evolutionary origins of human decision-making strategies. In fact, human and chimpanzees were both relatively more risk-seeking compared to bonobos. Finally, we investigated why people respond differently to money versus concrete rewards when making decisions. We found that people were more risk-prone when making decisions about money that was constrained as a store of value, compared to money that could be freely exchanged. This shows that people are sensitive to money's usefulness as a store of value that can be used to acquire other types of rewards. Our results indicate that humans exhibit different preferences when making risky decisions about money versus food, an important consideration for comparative research. Furthermore, different psychological processes may underpin decisions about abstract rewards compared to concrete rewards.

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## 1. Introduction

Monetary rewards fundamentally differ from primary biological rewards like food. While food is of central importance to both humans and other animals, money is an evolutionarily novel currency. Moreover, money has several properties that distinguish it from biological rewards: it serves as an abstract store of value, it can be flexibly converted into other rewards, and it can take on very large values. Indeed, some theoretical views suggest that money functions as a tool allowing people to acquire their actual goals (Lea & Webley, 2006). Although there have been few studies of the psychological underpinnings of money, some evidence indicates that money can have a large impact on people's goals and behavior. For example, rewarding people with money makes them more sensitive to tradeoffs between effort and compensation (Heyman & Ariely, 2004). Even priming people with monetary concepts can result in increased self-sufficiency and reduced willingness to help others (Caruso, Vohs, Baxter, & Waytz, 2013; Vohs, Mead, & Goode, 2006). Yet despite the influence of money on human behavior, most studies of human decision-making focus only on this currency. Studies involving money are critical for understanding present-day economic behavior, but it is unclear if these kinds of decision-making tasks also

capture the choice processes that humans use to make decisions about biologically-relevant rewards.

Do similar decision-making processes support choices about both money and biologically-central rewards like food? In fact, several pieces of evidence suggest that people may use different strategies when they are trying to accumulate money, compared to when they face decisions about food or other primary rewards that emulate foraging contexts. For example, people tend to discount delayed food or juice rewards more heavily than even small amounts of money (Estle, Green, Myerson, & Holt, 2007; Jimura, Myerson, Hilgard, Braver, & Green, 2009; McClure, Ericson, Laibson, Loewenstein, & Cohen, 2007; McClure, Laibson, Loewenstein, & Cohen, 2004; Odum, Baumann, & Rimington, 2006; Rosati, Stevens, Hare, & Hauser, 2007). Similarly, people are more risk-prone for juice compared to small amounts of money when tested in the same setup for both reward types (Hayden & Platt, 2009) (but see Estle et al., 2007). Patterns of lifespan change in decision-making also suggest an important distinction between the choice processes involved in decisions about money versus food: whereas younger adults discount monetary rewards more steeply than older adults, both age groups showed similar temporal choices about juice (Jimura et al., 2011). Finally, neuroimaging data examining the neural substrates supporting value-based decision-making indicate that the brain regions encoding value are distinguishable based on whether the rewards are money versus consumable rewards (see Clithero & Rangel, 2014 for a meta-

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analysis of imaging studies examining different reward currencies). Overall, this evidence suggests that people make value-based decisions differently when faced with decisions about food versus money. One possibility is that this stems from a magnitude effect: decisions about higher-value rewards are sometimes treated differently from lower-value rewards (Green, Myerson, & McFadden, 1997; Holt & Laury, 2002), so money and consumables might fall into those respective categories. Alternatively, there may be something fundamentally different about money versus food rewards, even if their values are relatively well-matched. Either way, this evidence suggests that reward type can alter the strategies that people use when making decisions.

These results pose a challenge to understanding the evolutionary origins of human decision-making: nonhuman studies of decision-making typically involve choices about food rewards, hindering comparisons between humans and other species. Yet comparative studies of the traits of different species are one of the most powerful tools in evolutionary biology for illuminating the historical process of natural selection. The comparative method can help pinpoint when specific traits emerged in phylogeny, as well as illuminate the emergence of these traits in relation to variation in species' socioecological characteristics (Clutton-Brock & Harvey, 1979; Harvey & Purvis, 1991; Mayr, 1982). Such comparisons have been critical for understanding the evolution of behavioral and morphological characters, and more recently have been fruitfully applied to the problem of cognitive evolution as well (Amici, Aureli, & Call, 2008; MacLean et al., 2012; Sherry, 2006). Indeed, comparisons of human cognition with that of other species, especially our closest relatives the great apes, have been a critical source of evidence for evaluating hypotheses about human uniqueness (Hare, 2011; Hill, Barton, & Hurtado, 2009; Kaplan, Hill, Lancaster, & Hurtado, 2000; Penn, Holyoak, & Povinelli, 2008; Suddendorf & Corballis, 2007; Tomasello, Carpenter, Call, Behne, & Moll, 2005), including understanding the origins of human economic decision-making (Santos & Rosati, 2015). However, given that humans can respond differently to decisions about different currencies, human and animal tasks that appear similar may actually recruit different psychological processes (Blanchard, Wolfe, Vlaev, Winston, & Hayden, 2014).

To understand the evolution of human-like decision-making, it is therefore critical to equate the problems faced by humans and other animals. In fact, studies of decision-making in humans and nonhumans differ in several other relevant ways in addition to the differences in reward currencies used across species. For example, human decision-making tasks often involve one-shot choices about (hypothetical) monetary amounts presented in a linguistic format (e.g., "Would you prefer a 50% chance of winning \$20?"). In contrast, nonhuman studies typically involve a series of iterated choices about consumable rewards, where animals learn about reward payoffs through direct experience. There is some evidence that all of these contextual factors can influence human preferences. For example, people exhibit steeper temporal discounting when making iterated compared to one-shot decisions (Schweighofer et al., 2006). People also show different risk preferences when choosing from description versus experience (Barron & Erev, 2003; Hertwig, 2012; Hertwig & Erev, 2009), by overweighting rare outcomes when making risky decisions from description but relatively underweighting these outcomes when making decisions from experience (Hertwig, Barron, Weber, & Erev, 2004). Finally, the potential disparity between real and hypothetical responses is also a major concern in both psychological and economic research (Green & Myerson, 2004; Hertwig & Ortmann, 2001; List & Gallet, 2001). Some evidence indicates that people can exhibit greater risk-aversion when monetary rewards are real than when they are hypothetical (Holt & Laury, 2002, 2005), whereas other studies have found similar choices for real and hypothetical monetary rewards (Johnson & Bickely, 2002; Lagorio & Madden, 2005; Madden, Begotka, Raiff, & Kastern, 2003; Wiseman & Levin, 1996). Overall, these findings suggest that contexts can affect human decision-making patterns, and many of the ways in which typical human studies differ from typical nonhuman studies make direct comparisons challenging.

In the current studies, we examine how reward currency influences people's preferences risk, or probabilistic variation in payoffs. Decision-making under risk is a critical theoretical issue in psychology and economics as well as biology (Kacelnik & Bateson, 1996, 1997; Platt & Huettel, 2008; Tversky & Kahneman, 1981), so risky choice is a domain that is well-suited for evolutionary approaches to decision-making. Some theories have proposed that risk-aversion is a widely conserved foraging strategy, as a variety of nonhuman species ranging from insects, birds, and mammals are broadly risk-averse for gains when making decisions about food (Kacelnik & Bateson, 1996, 1997). Given that humans also tend to be risk-averse when making decisions about monetary gains (Kahneman & Tversky, 1979, 2000; Tversky & Kahneman, 1981), this suggests that humans and many nonhumans may exhibit risk aversion due to shared common descent. However, several primate species – including rhesus macaques (*Macaca mulatta*), capuchins (*Cebus apella*), and chimpanzees (*Pan troglodytes*) – show more risk-seeking patterns of choice than other species in similar contexts (De Petrillo, Ventricelli, Ponsi, & Addressi, 2015; Heilbronner & Hayden, 2013; Heilbronner, Rosati, Stevens, Hare, & Hauser, 2008). Importantly, chimpanzees are specifically more risk-seeking when contrasted with bonobos (*Pan paniscus*) on matched comparisons across several different tasks (Haun, Nawroth, & Call, 2011; Heilbronner et al., 2008; Rosati & Hare, 2012, 2013). Although chimpanzees and bonobos are humans' two closest living relatives – diverging from each other less than 1 mya (Prüfer et al., 2012) – most theoretical claims about behavioral and cognitive evolution in humans tend to use chimpanzees alone as a model for the last common ancestor of humans with apes (Wrangham & Pilbeam, 2001). However, recent work involving comparison of both species suggests that the last common ancestor may in fact have had a mosaic of chimpanzee-like and bonobo-like traits across different behavioral domains (Hare & Yamamoto, 2015). The critical test of whether human risk preferences are evolutionarily derived or evolutionary conserved is to therefore to examine humans and our closest phylogenetic relatives in a matched decision-making context.

Our study therefore had two main goals. First, we examined how currency influences human choice preferences. While previous research has shown that humans differentiate money (secondary reinforcers) and consumable rewards like food (primary reinforcers) when making decisions (including when making decisions under risk; Hayden & Platt, 2009), it is currently unclear why people respond differently to these currencies. One possibility is that consumables like food are treated as a 'special' or distinct category of reward (Rosati et al., 2007). However, humans may also respond differently to abstract markers of value, like money, compared to other more concrete rewards—regardless of whether they are consumable. To test this, in Study 1 we compared human risk preferences in the same setup for food, prizes, and money. As prizes are not a primary reward (in contrast to food) but are also not an abstract marker of value (in contrast to money), this comparison can disentangle why humans might treat these currencies as different. Importantly, we used small amounts of food, small amounts of money (\$1 or less), and prizes with matched economic values to the money. Many magnitude effects in human decision-making stem from comparisons involve very large differences ranging from 20 to 1000 times as large (e.g., \$100 versus \$100,000; Green et al., 1997; Holt & Laury, 2002, 2005; Kirby & Marakovic, 1996), whereas comparative studies of animal decision-making comprising these smaller variations in value have not revealed consistent magnitude effects (Green, Myerson, Holt, Slevin, & Estle, 2004; Stevens, Rosati, Ross, & Hauser, 2005) (but see Ludvig, Madan, Pisklak, & Spetch, 2014). This methodological approach therefore minimizes the likelihood that our comparison was capturing magnitude effects alone. In Study 2, we then examined how money's unique characteristics may influence people's preferences. In particular, we examined whether risk preferences for money depend on that money's usefulness as a store of value that can be exchanged for other rewards. Finally, all participants completed a hypothetical risk questionnaire involving choices about small amounts of money

(based on Holt & Laury, 2002), allowing us to directly compare individuals' performance in the main behavioral task to their performance in a more standard economic task.

Our second goal was to illuminate the evolutionary origins of human decision-making by comparing the performance of humans to chimpanzees and bonobos, tested in a previous study (Rosati & Hare, 2013). Although humans may use adaptive decision-making rules derived from optimal foraging theory when faced with uncertainty (Rode, Cosmides, Hell, & Tooby, 1999), and some work has compared human and chimpanzee preferences for variability (for different reward types) in similar contexts (Proctor, Williamson, Lutzman, de Waal, & Brosnan, 2014), there have been no previous comparisons of risk preferences in humans and apes when faced with matched foraging decisions for food rewards. Our setup – involving an experiential task with real rewards and trial-by-trial feedback about contingencies – was designed to be similar to previous work on nonhuman ape decision-making (see also Rosati et al., 2007). One possibility is that humans might exhibit preferences more similar to bonobos, given that humans are also generally risk-averse. Conversely, human may show risk-prone preferences, like chimpanzees, specifically when faced with experiential decisions about food rewards. This sort of comparison is critical to identify the most appropriate comparative model for the last common ancestor's decision-making capacities, as our model of the last common ancestor impacts biological inferences about what traits are novel or derived in the human lineage.

## 2. Study 1: Risk preferences across currencies

In study one, participants made a series of choices between a safe option and risky option. The risky option provided either a preferred reward (good outcome) or non-preferred reward (bad outcome) with equal probability, but participants did not know which outcome they would receive in advance. The safe alternative provided an intermediately-preferred reward type; this reward could vary in amount across trials, but participants always know what they would receive from this option before they chose on any given trial. This allowed us to assess whether individuals modulated their choices according to the relative value of the two options.

Participants were assigned to one of three conditions. In the *food condition* they made decisions about small amounts of food (with different food types determined based on the participant's own subjective preferences across several available types). In the *money condition*, they made decisions about small amounts of money. In the *prize condition* participants made decisions about different types of prizes (also determined based on the participant's own ratings as with the food rewards, and approximately matched in value with the monetary rewards). As prizes are concrete yet non-consumable rewards, the prize condition allowed us to assess whether people generally treat food differently from non-consumable rewards, versus whether they treat abstract money differently from concrete rewards. Finally, we compared the performance of the participants in the food condition with those of chimpanzees and bonobos previously tested on a matched version of this task.

### 2.1. Methods

#### 2.1.1. Participants

We tested 75 people (25 per condition), recruited from Duke University and the surrounding community (36 females, 39 males; age range: 18–32 years; mean age = 21.0 years). Additional subjects were tested but excluded in each condition based on predetermined exclusion criteria described in more detail below (in particular, criteria to ensure that individuals found the food and prizes to actually be rewarding). We matched the subject number per condition to those of the apes tested in the food-based version of task.

#### 2.1.2. Consent and reward selection procedure

Experimental procedures complied with guidelines of the Duke University Health System IRB. All participants were tested individually in a room at Duke University. After giving written informed consent, participants in the food and prize conditions were first asked to rate and rank five potential reward types. The rewards used in the main behavior task in these conditions were based on each subject's personal preferences (e.g., given individual variation or idiosyncrasies in preferred food types). As participants in the money condition made decisions about small amounts of money with known values, we did not have those participants rank their rewards.

Participants in the food condition were asked to taste five foods (chocolate-covered raisins, Cheezit crackers, M&M's, pretzels, and Cheerios). They rated how much they liked each type on a six-point scale (multiple items could be given the same rating), and then uniquely ranked the items in order of preference (see ESM for scales). These rankings determined the food items used in the task: each participant's highest-ranked item was assigned as the good risk outcome, the lowest-ranked item as the bad risk outcome, and the middle-ranked type as the safe option. The prize condition followed the same general procedure. Participants first viewed five prize items, whose value approximated the same range as the monetary rewards (a notebook valued \$1.09, an eraser valued \$0.79, a pen valued \$0.39, a blank CD valued \$0.32, and a paperclip valued \$0.01). Participants were not explicitly informed of these costs, as directly attaching monetary amounts can lead people to treat other rewards like money (e.g., Heyman & Ariely, 2004). Then participants rated and ranked the five prizes, using the same scales as in the food condition.

#### 2.1.3. Behavioral task: instructions and practice trials

After the initial consent and reward rankings, the participant sat across a table from the experimenter for the main behavioral task. This task was designed to match a nonverbal risk task designed for use with apes, in order to facilitate direct comparisons across species. As we thought participants would be uncomfortable if the experimenter did not speak as all (e.g., ran the study exactly as it had been executed with nonhumans), the experimenter initially read instructions while demonstrating the procedure (see ESM Fig. S1 for photos of setup, and ESM Appendix 3 for script). However, the verbal instructions focused on the physical procedure the participant would witness, and did not involve verbal descriptions of the reward contingencies and did not label the two options as risky and safe. Thus, human participants had to make the same kinds of inferences about reward outcomes based on their own experience that the apes did.

Participants were told that they would make decisions between two containers that would contain different rewards. On each trial they would first see the experimenter place one reward (*the safe option*) under one of the overturned containers. Thus, the participant had always seen what that safe option would provide on a given trial. For the alternative (*the risky option*), the experimenter would first show two potential outcomes in a tray (e.g., the good outcome and the bad outcome), but then place only one of them under the second container. In particular, experimenter always occluded this container before baiting it, so the participant did not know whether they would receive the good or bad outcome in advance. The food rewards had always been pre-distributed into small clear cups so they were easily visible, and the money was displayed small black boxes with coin-slots so the amounts were clearly visible (the prizes did not need to be displayed in this fashion to see the amounts).

To gain experience with the task procedure and reward contingencies, participants first completed three *practice trials*. Here, the experimenter baited only one option per trial (two risk trials resulting in each possible outcome, and one low-value safe trial) so that all participants had experience with both the safe and risk options before they started making choices between them. These trials also allowed us to check the participant's task comprehension. In particular, on each

practice trial the participant had to report how many items were under the container before they received the reward. Participants therefore had to remember the number of items they had seen, and also correctly report that only one item was under the risk option container (despite having initially seen both the good and bad outcome in the tray). Participants were reminded of the procedure and then asked again if they initially answered incorrectly.

#### 2.1.4. Behavioral task: Choice phase

Immediately following the practice trials, participants then completed 12 choice trials. The experimenter baited the safe and then the risky option (the side assignment was counterbalanced across trials). The outcome of the risky option was predetermined; half of trials resulted in the good payoff, with outcome order pseudo-randomized with no more than three trials in a row with the same outcome. After baiting both containers, the experimenter asked the participant which option they preferred, and participants could point or verbally indicate one of the cups; otherwise the experimenter did not talk to the participant. They did not see the outcome associated with the risky option if they did not choose it. The experimenter informed participants that there was no right or wrong way to complete the task, and looked down the middle of the table when the participant chose to avoid inadvertent social cuing, as in the ape procedure. In the food condition, participants consumed their selected reward on a trial-by-trial basis (like apes). In the prize and money conditions, they accumulated their rewards in a tray, and knew they would keep their accumulated rewards. There was a 30 s inter-trial interval starting when the participant placed the last food piece in their mouth, or placed the last item in the tray.

In all three conditions, the risky option provided either the good or bad outcome, and the value of the safe option varied between low, medium, or high across trials (order was pseudo-randomized, with no more than two trials in a row with the same safe value). This ensured that participants modulated their choices according to the relative value of the two options. In the food condition, the safe option provided one, three, or six pieces of the intermediately-preferred type; these contingencies matched those in the ape food task. In the prize condition, the value of the safe option again varied across trials (low, medium, or high), but here could provide one, two, or three items. In the money condition, the risky option provided one dollar or one penny, and the safe option provided different quantities of dimes: low (40 cents), medium (50 cents) or high (60 cents). As directly equating the value of the food, prizes, and money was difficult, we were conservative in that the low safe value in the money condition (40 cents) was less than the average expected value of the risky option (e.g., 50 cents), biasing individuals toward the risky option contrary to our main hypotheses.

#### 2.1.5. Reward motivation and subject exclusions

One potential issue with our setup was that participants might have felt pressure to consume food they did not want (unlike the apes). To address this, we asked participants to refrain from eating for two hours before the session. Second, the food types were determined by each individual's subjective preferences, and participants were also provided with water to ensure they did not become thirsty. Finally, participants could throw away food. In particular, we provided a small trashcan immediately adjacent to the testing table, and informed participants that they could simply throw away any food they did not want. We included this trashcan in order to exclude individuals who did not want to eat the food. Participants in the prize condition were also given the option of throwing their prizes away, as their rewards were also based on the same ranking system as in the food condition. We did not provide this option to participants in the money condition (where the rewards had objective values), but participants were informed beforehand that they could exchange their accumulated coins for the equivalent bills after the task to ensure that participants did not find it aversive to acquire large amounts of change.

We excluded participants for two main reasons. First, we excluded subjects that threw away the good or safe options in the main task; participants were not excluded for discarding the bad risk outcome, as this was designed to be a non-preferred reward category. Second, we excluded subjects that explicitly reported that they did not like the rewards, or liked them in a different order than the initial rankings, in an open-ended post-test questionnaire. A typical example of this is the following statement: "I wanted something sweet, so I chose [good risk outcome] or [bad risk outcome] over [safe outcome]." That is, this participant reported preferring both their potential risk payoffs more so than the safe payoff.

In the food condition, we excluded eleven additional participants: nine threw away the safe option or good risk outcome; one threw the safe food away and reported they did not like it in the questionnaire; and one participant reported not liking their safe reward outcome after refusing to taste the food in the ranking phase. We excluded six additional individuals in the prize condition: three threw away good or safe prizes, two reported disliking the good and safe prizes in the questionnaire; and one individual refused to take the prizes with them after the task. We did not exclude any individuals in the money condition, as no individuals reported not liking money (or preferring less over more money).

#### 2.1.6. Post-task procedure

After the task, participants completed a series of questionnaires. The first part consisted of demographic information (age and gender), their relative hunger, and an open-ended question ("Please briefly explain why you chose the options that you did in the test") that we used to exclude subjects. Second, subjects completed a hypothetical risk questionnaire about monetary rewards (derived from Holt & Laury, 2002; see ESM for complete set of questions). This risk questionnaire assessed the participants' risk preferences in a more standard hypothetical task involving decision descriptions with relatively small amounts of money (ranging from \$0.10 to \$3.85), similar to our money condition. This allowed us to assess the relationship between choices in the behavioral task, and preferences in a standard risk questionnaire. After completing the rest of the study, participants also completed additional questionnaires examining aspects of decision-making styles (see ESM). However, those questionnaires did not involve discrete choices between different options and therefore did not pertain to the current work, which focused on economic risk preferences across contexts. Those additional surveys were therefore not analyzed in relation to the main behavioral task reported in the current manuscript, but are mentioned for methodological transparency. Following the testing session, all participants were paid \$10 (by check) for participation.

#### 2.1.7. Data coding and analysis

Participants' choices were recorded by the experimenter, and checked by a second coder from videotape. We first used repeated-measure ANOVAs to compare each subject's average preferences for the risky option across different values of the safe alternative. We also report generalized linear mixed models (GLMM) where choices were analyzed trial-by-trial as binary outcome variable, accounting for within-subjects repeated measures, and compared fit of models with different predictive factors using likelihood ratio tests (Bolker et al., 2008).

#### 2.1.8. Comparison with apes

We compared the performance of humans in the food condition with choices from wild-born chimpanzees ( $n = 24$ ) and bonobos ( $n = 13$ ), previously reported in Rosati and Hare (2013). We used the apes' performance in the low variance condition, which matched the contingencies in the human task. All behavioral studies had IACUC approval from Duke University (A078-08-03) and adhered to host country laws. The chimpanzee research was conducted at Tchimpanzee Sanctuary in the Republic of Congo (permit 009/MRS/DGRST/DMAST), and the bonobo research was conducted at Lola ya Bonobo

Sanctuary in the Democratic Republic of Congo (permit MIN.RS/SG/004/2009). All apes at both sites were socially housed, and most semi-free-ranged in tropical forest during the day (5–40 ha across groups). Apes were tested individually in familiar night dormitories, and had *ad libitum* access to water. The apes were never food-restricted for testing, and the majority of their food came from foraging in their enclosures and multiple feedings of food 2–4 times per day.

Apes made decisions between a safe option that provided an intermediately-preferred food type, and a risky option that provided either a highly-preferred or non-preferred food type. The procedure followed that used with the humans, with only minor differences. Ape food types were determined in an initial preference test (involving 20 dyadic choices between five food types). The five food types were based on availability at the different sanctuaries, and represented food types the apes were familiar with and received in other contexts such as daily feedings. Based on the preference test, chimpanzees received banana slices as their good risk outcome, cucumber slices as their bad risk outcome, and peanuts as their safe outcome; bonobos received banana slices as their good risk outcome, lettuce leaf as their bad risk outcome, and papaya as their safe outcome. The species did not differ in their relative preferences for these outcome categories (see Rosati & Hare, 2013 for all details). In the main test, the experimenter and ape sat across from each other at a table with a sliding top, the experimenter demonstrated the baiting of the safe and risky option as in the human task, and the apes could choose by pointing at or touching one of the options. To ensure the apes understood the task, they completed a separate introductory session with 14 exposure and 8 control trials. Their test session had 18 choice trials with 4 additional intermixed control trials to ensure that apes paid attention.

In our species comparison, we additionally accounted for any potential differences in food preferences across species by controlling for individual subject's relative preferences across the available food types. For humans, we took the difference between each participant's average ratings for the good and bad risk outcomes (on the six point scale), compared to the rating for the safe option. This was mapped onto an index ranging from zero to one such that an individual who exhibited completely ordinal preferences (e.g., rated the good risk outcome as higher than the safe option, which was rated equally higher than the bad risk outcome) would have a score of 0.5, an individual who preferred the safe option when relatively more would have a lower score, and an individual preferred the bad outcome would have a higher score. For apes, we calculated this score from each individual's pattern of choices in a food preference pretest, by averaging across all trials where they chose between the safe option food type and one of the risk outcome food types (reported in Rosati & Hare, 2013), resulting in the same index.

## 2.2. Results

### 2.2.1. Human preferences across currencies

Participants chose the risky option above chance on  $M \pm SE = 68.7 \pm 4.3\%$  of trials in the food condition, above chance [one sample *t*-test:  $t_{24} = 4.30, p < 0.001, d = 0.86$ ], and on  $69.0 \pm 3.4\%$  of trials in the prize condition, above chance [ $t_{24} = 5.67, p < 0.001, d = 1.13$ ], but only on  $53.0 \pm 3.3\%$  of in the money condition [ $t_{24} = 0.90, p = 0.38, n.s.$ ]. That is, humans preferred the risky option in the food and prize conditions, but not the money condition (see Fig. 1). We then conducted a repeated-measures ANOVA with *condition* (money, prize, or food) as a between-subjects factor, and *safe value* (low, medium, or high) as a within-subjects factor. There was a main effect of safe value [ $F_{2,144} = 35.36, p < 0.001, \eta^2 = 0.33$ ], with a significant linear contrast [ $F_{1,72} = 56.19, p < 0.001, \eta^2 = 0.44$ ]. That is, participants were less likely to choose the risky option as the value of the safe alternative increased, modulating their choices according to the relative value of their options. There was also a main effect of condition [ $F_{2,72} = 6.10, p < 0.005, \eta^2 = 0.15$ ]; pair-wise comparisons indicated that participants in the money

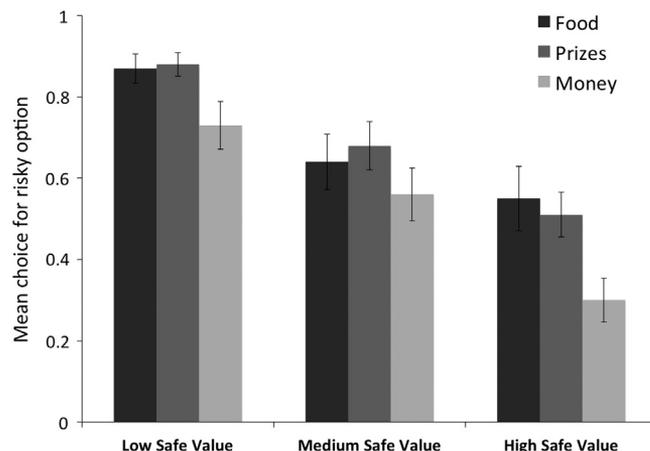


Fig. 1. Human risk preferences across currencies (Study 1). Humans made choices under risk for food rewards, prizes, and small amounts of money. Overall choices for the risky option in each condition, broken down by the value of the safe alternative. Error bars indicate SE.

condition chose the risky option less often than in the food and prize conditions [ $p < 0.05$  for significant comparisons]. There were no significant interaction between condition and safe value. The results from the GLMM analysis also indicated that individuals were less likely to choose the risky option in the money condition (see ESM for details and full parameters from the best-fit model). In particular, including condition a predictor significantly increased model fit [likelihood ratio test:  $\chi^2 = 11.62, df = 2, p < 0.005$ ].

We conducted several additional checks of these results. First, as it was difficult to equate reward value across these conditions, we also compared preferences on the subset of trials where the safe option had the intermediate value relative to the risk outcomes: when the safe option provided one item in the food and prize condition, or when the safe option provided 50 cents in the money condition. While participants choose the risky option on  $87.0 \pm 3.6\%$  of relevant trials in the food condition, and  $88.0 \pm 2.9\%$  in the prize condition, they chose it only  $56.0 \pm 6.5\%$  in the money condition [ $F_{2,72} = 15.62, p < 0.001, \eta^2 = 0.30$ ; pair-wise comparisons  $p < 0.001$  for significant cases]. This accords with the analyses including all safe value magnitudes.

We also confirmed that participants rated their food and prize categories appropriately (as reward assignments were based on the forced ranking). In the food condition, there was a significant effect of outcome category on ratings [ $F_{2,48} = 91.76, p < 0.001, \eta^2 = 0.79$ ], and pair-wise comparisons indicated that average ratings for the *good outcome* food type were higher than for the *safe outcome* food, which were higher than for the *bad outcome* food [ $p < 0.001$  for all cases; *good food* rating:  $5.8 \pm 0.1$ ; *safe food*:  $4.4 \pm 0.2$ ; *bad food*:  $2.4 \pm 0.2$ ]. Similarly, there was a significant effect of outcome category on ratings in the prize condition [*good prize*:  $5.1 \pm 0.2$ ; *safe prize*:  $3.60 \pm 0.2$ , *bad prize*:  $1.7 \pm 0.20$ ;  $F_{2,48} = 89.35, p < 0.001, \eta^2 = 0.79$ ; pair-wise comparisons indicated that all categories differed at  $p < 0.001$ ]. This indicates that our ranking procedure was successful in identifying food and prize types that the participants viewed as being appropriately desirable (or relatively undesirable for the bad risk outcome).

Finally, we examined whether differences in reward history could account for these findings by examining how often participants received the good versus bad risky payoff (as the payoffs were predetermined). Across conditions, participants received good payoff from the risky option at chance levels [*food condition*:  $51.5 \pm 3.5\%$  percent of trials, binomial test:  $p = 0.73, n.s.$ ; *prize condition*:  $50.2 \pm 3.5\%$ ,  $p = 0.99, n.s.$ ; *money condition*:  $55.3 \pm 4.0\%$ ,  $p = 0.20, n.s.$ ], with no in average reward outcomes across conditions [ANOVA with *condition* as a between-subjects factor:  $F_{2,72} = 1.01, p = 0.36, n.s., \eta^2 = 0.03$ ]. Thus, participants could not detect the payoff in advance using some

other cue, and did not differ in how often they got the good payoff across the three conditions.

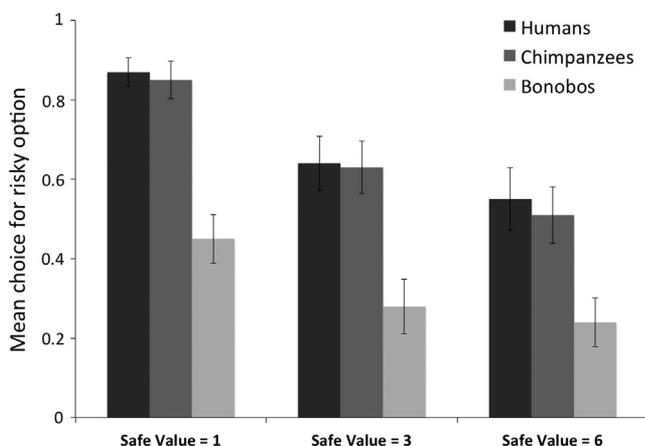
### 2.2.2. Human and ape risk preferences for food

We next compared human and ape risk preferences for food rewards. Chimpanzees chose the risky option on  $66.4 \pm 5.3\%$  of trials, above chance [ $t_{23} = 3.09, p = 0.005, d = 0.63$ ], whereas bonobos chose it on  $32.5 \pm 4.4\%$  of trials, below chance [ $t_{12} = -4.03, p < 0.005, d = 1.18$ ]. That is, chimpanzees preferred the risky option, whereas bonobos preferred the safe option (see Fig. 2). A repeated-measures ANOVA with *safe value* as a within-subjects factor, *species* as a between-subjects factor, and *preference score* as a covariate to account for any individual variation in relative food preferences revealed a main effect of safe value [ $F_{2,116} = 6.11, p < 0.005, \eta^2 = 0.095$ ], with a significant linear contrast [ $F_{1,58} = 9.45, p < 0.005, \eta^2 = 0.14$ ]: individuals were more likely to choose the safe alternative as its value increased. There was also a significant effect of species [ $F_{2,58} = 12.50, p < 0.001, \eta^2 = 0.30$ ]: pair-wise comparisons indicated that bonobos were less likely to choose the risky option than both humans and chimpanzees, who did not differ [ $p < 0.001$  for significant cases]. There was no significant effect of the food preference score, and no significant interactions. The results from the GLMM trial-by-trial analyses also revealed that chimpanzees and humans were more likely to choose the risky option than bonobos (see ESM for details and full parameters from the best-fit model). In particular, the inclusion of species as a predictor significantly increased model fit [LRT:  $\chi^2 = 19.66, df = 2, p < 0.001$ ].

As with the main analyses of currency condition, we also checked whether average risk payoffs could account for these results. However, the percentage of trials where subjects received the good payoff from the risky option did not differ across species [ANOVA with *species* as a between-subjects factor:  $F_{2,59} = 0.62, p = 0.54, n.s.$ ], indicating that differences in reward histories cannot account for their different preferences.

### 2.3. Discussion

Overall, these results indicate that humans treat decisions about abstract rewards differently from decisions about concrete rewards. In particular, humans were relatively more risk-prone for food and prizes compared to money. These results suggest that it is not the case that food or biologically relevant rewards have a 'special' status in decision making—rather, it seems that money is treated as distinct from other more concrete rewards, regardless of whether they are consumable. In



**Fig. 2.** Risk preferences for food in humans, chimpanzees, and bonobos (Study 1). Humans and apes made choices between risky option that provided a desirable or undesirable food type with equal likelihood, and a safe option that always provided an intermediately-preferred type of food. Overall choices for the risky option for each species, broken down by the value of the safe alternative (one, three, or six pieces of the intermediately-preferred food type). Error bars indicate SE.

addition, our results show that people exhibit a more risk-seeking pattern of choices for food rewards, closely resembling the responses chimpanzees and dissimilar from bonobos tested in a highly similar setup. Thus, although bonobos exhibited relative risk-aversion like many other taxa, humans seem to share more risk-prone preferences with chimpanzees when making decisions about food in the matched situation.

However, there are some important caveats for these results. Equating value across reward types was difficult, and there were some minor procedural differences across conditions. For example, participants evaluated their preferences for the set of options in the food and prize conditions, but did not in the money condition. Moreover, it is unclear why people responded differently to risky choices in the money condition. One possibility is that mere exposure to money influenced people's choices, as even subtle priming about money can shift people's goals across a variety of behavioral contexts (Caruso et al., 2013; Vohs et al., 2006). Alternatively, people may have responded to the characteristics of money compared to other rewards, as money can be flexibly used to acquire other rewards. That is, the value of money does not depend on its intrinsic characteristics, but rather on how it can be exchanged for other items. In Study 2 we therefore address whether this feature of money impacts how people make decisions.

### 3. Study 2: The psychological impact of money

We compared participant's preferences in two conditions where they played the same basic risk task for money. In the *keep condition* participants were told in advance that they could keep the money, whereas in the *trade condition* subjects were told that they would trade in the money for prizes after the task. Thus, individuals had the same exposure to money when making decisions – and all task parameters were equated – but participants had different expectations whether the money could be flexibly exchanged.

#### 3.1. Methods

##### 3.1.1. Subjects

We tested a new sample of 50 participants from the same population (28 females and 22 males; age range: 18–34 years; mean age = 22.3 years), who were assigned to either the *trade* or the *keep* condition.

##### 3.1.2. Procedure

We used the same general procedure as Study 1. Participants first rated the five prizes, and then completed the behavioral task accumulating monetary rewards. The risky option provided one dollar or one penny with equal probability, and the safe option always provided 50 cents (two quarters). We used the prizes from Study 1 (as the prizes had more equivalent value to the money amounts). The participants in the *trade condition* were informed that they would exchange their money for prizes after the task: each dollar would be exchanged for their highest-preferred item, each penny for their lowest-preferred, and the 50 cents for their intermediately-preferred item. In contrast, participants in the *keep condition* were informed of the 'exchange rate,' but told that they could keep as much money as they wished. Thus, the only difference in procedure was participants' expectations of whether the money was a flexible store of value, or was constrained such that they only could use it to acquire the prize items. An additional five participants were excluded due to experimenter error in reading instructions or assigning the correct prizes based on rankings.

#### 3.2. Results

Participants chose the risky option on  $50.7 \pm 6.1\%$  of trials in the *keep condition* [ $t_{24} = 0.11, p = 0.91, n.s.$ ], but in  $70.0 \pm 5.0\%$  of trials in the *trade condition*, above chance [ $t_{24} = 4.04, p < 0.001, d = 0.81$ ].

We then conducted an ANOVA with *condition* (keep or trade) as a between subjects factor, accounting for any potential variation in prize preferences by including each individual's *prize preference score* as a covariate (this score was calculated in the same way as the food preference score described in Study 1, as all participants here rated the prizes in the same fashion). This analysis revealed an effect of condition [ $F_{1,47} = 5.92, p < 0.05, \eta^2 = 0.11$ ]: individuals choose the risky option more when they knew they would trade the money for prizes (see Fig. 3a). There was no effect of prize preference score on risky preferences. The results from the GLMM also indicate that participants were more risk-seeking in the trade condition (see ESM for details and full parameters from the best-fit model). In particular, the inclusion of condition (keep or trade) as a predictor significantly increased model fit [LRT:  $\chi^2 = 5.80, df = 1, p < 0.05$ ].

As in the previous study, we also confirmed that subjects rated their prize rewards appropriately. There was a significant effect of outcome category on ratings [good prize:  $4.8 \pm 0.1$ ; safe prize:  $3.3 \pm 0.2$ ; bad prize:  $1.9 \pm 0.2$ ;  $F_{2,96} = 126.17, p < 0.001, \eta^2 = 0.72$ ] and pair-wise comparisons indicated that all categories differed [ $p < 0.001$  for all cases]. There was no difference in ratings across conditions [ $F_{1,48} = 0.01, p = 0.91, n.s.$ ], indicating that participants both conditions exhibited similar relative preferences for the prizes. In addition, participants received the good outcome at chance levels [keep condition:  $52.0 \pm 4.1\%$ ,  $p = 0.69, n.s.$ ; trade condition:  $51.9 \pm 3.5\%$ ,  $p = 0.63, n.s.$ ], with no difference in the average reward outcomes across conditions [five individuals never chose the risky option and could not be included;  $t_{43} = -0.97, p = 0.34, n.s., d = 0.29$ ]. Thus, these alternatives cannot account for difference between conditions.

### 3.3. Discussion

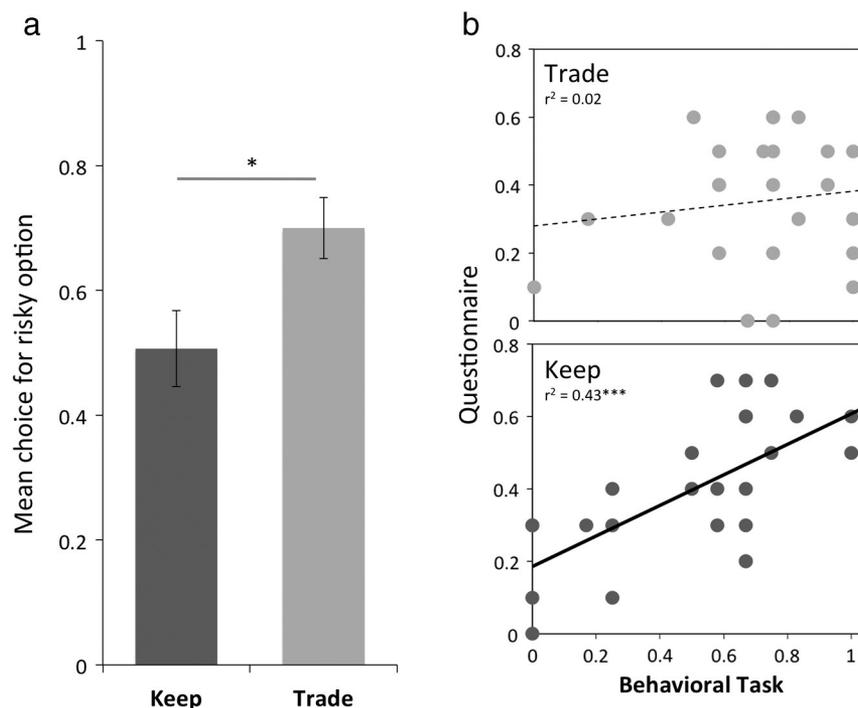
These results indicate that mere exposure to money was not sufficient to make people more risk-averse, as participants played for money in both conditions. Rather, participants' expectations about what they could do with the money influenced their patterns of choice: people were sensitive to whether they could freely exchange the money

after the task. Importantly, this study could exactly equate the procedure for participants, as all participants ranked the prizes in the same fashion and played for money in the actual task. Nonetheless, their expectations about whether they could keep the money influenced their preferences. The current results therefore show that mere exposure to money is not sufficient to shift preferences. However, it is important to note that money can both be exchanged for other rewards and be saved and accumulated into larger amounts—both are intrinsically intertwined aspects of how money is typically used. While we cannot distinguish the relative importance of these factors for the current results, disentangling these features is an important consideration for future research.

### 4. Questionnaire results

All 125 participants completed a hypothetical questionnaire following the behavioral task, involving 10 choices between a high-variance (risky) option and a lower-variance (safe) option that differed in expected value. Participants choose the risky option on  $39.5 \pm 1.6\%$  of questions, with no differences across the five conditions [ $F_{4,120} = 0.47, p = 0.76, n.s.$ ]. Individuals choose the risky option less often than would be expected from risk-neutrality (see ESM), showing that our population exhibited typical risk-averse preferences in this questionnaire (Holt & Laury, 2002).

Our main question was how questionnaire responses related to task performance. In fact, this relationship depended on reward type. In Study 2, participants' in the *keep condition* who were more risk-prone in the behavioral task were also more risk-prone in the questionnaire [ $r_p = 0.65, p < 0.001$ ]. However, there was no relationship between task and questionnaire responses in the *trade condition* [ $r_p = 0.14, p = 0.51, n.s.$ ; see Fig. 3b]. Notably, these conditions were identical except for individuals' expectations about whether they could keep the money. Similarly, in Study 1 questionnaire responses and task performance were unrelated in the *food condition* [ $r_p = -0.04, p = 0.85, n.s.$ ] and the *prize condition* [ $r_p = -0.04, p = 0.86, n.s.$ ], but were positively correlated in the *money condition* [ $r_p = 0.54, p = 0.005$ ].



**Fig. 3.** Human risk preferences for money (Study 2). Humans made risky choices for money they knew they could keep, or money they knew they had to trade for prizes. (a) Risk preferences across conditions in the behavioral task. (b) Relationship between preferences in the behavioral task and a hypothetical questionnaire involving risky decisions about small amounts of money. Larger values indicate greater preferences for risk in both the task and questionnaire. Error bars indicate SE, \*  $p < 0.05$ , \*\*\*  $p < 0.001$ .

Thus, the hypothetical questionnaire results correspond to real-life experiential decisions about risk when people made choices about money that they could keep. However, questionnaire responses and task choices were unrelated when participants made decisions about other currencies—or even money that knew they would later trade for prizes. This provides further support for the hypothesis that people treat decisions about money as distinct from those about concrete rewards (or money with atypical properties).

## 5. General discussion

Our findings support three main conclusions. First, Study 1 indicates that human decision-making under risk is sensitive to reward currency: choices for money are treated differently from choices about concrete rewards such as food or prizes. Second, the results from Study 2 suggest that money has a special status because it is a store of value that can be flexibly converted into other types of rewards. Finally, the comparison of human and ape risk preferences for food in Study 1 suggests that humans and chimpanzees are relatively more risk-prone than bonobos. In an experience-based task in which individuals ate food rewards on a trial-by-trial basis, humans exhibited more risk-seeking choices much like chimpanzees on a matched task. This indicates that bonobos have the more derived pattern of decision-making under risk, suggesting that chimpanzees may be a better model for the last common ancestor with regards to this particular cognitive trait.

While other studies have found that people will exhibit different patterns of decision-making for money compared to food, previous results are consistent with the possibility that people treat biological rewards as a distinct currency. However, our comparison indicates that it is in fact *money* that is treated differently from other concrete rewards, regardless of whether those rewards are actually consumable, primary reinforcers. One possibility is that these effects stem from variation in how humans value these different rewards: money may generally be more valuable than food to most humans. This finding in and of itself is important, as many comparative studies of human versus nonhuman decision-making utilize money and food rewards that might vary widely in value. However, we did attempt to mitigate this possibility by using very small amounts of money for comparison with the food rewards. Furthermore, most magnitude effects in human decision-making studies use very large values (Green et al., 1997; Holt & Laury, 2002, 2005; Kirby & Maraković, 1996). Studies of animal decision-making involving smaller variation in reward value have not found such consistent effects (Green et al., 2004; Stevens et al., 2005), and some evidence suggests that decision-makers may even be more risk-prone for higher-value rewards (Ludvig et al., 2014), an effect working against this explanation.

Another possibility is that abstract marks of value like money – including even the small amounts of money as used in the current studies – are treated differently from other rewards even when values are relatively well-matched. For example, the real-life value of our prize rewards was economically matched to the range of monetary values we used, and yet we found differences in how people responded to money versus prizes in both studies. Money may therefore have a special status in human decision-making specifically because it is an exchangeable store of value. Exposure to monetary rewards was not sufficient to induce more risk-averse choices, as people treated money more like concrete rewards when its use in acquiring other rewards was constrained. The results from the hypothetical questionnaire further support the distinction between decisions about money and decisions about other rewards. While responses in the questionnaire were predictive of choices in the behavioral task when people played for money they could keep after the fact, questionnaire responses were unrelated to task performance when individuals made decisions for food, prizes, or even money whose use had been constrained. Overall, these results suggest that humans use different psychological processes when

making decisions about abstract markers of value, like money, compared to decisions that involve concrete payoffs like food or prizes.

In Study 1, we also found that human patterns of risky decision-making for food were more similar to chimpanzees than bonobos. While it is obviously difficult to exactly match the procedure given to humans and nonhumans, we tested both humans and apes on an iterated decision-making task where they consumed real rewards on a trial-by-trial basis, and took several steps to best equate the situations and ensure that humans were actually motivated to consume the food. Our result has important implications for comparative studies of decision-making, highlighting that such comparisons may sometimes require studying human choices in foraging contexts more like those used with animals. Indeed, a comparison of human decisions about money with nonhuman decisions about food using the current task would erroneously suggest that humans more resemble bonobos than chimpanzees in their risk preferences.

Why might humans exhibit relatively risk seeking preference for food rewards? We have argued that different patterns of risk preferences in apes may be related to differences in their wild feeding ecology. While payoff contingencies, task design, and contextual factors can all clearly influence animal choices (Hayden & Platt, 2009; Heilbrunner & Hayden, 2013; Proctor et al., 2014), chimpanzees appear relatively more risk-seeking than bonobos across a variety of paradigms (Haun et al., 2011; Heilbrunner et al., 2008; Rosati & Hare, 2012, 2013). Evolutionarily, chimpanzees may be more willing to accept risk in their foraging payoffs compared to bonobos because they feed on more spatially-dispersed and therefore uncertain food resources, deal with greater seasonal variability, and engage in more risk-prone hunting than bonobos (Hare, Wobber, & Wrangam, 2012; Kano, 1992; Wrangham & Peterson, 1996). That is, ape psychology may be shaped by species-typical environments. Notably, human hunter-gatherer groups also engage in risk-prone hunting (involving economic variation in payoffs, as opposed to risk of physical injury), and humans exhibit the largest day range of any ape species (Marlowe, 2005). Indeed, some theories suggest that the human ecological niche is inherently risky in the sense of presenting the possibility of little or no food on a given day, as humans feed on relatively high-quality, difficult to access foods; food-sharing may represent a strategy for mitigating this risk (Kaplan, Schiniter, Smith, & Wilson, 2012; Kaplan et al., 2000). One possibility is therefore that human risk preferences for food are shaped by ecological variables much like other apes. An important caveat, however, concerns the generality of our results across human populations (Henrich, Heine, & Norenzayan, 2010). While there have been some cross-cultural comparisons of human decision-making preferences (Henrich & McElreath, 2002; Salali & Migliano, 2015; Weber & Hsee, 1998), to our knowledge there have been no previous comparisons involving experiential tasks with food rewards, which would be critical to assess the representativeness of the current findings.

Finally, these findings shed light on the evolutionary history of money. Although money is a ubiquitous facet of modern human life, surprisingly little is known about the psychological processes that people use when thinking about money (Vohs, Mead, & Goode, 2008). Importantly, humans are the only species to have invented and regularly use abstract markers of value. Although other species can learn to flexibly trade tokens in experiments (Addessi, Crescimbeni, & Visalberghi, 2007; Brosnan & de Waal, 2005), there are important differences in how animals represent tokens compared to humans (see Santos & Rosati, 2015 for a review). For example, there is not strong evidence that primates treat tokens as a store of value (but see Sousa & Matsuzawa, 2001). Primate token use is also highly dependent on the presence of human experimenters, and there is little evidence that primates trade tokens with conspecifics (Brosnan & Beran, 2009; Pelé, Dufour, Thierry, & Call, 2009). Moreover, while money can dramatically shift human behavior in a variety of contexts, abstract markers of reward have a more mixed effect on nonhumans. While primates are more successful at inhibiting a pre-potent motor response when faced

with symbolic rewards (Shifferman, 2009), the impact on other cognitive processes is unclear. For example, chimpanzees show similar patterns of temporal self-control for both food rewards and tokens (Evans, Beran, Paglieri, & Addessi, 2012).

Why do humans seem to have specialized psychological skills for thinking about money? In the current studies, expectations about whether money could be used as a tool for acquiring other rewards influenced how people made decisions. This suggests that a crucial distinction between money and other resources is its ability to stimulate flexible exchanges. Direct exchanges are seen in many other species, but such behaviors – such as swapping food or trading grooming for social support – require that both parties' desires to coincide in some fashion, either simultaneously (in a direct exchange of items) or over a longer period (in the case of reciprocal exchanges of different resources). Money, in contrast, provides a common metric that can account for all types of resources, such that different individuals' needs can be decoupled when they engage in a transaction (Davies, 2002). Indeed, theoretical models suggest that market-pricing is a distinct form of human social interaction, with monetary exchange as a prototypical example of such relationships (Fiske, 1992). Thus, while economic behaviors have evolutionary roots in other species, humans likely also have derived psychological skills for dealing with the abstract rewards that are uniquely utilized by our species.

### Supplementary Materials

Supplementary methods, analyses, and data to this article can be found online at <http://dx.doi.org/10.1016/j.evolhumbehav.2015.10.003>.

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