To bet or not to bet? Decision-making under risk in non-human primates

M. Pelé · M. H. Broihanne · B. Thierry · J. Call · V. Dufour

Abstract Animals deal with predictable and unpredictable events on a daily basis. Yet our knowledge of the cognitive processes involved in decisions remains limited. We tested capuchins, macaques and orang-utans in a food-gambling task to investigate whether or not individuals estimate the chances of different outcomes. Results highlighted that gambling decisions were negatively induced by the probability of losing and the frequency of previous losses, and positively induced by the probability of gaining. Actual decisions were consistent with first order stochastic dominance. The study of second order stochastic dominance revealed that macaques were risk-prone whereas capuchins and orang-utans were risk-adverse. We detected responses comparable to the hot-hand effect, a bias found in humans. Capuchins and orang-utans exhibited probability distortion and loss aversion, which were not systematically found in macaques. Given the heterogeneity among individuals, we implemented mixture

M. Pelé · B. Thierry · V. Dufour
Centre National de la Recherche Scientifique, Département Ecologie, Physiologie et Ethologie, Strasbourg, France

M. Pelé · B. Thierry · V. Dufour (✉)
Institut Pluridisciplinaire Hubert Curien, Université de Strasbourg, Strasbourg, France
e-mail: valerie.dufour@iphc.cnrs.fr

M. H. Broihanne
Laboratoire de Recherche en Gestion et Économie, EM Strasbourg Business School, Université de Strasbourg, Strasbourg, France

J. Call
Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

models and showed that attitudes towards risk and probabilities play complementary and different roles in the three species.

"*A person who has not made peace with his losses is likely to accept gambles that would be unacceptable to him otherwise.*" Kahneman and Tversky (1979)

People are regularly confronted with problems, choices, and alternatives that compel them to take decisions. There are different degrees of certainty about the consequences of decisions. The conditions in which individuals make these decisions could be split into three types: (1) *certainty*, where each action is known to lead invariably to a specific result, (2) *risk*, where each action leads to one of several possible outcomes, each of which has a known probability, or (3) *uncertainty*, where actions may lead to several outcomes, the probabilities of which are unknown (Luce and Raiffa 1957).

Human decision-making has been the subject of extensive research in economics, psychology and sociology. A main conclusion is that decision-making is not solely based on well-deliberated calculations (Tversky and Kahneman 1974, 1981; Kahneman and Tversky 1979). In risky or uncertain conditions, decisions often also rely on intuitions or on a hunch that seems correct but neglects normative rules, despite mature and sufficient cognitive power. Several reasoning biases limiting the optimality of choices have been identified—for example the hot hand effect (Tversky and Kahneman 1971), the gambler's fallacy (Croson and Sundali 2005), and the house money effect (Thaler and Johnson 1990).

Like humans, animals have to deal with risk and uncertainty when taking decisions. Traveling towards distant resources, for instance, is potentially associated with predation or depletion. The estimation of the odds for risky or uncertain outcomes is also a prominent feature of social life in non-human primates; monkeys and great apes can cooperate and make alliances to obtain a better position in the social hierarchy. Before challenging higher-ranking conspecifics, individuals need to assess whether their allies are liable to support their action without defection or risk of retaliation. Supporting allies is thought to be a "commodity" service that is potentially tradable for other goods or services in primate societies. Hence, it is in the interest of individuals to consider the possible advantages and drawbacks of their behaviors, and their risk sensitivity may therefore strongly affect decision-making.

The response of animals when facing a choice between predictable and unpredictable outcomes has mostly been investigated in the foraging context (Kacelnik and Bateson 1996). Two main variables are thought to affect decisions in animals: the quantity of food to be obtained and the time needed to acquire it. Subjects are typically

offered a choice between two options, one where food quantity or delay is held constant from one trial to another, and another where the same variable is manipulated to induce some variance from one trial to the next. For both variable and constant options, the overall amount of food or delay is equivalent. Although the potential reward is not predictable in any given variable trial, subjects can learn that consistently choosing one option over another leads to obtaining an equivalent amount of food (or waiting an equivalent duration); both options then become equally certain from the subject's perspective. Such tactics were found in starlings (*Sturnus vulgaris*: Bateson and Kacelnik 1997) and non-human primates (*Macaca mulatta*: Hayden and Platt 2007; *Pan troglodytes*, *P. paniscus*: Heilbronner et al. 2008). Non-human primates learned to anticipate the general pattern of reward delivery instead of choosing on a trial-by-trial basis. Thus, introducing variability is not always enough to experimentally assess risk-sensitivity in animals. More recently, Haun et al. (2011) tested four great apes species in a task where subjects could choose between a safe option (a large or small piece of banana) and a risky option. The authors found that the four species were more likely to choose the risky option when the size of the safe option decreased, and all four species were globally risk-prone, especially chimpanzees and orang-utans. As stated by Cartar and Smallwood (1996), animals may respond to risk differently according to their evaluation of the probabilistic consequences of their decision. In a study where rhesus macaques (*M. mulatta*) played against a computer in a simplified version of the "rock-paper-scissors" game, subjects mainly behaved according to the outcomes of their previous choices (Lee et al. 2005). When the computer response fitted the choices made by subjects, however, subjects took into account the choices operated by the computer in addition to their own (Lee et al. 2005). Their choices were not simply guided by a reinforcement learning model (the value of each choice is updated according to its outcome) but also by a belief learning model (a player's choice is based on his/her belief of how the other will play). Therefore, although the decision was based on previous outcomes, subjects could also take into account hypothetical outcomes. These studies therefore suggest that non-human primates are good models for the investigation of attitudes towards risk and decision-making determinants. To assess the propensity of non-humans to engage in risky situations and the cognitive processes underlying their decisions, it is necessary to study their behavior towards probabilistic payoffs with no absolute certainty about the outcome. This can allow us to determine how far individuals anticipate and calculate the outcomes of their choices.

In this study we hypothesized that the possibility of losing would affect primate subjects in an economic context such as the exchange of goods with a human partner. The intentional transfer of food is not frequent among adults in non-human primates (de Waal 1997; Dufour et al. 2009; Pelé et al. 2009, 2010a). However, they possess some of the cognitive pre-requisites necessary for the calculated transfer of goods. They remember past social interactions (Menzel 1991). They can also delay gratification (Amici et al. 2008; Dufour et al. 2007; Heilbronner et al. 2008), and in food exchange tasks, brown capuchin monkeys (*Cebus apella*) and long-tailed macaques (*Macaca fascicularis*) can wait 20–40 sec and 2–5 min respectively for a reward equivalent to 40 times the initial one (Pelé et al. 2010b, 2011). Non-human primates accurately estimate quality and quantity (Drapier et al. 2005; Ramseyer et al. 2006; Hanus and Call 2007). However, we know little about their sensitivity to risk and their skills in probabilistic evaluation.

We therefore tested two monkey species, brown capuchin monkeys and long-tailed macaques, and one ape species, orang-utans (*Pongo pygmaeus*), in an exchange task where each decision to trade was a gamble. We gave the individuals an opportunity to gamble a piece of cookie with a human experimenter for pieces of larger, equal or smaller sizes. Subjects could predict the odds of gaining by seeing the content of several cups, but they did not know with certainty which cup they would receive, and thus they could lose by obtaining less than the item they bet. Apes generally perform better than monkeys in cognitive tasks bearing on imitation, inference, mirror self-recognition and other-regarding abilities (Tomasello and Call 1997). This study of different species of primates aims to single out the factors affecting their decisions under risk, and identify any differences or common denominators in the risk sensitivity of human and non-human primates. To achieve this, we first analyze the determinants of primate decision-making within the theoretical context of decision-making in humans. We then compare the data observed in our primate subjects to the choices predicted by Expected Utility Theory (von Neumann and Morgenstern 1944), Cumulative Prospect Theory (Kahneman and Tversky 1979; Tversky and Kahneman 1992) and Rank Dependent Expected Utility Theory (Quiggin 1982, 1993). This paper also highlights the usefulness of these decision-making theories for understanding how non-human primates make their choices when faced with risk. Moreover, we identify specific behavioral traits (risk aversion, probability distortion) in non-human primates which give interesting results when compared with the traits usually found by researchers in humans. Finally, our paper is the first attempt to implement and test mixture models of theories of decision under risk for non-human subjects. The paper is presented as follows: Section 1 describes the subjects and methods, and Section 2 presents theories of decision-making and estimation methods. Sections 3 and 4 describe our results. Section 5 discusses our conclusions.

1 Methods

1.1 Subjects

We tested eight brown capuchin monkeys and five long-tailed macaques maintained at the Primatology Center of the University of Strasbourg, France, and four orang-utans kept at the Wolfgang Köhler Research Primate Centre, Leipzig Zoo, Germany (age, sex and rearing conditions of subjects are presented in Online Resource 1, Table S1). Prior to the study, all individuals had taken part in exchange tasks involving food items for monkeys (Drapier et al. 2005; Ramseyer et al. 2006; Pelé et al. 2010b, 2011) and tokens for apes (Pelé et al. 2009; Dufour et al. 2009).

1.2 Experimental procedure

During a trial the experimenter typically stood in front of the subject's compartment holding an initial piece of cookie measuring $2 \times 2 \times 0.5$ cm in one hand, and a tray of six aligned plastic cups in the other hand. Each cup contained a different sized piece of cookie: $1 \times 1 \times 0.5$, $2 \times 2 \times 0.5$, and $4 \times 4 \times 0.5$ cm (Online Resource 1, Figure S1).

Table 1 Number (#) and content of cups for each combination of rewards

Combinations of rewards			
#	Content of cups	#	Content of cups
1		10	
2		11	
3		12	
4		13	
5		14	
6		15	
7		16	
8		17	
9		18	

Small black squares represent pieces of cookie 1 x 1 x 0.5 cm in size, *medium black squares* represent pieces of cookie 2 x 2 x 0.5 cm, *large black squares* represent pieces of cookie 4 x 4 x 0.5 cm.

The experimenter made sure that the subject saw the contents of each cup and gave the initial piece of cookie to the subject while still presenting the tray. The experimenter then held out her empty hand, offering the subject the chance to give the initial item back. If the subject returned it, s/he received the contents of a randomly chosen cup. If the subject chose to keep the initial item, the experimenter ended the trial, leaving the subject to consume the initial item. The experimenter then waited 30 s after the end of food consumption before starting another trial. The chances of losing or gaining were manipulated via different combinations of rewards in the cups, giving the subjects a means to assess the chances of losing or gaining compared to the initial item already in hand. To ensure that individuals would understand the experimental set up (i.e. only one of the six cups is received in exchange), the study was conducted by offering a step-by-step decrease in the chances of winning from one combination to another. At the end of the study, subjects were tested with two additional combinations (# 17 and # 18) in which the chances of winning increased again; these combinations allowed us to check that subjects had understood the potential rewards. The 18 combinations tested for each species are shown in Table 1.

For each combination, four series of 12 trials each were administered to capuchins and macaques. The testing period for monkeys was spread over 2 years from July 2006 to March 2008. Due to experimental availability, only two series of 12 trials per combination were administered to orang-utans from June to July 2008. Individuals were tested at the maximal rate of two series per day, with a minimum of 2 h between series. This procedure allowed us to be certain that subjects consumed items with pleasure as they had not attained their satiation level.[1]

2 Theories of decision-making in humans

In this section, we present the general theories of decision-making under risk (Expected Utility Theory, Cumulative Prospect Theory and Rank Dependent Expected Utility Theory) that are commonly used to analyze human choices. We also show how decisions made by our subjects could be modeled under each theory, and how conditional log-likelihoods can be computed. In the results section, the maximization of these conditional log-likelihoods (see Harrison and Rutström 2009) is used to estimate parameters that best fit the actual choices made by our subjects.

2.1 Expected utility theory

Expected Utility Theory (hereafter referred to as EUT) states that the decision-maker chooses between risky prospects by comparing their expected utility values, i.e. the weighted sums obtained by adding together the utility values of outcomes multiplied by their respective probabilities (von Neumann and Morgenstern 1944). Let $x=((x_i,p_i), i=1,\ldots,n)$ denote a lottery where x_i is the ith outcome and p_i is the corresponding probability. Any subject who is offered a choice between the lottery x and a certain amount W should choose to keep the certain amount if:

$$u(W) > E[u(x)] \Leftrightarrow u(W) > \sum_{i=1}^{n} p_i u(x_i) \qquad (1)$$

We suppose that subjects evaluate outcomes in terms of quantities because they are consumption amounts. The utility function may take different mathematical forms and, as a first example, we choose $u(y)=y^{\delta}$, $\forall$ y, where y is the quantity of item and δ is the risk aversion parameter. This power function allows us to identify attitudes towards risk and to discriminate between risk averters ($\delta<1$), risk seekers ($\delta>1$) and risk neutral subjects ($\delta=1$).

A simple way to compute each item value y is to measure the item volume. Thereby, small pieces of cookie measuring $1\times1\times0.5$ cm take an item value equal to 0.5, pieces of cookies measuring $2\times2\times0.5$ cm are valued 2 and large pieces of cookie measuring $4\times4\times0.5$ cm are valued 8. For example, combination # 4 (containing two small, one medium and three large rewards) is evaluated $E[u(\#4)] = \left(\frac{2}{6} \times (0.5)^{\delta}\right) + \left(\frac{1}{6} \times (2)^{\delta}\right) + \left(\frac{3}{6} \times (8)^{\delta}\right)$ in EUT. Therefore, according to EUT, subjects should prefer the gamble

---

[1] The first combinations, i.e. those involving a high probability of getting a large cookie, were tested at the rate of one series of 12 trials per day.

to the neutral item if the expected utility of the gamble exceeds the utility of the certain outcome. For example, in # 4 the gamble is preferred if $E[u(\#4)]>(2)^\delta$.

In order to run our estimation procedure, we have to specify the likelihood of this model. The following steps of the maximization procedure are based on Harrison and Rutström's method (2009). We compute the expected utility for each individual choice for a candidate estimate of δ and the difference ΔEUT between this expected utility and the utility of the certain outcome, 2^δ. This difference is then used to define the cumulative probability of the observed choice using a standard cumulative normal distribution function $\Phi(\Delta EUT)$.

The conditional log-likelihood of the Expected Utility Theory (power utility function) is therefore:

$$\ln L^{EUT}(\delta; y) = \sum_i \ln l_i^{EUT} = \sum_i [y_i \ln \phi(\Delta EUT) + (1-y_i)\ln(1-\phi(\Delta EUT))] \quad (2)$$

Where $y_i=1$ denotes the choice of the exchange in task i ($y_i=0$ is for the choice of the certain outcome).

2.2 Cumulative prospect theory

Cumulative Prospect Theory (CPT in the following) differs from EUT in two ways. First, utility is derived from changes in wealth, and is relative to a reference point with respect to which gains and losses are defined. Losses are weighted more heavily than gains, and this feature is referred to as loss aversion. Second, individuals use decision weights instead of probabilities and overweight probabilities of extreme events. This feature captures the empirical evidence in humans, where many economic agents simultaneously demand lottery tickets and insurance contracts.

Under CPT, subjects evaluate the opportunity to play the lottery by computing a valuation function $V(x)$ defined as follows:

$$V(x) = V(x^+) + V(x^-) = \sum_{i=m+1}^{n} \pi_i^+ v(x_i) + \sum_{i=1}^{m} \pi_i^- v(x_i) \quad (3)$$

where $x^+=\max(0,x)$; $x^-=-\max(0,-x)$.

The first element of CPT is to define x in terms of net gains and losses, and to rank the outcomes of the lottery in increasing order. These are divided into two categories: the m first outcomes are negative (losses) and the n-m following outcomes are positive (gains). The evaluation function is defined over these two domains with different decision weights π_i and a specific value function $v(.)$.

The value function is analogous to the utility function of EUT but is defined differently over gains and losses.

$$v(x) = \begin{Bmatrix} x^\alpha \\ -\lambda x^\beta \end{Bmatrix} if \begin{smallmatrix} x \geq 0 \\ x < 0 \end{smallmatrix} \quad (4)$$

with $\lambda>1$ (loss aversion) and $0<\alpha,\beta\leq1$ (diminishing sensitivity) and where x is a gain or a loss relative to a reference point. The value function is generally concave on gains, convex on losses, and kinked at 0. The loss aversion parameter λ indicates that subjects are loss averse if $\lambda>1$, which means that in any choice where a loss of k is at stake, subjects accept the bet if the net potential gain is higher than λ times k. Tversky and Kahneman (1992) experimentally identified a median value of $\lambda=2.25$, indicating pronounced loss aversion.

In our experiment this value means that a subject accepts losing a medium size cookie if s/he can gain a cookie 2.25 times bigger than the medium cookie.

In our study, gains and losses are volumes of cookies that are higher or lower than the reference consumption amount two ($x=y-2$). For example, for subjects using CPT, combination # 4 is an opportunity to obtain three gains each evaluated 8–2=6, to incur two losses each evaluated 0.5–2=−1.5 and to have one null outcome (one medium size cookie).

The second ingredient of CPT is to associate weights to the gamble's outcomes instead of probabilities. This is achieved with a non-linear function $w(.)$ defined separately on the cumulative probability distribution of gains (+) and losses (−):

$$\pi_1^- = w^-(p_1) \tag{5}$$

$$\pi_i^- = w^-(F_x(x_i)) - w^-(F_x(x_{i-1})) = w^-\left(\sum_{j=1}^{i} p_j\right) - w^-\left(\sum_{j=1}^{i-1} p_j\right) for\ 2 \leq i \leq m \tag{6}$$

$$\pi_n^+ = w^+(p_n) \tag{7}$$

$$\pi_i^+ = w^+(1 - F_x(x_{i-1})) - w^+(1 - F_x(x_i))$$
$$= w^+\left(\sum_{j=1}^{n} p_j\right) - w^+\left(\sum_{j=i+1}^{n} p_j\right) for\ m \leq i < n \tag{8}$$

Where F_x is the cumulative distribution function of lottery x.

The probability weighting function put forward in the literature is generally inverse S-shaped which overweights low probabilities and underweights high ones.

For sake of simplicity we used $w^+(.)=w^-(.)=w(.)$ and made our computations with the Tversky and Kahneman (1992) probability weighting function:

$$w(p) = \frac{p^\gamma}{(p^\gamma + (1-p)^\gamma)^{1/\gamma}} \tag{9}$$

where γ is the probability distortion parameter, w (0)=0 and w (1)=1.

This specific probability weighting function takes the shape of an inverse S if $0 < \gamma < 1$, which is a very common characteristic of all weighting functions (Gonzalez and Wu 1999). In this function, γ controls both the level of the inflexion point and the curvature[2] (Figure S2, Online Resource 1). As an example (KT Computation example, Online Resource 1), under CPT with a power utility function, combination # 4 is evaluated $V(\#4)=1.3683$. As this value is positive, subjects following CPT with parameters $\gamma=0.6$ and $\lambda=2.25$ should accept exchanging the initial item against combination # 4.

Our estimation procedure with CPT uses the same steps as the EUT procedure, but uses the value function instead of the utility function, and a weighting function is defined over the cumulative probability distributions rather than the probabilities. The prospective utility of each individual choice (ΔCPT) is used

---

[2] There are also two-parameter weighting functions (see for example, Lattimore et al. 1992, and Prelec 1998) that separately control the inflexion point and curvature. Gonzalez and Wu (1999) suggest that one-parameter weighting functions and one-parameter value functions provide an excellent and parsimonious fit of data at an aggregate level.

to define [3] the cumulative probability of the observed choice using a probit function as previously described. The conditional log-likelihood of the Cumulative Prospect Theory is therefore:

$$\ln L^{PT}(\alpha, \beta, \lambda, \gamma; y) = \sum_i \ln l_i^{PT} = \sum_i [y_i \ln \Phi(\Delta CPT) + (1-y_i) ln(1-\Phi(\Delta CPT))] \quad (10)$$

Where $y_i=1$ (0) denotes the choice of the exchange in task i.

2.3 Rank dependent expected utility theory

Rank Dependent Expected Utility Theory (RDEUT in the following) is a model that incorporates probability distortion. More precisely, subjects are considered to use utility functions to evaluate outcomes but their perception of probability is not correct so they use weighting functions instead of probabilities. Although this feature is similar to CPT, decision weights under RDEUT are identically defined over gains and losses.

Under RDEUT, subjects evaluate the opportunity to play the lottery $x=((x_i,p_i),i=1,\dots,n)$ by computing a valuation function $V(x)$ defined as follows:

$$V(x) = \sum_{i=1}^n \pi(p_i).u(x_i) \quad (11)$$

The most parsimonious weighting functions in RDEUT are the power weighting function, and Tversky and Kahneman's (1992) weighting function. The latter has already been presented in 2.2, and the power weighting function $w(p_i)=p_i^\gamma$ is always convex for $\gamma>1$, is linear for $\gamma=1$ and is always concave for $\gamma<1$. Therefore, whatever the weighting function $w(p_i)$, RDEUT becomes equivalent to EUT when $w(p_i)=p_i$, that is when $\gamma=1$. As an example (RDEUT Computation example, Online Resource 1), under RDEUT, we obtain $V(\#4)=3.4194$. The gamble should be accepted in RDEUT if its evaluation under RDEUT exceeds the rank dependent evaluation of the certain outcome; $3.4194>2^\delta$ indicates that combination # 4 should be preferred to the certain outcome.

Our estimation procedure with RDEUT uses the same steps as EUT, but with a weighting function defined over the cumulative probability distributions instead of probabilities. The rank dependent expected utility of each individual choice (ΔRDEUT) is used to define the cumulative probability of the observed choice using a probit function as before. The conditional log-likelihood of the Rank Dependent Expected Utility Theory is therefore:

$$\ln L^{RDEUT}(\delta, \gamma; y) = \sum_i \ln l_i^{RDEUT} = \sum_i [y_i \ln\Phi(\Delta RDEUT) + (1-y_i)\ln(1-\Phi(\Delta RDEUT))] \quad (12)$$

Where $y_i=1$ (0) denotes the choice of the exchange in task i.

3 General results

Results were analyzed in three steps. First, we report general results relative to the exchange rate (i.e. the percentage of initial items returned) in each species according to

---

[3] Formally, we keep the notation of the difference ΔCPT between the prospective utility of each individual choice and the prospective utility of the certain outcome. This last value is 0.

the reward combinations proposed throughout the study. A second analysis is carried out for first and second order stochastic dominance of subjects' choices. Finally, we study which variables influenced decision-making in subjects. All the aforementioned analyses were conducted for 17 combinations, as the final combination was not tested in all subjects.

3.1 Exchange rate

Table 2 presents the mean exchange rate for each species according to the different combinations of rewards proposed to subjects.

There were significant differences across species in the exchange rate (Kruskal-Wallis test: $\chi^2=13.48$, df=2, $p=0.0012$). Macaques returned significantly more food than capuchins (Dunn's post-hoc, $p<0.05$) and orang-utans (Dunn's post-hoc, $p<0.05$). No significant difference was found between percentages of return of capuchins and orang-utans. Within each species, there were significant differences in the exchange rate across individuals (Kruskal-Wallis test; capuchins: $\chi^2=31.12$, df=7, $p=6e-0.5$, macaques: $\chi^2=13.38$, df=4, $p=0.0095$, orang-utans: $\chi^2=11.13$, df=3, $p=0.011$). Individual profiles are illustrated in Figure S3 (Online Resource 1).

3.2 First and second order stochastic dominance of subjects' choices

We employed the concepts of first and second order stochastic dominance in order to test whether subjects had preferences regarding the possible combinations. First order stochastic dominance (FOSD) is used to analyze choices between the certain outcome (medium piece of cookie) and the proposed gamble. In this sub-section, $F_{\#}(.)$ denotes the cumulative distribution function of combination # and $G(.)$ is the cumulative distribution function of the certain "medium piece of cookie" outcome. Figures S4 and S5 (Online Resource 1) show that, in accordance with FOSD, subjects should always exchange in combinations # 3, # 5 and # 10 and they should not exchange (and prefer the certain outcome) in # 16. FOSD does not give any decision rule for # 2, # 4, # 6 to # 9 and # 11 to # 15.

Second order stochastic dominance (SOSD) allows us to introduce a relative or comparison-based riskiness or dispersion. Formally, given two distributions $F(.)$ and $G(.)$ with the same mean (that is, with $\int xdF(x)=\int xdG(x)$) we say that $F(.)$ is riskier than $G(.)$ (or equivalently, $G(.)$ second-order stochastically dominates $F(.)$) if every risk-adverse individual prefers $G(.)$ to $F(.)$. SOSD is useful to analyze the choices made by subjects in # 14 where $F_{\#14}(.)$ and $G(.)$ have an identical mean value of two quantitative outcomes ($1/6 \times 8 + 1/6 \times 2 + 4/6 \times 0.5 = 2$). Therefore, a subject choosing the certain outcome in this particular combination is risk averter. SOSD also helps us to understand choices made by subjects in 9 and # 10 because $F_{\#9}$ and $F_{\#10}$ have an identical expected outcome of three ($2/6 \times 8 + 4/6 \times 0.5 = 1/6 \times 8 + 5/6 \times 2 = 3$); by SOSD, # 9 is riskier than # 10. Therefore, risk-adverse subjects are expected to choose the certain outcome in # 14 and to exhibit a lower propensity to gamble in # 9 than in # 10. We tested FOSD and SOSD by analyzing the average choices made by subjects in Table 3.

Table 3 presents the proportions of choices that are consistent with FOSD (Panel A) and SOSD (Panel B) predictions for the three species. Panel C tests the difference between the proportions of gamble choices in # 9 and # 10. "G" refers to the gamble

Table 2 Mean exchange rate of the initial item over 48 trials for capuchins and macaques (24 trials for orang-utans) for each combination of rewards in each species[a]

Combinations	Number of cups			Mean exchange rate across species		
#	Large	Medium	Small	Capuchins (48 trials×8 subjects)	Macaques (48 trials×5 subjects)	Orang-utans (24 trials×4 subjects)
1	4	2	0	94.01 (23.76)	100.00 (0)	90.63 (29.30)
2	4	0	2	88.28 (32.20)	100.00 (0)	94.79 (22.33)
3	3	3	0	86.20 (34.53)	99.17 (9.10)	80.21 (40.05)
4	3	1	2	96.61 (18.10)	100.00 (0)	79.17 (40.82)
5	2	4	0	92.45 (26.45)	99.17 (9.10)	72.92 (44.67)
6	2	3	1	80.73 (39.49)	100.00 (0)	89.58 (30.70)
7	2	2	2	85.68 (35.07)	98.75 (11.13)	91.67 (27.78)
8	2	1	3	82.29 (38.22)	100.00 (0)	73.96 (44.11)
9	2	0	4	77.08 (42.08)	96.67 (17.98)	54.17 (50.08)
10	1	5	0	75.70 (45.63)	95.00 (21.84)	53.13 (50.16)
11	1	4	1	53.38 (49.95)	96.67 (17.98)	60.42 (49.15)
12	1	3	2	52.60 (49.99)	82.92 (37.71)	50.0 (50.26)
13	1	2	3	39.59 (48.96)	73.34 (44.31)	52.08 (50.21)
14	1	1	4	32.29 (46.82)	74.58 (43.63)	39.58 (49.15)
15	1	0	5	22.14 (41.57)	62.50 (48.51)	12.50 (33.24)
16	0	0	6	2.34 (15.14)	16.66 (37.34)	1.04 (10.20)
17	3	1	2	34.90 (47.72)	76.67 (42.38)	51.04 (50.25)
Mean				64.18 (47.94)	86.59 (34.07)	61.58 (48.65)

[a] Standard deviations are in parentheses

choice and "CO" is the certain outcome choice. For example, FOSD success rate in # 1 consists of choosing "G". Table 3, Panel A results indicate that choices made by subjects are strongly consistent with FOSD, the lowest proportion of 79.17% being obtained by orang-utans. Note that capuchins and orang-utans exhibit higher proportions of consistent choices (97.65 and 98.95% respectively) when the FOSD choice is "CO" than when it is "G" (85.81 and 74.22% respectively), and their success rates are less dispersed (standard deviation of 15.13 and 10.15 respectively). The opposite is observed for macaques, which succeed better in FOSD gambling combinations (98.335% with std dev. of 12.8 in "G" choices and 83.33% with std dev. of 37.26 in "CO" choice). These results indicate that risk-taking behaviors differ between species. Panel B results showing SOSD consistent choices in # 14 indicate that macaques are risk-seeking (average rate of "CO" choice is 25.42%) whereas capuchins and orang-utans are risk-adverse (67.71 and 60.42% respectively). In Panel C, only capuchins exhibit significant higher gambling choices in # 9 than in # 10, which is not consistent with their risk preferences in # 14.

We analyzed behaviors at the individual level in all trials (Table S2, Online Resource 1). We found that the average behavior of almost all the subjects conforms to theory. These results highlight that, on average, decisions made by subjects were almost consistent with

Table 3 Percentage of subjects' choices in accordance with FOSD (Panel A) and SOSD (Panel B and C) with G: choice of the gamble, CO: choice of the certain outcome[a]

Panel A: Percentage of choices consistent with FOSD			
FOSD predicts:	Capuchins	Macaques	Orang-utans
G in # 1, # 3, # 5, # 10	85.8075% (34.9%)	98.335% (12.8%)	74.2225% (43.8%)
CO in # 16	97.65% (15.13%)	83.33% (37.26%)	98.95% (10.15%)
Average FOSD success rate (G in # 1, # 3, # 5, # 10 & CO in # 16)	88.178% (32.28%)	95.336% (21.09%)	79.17% (40.61%)
Panel B: Percentage of choices consistent with SOSD in # 14			
SOSD predicts:	Capuchins	Macaques	Orang-utans
CO in # 14	67.71% (46.82%)	25.42% (43.63%)	60.42% (49.15%)
Panel C: Difference between choices consistent with SOSD in # 9 and # 10			
	Capuchins	Macaques	Orang-utans
Z-test of the difference between G in # 9 & G in # 10	2.055[**]	0.914	0.144

[a] Standard deviations are given in parentheses. [*], [**], [***] respectively indicates significance at the 1, 2 and 5% levels

stochastic dominance (87.56% of all choices are consistent with FOSD, and 42.35% of all subjects always choose the FOSD outcome). In the next sub-section, we investigate what drives the observed decisions.

3.3 Decision-making determinants

To investigate the mechanisms underlying decisions, we consider the following linear model:

$$y_{it} = \beta' x_{it} + \propto_i + \varepsilon_{it} \tag{13}$$

where y_{it} is a binary variable equal to 1 if subject i exchanges in trial t, and otherwise has a value of 0. In this model, the decision to exchange depends on different variables (x is a vector of explanatory variables) and on individual specific parameters that do not change over time (α_i). The error term ε_{it} is i.i.d. $N(0,\sigma^2)$.

Our focus is to test the assumption that subjects consider current and past gains and losses when they decide to exchange. However, this impact may appear in different variables: i) the probability of gaining (getting a large cookie), or P_{Gt}, and the probability of losing (getting a small cookie), or P_{Lt}, in trial t; ii) the quantitative outcome (measured in units of small cookies) received during the preceding trial, or O_{Pt-1}, and the average of the quantitative outcomes previously received during the session, or O_{APt-1}; iii) the type of outcome (gain, +1, loss, −1, or neutral, 0) resulting from the preceding trial, $O_{Ptype t-1}$; iv) the frequency of the different types of outcomes previously received during the session, or F_{Gt-1} (frequency of gains) and F_{Lt-1} (frequency of losses and neutral items). For example, in the 5th trial of a session for a subject who received a small cookie in the 1st and 2nd trial, a medium-sized cookie in the 3rd trial and a large cookie in the 4th trial: O_{Pt-1} represented the quantitative outcome received at the 4th trial, i.e. +3; O_{APt-1} is the average of quantitative outcomes obtained

from the 1st to the 4th trials of the session, i.e. +1.5/4=+0.375; $O_{Ptypet-1}$ indicates the qualitative (type of) outcome received at the 4th trial, a gain, i.e. +1; F_{Gt-1} indicates the frequency of gains over the four preceding trials, i.e. 1/4=0.25; *and* F_{Lt-1} indicates the frequency of losses and neutral items over the four preceding trials, i.e. 3/4=0.75.

We tested the following conditional logit model (Chamberlain 1980):

$$Prob\left(y_{it} = 1\Big/x, \beta, \propto\right) = F\left(\beta' x_{it} + \propto_i\right) \qquad (14)$$

Table 4 presents results for the impact of the preceding variables in different specifications (M0 to M8) over the entire dataset. In M1 to M5 we add all explaining variables one by one to the probability of losing and gaining (M0). The relative significance of the variables may help us to understand whether subjects were mainly influenced by quantitative (O_{Pt-1}, O_{APt-1}) or qualitative ($O_{Ptypet-1}$, F_{Gt-1}, F_{Lt-1}) outcomes. We may also learn how past outcomes affect the choices made by subjects: actual decisions may be driven by the outcome of the preceding trial (O_{Pt-1}, $O_{Ptypet-1}$) or by the global history of outcomes (O_{APt-1}, F_{Gt-1}, F_{Lt-1}). We therefore analyzed the impact of quantitative and qualitative variables in M6, M7 and M8.

The results indicate that, over the entire dataset and for M0 to M8, exchange decisions were negatively influenced by the probability of losing and positively by the probability of gaining in the trial. The coefficients of these variables are significant at high levels and, according to the z-statistics, crucially explain the decisions made by subjects. Coefficient estimates of models M0 to M5 indicate that individually, the quantitative outcome obtained in the preceding trial (O_{Pt-1}), the average of previously received quantitative outcomes (O_{APt-1}) and the frequency of previous gains (F_{Gt-1}) during the session have a positive and significant effect on the decision to exchange. The negative impact of both the qualitative outcome obtained during the preceding trial ($O_{Ptypet-1}$) and the frequency of previous losses and neutral items (F_{Lt-1}) on the gambling decision is also significant. Interestingly, the positive effect of the average previous quantitative outcome during the session is comparable to the hot hand effect observed in human gamblers.[4]

In M6, the decision to exchange is modeled with explanatory variables about quantitative outcomes (O_{Pt-1}, O_{APt-1}) whereas in M7, only variables about qualitative outcomes are used ($O_{Ptypet-1}$, F_{Lt-1}) and M8 is our best mixed specification.[5] The examination of the log-likelihood and pseudo R^2 of these models indicates that the decision to exchange is better fitted by qualitative (frequency of losses in M7 and M8) than quantitative (amount of gains or losses in M6) outcomes. Our best estimation (in terms of both log-likelihood and pseudo R^2) is obtained in M5, where the frequency of previous losses (z-stat=−2.51) together with the probability of gains and losses in the current trial explain the exchange decision. Moreover, as the coefficients for P_{Gt} and P_{Lt} are very close and that gains are much greater than losses, it requires a much larger gain to elicit a similar behavioral response to a small loss. This is evidence of loss aversion[6] in subjects.

---

[4] The hot hand effect is observed when a series of gains increases the willingness to take future risks; it is related to the illusion of control (Langer 1975). The positive impact of the average quantitative outcome received previously could also be attributed to the house money effect; however, as subjects cannot bet their cumulated outcomes like humans, we can only retain the hot hand effect explanation here.

[5] We tested many specifications and present only our best ones here. Other results are obtainable upon request.

[6] We thank K. Chen for this valuable insight on our regression results.

Table 4 Influence of different variables on the exchange behaviors of the subjects (entire dataset) [a]

Models	M0	M1	M2	M3	M4	M5	M6	M7	M8
P_{Lt}	-.012 *** (−13.58)	-.012 *** (−12.27)	-.014 *** (−14.27)	-.009 *** (−8.49)	-.009 *** (−8.32)	-.013 *** (−14.07)	-.009 *** (−9.62)	-.013 *** (−13.38)	-.012 *** (−12.01)
P_{Gt}	.017 *** (11.41)	.015 *** (9.08)	.018 *** (11.45)	.008 *** (4.55)	.009 *** (5.93)	.017 *** (10.76)	.008 *** (4.56)	.018 *** (11.10)	.014 *** (8.49)
O_{Pt-1}		.083 *** (4.25)							.081 *** (4.18)
$O_{Pqpet-1}$			-.074 * (−1.88)				.002 (0.11)		
O_{APt-1}				.217 *** (6.21)			.214 *** (5.15)	-.062 (−1.58)	
F_{Gt-1}					.574 *** (3.76)				
F_{Lt-1}						-.242 ** (−2.51)		-.236 ** (−2.46)	-.219 * (−2.28)
Pseudo R^2	.1897	.1944	.2011	.1796	.1428	.2022	.1796	.1995	.1937
Obs. nber	12240	11220	11220	11220	11220	11220	11220	11220	11220
LogL	−4890.72	−4462.22	−4424.76	−4544.08	−4747.68	−4418.64	−4544.03	−4434.02	−4466.08

[a] For the tth trial, P_{Lt} is the probability of losing (getting a small cookie in this trial), P_{Gt} is the probability of winning (getting a large cookie in this trial), O_{Pt-1} is the quantitative outcome received at the t-1th trial, O_{Pt-1} is the average of the quantitative outcomes received from the 1st to the t-1th trials of the session, $O_{Pqpet-1}$ is the qualitative outcome (gain, +1, loss, −1, or neutral, 0) received at the t-1th trial, F_{Gt-1} and F_{Lt-1} are respectively the frequencies of gains (of losses and neutral items) among the outcomes previously received from the 1st to the t-1th trials of the session. Models M0 to M8 indicate the coefficients of the different explanatory variables; levels of significance are given according to the following rule: * for 5, ** for 1, and *** for 0.1% (z-statistics are given in parentheses). Obs. nber and LogL are respectively the number of observations and the log likelihood of the last iteration's estimation

As this latter result is in line with actual gambling behaviors in humans, we run the best fit regressions (M0 as a benchmark, M5 and M8) for the three species in Table 5. In capuchins and orang-utans, choices made by subjects are influenced by both the characteristics of the immediate trial and the complete history of outcomes. However, decisions in macaques were mainly explained by the probability of gains and losses in the previous trial. More precisely, the variable O_{Pt-1} has a relatively stronger explanatory power (z-stat=6.77) than the frequency of losses (z-stat=−2.52) for orang-utans than for capuchins (z-stats of respectively 4.62 and −2.49), but does not have a significant explanatory power regarding decisions to gamble in macaques. This result will be analyzed in the conclusion.

Taken together, the results of Tables 4 and 5 reinforce our preceding conclusion on the risk preference of subjects, because the decision to exchange is very sensitive to the qualitative history of outcomes.

4 Results on theories of decision making

In this section, we aim to determine the mechanisms that underlie decision-making by comparing our primate data to three theories of human decision-making: Expected Utility Theory (von Neumann and Morgenstern 1944), Cumulative Prospect Theory (Kahneman and Tversky 1979; Tversky and Kahneman 1992) and Rank Dependent Expected Utility Theory (Quiggin 1982). To assess how far these theories explain the decision of individuals and to estimate some parameters of these theories, we carried out maximum log-likelihood estimations on data samples for each species. To account for heterogeneity between subjects, we finally explain and fit mixture models of EUT / RDEUT and EUT / CPT. All preceding analyses were conducted for 17 combinations, as the final combination was not tested in all subjects.

4.1 Expected utility theory

Firstly, it is important to note that as expected from EUT, the mean percentage of return in each species progressively decreased throughout the study from combination # 1 to combination # 16 (Fig. 1). In all species, mean return rates remained significantly higher than 50% from combination # 1 to combination # 11 (they are significantly higher than 50% for combinations # 1 to # 12 for macaques, # 1 to # 9 for capuchins and # 1 to # 7 for orang-utans). Percentages of return did not significantly differ from 50% in combinations # 12 to # 14 in all species (macaques: # 13 to # 15, capuchins: # 10 to # 14, orang-utans: # 8 to # 14). When considering combinations # 15 and # 16, each species presented a percentage of return significantly lower than 50%, with the exception of # 15 in macaques. Subjects were tested at the end of sessions using control combination # 17, where the chance of gaining was high; the percentage of exchange in all three species increased again (capuchins: 34.9%, macaques: 76.67%, orang-utans: 51.04%), but was not significantly different from 50%.

Secondly, we compute conditional log-likelihood of the expected utility theory for two utility functions (where y is the quantity of item): The power utility function: $u(y)=y^{\delta}$, ∀ y (δ is the risk aversion parameter), and the negative exponential utility function: $u(y)=-exp(-y\rho)$, ∀ y (ρ is the risk aversion parameter). These two functional forms are

Table 5 Influence of the different variables on the exchange behaviors of the animals (for the three species) [a]

Models	M0			M5			M8		
	Capuchins	Macaques	Orang-utans	Capuchins	Macaques	Orang-utans	Capuchins	Macaques	Orang-utans
P_{Lt}	-.014 *** (−13.39)	-.015 *** (−7.72)	-.023 *** (−9.42)	-.015 *** (−12.89)	-.061 *** (−7.86)	-.024 *** (−9.14)	-.015 *** (−13.04)	-.016 *** (−7.57)	-.023 *** (−9.44)
P_{Gt}	.023 *** (12.45)	.014 *** (4.11)	.004 *** (10.82)	.024 *** (11.71)	.015 *** (4.11)	.047 *** (10.23)	.018 *** (9.24)	.014 *** (3.61)	.038 *** (9.00)
O_{Pt-1}							.118 *** (4.62)	.023 (0.59)	.39 *** (6.77)
F_{Lt-1}				-.351 *** (−2.82)	-.135 (−0.67)	-.648 ** (−2.48)	-.309 ** (−2.49)	-.135 (−0.67)	-.672 ** (−2.52)
Pseudo R^2	.2145	.2426	.2227	.2225	.2564	.2350	.2167	.2524	.2599
Obs. nber	6528	4080	1632	5984	3740	1496	5984	3740	1496
LogL	−2868.32	−1061.75	−763.42	−2603.62	−958.47	−689.36	−2623.18	−963.63	−666.88

[a] For the tth trial, P_{Lt} is the probability of losing (getting a small cookie in this trial), P_{Gt} is the probability of winning (getting a large cookie in this trial), O_{Pt-1} is the quantitative outcome received at the t-1th trial, F_{Lt-1} is the frequency of losses and neutral items among the outcomes previously received from the 1st to the t-1th trials of the session. Models M0, M5 and M8 indicate the coefficients of the different explanatory variables; levels of significance are given according to the following rule: * for 5, ** for 1, and *** for 1% (z-statistics are given in parentheses). Obs. nber and LogL are respectively the number of observations and the log likelihood of the last iteration's estimation

interesting because they exhibit different properties. The power function exhibits constant relative risk aversion (CRRA). CRRA means that attitudes towards proportional risks are constant with y, that is, the decision of a subject to accept gambles depends on their experience in food consumption resulting from past trials. The negative exponential utility function exhibits constant absolute risk aversion (CARA), which means that if subjects experience an increase in food consumption resulting from "winning" trials, this will not affect their decisions to accept next gambles. Testing these two specifications allows us to study decision-making in non-human primates for which we control the satiation level.

Table 6 presents estimates of the utility functions' parameters for the three primate species.[7] Our results indicate that the best fits are obtained with the power utility functions for all species. However, whatever the function retained, subjects significantly exhibit risk aversion ($\rho > 0$ or $\delta < 1$) with coefficients close to 0.7 for capuchins and orang-utans and close to 1 (but not significantly different from 1) for macaques in the CRRA utility function. Note that we found some individual heterogeneity within species (Table S3, Online Resource 1).

From these results we conclude that decisions made by subjects were generally consistent with EUT, but individual heterogeneity was present. However, one violation of EUT principles should be stressed regarding the effective choices of subjects: in the control condition # 17, the evaluation of combinations by subjects differed from the one of combination # 4 despite identical rewards. We use CPT to better understand the decision-making process of subjects in the next sub-section.

4.2 Cumulative prospect theory

The observed choices of subjects can be explained with CPT by the level of the weighting function and by the loss aversion parameters.[8] Table 7 presents estimates of the CPT parameters for the three primate species. Our results indicate that capuchins and orang-utans exhibit significant loss-aversion whereas the result is not clear-cut in macaques. For example, in capuchins and orang-utans, subjects accept losing a medium size cookie if they can gain a cookie 2.28 or 2.12 times its size. This is in line with the result obtained in humans by Tversky and Kahneman (1992), who experimentally identified a median value of $\lambda = 2.25$ indicating pronounced loss aversion. In all species we found significant probability distortion. With $\gamma = 0.83$ in capuchins (0.78 in macaques and 0.91 in orang-utans) the weighting function is inverse-S shaped, and subjects overweight low probabilities and underweight high ones. Note however, that γ is not significantly different from 1 in orang-utans.

To sum up, our results indicate that choices are consistent with CPT predictions. In the last sub-section we test RDEUT, then use a mixture model to take subject heterogeneity into account (Harrison and Rutström 2009).

---

[7] In our estimation we consider the residuals from the same subject to be potentially correlated and correct for this fact when calculating standard errors of estimates.

[8] As CPT is over-identified with the estimation of 4 parameters in choices where only outcome probabilities vary, here we assume that values are roughly linear in the range of gains and losses (i.e. $\alpha = \beta = 1$).
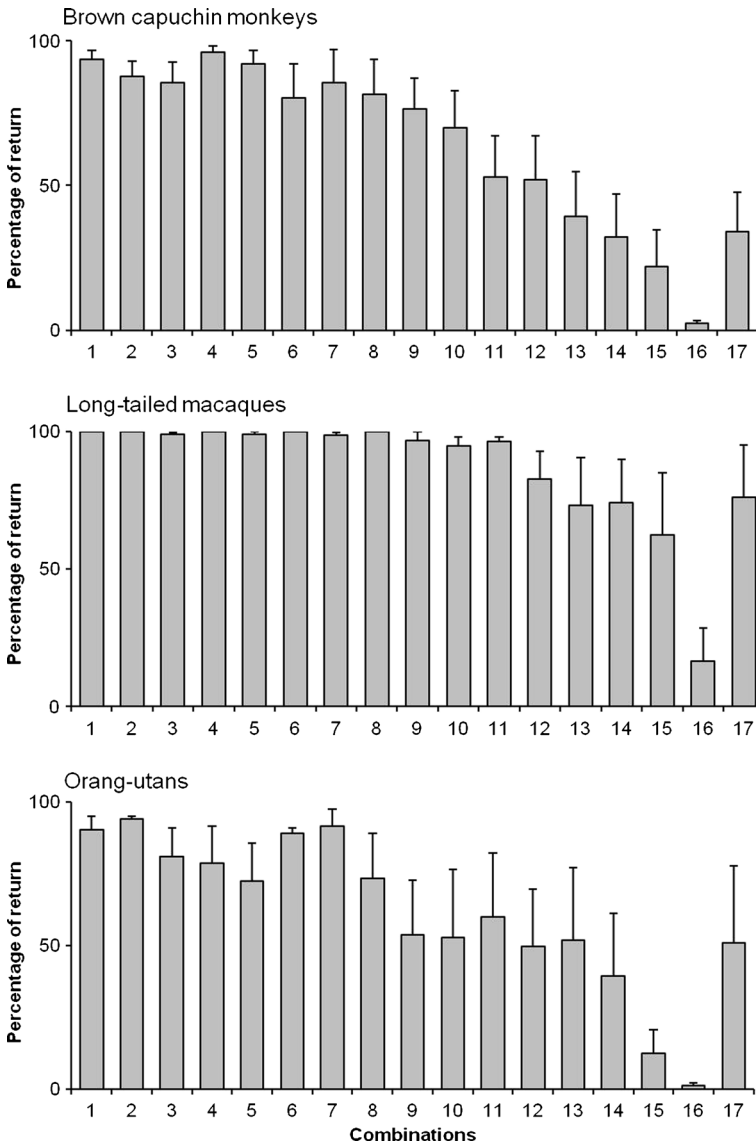
Fig. 1 Mean percentage of initial items exchanged (% of return) for each combination of rewards proposed to subjects in each species

4.3 Rank dependent expected utility theory

Under RDEUT, the decisions made by subjects may be explained by different attitudes towards risk and probability distortion, but the individuals do not differentiate between gains and losses as in CPT. Table 8 gives our estimates for four specifications of utility function and weighting function in RDEUT: CARA (negative exponential) utility function / Tversky and Kahneman (1992) weighting function, CARA / power, CRRA / KT and CRRA / power. Regarding the log-likelihood of all four specifications, we

Table 6 Estimates of parameters for EUT models [a]

Utility function	Parameters / Log L	Capuchins	Macaques	Orang-utans
Negative exponential	ρ	0.2334 *** (0.0426)	0.1661 *** (0.0146)	0.2458 *** (0.0694)
	Log L	−4148,78	−2549.32	−1042.36
Power	δ	0.6805 *** (0.0786)	1.0197 *** (0.1073)	0.6458 *** (0.0782)
	Log L	−3472.26	−1302.45	−902.87
Nber of obs.		6528	4080	1632

[a] This table presents estimates of two utility functions (negative exponential, power) parameters for three primate species. Robust standard errors (adjusted for clusters in subjects) are in parentheses. *, **, *** respectively indicates significance at the 5, 1 and 0.1% levels. Log L is the pseudo log-likelihood of the estimation

found CRRA / KT to be the best model (with a slight exception for macaques with CRRA / power). This model efficiently fitted the behavior of subjects, and our results in power / KT indicate that highly risk-adverse subjects (capuchins and orang-utans) strongly distort probabilities whereas there is no significant probability distortion in macaques. According to Chateauneuf and Cohen (1994), capuchins and orang-utans exhibit optimistic attitudes towards probabilities (γ is significantly higher than 1). Note that in macaques, probability distortion parameters are very different across the three models (1.5404 in CRRA / power, 0.0254 in CARA / KT and 0.9914 in CRRA / KT). However, we can conclude that capuchins and orang-utans are risk-adverse and optimistic whereas macaques are practically all risk-prone. As this last result complements the ones for EUT and CPT, we then built and analyzed different mixture models between EUT and RDEUT and between EUT and CPT in order to analyze the relationship between risk aversion and probability distortion in the three species.

4.4 Mixture models

Mixture models[9] allow the joint estimation of the probabilities and parameters of the conditional log-likelihood functions. They better characterize unobserved individual heterogeneity and were first used to address the debate over theories of choice under uncertainty by Harrison and Rutström (2009) for EUT and CPT and by Conte et al. (2011) for EUT and RDEUT. Our paper is the first attempt to use mixture models for non-human primates. We present our mixture model for EUT and RDEUT by first denoting π^{EUT} as the probability that the EUT model is correct and $\pi^{RDEUT} = (1 - \pi^{EUT})$ as the probability that the RDEUT model is correct. The grand log-likelihood can be written as the probability-weighted average of the conditional log-likelihoods:

$$\ln L(\delta, \gamma, \alpha, \pi^{EUT}; y) = \sum_i \ln\left[\left(\pi^{EUT} \times l_i^{EUT}\right) + \left(\pi^{RDEUT} \times l_i^{RDEUT}\right)\right] \quad (15)$$

This log-likelihood can be maximized in order to find parameter estimates for EUT (α) and RDEUT (δ, γ) and the log odds parameter κ. Actually, the probability for the EUT model is obtained in $\pi^{EUT} = 1/(1 + exp(\kappa))$. Moreover, since $\pi^{EUT} = \frac{1}{2}$ when $\kappa = 0$,

---

[9] A recent survey of mixture models since their early development in Pearson (1894) can be found in MacLachlan and Peel (2000).

Table 7 Estimates of parameters for CPT. This table presents estimates of CPT parameters for three primate species [a]

Parameters / Log L	Capuchins	Macaques	Orang-utans
λ	2.2875 [***] (0.4059)	0.9093 [*] (0.4551)	2.1213 [***] (0.5552)
γ	0.8305 [***] (0.0522)	0.7869 [***] (0.0514)	0.9134 [***] (0.0878)
Log L	−4413.03	−1164.37	−1212.05
Nber of obs.	6528	4080	1632

[a] Robust standard errors (adjusted for clusters in subjects) are in parentheses, except when convergence is not achieved (*cna*). [*], [**], [***] respectively indicates significance at the 5, 1 and 0.1% levels. Log L is the pseudo log-likelihood of the estimation

the p-value on the estimate of κ provides the estimate for the null hypothesis H_0: $\pi^{EUT} = \pi^{RDEUT}$.

Table 9 presents estimates of parameters for mixture model of RDEUT and EUT. First, note that EUT and RDEUT equally fit decisions in the three species (high Chi 2 test p-values). Therefore, heterogeneity among subjects does not allow us to discriminate between decision-making theories. The examination of results for capuchins and orang-utans leads us to conclude on risk-neutrality in EUT (α is not significantly different from 1) and/or risk-aversion (δ is significantly lower than 1), and on optimistic attitudes towards probabilities in RDEUT (but γ is not significantly different from 1). In macaques, we find significant risk-prone behavior under EUT but risk-aversion and

Table 8 Estimates of parameters for RDEUT. This table presents estimates of RDEUT parameters for two utility functions (power and negative exponential) and two weighting functions (power, KT) for three primate species [a]

Utility function / Weighting function	Parameters / Log L	Capuchins	Macaques	Orang-utans
Negative exponential / Power	ρ	0.5005 [***] (0.1993)	*Failed*	0.5313 [*] (0.2324)
	μ	3.3313 (1.83)		2.6790 (1.7885)
	Log L	−3934.67		−1011.30
Power / Power	δ	0.2286 [***] (0.0900)	0.5706 [***] (0.0762)	0.1915 (0.1058)
	μ	2.3072 [***] (0.66)	1.5404 [***] (0.1967)	2.3261 (1.8879)
	Log L	−3903.80	−1150.01	−1031.83
Negative exponential / KT	ρ	0.4137 [***] (0.0451)	0.3696 [***] (7.69 10^{-8})	0.3674 [**] (0.1453)
	γ	2.7500 (1.6402)	0.0254 [***] (0.0048)	2.0661 (1.4277)
	Log L	−3863.15	−1553.58	−1000.41
Power / KT	δ	0.3527 [***] (0.0914)	0.6852 [***] (0.0580)	0.3173 [***] (0.1044)
	γ	1.5725 [***] (0.1156)	0.9914 [***] (0.3189)	1.4961 [***] (0.2004)
	Log L	−3796.78	−1164.69	−990.71
Nber of obs.		6528	4080	1632

[a] Robust standard errors (adjusted for clusters in subjects) are in parentheses. [*], [**], [***] respectively indicates significance at the 5, 1 and 0.1% levels. Log L is the pseudo log-likelihood of the estimation. "*Failed*" indicates that we do not find starting values allowing us to maximize log-likelihood

non-significant, pessimistic attitudes towards probabilities under RDEUT. To sum up, macaques are risk-prone and seemingly overweight (resp. underweight) low (resp. high) probabilities whereas capuchins and orang-utans exhibit risk-aversion and underweight (resp. overweight) low (resp. high) probabilities. Therefore, taking into account heterogeneity among individuals can help us to understand that individual attitudes towards risk and probability distortion play complementary roles in decision-making in all three species.

We then moved on to a mixture model of EUT and CPT. Unfortunately, we were not able to find starting values that allowed us to maximize the log-likelihood (the maximization in question required four parameters, making the computations more difficult). In their paper, Harrison and Rutström (2009) give their estimates of a mixture model of EUT and Prospect Theory (and not for CPT), and obtain parameters consistent with theoretical predictions. It is important to note, however, that they only estimate parameters for Prospect Theory which probably alleviates the maximization process.

5 Conclusion

We found that all three species globally exchanged in a manner that was consistent with first and second order stochastic dominance. Brown capuchin monkeys, long-tailed macaques and orang-utans were capable of taking into account the chances of loss and gain when gambling one food item for another. Throughout the study, gambling remained frequent despite an increasing chance of losing from one combination to the next, and some individuals continued betting despite having experienced an accumulation of negative outcomes in a given session. When investigating general results (i.e. without any decision making model hypothesis), we found that decisions made by subjects were mostly in accordance with first order stochastic dominance, and exhibited risk aversion for capuchins and orang-utans and risk seeking for macaques with regard to second order stochastic dominance. The decisions taken by subjects to accept gambles were affected by the probability of winning and/or losing in the actual trial. In orang-utans, and to a lesser extent in capuchins, decisions to gamble were also positively and significantly driven by the outcome in the preceding trial and by the frequency of losses they had experienced in previous trials. Choices made by macaques were mainly driven by the characteristics of the immediate trial rather than by the history of outcomes. When investigating theories of decision under risk, we found that capuchins and orang-utans exhibit risk-aversion under EUT, distort probabilities and exhibit loss aversion under CPT and exhibit risk-aversion and optimism under RDEUT. In macaques, we find risk-seeking under EUT, probability distortion but no strong loss aversion under CPT and no probability distortion under RDEUT. Our estimations using a mixture model of EUT and RDEUT are helpful to understand macaque behaviors as opposed to those shown by capuchins and orang-utans, and contribute to the conclusion that attitudes towards risk and probability distortion play complementary roles in all three species' decisions.

There are many results in this study and we have described them in this section with the general idea that some human behavioral biases might be related to specific features of these species, and thus to divergences in their evolutionary history. First, our analysis of data in the context of EUT, CPT, RDEUT and mixture models show that macaques generally exhibit risk seeking whereas decision-taking in the other two species' decisions was characterized

Table 9 Estimates of parameters for mixture model of RDEUT and EUT [a]

Parameters / Log L	Capuchins	Macaques	Orang-utans
δ	0.5340 *** (0.1130)	0.5825 *** (0.1923)	0.5618 *** (0.1653)
γ	1.0361 *** (0.1347)	0.3172 (0.4481)	1.2431 *** (0.1709)
α	1.0174 *** (0.0948)	1.2108 *** (0.0417)	1.0354 *** (0.1709)
κ	0.3451 (1.41)	−0.5666 (1.2262)	1.2243 (3.118)
Log L	−3438.94	−1074.36	−898.73
π_{EUT}	41.45% (34.22%)	63.79% (28.32%)	34.86% (54.73%)
$H_0: \pi^{EUT} = \pi^{RDEUT}$	0.48	0.24	0.25
Chi 2 test p-value	0.8029	0.6261	0.6182
Nber of obs.	6528	4080	1632

[a] This table presents estimates of parameters for both RDEUT and EUT with power utility functions (coefficient α in EUT or δ in RDEUT) and KT weighting function (coefficient γ in RDEUT) for three primate species. Coefficient κ is used to compute the probability that subjects' behavior is fit by EUT, p_{EUT}, and to test whether the probabilities of EUT and RDEUT are identical (Chi 2 test). Robust standard errors (adjusted for clusters in subjects) are in parentheses. *, **, *** respectively indicates significance at the 5, 1 and 0.1% levels. Log L is the pseudo log-likelihood of the estimation

by risk aversion. Differences between species in attitudes towards risk have already been reported in a previous study, where a difference in risk-seeking behavior between chimpanzees and bonobos was attributed to differences between the natural foraging strategies of each species (Heilbronner et al. 2008). Hunting in chimpanzees, a rather risky foraging mode, was a suggested explanation of risk-seeking in this species, whilst fruit-gathering, a less unpredictable foraging habit, would explain risk-averse choices in bonobos (Heilbronner et al. 2008). We also found interspecific differences during our study. If we examine what elements may sustain those differences in the natural characteristics of each of the three species, we could relate the risk-prone attitudes of long-tailed macaques to their capacity to inhabit a wide range of habitats, including towns where they live in close proximity with humans (Fooden 1995). By contrast, orang-utans and capuchins may be more risk-adverse because they generally inhabit more uniform types of habitats (mainly tropical forests) (Groves 1993; Fragaszy et al. 2004). However, given both individual heterogeneity and results from previous studies, we think that it would be premature to draw conclusions on the generality of attitudes towards risk from a single experimental context. Indeed, in another study testing choices between safe versus risky options, both chimpanzees and bonobos exhibited risk proneness (Haun et al. 2011). This was also true of orang-utans (Haun et al. 2011), conflicting with our current results. However, it is important to note that although our conclusion on risk aversion in orang-utans is primarily based on SOSD, we also evaluate the strength of the risk-aversion parameter and its relative influence compared to others such as loss aversion or probability distortion.

Secondly, our experimental design gives us the opportunity to discuss some determinants of decision-making under risk for non-human primates. The first to consider is satiation, as it may also provide a better explanation for individual choices of the risky versus safe option (and vice-versa) than general attitudes toward risk per se. Many studies suggest that attitudes towards risk in animals may depend on energetic budget. This approach postulates that an animal with a positive energetic budget should not

take risks, whilst an animal with a negative budget, who therefore has nothing to lose, should take every risk in an attempt to replenish its reserves (Kacelnik and Bateson 1996). In our study, this would mean that the utility of the reward may not have remained constant across a test session as the satiation level of individuals increased from one trial to the next. Satiation would lead to a decrease in the perceived utility of the rewards. Interestingly, our results on risk attitudes take this satiation problem into account as the best-fitting utility function for our data considered that individual experience of food consumption affects decisions. In a nutshell, macaques are risk prone although their energetic budget is positive.

Our experimental design also allows us to discuss the ability of non-human primates to evaluate probabilities and to consider that successive trials are independent. These points are indeed at the core of the aforementioned experiments. For example, Haun et al. (2011) suggested that high individual rates of risky choices in their study may be due to "an inadequate ability to infer the chances of the risky option without experience". Theories of decision-making under risk are all based on the assumption that subjects evaluate the respective probabilities of outcome (Knight 1921). In all species in our study, probability of losses and gains were the variables that explained decisions the best, fitting with what is expected from a rational individual that considers each trial independently. However, orang-utans and capuchins also took previous outcomes into account although they did so to a lesser extent than for the two other variables. Macaques show a slightly different pattern as they were not significantly influenced by previous outcomes. They are also better at following FOSD prediction. This result is surprising as we could have expected orang-utans to perform better than other species. Interestingly, orang-utans attributed more weight to the quantitative outcome of the immediately preceding trial than capuchins. Cognitive capabilities in this species are well known (Tomasello and Call 1997; Mulcahy and Call 2006), and existing knowledge suggests that this cannot be explained by a poorer memory of previous incomes in orang-utans compared to the other species. One explanation would be that the orangutans remained focused on each trial and were thus more responsive to the most recent loss. Somehow, it would suggest that they were highly attentive to the result of each decision and may have understood well that the trials were independent from each other. Further studies are needed to detect whether the difference in performances between the three species is still detectable in other experimental setups.

As a third point, we discuss behavioral decision making in non-human/human primates. In humans, previous outcomes also affect actual decisions in economic situations where sequential choices are independent (Clotfelter and Cook 1993). The existence of behavioral biases and judgment errors has been documented in studies on how previous outcomes influence expectations concerning the future in the context of risky decisions; for example, the hot hand effect (Tversky and Kahneman 1971), the gambler's fallacy (Croson and Sundali 2005), and the house money effect (Thaler and Johnson 1990). Among these biases, the hot hand effect is the fact that individuals are ready to take more risks after a series of gains, an effect also referred to as the "illusion of control" (Langer 1975). Another bias, the gambler's fallacy, is the belief that if deviations from average are observed in repeated independent trials then these deviations are likely to be evened out by opposite deviations in the future. According to Tversky and Kahneman (1971), the gambler's fallacy is a cognitive bias that is due to the representativeness heuristic. The representativeness heuristic is a psychological trait wherein people

judge the probability or frequency of an event by considering how much the occurrence of the event resembles available data as opposed to using a "Bayesian probability" calculation. According to this view, "after observing a long run of red on the roulette wheel, for example, most people erroneously believe that black will result in a more representative sequence than the occurrence of an additional red" (Tversky and Kahneman 1974). Phenomena similar to the hot hand effect were detected in our results. After a series of gains, individuals were more prone to take risks. The analysis revealed that subjects were very sensitive to the qualitative aspects of their previous outcome (have I lost frequently?) more than the quantitative one (how much have I already won?). These findings represent a significant addition to previous research, suggesting that humans share several behavioral biases with other primate species.

In a last point, when comparing the data observed in non-human primates to the theories of economic decisions in humans, we have found that the three species exhibit different attitudes towards probabilities and different attitudes towards risk. Studies in humans have reported that decision-making in a risky context may vary according to the set-up used (Lévy-Garboua et al. 2012; Holt and Laury 2002). Individuals are risk-averse in the domain of gains when presented with value-increasing options, but take more risks in the domain of loss when faced with decreasing values (Kessler et al. 1996; Linveille and Fischer 1991; Thaler 1985). For example, individuals are ready to buy insurance for unlikely disasters and still play lotteries. Our experiment is the first to implement a loss, as individuals accept giving up a food already held in their hand. Thus, we may have provided a different framing compared to previous studies which could explain differences in attitudes towards risk in the tested species. We find that capuchins and orang-utans exhibit significant probability distortion and loss aversion, whereas similar conclusions could not be significantly and systematically established in macaques. In brown capuchin monkeys in particular, *reference dependence* and *loss aversion* have also been documented by Chen et al. (2006) in capuchins, and the *endowment effect* was described by Lakshminarayanan et al. (2008). Therefore our results extend those findings to other interesting species and show that the loss aversion coefficients in capuchins and orang-utans are comparable to those found in humans by Tversky and Kahneman (1992). Moreover, under CPT, we estimate weighting function parameters in accordance with the estimated values in humans in Tversky and Kahneman (1992), Camerer and Ho (1994) and Wu and Gonzalez (1996). Thus like humans, the evaluation of probability by non-human primates can be subjective. Further development of the current study in comparison with other work is needed before concluding on general "species-specific" attitudes towards risk. Yet this study indicates that some human behavioral biases may not emerge as a result of economic and market experience, but might rather be related to particular features of species, and thus to divergences in their evolutionary history.

References

Amici, F., Aureli, F., & Call, J. (2008). Fission-fusion dynamics, behavioral flexibility and inhibitory control in primates. *Current Biology, 18*(18), 1415–1419.

Bateson, M., & Kacelnik, A. (1997). Starlings' preferences for predictable and unpredictable delays to food. *Animal Behavior, 53*(6), 1129–1142.

Camerer, C. F., & Ho, T. (1994). Violations of the betweenness axiom and nonlinearity in probability. *Journal of Risk and Uncertainty, 8*(2), 167–196.

Cartar, R. V., & Smallwood, P. D. (1996). Risk-sensitive behavior: where do we go from here? *American Zoologist, 36*(4), 530–531.

Chamberlain, G. (1980). Analysis of covariance with qualitative data. *Review of Economic Studies, 47*, 225–38.

Chateauneuf, A., & Cohen, M. (1994). Risk seeking with diminishing marginal utility in a non-expected utility model. *Journal of Risk and Uncertainty, 9*, 77–91.

Chen, K. M., Lakshminarayanan, V., & Santos, L. R. (2006). How basic are behavioral biases? Evidence from capuchin monkey trading behavior. *Journal of Political Economy, 114*(3), 517–537.

Clotfelter, C. T., & Cook, P. J. (1993). The "gambler's fallacy" in lottery play. *Management Science, 39*, 1521–1525.

Conte, A., Hey, J. D., & Moffatt, P. G. (2011). Mixture models of choice under risk. *Journal of Econometrics, 162*(1), 79–88.

Croson, R., & Sundali, J. (2005). The gambler's fallacy and the hot hand: empirical data from casinos. *Journal of Risk and Uncertainty, 30*(3), 195–209.

de Waal, F. B. M. (1997). Food transfers through mesh in brown capuchins. *Journal of Comparative Psychology, 111*(4), 370–378.

Drapier, M., Chauvin, C., Dufour, V., Uhlrich, P., & Thierry, B. (2005). Food exchange with humans in brown capuchin monkeys. *Primates, 46*(4), 241–248.

Dufour, V., Pelé, M., Sterck, E. H. M., & Thierry, B. (2007). Chimpanzee anticipation of food return: coping with waiting time in an exchange task. *Journal of Comparative Psychology, 121*(2), 145–155.

Dufour, V., Pelé, M., Neumann, M., Thierry, B., & Call, J. (2009). Calculated reciprocity after all: computation behind token transfers in orang-utans. *Biology Letters, 5*(2), 172–175.

Fooden, J. (1995). Systematic review of Southeast Asian longtail macaques, *Macaca fascicularis* (Raffles [1821]). *Fieldiana Zoology, 81*, 1–206.

Fragaszy, D. M., Visalberghi, E., & Fedigan, L. M. (2004). *The complete capuchin*. Cambridge: Cambridge University Press.

Gonzalez, R., & Wu, G. (1999). On the shape of the probability weighting function. *Cognitive Psychology, 38*, 129–166.

Groves, C. P. (1993). Order primates. In D. E. Wilson & D. M. Reader (Eds.), *Mammalian species of the world: A taxonomic and geographic reference* (pp. 243–277). Washington: Smithonian Institution Press.

Hanus, D., & Call, J. (2007). Discrete quantity judgments in the great apes (*Pan paniscus*, *Pan troglodytes*, *Gorilla gorilla*, *Pongo pygmaeus*): the effect of presenting whole sets versus item-by-item. *Journal of Comparative Psychology, 121*(3), 241–249.

Harrison, G. W., & Rutström, E. E. (2009). Expected utility theory and prospect theory: one wedding and a decent funeral. *Experimental Economics, 12*, 133–158.

Haun, D. B. M., Nawroth, C., & Call, J. (2011). Great apes' risk-taking strategies in a decision making task. *PloS One, 6*(12), e28801.

Hayden, B. Y., & Platt, M. L. (2007). Temporal discounting predicts risk sensitivity in rhesus macaques. *Current Biology, 17*(1), 49–53.

Heilbronner, S. R., Rosati, A. G., Stevens, J. R., Hare, B., & Hauser, M. D. (2008). A fruit in the hand or two in the bush? Divergent risk preferences in chimpanzees and bonobos. *Biology Letters, 4*, 246–249.

Holt, C. A., & Laury, S. K. (2002). Risk aversion and incentive effects. *American Economic Review, 92*(5), 1644–1655.

Kacelnik, A., & Bateson, M. (1996). Risky theories – The effects of variance on foraging decisions. *American Zoologist, 36*, 402–434.

Kahneman, D., & Tversky, A. (1979). Prospect theory: an analysis of decision under risk. *Econometrica, 47*(2), 263–291.

Kessler, E. H., Ford, C. M., & Bailey, J. R. (1996). Object valence as a moderator of the framing effect on risk preference. *Journal of Economic Behavior and Organization, 30*, 241–256.

Knight, F. H. (1921). *Risk, uncertainty and profit*. Boston: Houghton Mifflin.

Lakshminarayanan, V., Chen, K. M., & Santos, L. R. (2008). Endowment effect in capuchin monkeys. *Philosophical Transactions of the Royal Society of London, Series B, 363*, 3837–3844.

Langer, E. (1975). The illusion of control. *Journal of Personality and Social Psychology, 32*, 311–328.

Lattimore, P. K., Baker, J. R., & Witte, A. D. (1992). The influence of probability on risky choice: a parametric examination. *Journal of Economic Behavior and Organization, 17*(3), 377–400.

Lee, D., McGreevy, B. P., & Barraclough, D. J. (2005). Learning and decision making in monkeys during a rock-paper-scissors game. *Cognitive Brain Research, 25*(2), 416–430.

Lévy-Garboua, L., Maafi, H., Masclet, D., & Terracol, A. (2012). Risk aversion and framing effects. *Experimental Economics, 15*(1), 128–144.

Linveille, P. W., & Fischer, G. W. (1991). Preferences for separating or combining events. *Journal of Personality and Social Psychology, 60*(1), 5–23.

Luce, R. D., & Raiffa, H. (1957). *Games and decisions*. New York: Wiley.

MacLachlan, G., & Peel, D. (2000). *Finite mixture models*. New York: Wiley.

Menzel, C. R. (1991). Cognitive aspects of foraging in Japanese monkeys. *Animal Behaviour, 41*(3), 397–402.

Mulcahy, N. J., & Call, J. (2006). Apes save tools for future use. *Science, 312*, 1038–1040.

Pearson, K. (1894). Contribution to the mathematical theory of evolution. *Philosophical Transactions A, 185*, 71–110.

Pelé, M., Dufour, V., Thierry, B., & Call, J. (2009). Token transfers among great apes: species differences, gestural requests and reciprocal exchange. *Journal of Comparative Psychology, 123*(4), 375–384.

Pelé, M., Thierry, B., Call, J., & Dufour, V. (2010a). Monkeys fail to reciprocate in an exchange task. *Animal Cognition, 13*, 745–751.

Pelé, M., Dufour, V., Micheletta, J., & Thierry, B. (2010b). Long-tailed macaques display unexpected waiting abilities in exchange tasks. *Animal Cognition, 13*, 263–271.

Pelé, M., Micheletta, J., Uhlrich, P., Thierry, B., & Dufour, V. (2011). Delay maintenance in Tonkean macaques and brown capuchin monkeys. *International Journal of Primatology, 32*(1), 149–166.

Prelec, D. (1998). The probability weighting function. *Econometrica, 66*(3), 497–527.

Quiggin, J. (1982). A theory of anticipated utility. *Journal of Economic Behavior and Organization, 3*(4), 323–43.

Quiggin, J. (1993). *Generalized expected utility theory. The rank-dependent model*. Boston: Kluwer Academic Publishers.

Ramseyer, A., Pelé, M., Dufour, V., Chauvin, C., & Thierry, B. (2006). Accepting loss: temporal limits in brown capuchin monkeys. *Proceedings of the Royal Society of London. Series B, 273*, 179–184.

Thaler, R. H. (1985). Mental accounting and consumer choice. *Marketing Science, 4*(3), 199–214.

Thaler, R. H., & Johnson, E. J. (1990). Gambling with the house money and trying to break even: the effects of prior outcomes on risky choice. *Management Science, 36*(6), 646–660.

Tomasello, M., & Call, J. (1997). *Primate cognition*. Oxford: Oxford University Press.

Tversky, A., & Kahneman, D. (1971). Belief in the law of small numbers. *Psychological Bulletin, 76*(2), 105–110.

Tversky, A., & Kahneman, D. (1974). Judgment under uncertainty: heuristics and biases. *Science, 185*(4157), 1124–1131.

Tversky, A., & Kahneman, D. (1981). The framing of decisions and the psychology of choice. *Science, 211*(4481), 453–458.

Tversky, A., & Kahneman, D. (1992). Advances in prospect theory: cumulative representation of uncertainty. *Journal of Risk and Uncertainty, 5*(4), 297–323.

von Neumann, J., & Morgenstern, O. (1944). *Theory of games and economic behavior*. Princeton: Princeton University Press.

Wu, G., & Gonzalez, R. (1996). Curvature of the probability weighting function. *Management Science, 42*, 1676–1690.