1 2 3	Systematic comparison of risky choices in humans and monkeys
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# 37 Abstract

- 38 The past decades have seen tremendous progress in fundamental studies on economic choice in
- 39 humans. However, elucidation of the underlying neuronal processes requires invasive
- 40 neurophysiological studies that are met with difficulties in humans. Monkeys as evolutionary closest
- 41 relatives offer a solution. The animals display sophisticated and well-controllable behavior that
- 42 allows to implement key constructs of proven economic choice theories. However, the similarity of
- 43 economic choice between the two species has never been systematically investigated. We
- 44 investigated compliance with the independence axiom (IA) of expected utility theory as one of the
- 45 most demanding choice tests and compared IA violations between humans and monkeys. Using
- 46 generalized linear modeling and cumulative prospect theory (CPT), we found that humans and
- 47 monkeys made comparable risky choices, although their subjective values (utilities) differed. These
- 48 results suggest similar fundamental choice mechanism across these primate species and encourage
- 49 to study their underlying neurophysiological mechanisms.

3

# 51 Introduction

- 52 Risky decision making has been investigated for more than 200 years (Stigler, 1950) and remains a
- 53 popular research topic (Blavatskyy et al., 2022; Bujold et al., 2022; Frey et al., 2017; Ruggeri et al.,
- 54 2020; Yang et al., 2022). While economists showed interest in building mathematical models to
- 55 explain risky decisions and relating them to society (Moscati, 2016; Ruggeri et al., 2020; Schneider &
- 56 Day, 2018), neuroscientists investigated the neural mechanism of decision making. To bridge the gap
- 57 between the two directions of research, neuroeconomic studies by neuroscientists and economists
- 58 have shown insightful results regarding the neural basis of risky decision-making (Bossaerts &
- 59 Murawski, 2015; Konovalov & Krajbich, 2016; Serra, 2021).
- 60 In neuroeconomic research, the model organisms used by economists and neuroscientists are
- 61 usually different. Economists tend to focus on human behavior and therefore conduct almost all
- 62 studies with human participants (Addessi & Bourgeois-Gironde, 2020). Human neuroeconomic
- 63 studies commonly use neuroimaging. While a powerful tool for studying reward value and economic
- 64 decision making, the temporal and spatial resolution limits the information one can obtain from the
- 65 experiments. On the other hand, more precise single-neuron studies using electrophysiology or
- calcium imaging are restricted to specific human patients (Nourski & Howard, 2015). Therefore,
- 67 experiments on closely related species are important for studying subjective reward value and
- 68 economic decision making.
- 69 While many animal species are suitable for neuroeconomic studies, neuroscientists often use rhesus
- 70 macaque monkeys because the animals can understand complicated tasks and are phylogenetically
- closely related to humans (Brosnan, 2021; de Petrillo & Rosati, 2021). Recently, many important
- neuroeconomic discoveries were made in monkeys. For example, neurons in monkey orbitofrontal
- cortex (OFC) encode type, magnitude, probability and subjective value of reward (Ballesta et al.,
- 74 2020; Padoa-Schioppa & Assad, 2006; Pastor-Bernier et al., 2019; Tremblay & Schultz, 1999),
- amygdala neurons encode emotional and social choices (Grabenhorst et al., 2019), and dopamine
- 76 neurons encode utility and update value (Lak et al., 2014; Stauffer et al., 2014). These important
- studies help us to understand the neuronal mechanism of value and choice. While both
- 78 neuroscientists and economists conducted valuable studies on risky decision-making, substantial
- 79 gaps remain because of their failure to directly compare risky decision making between humans and
- 80 monkeys. Without this information, researchers would not know whether humans and monkeys
- 81 perform risky choices in a similar or different way.
- 82 Comparisons of decision making between humans and monkeys are largely limited to literature
- 83 reviews (Addessi & Bourgeois-Gironde, 2020; Bourgeois-Gironde et al., 2021), but direct
- 84 experimental comparisons have not been performed. In monkeys, studies demonstrated that
- 85 monkeys maximize expected utility (Ferrari-Toniolo et al., 2019; Stauffer et al., 2015), cooperate
- 86 with others (Grabenhorst et al., 2019), show loss aversion (Chen et al., 2006), and exhibit different
- risk attitude under different conditions (Ferrari-Toniolo et al., 2019; Pelé et al., 2014). In humans, on
- the other hand, studies investigated mathematical models and the influence of culture, education
- and social norms on risky decision making (Blavatskyy et al., 2022; Nielsen & Rehbeck, 2022; Ruggeri
- 90 et al., 2020). By contrast, only a few behavioral studies that included both humans and non-human
- 91 primates focused on simple social and economic games (Brosnan et al., 2011, 2012, 2017; Duguid et
- 92 al., 2014; Farashahi et al., 2019; Möller et al., 2022), but not on quantifiable risky choices that are
- 93 most commonly investigated in neuroeconomic research. Moreover, these studies tested only small
- 94 choice sets, which limits the generality of the comparison between species.

4

- 95 Here, we investigated the similarity of risky choices between humans and monkeys, testing the
- 96 independence axiom (IA) of expected utility theory with exactly the same design and settings
- 97 between the two species. The IA states that extending both choice options of a binary option set by
- 98 a common outcome should not change the participant's preference. However, our previous work
- had shown violations of the IA separately in humans and monkeys (Ferrari-Toniolo et al., 2022; Jain
- 100 & Nielsen, 2020). Therefore, by using this axiom as a test, we systematically compared risky choices
  101 between the two species.
- 102

## 103 Methods

104 Animals

105 Two rhesus macaques (Macaca Mulatta) weighing 12.65 kg and 13 kg were used in this experiment.

106 The monkeys were born in captivity at the UK Medical Research Council's (MRC) Centre for

107 Macaques (CFM). Monkey A ("Aragorn") and Monkey T ("Tigger") were pre-trained with visual

108 stimuli and similar joystick tasks before the experiment. The protocol was approved by the Home

- 109 Office of the UK and the experiments were continuously regulated by institutional (University of
- 110 Cambridge) and national officers including the UK Home Office Inspector, the University of
- 111 Cambridge Biomedical Services (UBS) Named Veterinary Surgeon (NVS), and the UBS Named Animal
- 112 Care and Welfare Officer (NACWO). Monkey T was implanted with a recording chamber and a
- 113 headpost before the experiment for other neuronal recording tasks.
- 114 Experimental design for monkeys
- During the experiment, each monkey sat in a chair (Crist instruments) and chose between twogamble options using a cursor driven by a left-right joystick. The two gamble options were presented
- 117 on a computer monitor 50 cm in front of the animal. In each option, reward magnitude (varying
- between 0 and 0.5 ml water) and probability (varying between 0 and 1) were represented by the
- height and width of a horizontal bar, respectively (Fig. 1A). At the beginning of each trial, a white
- 120 fixation cross appeared at the center of the monitor, and the cursor was displayed to facilitate
- 121 centering the left-right joystick. After two gamble stimuli were shown, the animal chose using the
- 122 joystick. Further details of the experiment can be found in our previous studies using similar setups
- 123 (Ferrari-Toniolo et al., 2019, 2022).
- 124 We set up our list of tests according to the IA:

125 
$$\forall A > B \Rightarrow \lambda A + (1 - \lambda)G > \lambda B + (1 - \lambda)G; \forall G, \forall p \in [0, 1]$$
 Eq. 1

126 where A and B represent the two original options;  $\lambda$  (lambda) represents the probability of the 127 original option in the new gamble option; G represents a gamble that commonly extends both 128 original choice options. In this study, option A was always a safe option with a middle reward magnitude (0.25 ml); option B was a three-outcome (0, 0.25ml, 0.5ml) option. Option A and B were 129 130 extended by a new gamble G according to Eq.1, thus forming options C and D: option C =  $\lambda A$  + (1-131  $\lambda$ )G, and option D =  $\lambda$ B + (1-  $\lambda$ )G. For gamble G, we set reward magnitude to 0 (no reward) and used three different probabilities  $\lambda$ : 0.75, 0.5 and 0.25, together with the original test set ( $\lambda$  = 1), thus 132 133 forming four different test settings. All choice options were pseudorandomly intermixed.

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## 136

## 137 Experimental design for humans

We conducted 180 different online tests on 126 human participants. Each participant performed 138 139 34.254 ± 7.2354 tests for each of the 4 lambdas (mean ± Standard Deviation). These tests were 140 selected from a previous study (Jain & Nielsen, 2020) and had similar probability distributions as 141 used for monkeys, including option A having only one reward amount delivered with p = 1.0 (Fig. 142 1B). Specifically, the monkeys were tested with reward magnitudes of 0 ml, 0.25 ml and 0.5 ml, and 143 the human participants were tested with reward magnitudes of \$0, \$10 and \$20. All tests were pseudorandomly ordered with each participant. In each trial, two different options were shown to 144 145 the participant on a computer monitor. Each option was shown as a pie chart, indicating the 146 probability of reward, together with numbers indicating each option. Participants were paid for one 147 randomly selected choice after completing the session, as described in previous economic studies 148 (Azrieli et al., 2020).

## 149 Statistical test of IA violations

- 150 To test IA violations, we assessed the probabilities P(AD) and P(BC) that represent the two directions
- 151 of violations across sessions in each monkey and across individual human participants. The violation
- AD indicates an Allais-type reversal: a participant who prefers the safe option A in option set AB
- prefers the "riskier" option D in option set CD, which can be stated as: p (A|{A,B}) > 0.5 and p
- 154 (D|{C,D}) > 0.5. By contrast, the violation BC indicates a reverse Allais-type reversal: a participant
- 155 who prefers option B in option set AB prefers option C in option set CD, which can be stated as: p
- (B|{A,B}) > 0.5 and p (C|{C,D}) > 0.5. The probability of a preference reversal in each direction, P(AD)
- 157 or P(BC), was computed as proportion of monkey choice sessions or as proportion of single-shot
- 158 human choices that switched in the corresponding direction.
- 159 To confirm the preference changes across sessions in each monkey and across individual human
- 160 participants, we performed two binomial tests for the two option sets (AB, CD). Significant
- 161 preference changes in both option sets would be counted as a (strong) violation of IA (P < 0.05; one-
- 162 sided binomial test).

# 163 Comparison of risky choices between humans and monkeys using a General Linear Model (GLM)

- 164 We used Matlab to build GLMs (fitglm with normal distribution and linear link function) with human
- data to predict monkey behavior. The GLMs predicted the probability y of choosing option B or D
- based on three regressors, namely lambda ( $\lambda$  in Eq. 1), the probability p of obtaining the highest
- 167 outcome, and the probability p of obtaining the lowest outcome) (fig. 1C):

168 
$$y = \beta_0 + \beta_1 \lambda + \beta_2 p$$
 (highest outcome) +  $\beta_3 p$  (lowest outcome) +  $\varepsilon$  Eq. 2

- After fitting the model (Eq. 2) to the human data, we entered the reward probabilities for the
  monkeys into Eq. 2 and predicted the probability of choosing option B or D. Inversely, after fitting
  the model to the monkey data, we entered the reward probabilities for the humans into Eq. 2 and
  predicted the probability of choosing option B or D. The predicted probabilities of choices were
- 173 compared with the actual choice probabilities using Pearson's correlation analysis. We compared the
- 174 predictions of the human-fitted model to each monkey separately, and we compared the prediction
- 175 of the monkey-fitted model to all humans' data. To further investigate how each variable
- 176 contributed to the GLM, we also assessed the beta coefficients (slope) for the regressors of the
- 177 models. In order to fit the single-shot human choices, we calculated the GLM using the binomial

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distribution and logit link function, repeating the procedure for each human participant and for each
monkey session. We then plotted the betas of each model in a three-dimensional scatter plot after
normalization (deducting the minimum value and log10 transformation) and after removing outliers
with more than three median absolute deviations (Fig. 3).

## 182 Cumulative prospect theory model

Similar to previous studies (Ferrari-Toniolo et al., 2019, 2022), we used a softmax function to
describe the choices as follows: the probability (p) of choosing an option M over an option N, given
the option set MN, was defined as:

186  $p(M|MN) = 1/(1+e^{-\gamma(VA-VB)})$  Eq. 3

where γ is the noise parameter and V is the prospect value (i.e. the subjective value as defined in the
cumulative prospect theory model. We defined the prospect value (V) using the utility function (u)
and probability weighting function (w) in a cumulative form (Kahneman & Tversky, 1979; Tversky &
Kahneman, 1992):

191  $V = \sum_{i} \pi_{i} \cdot u(outcome_{i})$  Eq. 4

192 
$$\pi_{i} = w(p_{i} + \dots + p_{n}) - w(p_{i+1} + \dots + p_{n})$$

where n is the number of outcomes and i is the corresponding current outcome (ordered from worstto best).

Eq. 5

As in previous studies (Ferrari-Toniolo et al., 2019; Hsu et al., 2009), we used a power function as utility function, with parameter  $\rho$  (>1 convex, <1 concave):

197 
$$u (outcome_i) = (\frac{outcome_i}{max (outcome)})^{\rho}$$
 Eq. 6

198 For the probability-weighting function, we used the two-parameter Prelec function with  $(\alpha, \beta)$ :

199  $w(p) = e^{-\beta(-\ln(P))^{\alpha}}$  Eq. 7

200 The  $\alpha$  and  $\beta$  represent the shape ( $\alpha < 1$ : inverse S shape,  $\alpha > 1$  regular S shape) of the probability-201 weighting function and the position of the inflection point, respectively.

202 Similar to our previous work (Ferrari-Toniolo et al. 2022), we estimated the parameters of the utility

203 function and weighting function by maximum likelihood estimation (MLE). Choice data from each

204 human participant or each monkey session were entered into Matlab (fminsearch function) to

205 estimate the four parameters ( $\gamma$ ,  $\rho$ ,  $\alpha$ ,  $\beta$ ).

206

### 207 Results

## 208 Experimental design

209 We used a common experimental design to compare risky decisions between humans and monkeys.

210 For monkeys, we showed two stimuli on a computer monitor at 0.5 - 1.0 s after appearance of a

211 central fixation cross. Subsequently, the animal chose between the two options using a joystick and

received the reward 1s later. As shown in Fig. 1A, each of the option stimuli contained one, two or

213 three horizontal bars whose width and height represented reward probability (p = 0 - 1) and

- 214 magnitude (m = 0 0.5 ml), respectively. For example, a full-width horizontal bar in the middle would
- represent a safe option (p = 1) of a middle reward (m = 0.25 ml) (Fig. 1A right). For humans, we

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- 216 presented each option as a pie chart and numbers that indicated reward amount (US\$ 0 - 20) and
- 217 probability (p = 0 - 1) (Fig. 1B).
- 218



### 219

220 Figure 1. Experimental design.

221	(A)	Example stimuli shown on the computer monitor to monkeys. Width and height of horizontal bars
222		represent outcome probability and magnitude, respectively. The example shows options A and B.
223	(B)	Example stimuli shown to human participants (options A and B).

- (B) Example stimuli shown to human participants (options A and B).
- 224 (C) Stimuli showing two option sets for independence axiom testing. Option A had only the middle 225 outcome with p = 1. Option C had a middle outcome with a specific probability and a low outcome of 226 m = 0 ml and p (low outcome) = 1 - p (middle outcome). Options B and D each had three outcomes 227 with specific probabilities. Preferring option A (A > B) and option D (C < D) represents an example 228 violation of the independence axiom.
- 229 (D) Marschak-Machina triangle with the two option sets shown in panel C. Dot positions in the triangle 230 represent the outcome probabilities for options A, B, C and D. The probability of the middle outcome 231 is 1 - p (low outcome) – p (high outcome). Thus, option A is a safe option with p = 1.0 of getting the 232 middle outcome.
- 233 Each test of the independence axiom (IA) employed two option sets. As shown in the example
- stimuli (Fig. 1C) and Marschak-Machina triangle (Fig. 1D), one option set (options C and D) was 234
- derived from the original option set (options A and B) according to the definition of the IA (Eq. 1). To 235
- 236 comply with the IA, the participant's preference should not change (e.g. if option A is preferred to

- option B, then option C should also be preferred to option D). In order to test the IA fully, we varied
   the options widely across the full Marschak-Machina triangle in both humans and monkeys.
- 239 Characteristics of risky choice in humans and monkeys
- 240 The monkeys performed a total of 92 tests in each daily session (23 tests for each of the 4 lambdas)
- 241 (30,997 trials in 34 sessions for Monkey A; 11,492 trials in 26 sessions for Monkey T). On average,
- each session consisted of a total of 911.68 ± 178.69 trials in Monkey A, and 442.00 ± 123.93 trials in
- 243 Monkey T (mean ± Standard Deviation).
- 244 Both monkeys preferred options A and C more (compared to the respective options B and D) when

the probability of the high outcome of options B and D decreased, as shown by the decrease of dot

- size towards the bottom in the Marschak-Machina triangle (Fig. 2A, B). This observation suggested
- that the animals understood the stimuli and the task.



248

Figure 2. Differential risk attitude across reward probabilities in the Marschak-Machina triangle.

250 (A) Choice between options A and B ( $\lambda$  = 1.0).

251 (B) Choice between options C and D ( $\lambda = 0.5$ ).

252 The size of black dots in the Marschak-Machina triangles represents the probability of choice in 34 daily

253 sessions for Monkey A, 26 daily sessions for Monkey T, and 126 human participants. Red solid dots show

254 choice indifference points (IPs); red lines show indifference curves from averaged session IPs in monkeys, and

averaged IPs of all human participants.

9

- 256 Using the softmax function (Eq. 3), we estimated choice indifference points between option A (P
- 257 (middle outcome) = 1.0; red circles in Fig. 2A) and option B (three outcomes; black dots) in each
- 258 monkey in one daily session. The three lambda values tested ( $\lambda = 0.25$ ,  $\lambda = 0.5$ ,  $\lambda = 0.75$ ) allowed
- three comparisons against  $\lambda = 1.0$  (option set AB in Fig. 1C). Then we applied the three lambda
- values (0.25, 0.5 or 0.75) to options A and B to obtain option C (p (middle outcome) = 0.25, 0.5 or
   0.75; p (low outcome) = 1 p (middle outcome)) and option D (three outcomes) (Fig. 1C, D) and
- estimated choice indifference points between option C (red circles in Fig. 2B) and option D in each
- 263 monkey. All indifference points are shown as small red dots in Figs. 2 and S1.
- 264 Interestingly, the probability of risky choices and the shape of indifference points differed between
- the two animals (Fig. 2A, B, top vs. middle). The difference was also apparent in the indifference
- 266 curves (IC) connecting the averaged indifference points across sessions (red lines). Monkey A
- showed convex ICs with  $\lambda = 1.0$  but inverse-S-shaped ICs with  $\lambda = 0.5$ . Monkey T showed inverse-S-
- shaped ICs with both  $\lambda$  =1.0 and  $\lambda$  =0.5. These data demonstrated subject-specific risk attitudes.
- 269 Many economics tests on humans use only one trial per participant in a larger number of
- 270 participants (as compared to many repeated trials in much fewer individual monkeys). Accordingly,
- 271 we performed 180 tests in our 126 human participants (45 tests for each of the 4 lambdas without
- any repetition of trial. As shown in Fig. 2, our human participants showed a similar trend (choosing
- the less risky option with higher probability of getting the high outcome), although their ICs differed
- 274 substantially from those of our monkeys.
- 275

## 276 GLMs reveal similarity of risky choices across species

277 To quantitatively measure the similarity of risky choices between humans and monkeys, we first 278 fitted a generalized linear model (GLM; Eq. 2) to the data of one species and then used the model to 279 predict the other species' behavior. Fig. 3A shows strong significant correlations between the 280 predicted probability of choices (choosing safer option; same option set across sessions in monkey, 281 across participants in human) and the actual probability of choices. The GLM fitted to the human data top panel) predicted well the behavior of both monkeys (Rho = 0.809, p =  $3.76 \times 10^{-20}$  for 282 Monkey A; Rho = 0.833, p =  $3.17 \times 10^{-22}$  for Monkey T). Vice versa, the GLM fitted to the data of one 283 monkey (bottom panel) predicted well the behavior of the humans (Rho = 0.732, p =  $1.57 \times 10^{-31}$  for 284 data by Monkey A; Rho = 0.688,  $p = 1.35 \times 10^{-26}$  for data by Monkey T). These results indicated 285

similar risky choices between the two species.

287 Next, we investigated whether humans' and monkeys' choices similarly reflected changes in the 288 options' parameters (probability of getting different reward magnitudes). To do so, we analyzed the 289 beta coefficients of the GLMs. While the GLMs described the prediction of risky choices, the beta 290 coefficients (regressors) of the GLMs indicated how much each parameter contributed to the risky 291 choice. We fitted one GLM for each human participant and one GLM for each monkey session. As 292 choices were not repeated in the individual human participants, we set up the model to predict 293 single binary choices; the analysis used a binomial distribution and logit link function in the GLM. We 294 found similar ranges of beta coefficients across the two species (Fig. 3B), suggesting similarity in risky 295 choices between humans and monkeys.

10



- Figure 3. General Linear Models (GLM's) of human data (probability of safer choices) predict monkeys'behavior and vice versa.
- (A) Correlations of choice probabilities predicted by GLM and actual choices. Each circle represents one
   test in the Marschak-Machina triangle (see Figs. 2 and S1). Pearson's Rho, least squares lines.
- 301 (B) Beta coefficients of GLMs fitted to data from humans (each participant; blue open circles) and
   302 monkeys (each session; red or black dots for Monkey A and Monkey T, respectively). The average
   303 betas for monkeys are represented by large open circles (red for Monkey A and black for Monkey T).
   304 PH and PL represent reward probability: PH represents p (high outcome) and PL represents p (low
   305 outcome) for the riskier option.

#### 306 Choice differences between the species

- 307 We compared choice probabilities between lambda = 1 (i.e. option set AB) and other lambdas (0.75,
- 308 0.5, 0.25; option set CD) and checked for any choice shifts to identify violations. We quantified
- 309 violations in two directions, the Allais paradox as originally described (Allais, 1953), and the reverse
- Allais paradox (Blavatskyy, 2013). Both monkeys showed significant IA violations in both directions;
- 311 when preferring option A to B, they also preferred option D to C ('Allais-type'; P < 0.05, binomial
- test; Fig. 4A); vice versa, when preferring option B to A, they also preferred option C to D ('reverse
- Allais-type'; Fig. 4B); see Fig. S2 for additional tests in both directions. These violations differed
- between the two monkeys (Fig. 4, top vs. middle). Interestingly, choice variability may partly explain
- 315 IA violations in monkeys (Fig. S3).



316

- Figure 4. Violations of independence axiom in monkeys and humans displayed in the Marschak-Machinatriangle.
- 319 (A) Allais-type violations.
- 320 (B) Reverse-Allais-type violations.

321 Dot size represents violation probability across 34 sessions in Monkey A, 26 sessions in Monkey T, and 126

- human participants, respectively. Hollow black circles indicate no violation for that option set. \* significance (P  $\sim 0.05$ ; binomial text). Data shown are for lambda = 0.5; for full results, see Fig. S2
- 323 < 0.05; binomial test). Data shown are for lambda = 0.5; for full results, see Fig. S2.

A number of human participants violated the IA (non-null probability of violation), as shown before (Blavatskyy et al., 2022; Jain & Nielsen, 2020; Nielsen & Rehbeck, 2022), although their averaged choices failed to reveal significant IA violations (P > 0.1; binomial test) (Fig. 4 bottom). Tour surprise, the violation patterns between humans and monkeys were quite different. For example, in Fig. 4, more violations were found at the left bottom corner in the Marschak-Machina triangle in humans than in monkeys. In contrast to the GLMs fitted to the human choice probabilities (Eq. 2), the GLMs

- fitted to the human IA violations (Eq. 2) failed to predict our monkeys' behavior (Rho = 0.0786, P =
   0.5541, Pearson's correlation analysis). Thus, despite the described inter-species similarities in risky
- 332 choices, the more stringent IA tests nevertheless demonstrated some differences between the
- 333 species.



### 334

335 Figure 5. Utility and probability-weighting functions in humans and monkeys.

- Each black line indicates the function in each human participant or in each monkey session. The estimations
  used power utility functions and two-parameter Prelec probability-weighting functions (Eqs. 3 7). Blue lines
- and purple bands show averaged functions and 95% confidence intervals, respectively.
- 339

340 Utility differences explain the choice differences between the species

In order to explain the differences between the two species, we fitted power utility functions and
 two-parameter Prelec probability-weighting functions to the choices of both humans and monkeys

- according to Cumulative Prospect Theory (Eqs. 3 7; see Methods) (Fig. 5). The two species showed
- 344 very different utility functions. Specifically, the utility parameter  $\rho$  differed significantly between the
- two species (P = 2.0950 x  $10^{-13}$ , Wilcoxon rank sum test), whereas the shape parameter  $\alpha$  of the
- probability-weighting function varied only insignificantly between the two species (P = 0.4409). The
- 347 more concave utility functions in humans compared to monkeys indicated more pronounced risk
- 348 avoidance in our human participants. However, some utility function in individual human
- 349 participants resembled those of individual monkeys (Fig. 5, individual black lines).
- 350

# 351 Discussion

This study investigated similarities and differences in risky choices between humans and monkeys. We compared risky choices between the two species in a systematic way by using exactly the same experimental design. Although we found overall similar choices in the two species, specific tests of the independence axiom (IA) revealed substantial differences in utility functions between the two

356 species, whereas their probability weighting functions were similar.

357 Current electrophysiological research in monkeys aims to elucidate neuronal mechanism of risky 358 choices. For example, recent monkey studies demonstrated that neurons in the orbitofrontal cortex, amygdala and anterior insular cortex compute reward value in risky choices (Ballesta et al., 2020; 359 360 Grabenhorst et al., 2019; Suzuki et al., 2017; Yang et al., 2022). Follow-up studies propose more 361 advanced reinforcement learning and economic models based on neuronal recording data (Dabney 362 et al., 2020; Serra, 2021). While these studies provided critical information about neuronal decision 363 mechanisms, it remains unknown to which extent these results in monkeys may explain human 364 economic decision mechanism. Surprisingly, no previous study systematically compared human 365 choice behavior and monkey choice behavior under risk. Therefore, our results demonstrating 366 similar risky choices in humans and monkeys may provide foundations for these neurophysiological

367 studies.

368 Previous economics studies demonstrated that risk attitude depends on many factors, such as

369 sequence of option presentation, loss or gain frames, social and cultural factors, and personality

370 (Malenka et al., 1993; Mikels & Reed, 2009; Ruggeri et al., 2020; van den Bos et al., 2013). Even in

371 well-controlled experimental setting, monkeys show differences in performing risk choices

372 compared to humans, as shown in Figs. 4 and 5. Therefore, even with a strict experimental design

and an absence of cultural influence, individual risk attitudes still exist that can be explained by

differences in the subjective evaluation of rewards as shown by the differences of utility functions.

375 Our previous work showed similar violations of the IA in monkeys and humans in specific settings of

the IA (Ferrari-Toniolo et al., 2022). Our current study used a far larger range of IA tests in humans

and option sets that directly reflected the axiom definition in monkeys. Using this extended design,

378 we still found violations of the IA in monkeys that occurred in both directions (Allais and reverse

- Allais). These results confirm that expected utility theory cannot explain all choices under
- 380 uncertainty and that the IA violations are not restricted to special circumstances (common
- 381 consequence and common ratio effects). The monkeys had different individual risk attitudes and
- 382 violation patterns, which is consistent with previous human studies on risky decision-making
- 383 (Blavatskyy et al., 2022; Ruggeri et al., 2020). It would be interesting to investigate whether

384 monkeys' behavior is more similar to some (but not all) humans.

In line with cumulative prospect theory, we interpreted IA violations as resulting from the subjective
non-linear evaluation of reward probabilities, formally represented by the probability weighting
function. On the other hand, the subjective non-linear evaluation of reward magnitudes (i.e. the
utility function) cannot by itself generate IA violations but can contribute to their specific patterns.
Our data revealed systematic IA violations in both humans and monkeys, suggesting a common
probability weighting mechanism, while different utility functions generated different patterns of
violations in the two species. Overall, these data suggest a brain mechanism for the evaluation of

392 risky choice options that is compatible with cumulative prospect theory and, importantly, is common

to humans and monkeys.

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- 394 While most previous economic studies focused only on single deterministic choices (Blavatskyy et
- al., 2022; Blavatskyy, 2007), our study on monkeys tested choices repeatedly. The repeated choices
- 396 reduced the chance of mistakes and noise that might explain some axiom violations (Blavatskyy,
- 397 2007; Hey & Orme, 1994). The probability of IA violations was positively correlated with choice
- variability (standard deviation of choice probability; Fig. S3), which might be explained by the
- 399 observation that most violations occurred close to the indifference points and curves of the
- 400 Marschak-Machine triangle (Figs. 2 and S1) (McGranaghan et al., 2022). To conclude, our extensive
- 401 and inter-species study confirms the well-known systematic and subject-specific violations of the IA.
- 402 Critically, our study showed not only similarities but also differences between the two species,
- 403 notably in subjective value (utility). The differences may be due to at least two factors. First, typical
- for monkey studies, we used large numbers of trials that provided substantial experience for the animals. By contrast, typical human studies use single-shot choices that fail to provide much
- 406 experience with the tested option sets. This difference in experience between the two species may
- 407 partly explain their different utility functions. Second, reward types and their amounts differed
- 408 between the two species. Our human participants were tested with money, whereas our monkeys
- 409 were tested with juice. Further, humans and monkeys seem to be risk seeking with small reward
- amounts and become gradually more risk avoiding with larger amounts, which is expressed by the
- 411 curvature of utility functions that changes from convex via linear to concave (Stauffer et al., 2014;
- 412 Farashahi et al., 2018). The risk-seeking with small reward amounts is recognized as the peanuts
- 413 effect (Prelec, 1991). Thus, despite the difficulties of inter-species comparisons, different reward
- types and amounts may have contributed to the differences in utility functions. Future research may
- elucidate in more detail the differences between human and monkey utility functions with a more
- 416 quantitative approach towards task experience and reward amount.
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#### 18

#### 541 Supplementary figures



542

### 543 Figure S1. Differential risk attitude across probabilities in the Marschak-Machina triangle.

544 (A) Choices in the two monkeys: 34 sessions for Monkey A and 26 sessions for Monkey T.

545 (B) Choices in the 126 human participants: four safer options (\$10, p = 1; \$10, p = 0.75; \$10, p = 0.5;
546 \$10, p = 0.25).

Each panel shows the probability of choosing a risky option. Each trial offered two options, a safer option (blue solid dot) and a riskier option (one of the black solid dots). We tested four safer options (0.25ml, p=1; 0.25ml, p = 0.75; 0.25ml, p = 0.5; 0.25ml, p = 0.25), as represented by the four Marschak-Machina triangles (lambda = 1.0, lambda = 0.75, lambda = 0.5, and lambda = 0.25). The probability of choosing the risky option across sessions is represented by the size of the black solid dot. Indifferent points (IP) in each session, indicating p = 0.5 of choosing the risky option (as estimated by softmax function), are represented by red dots. Red hollow circles represent average IPs across all sessions; blue dots represent the safer options.

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557 Figure S2. Violations of independence axiom across probabilities

Frequency and direction of the independence axiom violation across different probabilities. Dot size
represents the probability of violation across (monkey) sessions or (human) participants, comparing different
lambdas to the initial choice between options A and B (lambda = 1.0). (A) Red dots represent the probability of
Allais-type violations. (B) Blue dots represent the probability of reverse-Allais-type violations. Hallow black
circles indicate no violation for that choice set. \* significance P < 0.05; binomial test in the two test sets. The</li>
correlation between predicted and actual violation was significant (GLM model with human data to predict
monkey behavior, Spearman Rho = 0.201, P = 0.029), when lambda was used as the regressor.

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567 Figure S3. Choice variability partly explains independence axiom (IA) violations in monkeys.

- 568 (A) Choice variability (standard deviation) across different probabilities. Size of dots representing the
   569 variability (standard deviation) of choices averaged across sessions (34 sessions for Monkey A and 26
   570 sessions for Monkey T).
  - (B) Correlation of choice variabilities (sum of two tests) and IA violations.
- 572