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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.

50

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 (Addressi & 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
66 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
71 closely related to humans (Brosnan, 2021; de Petrillo & Rosati, 2021). Recently, many important
72 neuroeconomic discoveries were made in monkeys. For example, neurons in monkey orbitofrontal
73 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),
75 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
77 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 (Addressi & 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
87 risk attitude under different conditions (Ferrari-Toniolo et al., 2019; Pelé et al., 2014). In humans, on
88 the other hand, studies investigated mathematical models and the influence of culture, education
89 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.

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
99 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*

115 During the experiment, each monkey sat in a chair (Crist instruments) and chose between two
116 gamble 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
118 between 0 and 0.5 ml water) and probability (varying between 0 and 1) were represented by the
119 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:

$$125 \quad \forall A > B \Rightarrow \lambda A + (1 - \lambda)G > \lambda B + (1 - \lambda)G; \forall G, \forall \rho \in [0, 1] \quad \text{Eq. 1}$$

126 where A and B represent the two original options; λ (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
129 magnitude (0.25 ml); option B was a three-outcome (0, 0.25ml, 0.5ml) option. Option A and B were
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
132 three different probabilities λ : 0.75, 0.5 and 0.25, together with the original test set ($\lambda = 1$), thus
133 forming four different test settings. All choice options were pseudorandomly intermixed.

134

135

136

137 *Experimental design for humans*

138 We conducted 180 different online tests on 126 human participants. Each participant performed
139 34.254 ± 7.2354 tests for each of the 4 lambdas (mean \pm 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
144 pseudorandomly ordered with each participant. In each trial, two different options were shown to
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
152 AD indicates an Allais-type reversal: a participant who prefers the safe option A in option set AB
153 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
156 $(B|\{A,B\}) > 0.5$ 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
165 data to predict monkey behavior. The GLMs predicted the probability y of choosing option B or D
166 based on three regressors, namely lambda (λ in Eq. 1), the probability p of obtaining the highest
167 outcome, and the probability p of obtaining the lowest outcome) (fig. 1C):

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

169 After fitting the model (Eq. 2) to the human data, we entered the reward probabilities for the
170 monkeys into Eq. 2 and predicted the probability of choosing option B or D. Inversely, after fitting
171 the model to the monkey data, we entered the reward probabilities for the humans into Eq. 2 and
172 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

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

182 *Cumulative prospect theory model*

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

$$186 \quad p(M|MN) = 1 / (1 + e^{-\gamma(V_A - V_B)}) \quad \text{Eq. 3}$$

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

$$191 \quad V = \sum_i \pi_i \cdot u(\text{outcome}_i) \quad \text{Eq. 4}$$

$$192 \quad \pi_i = w(p_i + \dots + p_n) - w(p_{i+1} + \dots + p_n) \quad \text{Eq. 5}$$

193 where n is the number of outcomes and i is the corresponding current outcome (ordered from worst
194 to best).

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

$$197 \quad u(\text{outcome}_i) = \left(\frac{\text{outcome}_i}{\max(\text{outcome})} \right)^\rho \quad \text{Eq. 6}$$

198 For the probability-weighting function, we used the two-parameter Prelec function with (α , β):

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

200 The α and β 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 (γ , ρ , α , β).

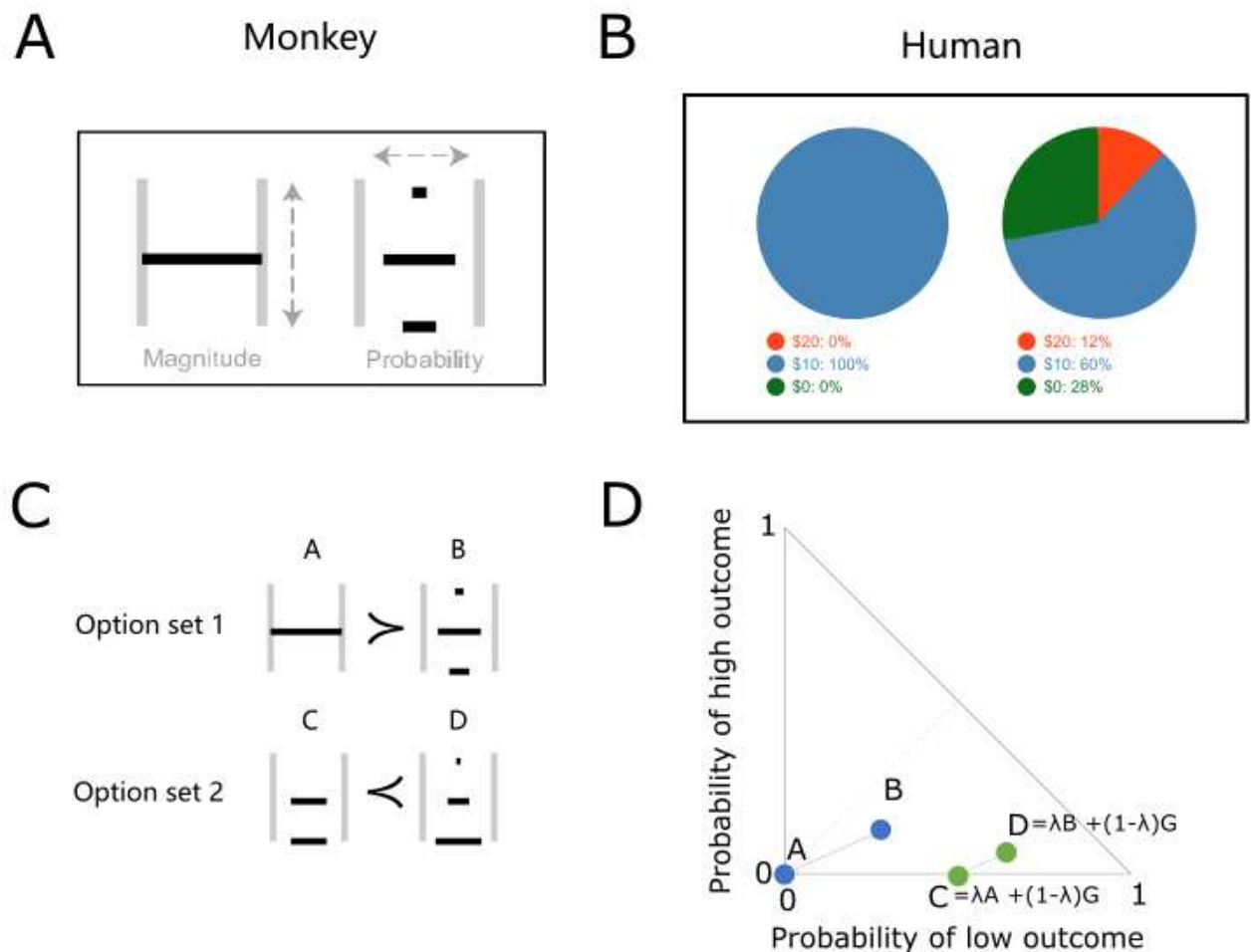
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207 **Results**

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
212 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
215 represent a safe option ($p = 1$) of a middle reward ($m = 0.25$ ml) (Fig. 1A right). For humans, we

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).
 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.

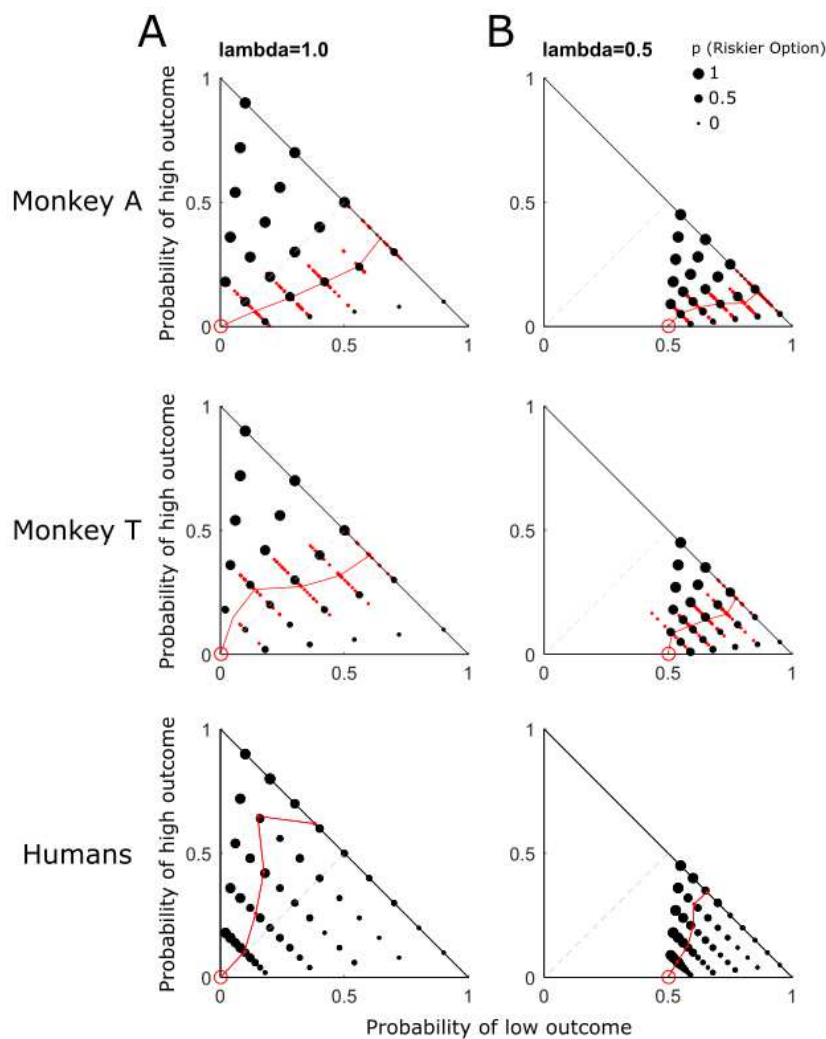
233 Each test of the independence axiom (IA) employed two option sets. As shown in the example
 234 stimuli (Fig. 1C) and Marschak-Machina triangle (Fig. 1D), one option set (options C and D) was
 235 derived from the original option set (options A and B) according to the definition of the IA (Eq. 1). To
 236 comply with the IA, the participant's preference should not change (e.g. if option A is preferred to

237 option B, then option C should also be preferred to option D). In order to test the IA fully, we varied
238 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,
242 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 \pm Standard Deviation).

244 Both monkeys preferred options A and C more (compared to the respective options B and D) when
245 the probability of the high outcome of options B and D decreased, as shown by the decrease of dot
246 size towards the bottom in the Marschak-Machina triangle (Fig. 2A, B). This observation suggested
247 that the animals understood the stimuli and the task.



248

249 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
255 averaged IPs of all human participants.

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
259 three comparisons against $\lambda = 1.0$ (option set AB in Fig. 1C). Then we applied the three lambda
260 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
261 0.75; p (low outcome) = $1 - p$ (middle outcome)) and option D (three outcomes) (Fig. 1C, D) and
262 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
265 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
267 showed convex ICs with $\lambda = 1.0$ but inverse-S-shaped ICs with $\lambda = 0.5$. Monkey T showed inverse-S-
268 shaped ICs with both $\lambda = 1.0$ and $\lambda = 0.5$. These data demonstrated subject-specific risk attitudes.

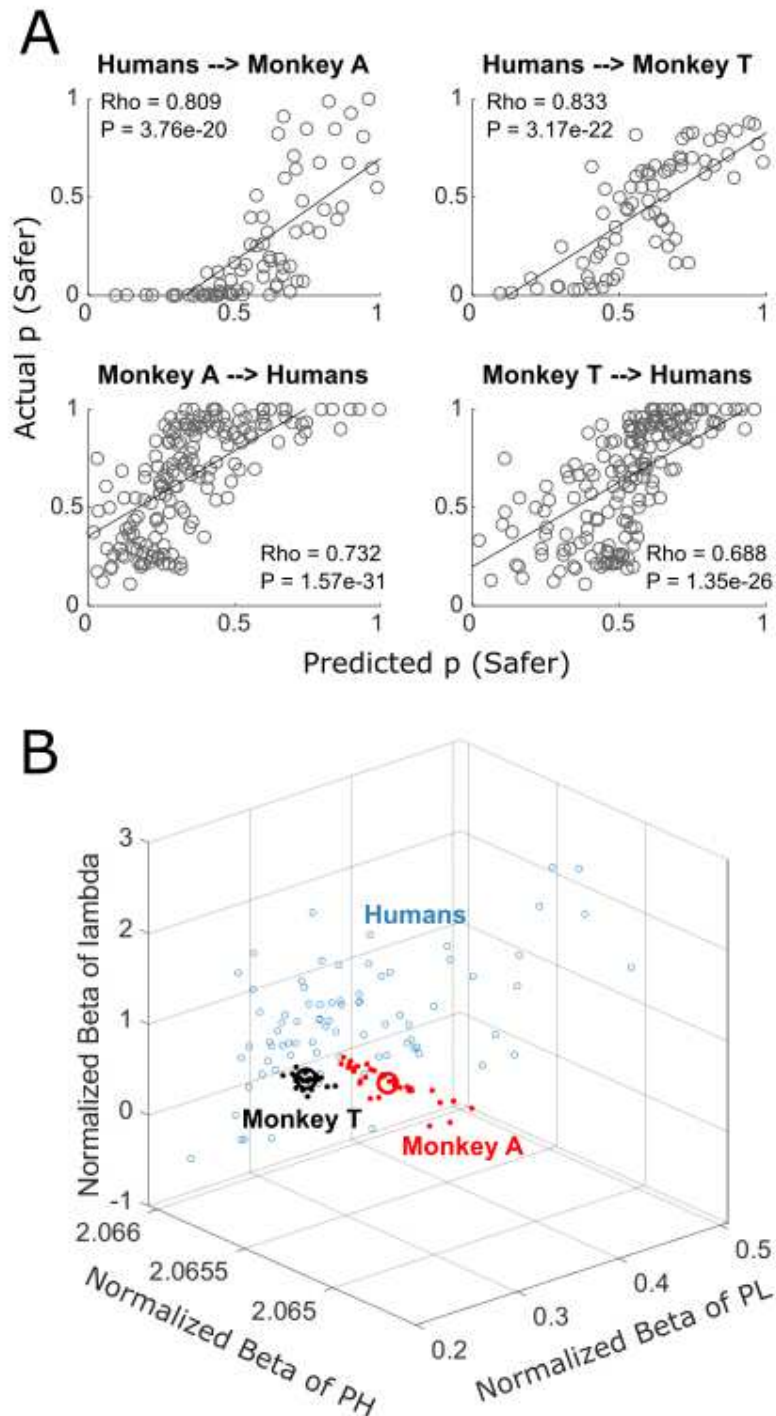
269 Many economics tests on humans use only one trial per participant in a larger number of
270 participants (as compared to many repeated trials in much fewer individual monkeys). Accordingly,
271 we performed 180 tests in our 126 human participants (45 tests for each of the 4 lambdas without
272 any repetition of trial. As shown in Fig. 2, our human participants showed a similar trend (choosing
273 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
282 data (top panel) predicted well the behavior of both monkeys ($Rho = 0.809$, $p = 3.76 \times 10^{-20}$ for
283 Monkey A; $Rho = 0.833$, $p = 3.17 \times 10^{-22}$ for Monkey T). Vice versa, the GLM fitted to the data of one
284 monkey (bottom panel) predicted well the behavior of the humans ($Rho = 0.732$, $p = 1.57 \times 10^{-31}$ for
285 data by Monkey A; $Rho = 0.688$, $p = 1.35 \times 10^{-26}$ for data by Monkey T). These results indicated
286 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.



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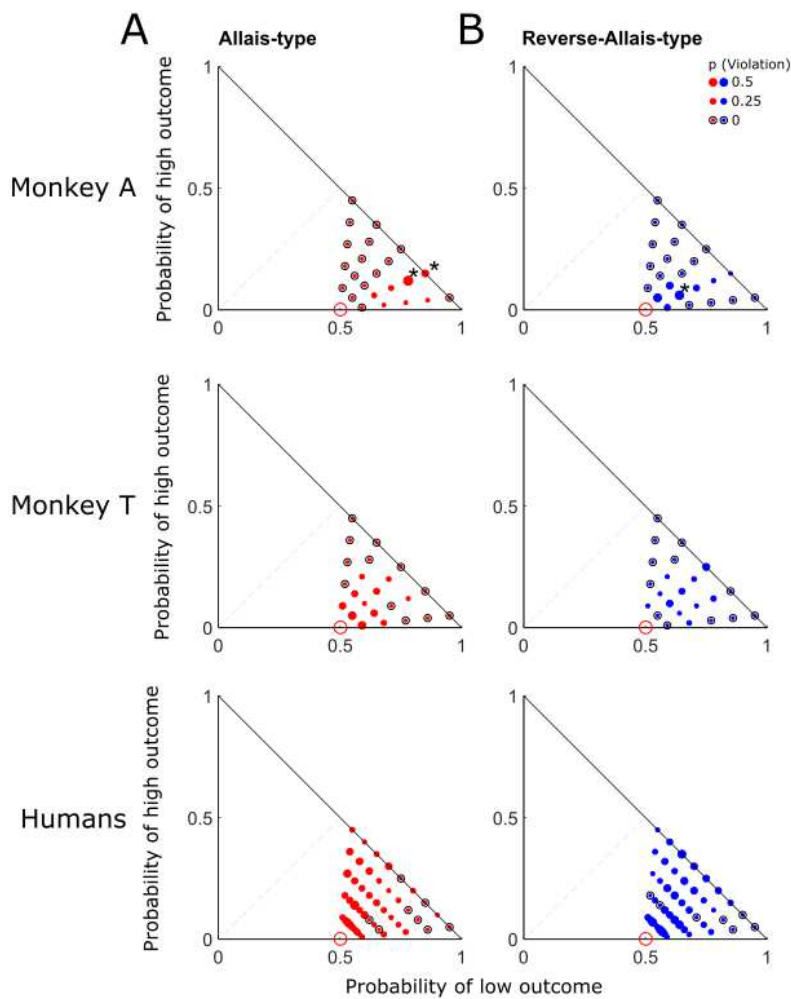
297 Figure 3. General Linear Models (GLM's) of human data (probability of safer choices) predict monkeys'
298 behavior and vice versa.

299 (A) Correlations of choice probabilities predicted by GLM and actual choices. Each circle represents one
300 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 λ s (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
310 Allais paradox (Blavatsky, 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
312 test; Fig. 4A); vice versa, when preferring option B to A, they also preferred option C to D ('reverse
313 Allais-type'; Fig. 4B); see Fig. S2 for additional tests in both directions. These violations differed
314 between the two monkeys (Fig. 4, top vs. middle). Interestingly, choice variability may partly explain
315 IA violations in monkeys (Fig. S3).



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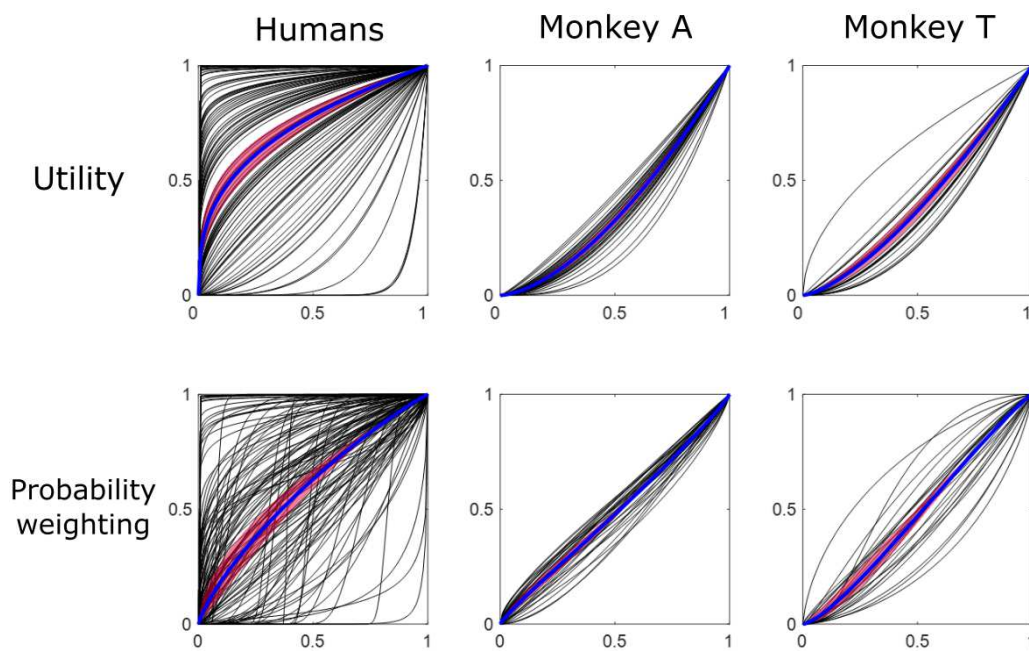
317 Figure 4. Violations of independence axiom in monkeys and humans displayed in the Marschak-Machina
318 triangle.

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

324 A number of human participants violated the IA (non-null probability of violation), as shown before
325 (Blavatsky et al., 2022; Jain & Nielsen, 2020; Nielsen & Rehbeck, 2022), although their averaged
326 choices failed to reveal significant IA violations ($P > 0.1$; binomial test) (Fig. 4 bottom). Tour surprise,
327 the violation patterns between humans and monkeys were quite different. For example, in Fig. 4,
328 more violations were found at the left bottom corner in the Marschak-Machina triangle in humans
329 than in monkeys. In contrast to the GLMs fitted to the human choice probabilities (Eq. 2), the GLMs
330 fitted to the human IA violations (Eq. 2) failed to predict our monkeys' behavior ($Rho = 0.0786$, $P =$
331 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.

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

339

340 Utility differences explain the choice differences between the species

341 In order to explain the differences between the two species, we fitted power utility functions and
342 two-parameter Prelec probability-weighting functions to the choices of both humans and monkeys
343 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 ρ differed significantly between the
345 two species ($P = 2.0950 \times 10^{-13}$, Wilcoxon rank sum test), whereas the shape parameter α of the
346 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**

352 This study investigated similarities and differences in risky choices between humans and monkeys.
353 We compared risky choices between the two species in a systematic way by using exactly the same
354 experimental design. Although we found overall similar choices in the two species, specific tests of
355 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,
359 amygdala and anterior insular cortex compute reward value in risky choices (Ballesta et al., 2020;
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
373 and an absence of cultural influence, individual risk attitudes still exist that can be explained by
374 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
376 the IA (Ferrari-Toniolo et al., 2022). Our current study used a far larger range of IA tests in humans
377 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
379 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 (Blavatsky 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.

385 In line with cumulative prospect theory, we interpreted IA violations as resulting from the subjective
386 non-linear evaluation of reward probabilities, formally represented by the probability weighting
387 function. On the other hand, the subjective non-linear evaluation of reward magnitudes (i.e. the
388 utility function) cannot by itself generate IA violations but can contribute to their specific patterns.
389 Our data revealed systematic IA violations in both humans and monkeys, suggesting a common
390 probability weighting mechanism, while different utility functions generated different patterns of
391 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
393 to humans and monkeys.

394 While most previous economic studies focused only on single deterministic choices (Blavatskyy et
395 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
398 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
404 for monkey studies, we used large numbers of trials that provided substantial experience for the
405 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
410 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
414 types and amounts may have contributed to the differences in utility functions. Future research may
415 elucidate in more detail the differences between human and monkey utility functions with a more
416 quantitative approach towards task experience and reward amount.

417

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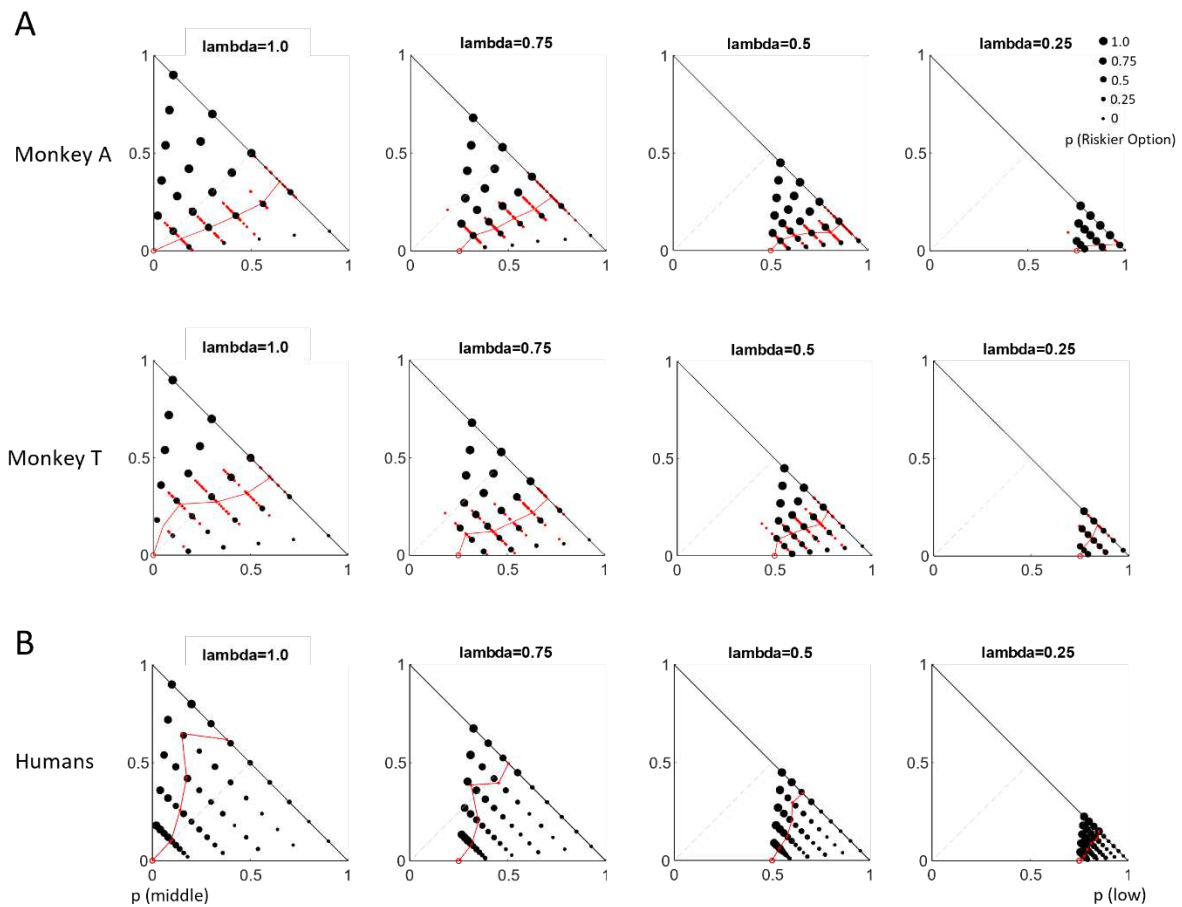
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541 **Supplementary figures**



542

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

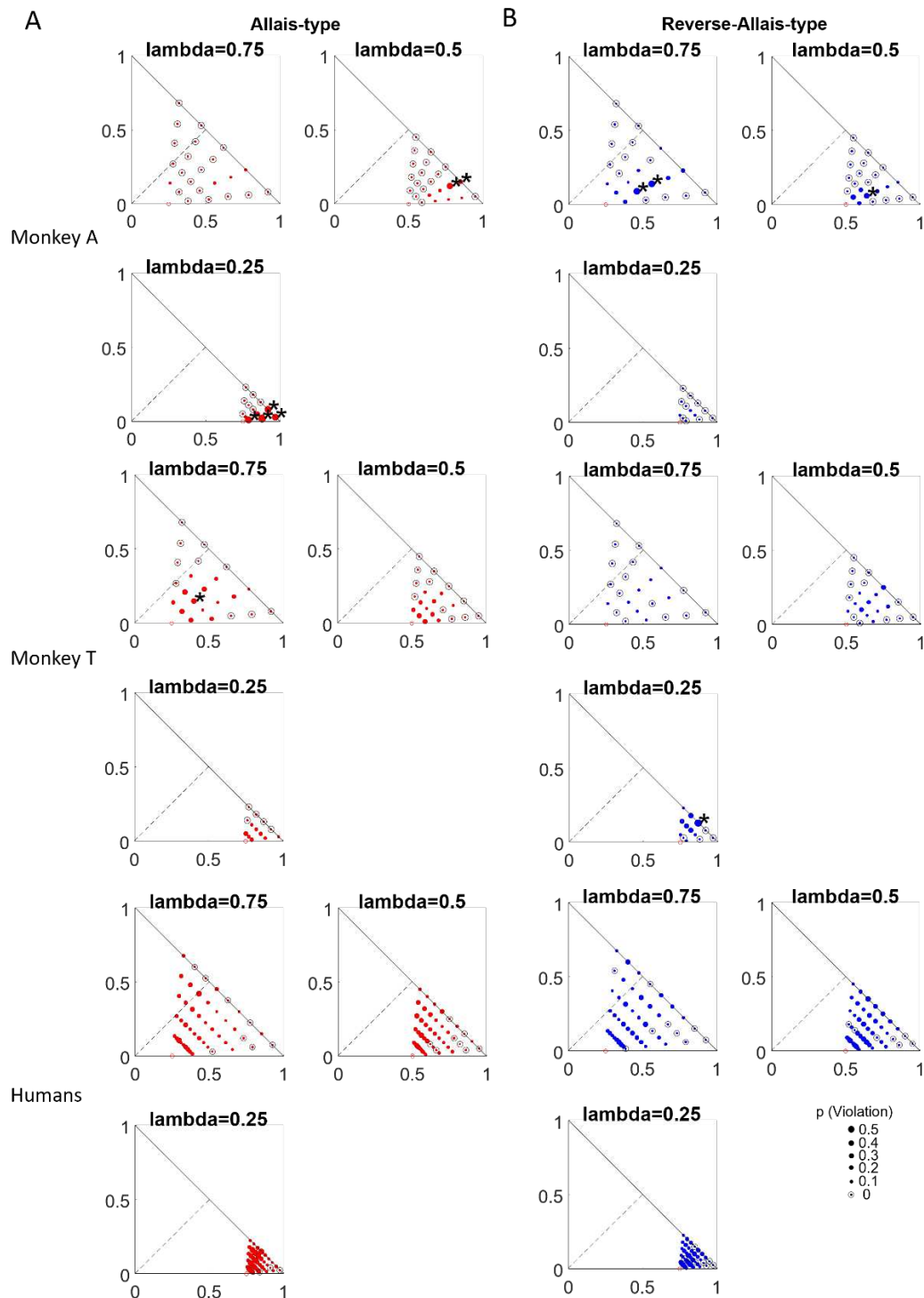
544 (A) Choices in the two monkeys: 34 sessions for Monkey A and 26 sessions for Monkey T.

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

547 Each panel shows the probability of choosing a risky option. Each trial offered two options, a safer option (blue
548 solid dot) and a riskier option (one of the black solid dots). We tested four safer options (0.25ml, $p = 1$; 0.25ml,
549 $p = 0.75$; 0.25ml, $p = 0.5$; 0.25ml, $p = 0.25$), as represented by the four Marschak-Machina triangles ($\lambda =$
550 1.0 , $\lambda = 0.75$, $\lambda = 0.5$, and $\lambda = 0.25$). The probability of choosing the risky option across
551 sessions is represented by the size of the black solid dot. Indifferent points (IP) in each session, indicating $p =$
552 0.5 of choosing the risky option (as estimated by softmax function), are represented by red dots. Red hollow
553 circles represent average IPs across all sessions; blue dots represent the safer options.

554

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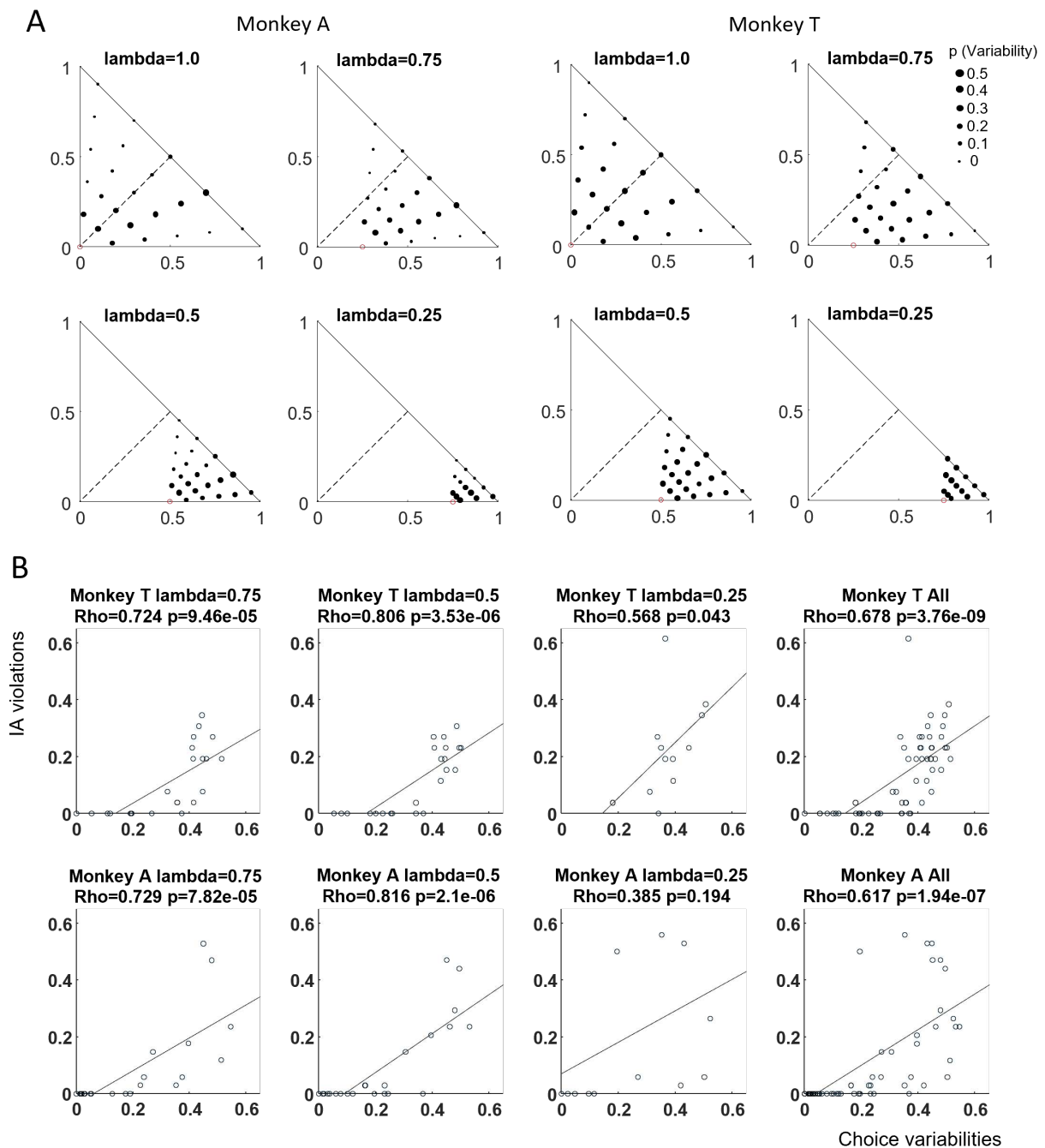


556

557 **Figure S2. Violations of independence axiom across probabilities**

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

565



566

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).

571 (B) Correlation of choice variabilities (sum of two tests) and IA violations.

572