Title page

- Title: Probability distortion depends on choice sequence in rhesus monkeys

- Abbreviated Title: Choice sequence shapes probability distortion

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1 Abstract

2 Humans and other primates share many decision biases, among them our subjective distortion of objective probabilities. When making choices between uncertain rewards, we typically treat 3 4 probabilities non-linearly: overvaluing low probabilities of reward, and undervaluing high ones. A 5 growing body of evidence, however, points to a more flexible pattern of distortion than the classical 6 inverse-S one, highlighting the effect of experimental conditions in shifting the weight assigned to 7 probabilities, such as task feedback, learning, and attention. Here we investigated the role of 8 sequence structure – the order in which gambles are presented in a choice task – in shaping the 9 probability distortion patterns of rhesus macaques. We presented two male monkeys with binary choice sequences of MIXED or REPEATED gambles against safe rewards. Parametric modeling 10 11 revealed that choices in each sequence type were guided by significantly different patterns of 12 probability distortion. Whereas we elicited the classical inverse-S shaped probability distortion in 13 pseudorandomly MIXED trial sequences of gamble-safe choices, we found the opposite pattern 14 consisting of S-shaped distortion, with REPEATED sequences. We extended these results to binary choices between two gambles, without a safe option, and confirmed the unique influence 15 of the sequence structure in which the animals make choices. Finally, we showed that the value 16 17 of past experienced gambles had a significant impact on the subjective value of future ones, shaping probability distortion on a trial-by-trial basis. Taken together, our results suggest that 18 differences in choice sequence are sufficient to reverse the direction of probability distortion. 19

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21 Significance Statement

Our lives are peppered with uncertain, probabilistic choices. Recent studies showed dynamic subjective weighting of probability. In the present study, we show that probability distortions in macaque monkeys differ significantly between sequences in which single gambles are repeated (S-shaped distortion), as opposed to being pseudorandomly intermixed with other gambles

(inverse-S shaped distortion). Our findings challenge the idea of fixed probability distortions resulting from inflexible computations, and points to a more instantaneous evaluation of probabilistic information. Past trial outcomes appeared to drive the 'gap' between probability distortions in different conditions. Our data suggest that probability values are slowly but constantly updated from prior experience – like in most adaptive systems – driving measures of probability distortion to either side of the S/inverse-S debate.

32

33 Introduction

34 Choices between uncertain rewards require decision-makers to evaluate each option along 35 multiple dimensions. At the very least, a decision-maker needs to simultaneously consider the quantity and probability of a reward's occurrence if he is to evaluate its attractiveness in relation 36 to other choice prospects. The von Neumann and Morgenstern utility theorem, commonly referred 37 to as Expected Utility (EU) theory, was the first axiomatic model of rational behavior capable of 38 describing people's choices in these situations (Von Neumann & Morgenstern, 1944). EU theory 39 rigorously introduced the concept of utility as a representation of a decision-maker's subjective 40 41 value for an objective reward quantity. Through the metric of utility, EU theory was able to describe 42 different risk attitudes, like the risk-seeking behavior of a gambler or the risk aversion of an 43 insurance buyer; it was, however, soon challenged by the various experimental results of behavioral economics (for review see e.g., Machina, 1987; Starmer, 2000; Weber & Camerer, 44 45 1987). Attempts to resolve some of these challenges led to the development of several generalized expected utility theories, many of which (notably prospect theory, rank-dependent 46 utility theory and cumulative prospect theory) incorporated the concept of probability distortion 47 (Kahneman & Tversky, 1979; Quiggin, 1982; Tversky & Kahneman, 1992). While maintaining the 48 49 non-linear relationship between subjective utility and objective reward magnitudes, these theories

made use of subjective probability weightings, or probability distortions, to account for the idea
that reward probabilities were also treated non-linearly during choice.

Experimental measures of probability distortion in humans and monkeys typically show that while 52 small probabilities tend to be overweighted by decision-makers, large probabilities are instead 53 54 underweighted (Gonzalez & Wu, 1999; Kahneman & Tversky, 1979; W. R. Stauffer, Lak, 55 Bossaerts, & Schultz, 2015). There is, however, dramatic variation in this pattern of distortion across both different subjects (Bruhin, Fehr-Duda, & Epper, 2010; Burke et al., 2018; Gonzalez 56 57 & Wu, 1999) and between different task contexts (Farashahi, Azab, Hayden, & Soltani, 2018; Hertwig, Barron, Weber, & Erev, 2004; Wu, Delgado, & Maloney, 2009). While the causes of such 58 variability have yet to be identified, differences in probability distortions could relate to the way in 59 60 which probability information is presented to decision-makers (Hertwig et al., 2004), or the way in 61 which probability knowledge is acquired and stored by the decision-maker (Camilleri & Newell, 62 2013). Some studies suggested that prospect theory might, altogether, be incapable of explaining differences in risk attitudes across these contexts (Kellen, Pachur, & Hertwig, 2016). 63

64 Here we investigated the role of choice context, specifically sequential structures, as a possible 65 source of probability distortion variability in rhesus macagues: animals known to show quantifiable and reproducible probability distortions (W. R. Stauffer et al., 2015). To achieve this, we first 66 67 measured the certainty equivalents (CE) of specific gambles, defined as the amount of reward for which the animal was choice-indifferent with regards to said gambles; the CE therefore indicated 68 the subjective value of the gamble in the 'currency' of the safe reward. We then simultaneously 69 70 estimated the contributions of utility and probability distortion to these subjective values, allowing 71 us to model the shape of the monkeys' probability distortion independently from utility.

We used this technique to investigate the possible influence of trial sequence structure on the shape of the probability distortion in two different task situations: randomly intermixing the trials required for the CE measurements of all gambles simultaneously, or determining the CEs of

different gambles via separate blocks of trials. We performed an out-of-sample test to validate and extend the results of our main task, and investigated the contribution of the trial history as a possible correlate of probability distortion variance. Our data showed that a change in the presentation order of probability information indeed altered the observed probability distortion pattern, inducing a reversal in probability distortion shape.

80

81 Materials and Methods

82 Animals and Experimental Setup

83 Two male rhesus macaques (Macaca mulatta) were used in this study (11.2kg and 13.2kg). During experiments, the monkeys sat in a primate chair (Crist Instruments) and made choices 84 between rewarding stimuli presented on a computer monitor positioned 30cm in front of them. 85 86 The animals reported their choices between options with a left-right motion joystick (Biotronix 87 workshop, Cambridge). Joystick position and task event times were sampled and stored at 1kHz on a Windows 7 computer running custom-made software written in MATLAB (The MathWorks, 88 89 Natick, MA) using Psychtoolbox (v3.0.11). All experimental protocols were assessed and approved by the Home Office of the United Kingdom. 90

91 Experimental Design

We trained the monkeys to associate visual stimuli with specific juice rewards that varied along two dimensions: the quantity of juice delivered (reward magnitude, *m*), and the delivery probability of the reward (reward probability, *p*). To capture both dimensions descriptively, the visual stimuli consisted of a horizontal bar or of a pair of horizontal bars framed between two vertical framing lines. The vertical position of the horizontal bars signaled the magnitude of juice delivered; the width of the bar signaled the probability of their delivery from no bar (no reward) to touching the frame on both side (certain reward). To ensure that the bar edge position was not used as a cue

for the gamble's mathematical expected value (EV), i.e. the product of *m* and *p*, the bars were randomly shifted horizontally on each trial. This guaranteed that magnitude and probability information were independently presented and used to make choices. Multiple partial bars found between the vertical frames signaled gambles between 'risky' rewards, while a singular, full width horizontal bar signaled a safe, riskless reward. Across all trials, monkeys experienced rewards ranging from 0 ml to 0.5 ml in 0.05 ml increments, and gamble probabilities varying between 0.1 and 1 in decimal increments (0.1).

The animals learned to associate rewards and magnitudes with the visual stimuli schema through more than 5000 single-outcome, or imperative, trials. For these trials, only one option was presented on either side of the screen. To obtain the cued reward, the animals were required to select the side on which the reward was presented. All reward options were repeated on both the left and right sides of the computer screen, alternating pseudorandomly to control for any sidepreference.

112 Following imperative training, we presented the animals with a binary choice paradigm where they had to choose one of two reward options presented simultaneously. Most binary choice trials 113 pitted a safe reward against a gamble. All gambles consisted of two probabilistic rewards: the 114 115 monkey could either get a fixed 0.5 ml of juice with probability p, or 0 ml of juice with probability 1 116 - p. Safe options varied in terms of reward magnitude only. In separate sets of trials, we presented the animals with choices between two gambles with two outcomes each (possible outcomes: 0 117 ml, 0.25 ml, 0.5 ml). In these trials, one of the gambles could have two non-zero outcomes (0.25 118 119 ml and 0.5 ml). In all cases, reward was delivered probabilistically, matching the probabilities cued 120 by each stimulus. Trials began with a white cross at the center of a black screen, followed by the appearance of a joystick-driven cursor. The cursor had to be moved to the center cross in order 121 for a trial to begin. After successfully maintaining the cursor on the central cross for 0.5 to 1 s, two 122 123 visual option cues appeared left and right of the central cross (Fig. 1a). In the case of imperative

124 trials, only one option appeared while the other side remained dark. The animal had 3 seconds to 125 convey his decision by moving the joystick to the selected side, after which the unselected option would disappear. The animal's response time (RT), i.e. the time interval between the cues 126 appearance and the beginning of the joystick movement, was collected for individual trials. 127 128 Reward delivery occurred after the holding time (0.1 s to 0.2 s), and the selected option lingered 129 on the screen for 1 s post reward delivery to reinforce stimulus-reward associations with visual feedback. A variable inter-trial period of 1 to 1.5 s (blank screen) led to the next trial onset. 130 131 Unsuccessful central hold, side selection hold, or trials where no choices were made resulted in a 6 s timeout for the animal, after which the trial would be repeated. 132

133 Psychometric Elicitation of Certainty Equivalents

The likelihood of a monkey choosing a specific, individual gamble over different safe options was assessed through the binary choice paradigm (Fig. 1b). The resulting choice ratios were then used to fit a logistic sigmoid function, or psychometric curve, to estimate choice likelihoods for every possible safe-gamble pairing within the tested reward range.

$$\mathsf{P}_{(\mathsf{ChooseSafe})} = 1/(1 + e^{-\left(\frac{SafeReward_{ml} - x_0}{\sigma}\right)}) \tag{1}$$

These psychometric curve captured the likelihood of choosing a safe option over a gamble through two free parameters: x_0 , measuring the x-position of the curve's inflection point, and σ , the function's temperature parameter, reflecting the steepness of the curve. Importantly, only sequences that contained choices between a gamble and a minimum of three different safe options (repeated at least 4 times) were used in the analysis.

The point of choice indifference between gamble and safe options, corresponding to the inflection point x₀ of the resulting model, represented a gamble's certainty equivalent (CE): the certain safe reward that was of equal subjective value to the gamble. CEs could then be used to categorize behavior. Gambles where the CEs were of greater value than the predicted EV signaled riskseeking behavior for that gamble's probability value. Gambles with CEs lower than their EVs indicated risk-averse behavior for that option. For cases where CEs were equal to EVs, the animals were seen as being risk-neutral.

To explore the role of task structure on the variability of one's probability distortion pattern, we 151 152 measured CEs in one of two elicitation conditions: MIXED or REPEATED trial sequences (Fig. 153 1c,d,e). In the case of MIXED sequences, multiple CEs were elicited through single blocks of randomized choice trials involving different gambles and safe options. Such blocks were repeated 154 until each gamble-safe pair had been presented a minimum of 4 times each. In the case of 155 156 REPEATED sequences, CEs were elicited using blocks of trials that contained a unique gamble. These REPEATED trial blocks pitted multiple safe options against a single gamble for the 157 158 elicitation sequence. Other than these sequence designs, everything from visual cues to 159 timescales was identical. The only difference between elicitation conditions was the number of 160 different probabilities of reward (gambles) experienced within a trial block. Testing for each elicitation condition was done consecutively over multiple days, with each monkey receiving 161 imperative training before their daily elicitation sessions. We collected on average 172.95 ± 20.24 162 (SEM) trials per daily session over 56 sessions for monkey A (22 REPEATED and 34 MIXED 163 sessions, in consecutive days), and 414.63 ± 27.87 trials over 59 sessions for monkey B (31 164 REPEATED and 28 MIXED sessions, in consecutive days). 165

166 Analysis of Behavioral Data

All data were collected, stored, and analyzed using custom MATLAB and Python (SciPy 1.1.0: Oliphant, 2007) software. Analyses were run on trial-by-trial choice data, and on the CEs elicited psychometrically from these trial-by-trial choices. The data were stored and analyzed separately for the two animals.

Before any comparative analyses, the use of visual stimuli to guide the monkeys' decision behavior was verified through analyzing all CE elicitation trials (excluding error trials where the animals made no choices) in a logistic regression model:

174
$$y = \beta_0 + \beta_1 (V_{Gamble}) + \beta_2 (V_{Safe}) + \beta_4 (Risk) + \beta_3 (Position_{LR}) + \varepsilon$$
(2)

175 The dependent variable took a value of y = 1 if the gamble was chosen and y = 0 if the safe option was chosen instead. As had been previously done (W. R. Stauffer et al., 2015), we fitted four 176 177 independent variables: option values (V_{aamble} , V_{safe}) were defined as the EV of gamble and safe rewards; gamble position (Position_{LR}) as 0 for left, 1 for right screen side; and the outcome's risk 178 value was defined as $\sqrt{p * (1-p)}$, a proportional representation of probabilistic variance. We 179 180 fitted individual testing days separately, fully standardizing the β -coefficients and then testing for statistical significance (one sample t-test, p<0.05) in order to identify relevant decision variables. 181 182 Positive regression coefficients indicated an increase in the likelihood of choosing a gamble over 183 a safe option with increasing independent variable value; negative regression coefficients indicated a decrease in the likelihood of choosing the gamble. 184

Once the use of onscreen stimuli to guide choices had been confirmed, CEs were measured using the aformentioned psychometric fit (see *Psychometric Elicitation of Certainty Equivalents*). CEs gathered in the MIXED condition were compared with CEs gathered under the REPEATED condition using a two-factor ANOVA with gamble probability and elicitation condition as main factors. The ANOVA also captured any interaction between the two factors, highlighting any condition effects present at a sequence level.

We pooled trial-by-trial choices to parametrically model the respective effects of utility and probability distortion on single choices, and more generally, on the subjective value of gambles (CEs). For each daily testing session, we simultaneously estimated both the utility and probability distortion functions from within a standard discrete choice model. Functional parameters that best-

described choices between gamble-safe pairs were elicited in this way, capturing the individual effects of non-linear utility and probability distortion. The model ran on trial-by-trial choice data, with data binned into several sets containing one gamble and all safe options presented against it on the day (CE elicitation sequence). The discrete choice (softmax) function returned the probability of choosing the gamble option based on the subjective value of both the gamble (V_G) and the safe reward presented (V_S).

$$P_{choose \ Gamble} = 1/(1 + e^{-\lambda(V_G - V_S)})$$
(3)

The softmax parameter, λ , defined the likeliness of choosing the better prospect; each option's value (V) was defined according to prospect theory (Kahneman & Tversky, 1979), as the product of utility (*u*) and probability distortion (*w*) outputs:

205
$$V(p,m) = w(p) * u(m)$$
 (4)

206 Utility was modeled through a power function

207
$$u(m) = \left(\frac{m_{outcome}}{m_{max}}\right)^{\rho}$$
(5)

where ρ >1 captured risk-seeking choice behavior, ρ <1 captured risk-averse choice behavior (ρ <1), and p=0 implied risk neutrality (Hsu, Krajbich, Zhao, & Camerer, 2009). Magnitude values were divided by 0.5 ml (m_{max}), such that the maximal reward a monkey could get was anchored at 1 unit of utility.

We compared four functional models of probability distortion in an attempt to best capture changes in probability distortion across conditions. Of these classical models, two had a single fitting parameter: the one-parameter Prelec function (Eq. 6, *Prelec-1*, parameter: α) and the Kahneman and Tversky probability weighting function (Eq. 7, *Tversky*, parameter: ϵ); the others had two fitting parameters: the two-parameter Prelec function (Eq. 8, *Prelec-2*, parameters: α , β) and the Gonzalez and Wu log-odds model (Eq. 9, *Gonzalez*, parameters: γ , δ). Formally:

218
$$w(p) = e^{-(-\ln(p))^{\alpha}}$$
 (6)

219
$$w(p) = \frac{p^{\varepsilon}}{(p^{\varepsilon} + (1-p)^{\varepsilon})^{1/\varepsilon}}$$
(7)

220
$$w(p) = e^{-\beta(-\ln(p))^{\alpha}}$$
 (8)

221
$$w(p) = \frac{\delta p^{\gamma}}{\delta p^{\gamma} + (1-p)^{\gamma}}$$
(9)

Using a maximum likelihood estimation (MLE) method we simultaneously estimated the functional
 parameters from the experimental data. We defined the log-likelihood function as:

224
$$LL(u(m), w(p)|y) = \sum_{i=1}^{n} y_i * \log(P_{Choose \ Gamble}) + \sum_{i=1}^{n} y'_i * \log(P_{Choose \ Safe})$$
(10)

225 The log-likelihood function was defined on all trials in a session (n), the trial number (i) and the 226 choice outcome parameter for the gambles and safe options (y and y' respectively). The outcome 227 parameters took a value of 1 if their respective option was chosen; 0 otherwise. We used an 228 unconstrained Nelder-Mead search algorithm (MATLAB: fminsearch) to compute the functional parameters that minimized the negative log-likelihood (-LL). This maximum likelihood estimation 229 230 approach allowed for the simultaneous estimation of the model's free parameters, placing no constraints on their values (Abdellaoui, 2000; Pelé, Broihanne, Thierry, Call, & Dufour, 2014; W. 231 232 R. Stauffer et al., 2015).

The algorithm identified the best fitting softmax, utility, and probability distortion parameters with respect to each monkey's daily choices on CE elicitation sequences. Four complete models were parametrized, accounting for the different probability distortion functions investigated. From these, we calculated the Bayesian Information Criterion (BIC) to pinpoint the probability distortion function most reliable in capturing behavior. Four sets of parameters and their BIC were estimated for every testing day, independently for each model. We selected a single model for further

analysis, based on the flexibility of the functional model, its comparative BIC score (one-factor
 ANOVA with repeated measures, Greenhouse-Geisser corrected p-values: pGGc), and the
 deviance between the model's predicted CEs and the experimental ones (one-factor ANOVA with
 repeated measures, Greenhouse-Geisser corrected p-values).

243 We further validated the parameter estimation procedure by running 10 simulated choice datasets 244 within the fitting algorithm. Datasets used for testing were generated by fixing the utility parameter (p) and varying the probability distortion parameter (α), or vice-versa. The softmax temperature 245 parameter was kept constant (λ =10) as we specifically wanted to test the robustness of the 246 247 estimation procedure in relation to variability in the utility and probability parameters. These fixed models were used to simulate individual trial choices. We simulated 6 trials for every gamble-safe 248 249 pair (safe magnitude levels: 0 ml to 0.5 ml in steps of 0.05 ml). Five datasets varied in terms of 250 utility ($\rho = 0.20, 0.50, 1.00, 1.50, 3.00$), five in terms of probability distortion ($\alpha = 0.33, 0.67, 1.00$, 251 1.50, 3.00). We measured estimation accuracy as the 95% confidence interval on estimated 252 parameters from Monte Carlo simulations on the parameter-derived datasets.

253 The final estimated parameters were first log-transformed to account for the asymmetric 254 distribution of the utility and probability distortion parameters (ranging from 0 to ∞ , with a value of 255 1 defining the linear case). We then compared the parameter estimates via one-way MANOVA 256 analysis with elicitation condition as main factor. From this multivariate analysis, we identified any significant effect of individual decision functions, while recognizing the collective role all three 257 parameters in capturing risk preference. More specifically, the MANOVA identified which model 258 function parameters (choice softmax, utility, or probability distortion) differed significantly between 259 260 CE elicitation conditions.

In the REPEATED condition, the gamble option did not change for long sequences of trials and
 could, theoretically, be ignored. In order to test the possibility of an attentional shift towards the

safe option in this condition, we defined a model with different weights applied to the two options'values:

$$P_{choose \ Gamble} = 1/(1 + e^{-\lambda((1-k)*V_G - k*V_S)})$$
(11)

The weight parameter (*k*) captured the attentional shift towards one option, if significantly larger than 0.5. The options' values (V_G , V_S) were computed, as in the previous model, using the power utility function and the selected probability distortion function (Prelec-1).

269 Evaluation of probability distortion in the Marschak-Machina triangle

We introduced the Marschak-Machina triangle (Machina, 1982; Marschak, 1950) to compare the choice behavior between the MIXED and REPEATED conditions in an out-of-sample test, and to evaluate the theoretical predictions of the discrete choice model vis-à-vis utility and probability distortions.

274 The Marschak-Machina triangle defines a two-dimensional space where any probabilistic 275 combination of three fixed reward magnitudes m₁<m₂<m₃ can be represented (see Results for 276 details). The x- and y-axes correspond to the probability of obtaining the lowest (p_1) reward m_1 and the highest (p_3) reward m_3 , respectively. The probability of the middle magnitude is not 277 278 explicitly represented in the diagram, but it can be readily obtained as $p_2=1-(p_1+p_3)$. Points on the 279 horizontal axis therefore correspond to gambles with outcomes m_1 and m_2 , while points on the 280 vertical axis identify gambles with m_2 and m_3 as possible outcomes; the hypotenuse comprises 281 all gambles containing outcomes m_1 and m_3 only. In our experiment we set the fixed magnitude levels to $m_1 = 0$ ml, $m_2 = 0.25$ ml and $m_3 = 0.5$ ml. 282

We characterized monkey A's behavior within the Marschak-Machina triangle, by defining indifference lines between points on the triangle edges as follows: we presented choices between a fixed gamble (A), defined on one of the axes, and a set of gambles (B_i) located on the triangle's hypotenuse; by fitting a psychometric curve to the ratio of B_i and A choices, we identified the indifference point on the hypotenuse as the probability p_3 corresponding to a choice ratio of 0.5. We then defined an indifference line as the segment connecting the fixed gamble on the axis with its corresponding indifference point. This procedure was repeated for four fixed gambles on the x-axis ($p_1 = 0.2, 0.4, 0.6, 0.8$) and for another four fixed gambles on the y-axis ($p_3 = 0.2, 0.4, 0.6, 0.8$) 0.8), resulting in 8 indifference lines.

292 Note that such indifference lines characterized points on the triangle edges (two-outcome gambles): they did not represent complete indifference curves within the Marschak-Machina 293 triangle (three-outcome gambles). Nevertheless, the slopes of the indifference lines univocally 294 295 identified a directional property a monkey's risk preference pattern: a gradual change in the slope (fanning-in or fanning-out) of indifference lines has been extensively used in the economic 296 297 literature to characterize choice behavior, particularly in relation to the predictions of generalized 298 expected utility theories. This property allowed us to quantify behavioral changes across elicitation 299 conditions and to compare the observed data with predictions from the theoretical economic model. 300

301 Crucially, gambles resting on the two axes were never used in the elicitation of CEs. representing 302 an out-of-sample test. As a consequence, the choice behavior observed in the Marschak-Machina 303 triangle could be used as independent validation for our previous results.

We computed the theoretical indifference lines by calculating, for each of the eight fixed gambles defined above, the probability p_3 for which the theoretical subjective value of the fixed gamble was equal to that of the gamble on the hypotenuse. The subjective value of a two-outcome gamble was defined according to cumulative prospect theory as

308
$$V(gamble) = u(m_H) \cdot w(p_H) + u(m_L) \cdot (1 - w(p_H))$$
(12)

where m_{H} and m_{L} represent the magnitude of the highest and lowest outcome respectively, p_{H} the probability of occurrence of the highest outcome, *u* the power utility function and *w* the *Prelec-1* probability distortion function.

The indifference point was defined as the point on the hypotenuse with subjective value equal to the subjective value of the fixed gamble. Thus, knowing the value of the fixed gamble, one could identify the indifference point as the probability p_3 satisfying the equation $u(m_3) \cdot w(p_3) = V(qamble)$:

315
$$p_3 = w^{-1} \left(\frac{V(gamble)}{u(m_3)} \right)$$
 (13)

316 where w^{-1} represents the inverse of the probability distortion function, i.e. $w^{-1} = exp(-(-ln(w))^{1/\alpha})$.

Each daily set of indifference points was elicited after CE elicitation sequences, for both the MIXED and REPEATED CE elicitation sessions. This resulted in two sets of indifference lines, distinctly associated with the REPEATED and MIXED conditions. Both datasets were obtained using intermingled gamble sequences, so any difference in the pattern of indifference lines could only be attributed to the effect of the previous block of trials, i.e. REPEATED or MIXED CE elicitation.

The directional pattern of the indifference lines was characterized by a measure of the "fanning" direction, corresponding to a gradual change in the slopes of indifference lines. When moving from the lower right to the top left corner of the Marschak-Machina triangle, indifference lines decreasing their slope would fan-in, while indifference lines increasing their slope would fan-outmuch like the structural slats of a folding fan.

A linear regression analysis on the indifference line slopes was used to statistically characterize the fanning pattern. A positive regression coefficient identified fanning-out of the indifference lines, while a negative regression coefficient identified fanning-in. It should be noted that the relation between the slopes of the indifference lines, as we defined them, was not expected to be linear,

but the linear regression served as a reasonable description of the expected theoretical patternand was then used to characterize the measured behavior.

In order to statistically compare the predicted and observed sequence effects on the steepness of the indifference lines, we first calculated the shift of indifference points (change in p₃ value) between the REPEATED and MIXED conditions; we did this for each of the eight indifference lines, for both the measured data and the model's predicted lines. We then carried out a correlation analysis on the modeled and measured shifts.

339 Trial History Effects

Since gamble presentation order was the only difference between the MIXED and REPEATED elicitation sequences, we sought to categorize the effects of said order on the subjective distortion of probabilities. Using past gamble EVs as a quantitative measure of past experiences – specific to probabilities – we compared the distribution and use of previous gamble EVs across elicitation condition.

We first compared the variability of consecutive gamble probabilities in both conditions using a two-sample t-test. We used the absolute value of consecutive gamble EV differences to contrast order in an unsigned matter, as signed differences would amount to zero in both cases. We then assessed the use of past gamble EVs using the following logistic regression:

349
$$y = \beta_0 + \beta_1(EV_{Gamble}) + \beta_2(EV_{Safe}) + \beta_3(EV_{Gamble-1}) + \dots + \beta_n(EV_{Gamble-n}) + \varepsilon$$
(14)

Again, the dependent variable took a value of y = 1 if the gamble was chosen and y = 0 if the safe option was chosen instead. The EV of both the current gamble and safe (EV_{gamble}, EV_{safe}), as well as the gamble EV of up to 8 trials in the past (EV_{gamble-n}) served as independent variables. Trials that did not have a minimum of 8 previous trials, in individual sessions, were removed for this analysis. We again standardized regression coefficients, and identified how many past gamble EVs had a significant impact on current choice (one sample t-test, p<0.05). Refining the analysis to a singular preceding trial – we investigated the use of a win-stay/lose-shift (WSLS) strategy by the animals. A common strategy for human and non-human primates alike, a WSLS choice pattern involves repeating a 'winning' choice until it results in a 'loss', one would then shift and try their luck on another choice option. Since choice options in the CE elicitation sequences involved many different values for both the gamble and the safe options, we instead explored a more relaxed WSLS model:

$$y = \beta_0 + \beta_1(EV_{Gamble}) + \beta_2(EV_{Safe}) + \beta_3(Outcome_{past}) + \beta_4(Position_{LR}) + \varepsilon$$
(15)

If the previous choice had been that of a gamble, and that gamble had won (i.e. resulted in a 0.5 363 ml reward), the 3rd independent variable (Outcome_{past}) took a value of 1; if the past chosen gamble 364 had instead been unsuccessful, Outcome_{past} was 0. By including current EV_{Gamble}, EV_{Safe}, and 365 *Position_{LR}*, we could identify the relative effect of a previous gamble's outcome on current choice. 366 The logistic regression analysis was only applied to trials in which the previous trial's gamble was 367 368 chosen. A positive regression coefficient for Outcome_{past} implied a greater likelihood of picking the gamble after a 'win', regardless of its value. A negative coefficient would, instead, capture a 369 decrease in the likelihood of picking the gamble, whatever it may be, after a 'loss'. 370

In order to compare the performance of this model with the previously defined model (Eq. 2), which did not include the contribution of past trials, we computed the BIC scores of the two models only in trials in which the previous gamble was chosen. After this trial selection, we removed 5 sessions in Monkey A's data, as they had fewer than 4 trials per gamble-safe pair.

To further investigate the effect of past outcomes on the risk patterns, we defined a reinforcement learning model, in which each gamble value was updated, starting from its EV, by adding or removing a fixed amount following a win or a loss respectively. Formally, choices were evaluated according to the discrete choice model defined earlier (Eq. 2), in which the safe value (V_s) was

the certain option's magnitude (linear coding of magnitudes), while the gamble value (V_G) was updated on each trial according to the rule:

$$V_G = V_G + \eta \cdot pre_{Win} - \eta \cdot pre_{Loss}$$
(16)

Where pre_{Win} and pre_{Loss} are variables encoding the last trial's outcome, i.e. $pre_{Win}=1$ if a gamble was won in the previous trial, 0 otherwise, and vice versa for pre_{Loss} . The value-updating parameter η represents the amount of value (in ml) added or removed to the gamble value based on the previous outcome. According to this model, the gamble value was not updated if the safe option had been chosen on the previous trial.

We retrieved the η parameter value using MLE, and used the resulting average value to simulate choices and compute the resulting CEs. The simulation was run on MIXED and REPEATED sequences separately, in order to compare the effect of a value-updating model on the CEs in the two sequence conditions.

391 Statistical Analysis

392 We used MATLAB and/or Python for all statistical analyses. Logistic regressions were computed per session and results were standardized by multiplying each coefficient with the ratio of the 393 corresponding independent variable's standard deviation over the standard deviation of the 394 395 predicted variable (Menard, 2011). Standardized regression coefficients were tested for statistical 396 significance through one sample t-test. Two-factor ANOVA, one-factor MANOVA, linear 397 regression, and t-test results were considered significant at p<0.05, while one-way repeatedmeasures ANOVAs were Greenhouse-Geisser corrected (degrees of freedom adjustment) to 398 399 account for sphericity violations (Mauchly's test p<0.05; Greenhouse & Geisser, 1959). Post-hoc 400 analysis with Bonferroni-Holm correction for multiple comparisons were applied to ANOVA 401 results. Cohen's d values were used as a measure of effect sizes. In all analyses of data from 402 single sessions, we reported mean ± SEM across sessions.

403

404 Results

405 Design

406 We tested whether the shape of the probability distortion would be influenced by the order in 407 which probability information is presented in a sequence of decisions.

Once the animals had been extensively trained with the reward-predicting stimuli (>10,000 trials), 408 409 we presented them with sequences of binary choices between different probabilistic rewards (or 410 gambles) and safe rewards (Fig. 1). We then used the choice ratios to measure the value of gambles relative to certain rewards - pinpointing the certain rewards that were subjectively 411 equivalent to gambles, or a gamble's certainty equivalent (CE). This procedure revealed the 412 413 animals' attitude towards risky choices: gamble CEs larger than said gamble's objective expected 414 value (EV) reflected risk-seeking behavior; risk-aversion was characterized instead by gamble CEs smaller than the gamble's EV. 415

By simultaneously estimating the individual contributions of utility and probability distortion to these measures of risk attitudes, we could model the shape of the monkeys' probability distortion irrespective of the utility function.

419 Basic behavioral performance

A logistic regression analysis demonstrated that the monkeys used the information from the visual stimuli to guide their decisions on all daily testing sessions (Fig. 2a). A positive regression coefficient for gamble value (one-sample t-test, Monkey A: t(55)=29.41, $p=2.5\times10^{-35}$; Monkey B: t(58)=30.16, $p=3.9\times10^{-37}$) indicated that animals were more likely to choose higher probability gambles than lower probability ones; conversely, the negative coefficient for safe reward value (Monkey A: t(55)=-44.65, $p=6.8\times10^{-45}$; Monkey B: t(58)=-58.61, $p=2.6\times10^{-53}$) indicated that monkeys chose the safe option more frequently when its value was of higher magnitude. Both animals preferred gambles of higher over lower probabilistic variance, i.e. they preferred gambles that were more uncertain, regardless of the outcome (positive coefficient for risk; Monkey A: t(55)=4.58, p=2.7×10⁻⁵; Monkey B: t(58)=7.79, p=1.4×10⁻¹⁰). Monkey A, but not monkey B, showed a side bias (positive coefficient for the position variable), which was taken into account by balancing the positions of gambles and safe rewards: every option was presented the same number of times on each side of the computer monitor.

433 Estimation of subjective values using different sequence structures

We used a binary choice paradigm to estimate the monkeys' subjective valuation of specific gambles. We measured the choice ratios between different safe rewards and gambles ranging in probabilities from p=0.1 to p=0.9. Fitting a softmax curve to each of these gamble-safe groups allowed us to estimate the CEs corresponding to different gamble probabilities (*see Materials and methods*). These CEs served as a measure of subjective value for unique probabilities and provided us with a precise measure of an animal's risk preference over the range of probabilities tested.

We elicited CEs in both monkeys using two different elicitation conditions: MIXED and 441 REPEATED gamble sequences (Fig. 2b). In the MIXED condition, we estimated CEs from 442 443 sequences of binary choices containing several different gambles pitted against safe rewards. All 444 gamble and safe options presented were randomly intermixed, and multiple CEs were estimated from these sequences – one for each gamble. In the REPEATED condition, we elicited CEs from 445 blocks of trials that contained a single, unique gamble versus different safe rewards. In this way, 446 we elicited a unique gamble's CE for each given block. Importantly, the two conditions used the 447 same visual stimuli; any difference between estimated CEs would therefore be due to the 448 elicitation sequence in which CEs were estimated. 449

450 We aggregated the daily CEs of individual monkeys, for both conditions, to determine the risk-451 preference pattern derived from the CEs measured in each elicitation sequence. The riskpreference pattern was therefore directly inferred from the relation between the CEs and the 452 453 respective EVs, as opposed to being theoretically derived from the shape of utility and probability 454 distortion functions. We found a significant difference between the distribution of CE values 455 elicited in REPEATED versus those elicited in MIXED sequences (two-way ANOVA, factors: gamble probability, elicitation condition). As expected, we found a significant main effect of reward 456 457 probability on a gamble's CE: higher probability gambles had a higher certainty equivalent in both animals (Monkey A: F(8,237)=444.12, p=5.2×10⁻¹³⁸; Monkey B: F(8,337)=241.14, p=1.4×10⁻¹³⁴). 458 We also saw a main effect of elicitation conditions (Monkey A: F(1,237)=7.69, p=0.006; Monkey 459 B: F(1,337)=20.21, $p=9.6\times10^{-6}$), where CEs elicited in the MIXED condition were significantly 460 461 different to those in the REPEATED condition. Adding to this effect, we observed a significant 462 interaction effect between probability and condition (Monkey A: F(8,237)=7.73, p=3.3×10⁻⁹; Monkey B: F(8,337)=12.56, p=8.5×10⁻¹⁶), suggesting that the different elicitation sequences had 463 464 a more complex effect on CE values than a mere monotonic increase or decrease. This effect was readily observable from the condition-specific CE distributions (Fig. 2c), where the concave 465 466 pattern of the MIXED-condition CEs contrasts with the S-shaped distribution of the REPEATEDcondition CEs. 467

468 Sequence-dependent changes in probability distortion

Since CE elicitation rested on reward options that varied in both magnitude and probability, any risk-preference changes could be attributed to non-linear utility, probability distortion, or a combination of both. To better understand the role of these decision variables in shaping a gamble's subjective value, we simultaneously estimated the shape of both functions from the monkeys' daily binary choices. Using a standard discrete choice model (Eq. 3), we elicited functional parameters that best explained each animal's choices between gamble-safe choice

pairs on individual days, assuming non-linear utility and probability distortion. The estimation
procedure allowed parameters to take on any value, imposing no constraints beyond the
functional forms of the discrete choice softmax, probability distortion, and utility curves.

478 We defined the value of each reward option as the product of its subjective probability and utility, 479 consistent with prospect theory and other modern decision theories (Kahneman & Tversky, 1979; 480 Tversky & Kahneman, 1992). As is traditionally done, we modeled utility through a one-parameter power function. The simple power function accounted well for risk-seeking (p>1), risk-aversive 481 482 (p<1), or risk neutral attitude (p=1) for the range of reward magnitudes. We tested only one model 483 for utility, as magnitude presentations did not differ across conditions. Instead, we sought to optimize our choice model with regards to subjective probability, since CE elicitation sequences 484 485 differed in terms of the order in which gamble probabilities were experienced. We tested four 486 classical models of probability distortion to maximize the reliability of our model in capturing real 487 choices; two of these functions had one free parameter, the others had two. Finally, we defined cumulative log-likelihood functions for each of these models and estimated the best-fitting 488 parameters for each decision function through maximum likelihood estimation (MLE) (see 489 Materials and methods). 490

491 Across all testing sessions, the BIC scores of the Prelec curves were consistently lower than the 492 one-parameter Tversky and lower than the Gonzalez models in at least monkeys (Fig. 3a). However, while the two-parameter Prelec had a marginally lower BIC score in both animals, the 493 one-parameter Prelec showed had a marginally lower sum of squared errors (SSE) between 494 predicted and average experimental CEs (one-factor ANOVA with repeated measures, Monkey 495 496 A: F(3,144)=6.166, pGGc=5.7×10⁴; Monkey B: F(3,168)=3.699, pGGc=1.3×10⁻²). We ultimately 497 selected the one-parameter Prelec due to this lower SSE, lower parameter count, and because 498 of its ease of interpretation: for the curvature parameter $\alpha > 1$ the function underweighted low probabilities and overweighted high ones, for $\alpha < 1$, low probabilities were overweighted and high 499

500 ones were underweighted. With an α =1, probabilities were treated linearly. Monte Carlo 501 simulations from predefined parameters confirmed the reliability of the MLE method for the 502 selected model: we recovered accurate parameters for both the utility (Fig. 3b) and probability 503 distortion (Fig. 3c) functions.

Having selected the one-parameter Prelec as the best-fitting probability distortion function, we estimated the functional parameters of our choice model (Eq. 3) using the MLE method. The model was able to capture the characteristic pattern of risk attitudes observed in our experimental data: CEs of low probability gambles resulted larger than the respective EVs in the MIXED condition, while CEs of high probability gambles were larger than their EVs in the REPEATED condition (Fig. 3d), in accordance with the measured behavior (Fig. 2b).

510 We compared daily estimated parameters across CE elicitation conditions for utility and 511 probability distortion (Fig. 4a). Both animals exhibited convex utility (ρ >1) in the tested range of 0-0.5 ml accounting for risk-seeking behavior, with linearity only in the case of Monkey B's 512 513 REPEATED condition. Importantly, probability distortions inverted across elicitation condition. In the MIXED elicitation condition, both animals overweighted low probabilities and underweighted 514 high ones (α >1), while they instead underweighted low probabilities and overweighted high ones 515 516 within the REPEATED condition (α <1) (Fig. 4b). MANOVA analysis confirmed the impact of the 517 different elicitation sequences on both animals' choice pattern (Monkey A: F(1,54)=24.96, Wilks's λ =0.41, p=3.85×10⁻¹⁰, η^2 =0.59; Monkey B: F(1,57)=40.78, Wilk's λ =0.31, p=5.2×10⁻¹⁴, η^2 =0.69) 518 with only the probability distortion parameter (α) consistently different across conditions (Fig. 519 520 4a,c). The change in risk-attitude between the two conditions could therefore, at least in the case 521 of gamble-safe choices, be reduced to a reversal in the probability distortion function.

The REPEATED condition was a much less complex decision situation compared to the MIXED one, theoretically allowing for a simpler choice strategy: it would have been sufficient to evaluate the certain option, ignoring the gamble option in the majority of trials, to make choices.

We tested for this possibility by fitting a model with an attentional parameter to the choice data (Eq. 11). We found that there was no significant difference in attention given to the safe compared to the gamble option (the weight parameter was not significantly different from 0.5; Monkey A: t(21)=-2.01, $p=5.7\times10^{-2}$ (t-test), Monkey B: t(30)=-1.25; $p=2.2\times10^{-1}$), suggesting that both options were fully considered when making choices in the REPEATED condition.

530 Reversal of probability distortion in the Marschak-Machina triangle

531 To extend our findings past gamble-safe choices, we characterized the choice behavior of one 532 monkey in a different set of gambles using the Marschak-Machina triangle. This diagram was first 533 introduced as a way of "organizing" a series of anomalies observed in risky choices, most notably 534 the common ratio and common consequence effects, which violated the independence axiom of EU theory. Several economic theories were developed to explain these apparent paradoxes. 535 536 Each theory predicted indifference curves with distinctive shapes in the Marschak-Machina 537 triangle, making it an ideal framework to evaluate and compare the alternative theories (Machina, 1982). 538

539 The use of this diagram, which makes it possible to represent a more general class of choice options, i.e. gambles with three fixed outcomes of varying probabilities (Fig. 5a), allowed us to 540 541 extend our results to a wider range of problems. We did this to test the robustness of the 542 parametric modeling (out-of-sample test) and, most importantly, to investigate the effect of elicitation condition from a different perspective: by looking at the change in direction of 543 indifference lines, which connected points of the triangle edges for which the animal expressed 544 choice indifference (Fig. 5b), we could quantify the effects of elicitation condition that were 545 546 specifically dependent on changes in probability distortion, and independent of changes in the shape of the utility function. 547

548 One of the theoretical consequences of probability distortions in the Marschak-Machina triangle 549 is that indifference lines would not be parallel to each other, as in the case of linear probability 550 weighting, but would instead fan-out or fan-in depending on the probability distortion (Fig. 5c): an 551 inverse S-shaped probability distortion would induce fanning-out, while an S-shaped one would 552 result in indifference lines fanning-in. Fanning-out would in fact correspond to an increase in the steepness of the indifference lines when shifting "probability mass" from worse to better 553 outcomes. As steeper lines correlate with more risk-seeking behavior, fanning-out would imply an 554 inverse S-shaped probability distortion. The opposite would happen with fanning-in indifference 555 556 lines, then corresponding to an S-shaped probability distortion function (Camerer, 1989). Crucially, because the outcome magnitudes used in the Marschak-Machina triangle are fixed, the 557 558 fanning direction is independent of the utility function and is therefore solely determined by the 559 shape of the probability distortion. In that sense, any observed change in the fanning direction of 560 the indifference lines with a change in elicitation sequence could only be due to a change in the probability weighting function (Fig. 5c). 561

562 We used the previously recovered parameters for utility and probability distortion to estimate the expected pattern of indifference lines in the two experimental conditions, MIXED and REPEATED 563 564 sequences. We then compared the predicted directions of the indifference lines with the measured ones. As expected, the theoretical indifference lines, modeled using the previously 565 elicited parameters, showed a slight fanning-out pattern for the MIXED condition, where a weakly 566 567 inverse S-shaped probability distortion was measured. Conversely, we saw a fanning-in pattern 568 in the REPEATED condition, for which we had observed an S-shaped probability distortion (Fig. 6a, left). 569

570 The direct experimental measure of indifference lines was carried out by presenting the animals 571 with binary choices between a gamble represented by a fixed point on the triangle edge and one 572 of several points on the triangle's hypotenuse. The indifference line was defined as the segment

573 connecting the fixed point with the point corresponding to choice indifference on the hypotenuse. 574 This procedure resulted in a directional pattern of indifference lines compatible with the theoretically predicted one, with no clear fanning direction of indifference lines in the MIXED 575 576 condition, and clear fanning-in in the REPEATED condition (Fig. 6a, right). We quantified this 577 directional pattern of indifference lines using a measure for the fanning direction. The fanning of 578 indifference lines corresponds to a gradual change in the slope of indifference lines: when moving from the lower right corner of the probability triangle to the upper left corner, an increasing slope 579 580 would produce fanning-out, whereas a decreasing slope would produce fanning-in. Following this 581 principle, we statistically assessed the fanning direction of the indifference lines by computing a linear regression on the slopes of the indifference lines. Results show no significant regression 582 slope in the MIXED condition (R²=0.08, p=0.50), indicating no fanning of indifference curves, while 583 584 in the REPEATED condition a significant linear regression (R²=0.98, p=4.4×10⁻⁶) indicated 585 fanning-out of the indifference lines. These results are consistent with predictions from the modeled indifference lines, which show a similar pattern of fanning directions (Fig. 6b). 586

We statistically compared the measured and predicted patterns of indifference lines by calculating the shift in the location of indifference points across conditions; the latter corresponding to changes in the slope of indifference lines. A significant correlation between the predicted and measured shifts (Pearson's correlation coefficient r=0.78, p= 4.0×10^{-3}) confirmed that the experimental data complied with our theoretical predictions (Fig. 6c), and supported the finding that probability distortion drove the change in risk attitude between REPEATED and MIXED conditions.

594 The Effect of Trials History on the Probability Distortion

595 Because CE the structure of elicitation sequences appeared to affect probability distortions 596 specifically, we investigated whether the differences in choice behavior could be explained in 597 relation to past experiences, or trial history. One key difference between elicitation sequences

was the order of the probabilities presented on the screen. In the MIXED sequences, the monkeys were much more likely to have experienced different gambles in their immediate past than in trials from REPEATED sequences, where the same gamble was repeated numerous times. Consequently, while the range of probabilities, magnitudes, and safe outcomes was identical in both conditions, the variability of past gambles was significantly different between the two conditions (Fig. 1d,e).

604 Since humans and non-human primates, much like rodents, often base part of their risky decisions on recent experiences (Barron & Erev, 2003; Hayden, B; Heilbronner, S; Nair, A; Platt, 2013; 605 606 Marshall & Kirkpatrick, 2013; Nowak & Sigmund, 1993), we again ran a logistic regression on the probability of choosing the gamble option: this time to verify if the EV of past gambles had any 607 608 impact on the animals' decisions (Eq. 14). We found that, in the MIXED condition, both monkeys 609 made use of at least one past gamble to make their decision (Fig. 7a). The monkeys appeared to 610 bias their choices in favor of the gamble (positive regression coefficient) when the prior gamble's EV was higher. In game-theoric terms, and taking the gamble's EV as a proxy for its 'win rate', 611 monkeys seemed to follow a win-stay/lose-shift (WSLS) strategy, whereby receiving a reward 612 from a risky choice option increased the likelihood of choosing a similar option again; the opposite 613 614 true for choices where the risky option resulted in a loss (no reward). To validate this hypothesis, we applied a WSLS-compatible model (Eq. 15) on the immediate trial history of both monkeys, 615 looking at their propensity to choose a gamble over a safe outcome when they had previously 616 617 chosen a gamble and won (Fig. 7b). As expected, we found a significant effect of both the current 618 gamble's EV (one-sample t-test, Monkey A: t(50)=29.41, p=3.19×10⁻³³; Monkey B: t(58)=32.28, p=9.38×10⁻³⁹) and the current safe outcome's EV on the likelihood of choosing a gamble (one-619 sample t-test, Monkey A: t(50)=-38.71, p=6.05×10⁻³⁹; Monkey B: t(58)=-46.19, p=1.9×10⁻⁴⁷). Both 620 monkeys had a small but significant side bias (one-sample t-test, Monkey A: t(50)=-4.59, 621 $p=2.97 \times 10^{-5}$; Monkey B: t(58)=-2.55, $p=1.3 \times 10^{-2}$). More importantly, there was a significant 622

positive effect of 'winning' the preceding gamble on the likelihood of selecting the gamble option again, regardless of value (one-sample t-test, Monkey A: t(50)=10.75, $p=1.3\times10^{-14}$; Monkey B: t(58)=8.32, $p=1.76\times10^{-11}$). In other words, receiving a reward from a risky gamble made the next gamble more attractive relative to the safe outcome.

627 We investigated this effect further, by estimating separate utility and probability distortion 628 parameters in trials where a past gamble had been selected and 'won', and in trials where the past selected gamble had been 'lost'. Due to lower trial counts per session after this trial selection, 629 630 all sessions were pooled for each condition. In both animals, the utility function estimated from the former class of trials was more convex than the utility estimated from unrewarded trials (Fig. 631 7c). Probability distortions, however, were not consistently different between these two classes of 632 633 trials, maintaining their respective inverse-S and S-shapes for MIXED and REPEATED 634 conditions. Much like in the logistic regression, these results suggested a tendency to choose the 635 gamble option more often after rewarded (win) trials, compared to unrewarded trials (a more convex utility function corresponding to stronger risk-seeking behavior). What it also highlighted, 636 however, was a change in the relative value distribution between gambles and safe options - one 637 that varies with past experience. In other words, gambles following a rewarded trial would be of 638 639 higher relative value for the monkeys than those following unrewarded trials, at least in terms of safe rewards. 640

Past win or lost effects on subjective value could account for some of the gap in probability distortion observed across our two conditions. A MIXED sequence of gambles would drive subjective value estimates in an opposing pattern to that of a REPEATED elicitation sequence simply due to task structure. In the case of MIXED sequences, the random distribution of gamble probabilities would indeed result in an inverse-S probability distortion. Gambles with probabilities larger than 0.5 would, more often than not, follow a gamble of lower EV; the monkey would then, on average, be less likely to pick said gamble due to the decrease in subjective value estimate

648 following lower past returns. This would drive down the CE value of high probability gambles. In 649 the case of low probability gambles, high past returns would drive CEs up. From this, we would 650 expect an opposing distortion pattern in a REPEATED condition. For any gamble, the CE value would be distorted in a way proportional to its own probability: a low probability gamble would be 651 652 driven down in value by repeated experience, whereas a high probability gamble would see its 653 value go up. A change in gamble value, rather than a simple WSLS strategy, might also have longer lasting effects and could explain the persistence of sequence type effects when looking at 654 655 choices in the Marschak-Machina triangle paradigm.

656 To test this hypothesis directly, we developed a simple reinforcement learning model in which gamble values were updated based on the previous trial's outcome: the value of a gamble 657 658 increased by a fixed amount after a win, and decreased by the same amount after a loss (Eq. 16). 659 Importantly, in the choice model, the gambles' starting values were the respective objective EVs, 660 which were compared to the objective safe magnitudes in order to make choices. No utility or probability distortion were included, only the previous choice softmax function, and we made no 661 distinction between parameters estimated in repeated or mixed sequences. We again estimated 662 the model parameters through MLE on each session's trial-by-trial choice data, and retrieved a 663 significant, mean value-updating parameter for both monkeys (Monkey A: $\eta = 4.5 \times 10^{-3} \pm 9.0 \times 10^{-1}$ 664 ⁴ SEM; t(55)=4.96, p=7.1×10⁻⁶; Monkey B: $\eta = 4.1 \times 10^{-3} \pm 5.8 \times 10^{-4}$ SEM; t(58)=7.1, p=2.0×10⁻⁹). 665 The value of n corresponded to the fixed amount of value being added to or removed from the 666 gamble's subjective value estimate following "win" and "lose" trials respectively. 667

After running the estimation procedure on all sessions, we tested if the average observed valueupdating parameter could explain the different CE distributions seen across the MIXED and REPEATED conditions. We computed CEs from simulated choices using the learning model defined above (Eq. 16), using the mean softmax and value-updating parameters, still holding utility and probability weights linear. The resulting pattern of simulated CEs (Fig. 7d) followed the experimental pattern. In particular, it captured the clear separation between the two CE elicitation sequences. Although this model appeared to have a lower BIC score than the "classical" prospect theory model (Eq. 3) (Monkey A: BIC_{Eq16}=160.7, BIC_{Eq3}=137.5, t(55)=6.92, p= 5.01×10^{-9} ; Monkey B: BIC_{Eq16}=419.8, BIC_{Eq3}=392.7, t(58)=4.69, p= 1.70×10^{-5}), it accounted for the change in the pattern of CEs across both conditions using a single set of parameters. Conversely, two different sets of parameters were necessary for the prospect theory counterpart to capture the different CE patterns.

Taken together, these results suggest that a simple value updating mechanism that modifies gamble values based on the previous outcomes, applied to different elicitation sequences, would be sufficient to induce a reversal in the observed probability distortion patterns of monkeys during choice.

684

685 Discussion

This study demonstrated that the shape of the probability weighting function guiding value-based 686 687 choices in monkeys depended largely on the task's sequence structure. When deriving CEs from 688 sequences in which different probabilistic rewards pseudorandomly alternated (MIXED), we found that monkeys overweighted low probability rewards and underweighted high probability ones. 689 Conversely, the same CE elicitation method yielded the opposite choice pattern (underweighting 690 691 of low probabilities and overweighting of high ones) when choice sequences consisted of trial 692 blocks each containing a unique, REPEATED gamble. By simultaneously eliciting utility and probability weighting functions from each of these elicitation conditions, we showed that the two 693 694 opposing choice patterns we observed could be explained by a reversal of the standard inverse 695 S-shaped probability distortion function, seen when gambles were MIXED, to an S-shaped distortion when identical gambles were REPEATED. We confirmed and extended these results 696 697 by comparing choice indifference lines in the Marschak-Machina triangle representations of the

two elicitation conditions. The triangle's indifference maps were compatible with the observed inversion of probability distortions, preserving the weighting patterns in trials where no safe options were presented. Finally, by analyzing both sequence structure and monkeys' choices in relation to previous trials, we showed that a past-driven update of subjective values could partially explain the observed reversal in probability distortion.

703 Modern economic theories of choice under risk introduced distorted probability weightings to 704 account for biases and departures from expected utility theory's predictions (Allais, 1953; 705 Kahneman & Tversky, 1979; Von Neumann & Morgenstern, 1944). Since then, the typical finding 706 has been that humans overweighted low probabilities all the while underweighting high ones 707 (Abdellaoui, 2000; Gonzalez & Wu, 1999; Lattimore, Baker, & Witte, 1992; Tobler, Christopoulos, 708 O'Doherty, Dolan, & Schultz, 2008), an inverse-S probability distortion (Kahneman & Tversky, 709 1979). This shape has also been replicated in monkeys (W. R. Stauffer et al., 2015), where 710 human-ported tasks resulted in a reliable inverse-S probability distortion. The current study tiesin with these findings, using a coherent set of visual stimuli for both gambles and safe reward 711 712 options to control for any bias introduced by the different visual representations of the two option types. Our results, in addition to reliability capturing macaque behavior using modern economic 713 714 choice theories, further characterize the effects of sequence structure on utility and probability 715 distortion.

In contrast to the generally reported inverse-S shaped probability distortion, a growing number of studies on human and animal subjects have highlighted the variability in probability distortion shapes, both across subjects and between task conditions (Bruhin et al., 2010; Farashahi et al., 2018; Hey & Strazzera, 1989). Recent work by Farashahi et al. (2018), emphasized the flexibility of probability weights in adapting to contextual changes, after finding that S-shaped and linear probability distortions could be seen in monkeys when performing different tasks. Our experimental data confirmed this high level of behavioral flexibility in monkeys, whereby directly

manipulating the order of presented gambles in a single task produced opposing patterns ofprobability distortion.

725 Other findings from human experiments suggest that the way in which probability information is 726 presented could account for the reported variability in subjects' risk attitudes. For example, when 727 reward probabilities are explicitly described (choice from description) to human subjects, they act 728 as if overweighting the probability of rare events, but when probabilities are learned from 729 experience (choice from experience), subjects choose as if underweighting the probability of rare 730 events. This effect has been aptly referred to as the description-experience (DE) gap (Hertwig et 731 al., 2004), and appears to extend to other primates. Indeed, monkeys have been shown to be more risk-seeking for experienced than for described gambles, implying a DE gap effect in non-732 733 human primates (Heilbronner & Hayden, 2016). While some authors have called for two separate 734 theories explaining choices from description and choices from experience (Abdellaoui, L'Haridon, 735 & Paraschiv, 2011; Hertwig & Erev, 2009), others have suggested that prospect theory could effectively describe choice in the two situations when allowing for a change in the probability 736 distortion function between the two settings (Frey, Mata, & Hertwig, 2015; Ungemach, Chater, & 737 Stewart, 2009). 738

739 While the dichotomous choice patterns we observed are comparable to those described in the 740 DE gap studies, here the cues representing reward probabilities were identical in the two sequence conditions. In both MIXED and REPEATED sequences, probabilities were described 741 742 explicitly through cues, learned from experience by the animals; the conditions only differed in the presentation order of the probability information. While the task design was different from previous 743 744 human DE studies in this respect, the repeated sampling of outcomes typically used to 'learn' the value of risky prospects in choices from experience (for review see Wulff, Mergenthaler-Canseco, 745 & Hertwig, 2018) echoes the repetitive structure of our REPEATED sequence; conversely, 746 described prospects are typically presented in a less structured, randomized sequence, 747

analogous to our MIXED condition. While a direct comparison remains to be done, findings in
both the DE gap experiments and in the present study suggest that past trial outcomes play a role
in shaping the subjective perception of reward probabilities.

751 Sampling bias has been identified as a source of variability in probability distortions, particularly 752 in relation to the DE gap. Indeed, sampling bias is particularly problematic in 'experienced' 753 conditions due to the limited number of trials used in learning the options' values: with small sample sizes, low probability gambles are often rewarded less frequently than would be 754 755 prescribed by their nominal probability (Camilleri & Newell, 2013; Hertwig & Erev, 2009; Hertwig 756 & Pleskac, 2010). The use of identical descriptive cues and elicitation procedures in the present study ensured that similar sampling sizes were applied, and indeed required, to estimate CEs for 757 758 every gamble. Any bias would therefore affect the two conditions in a similar manner. With no 759 obvious sampling biases, our data suggest that the DE gap could be modeled on the probability 760 distortion changes we observed across task conditions, and that much like in the present study, the observed changes in risk-preferences - from described to experienced reward probabilities -761 762 might result from differences in the task's presentation order of probability information.

A final source of variability we considered was that the REPEATED condition was a much less complex decision situation than the MIXED one: one could ignore the gamble in long, repeated sequences. However, we found that the animals neither differentially weighed the options, nor made choices faster in the REPEATED condition, indicating that they were not using widely differing valuation strategies.

The Marschak-Machina triangle, a diagram widely used in the economics literature, allows for the intuitive representation of choices between two- and three-outcome gambles, serving as an ideal framework for investigating complex economic choice problems (Camerer, 1989; Machina, 1987). In the current experiment we elicited indifference points in the Marschak-Machina triangle representation of the monkeys' behavior, which crucially provided a link between animal and

human studies. Although full indifference curves within the Marschak-Machina triangle remain to be tested, we showed that indifference points on the triangle edges complied with economic theories of choice, and confirmed the reversal of probability distortion across conditions – this time with probabilistic rewards only. Consequently, we demonstrated the possibility of rigorous behavioral characterization in non-human primates, paving the way for future investigations into the neurophysiological basis of advanced economic constructs like probability distortion, specific economic axioms, or the neural counterparts of alternative economic theories.

780 In conclusion, our results demonstrated the effect of a task's sequence structure on the shape of 781 a monkey's elicited probability distortion, and highlighted the potential influence of past rewards on subjective value. Moreover, and perhaps most significantly, these adaptive effects extended 782 783 through time: the patterns of indifference lines observed in the Marschak-Machina triangle after a 784 session of MIXED or REPEATED sequences were compatible with the probability distortion 785 shapes measured in the preceding CE elicitation session, even though the paradigm used in the Marschak-Machina triangle was always randomized. In this sense, the CE elicitation sequences 786 preceding the Marschak-Machina triangle paradigm might have driven and reinforced a gap 787 between the subjective values of identical probabilities, one that influenced choices between 788 789 gambles in the Marschak-Machina triangle. The reinforcement learning model we used supports 790 this hypothesis, implying that each experienced outcome could reinforce and update the subjective value of probabilities, leading to a flexible, and contextually driven judgement of 791 792 probabilistic information. More sophisticated models, such as the addition of a standard Rescorla-793 Wagner learning rule or a non-linear transformation of safe magnitudes to the current value 794 updating mechanism, could be more biologically plausible and successful in explaining the choice mechanism - and so remain to be explored. It should be noted that the monkeys' initial 795 learning/association phase was not analyzed here in reinforcement learning terms, as it was 796 797 carried out with imperative trials. A better understanding of probability learning, and the

permanence of subjective values reinforced across different conditions could shed light on the
core elements of prospect theory, and on the undeniably-adaptive nature of utility and probability
distortions.

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905

907 Legends

908 Figure 1. Experimental design. a, Trial sequence. Each trial started with the monkey moving a white cursor, through 909 left/right arm movements with a joystick, to the center of the screen. After 0.5 to 1 s (center holding), two cues appeared 910 indicating the two offered options (choice period): possible reward magnitudes and probabilities were indicated by the 911 vertical position and width of a horizontal bar, respectively. A single horizontal bar indicated a sure reward, two bars 912 indicated a gamble with two possible outcomes. The monkey moved the cursor to the side of the preferred option, 913 within 2 s. After 0.1 to 0.2 s (holding time) the juice reward was delivered according to the chosen option's reward 914 magnitude and probability. A further 1 s (association period) followed to reinforce the association between chosen cue 915 and reward. **b**, Psychometric elicitation of CEs. Left: three example gambles with different reward probabilities (p=0.3, 916 p=0.5, p=0.7) paired with varying safe magnitudes to elicit each gamble's CE. Right: each point represents the 917 probability of choosing the safe option in choices between a fixed gamble (identified by the color) and a varying safe 918 magnitude (horizontal axis). Lines are psychometric curves obtained by fitting a softmax function to the choice ratios. 919 Each line is associated to one specific gamble, and identifies its CE as the magnitude corresponding to a choice ratio 920 of 0.5 (vertical dashed line). c, Task conditions. The CEs were elicited using two sequence structures: in the MIXED 921 condition different gambles and different safe options were randomly intermixed, while in the REPEATED condition the 922 CE measurement for one gamble was completed before presenting a different gamble. d, Temporal sequence of the 923 presented gamble EV in the two elicitation conditions for one sample session (first 200 trials). The trial-by-trial variation 924 of the gamble EV highlights the difference in sequence structure between MIXED (red) and REPEATED (blue) 925 conditions. e, Variability of gamble EV across consecutive trials. Absolute value of the gamble EV difference (mean ± 926 SEM) between two consecutive trials, showing the main distinction between the two elicitation sequences: the previous 927 trials' gamble EV was consistently different from the current one in the MIXED condition, while it stayed constant in the 928 REPEATED condition. Asterisk indicates significant difference (t-test, p<0.05) between conditions.

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Figure 2. Basic choice behavior and estimation of certainty equivalents. **a**, Logistic regression of choice behavior. Four task variables (gamble EV, safe EV (magnitude), risk variance, gamble position) were used as regressors for the gamble choice. Positive standardized coefficients for gamble EV and risk indicated that monkeys preferred gambles with higher EV to gambles with lower EV, and more risky gambles to less risky ones. Negative coefficient for safe EV confirmed that monkeys preferred higher reward magnitudes to lower ones. The positive position factor for one monkey indicated a side bias, that was taken into account by repeating all choice pairs with inverted left-right positions. **b**, Psychometric estimation of CEs. CEs of two example gambles with probabilities 0.1 (top) and 0.8 (bottom), estimated 937 in the two different elicitation sequences: MIXED (red) and REPEATED (blue) sequences. The percentages of safe 938 choices as a function of safe magnitude (circles) were fitted to softmax functions (curves). Vertical lines indicate the 939 gambles EVs (dashed lines); filled circles indicate the CEs. In both monkeys, low probability gambles (top) had a lower 940 CE in the REPEATED condition than in the MIXED condition, where the CEs were consistently higher than the EVs, 941 indicating a risk seeking attitude. High probability gambles (bottom) showed the inverse pattern, indicating a risk 942 seeking behavior only in the REPEATED condition. c, Pattern of CEs across the two elicitation sequences (MIXED vs. 943 REPEATED). Single sessions' CEs (small data points) and average CEs across sessions (large data points) plotted as 944 a function of gamble EV, with cubic spline interpolated curves. The full pattern of CEs shows a smooth transition from 945 low to high probability gambles in terms of CE difference across the two elicitation sequences. For low probability 946 gambles, both monkeys showed higher CEs in the MIXED than in the REPEATED conditions; when increasing gamble 947 probabilities, the CE difference across conditions gradually reduced and inverted, resulting in lower CEs in the MIXED 948 than in the REPEATED condition for high reward probabilities. Single sessions' data points were shifted horizontally 949 (REPEATED condition: left; MIXED condition: right) for visualization purpose. d, Response times. Mean RT (± SEM 950 across sessions) in the two elicitation conditions. RT for monkey A were similar in the two conditions (RT difference = 951 3.0 ms, t(9088)=-0.59 p=0.56); Monkey B showed faster response in the MIXED condition compared to the REPEATED 952 condition (RT difference = 30.0 ms, t(22233)=-15.88 p=1.77×10⁻⁵⁶). See Figure 2-1 for RT as a function of the options' 953 EV.

954

Figure 2-1. Response time vs EV. Top: Mean RT (± SEM across sessions) as a function of EV difference between the
two presented options (gamble EV – safe magnitude). Choices between options with similar EV produced higher RT.
Bottom: Mean RT (± SEM across sessions) as a function of the EV of the chosen option. Faster RTs were associated
to higher EV of the chosen option, while slower RTs corresponded to choices where a low EV option was selected.

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Figure 3. Choice model selection and validation. a, Goodness-of-fit for choice behavior using four models with different
probability weighting functions. Bars represent mean BIC values (±SEM) across all sessions (Monkey A: N=56; Monkey
B: N=59). BIC scores for daily parametric fits differed significantly across models (one-factor ANOVA with repeated
measures, Monkey A: F(3,150)=8.32, pGGc=3.1×10⁻³; Monkey B: F(3,174)=13.575, pGGc=5.3×10⁻⁰⁸). Lower BIC
values for the Prelec weighting functions (Tversky, Prelec-1) indicate a better fit of the data compared to the oneparameter Tversky or two-parameter Gonzalez functions. BIC values for all model pairs except for Prelec-1 vs Prelec2, Prelec-1 vs Gonzalez, and Prelec-2 vs Gonzalez in Monkey A, and the Prelec-2 vs Gonzalez in monkey B, were

967 significantly different (post-hoc analysis, p<0.05) for both monkeys. The sum of squared errors in CE estimation was 968 the lowest in the Prelec models. b, c, Validation of the parameter estimation procedure using the Prelec-1 probability 969 weighting function. Upper plots in **b** and **c** represent the utility (left) and probability distortion (right) functions used to 970 simulate choices; lower plots represent the functions recovered with the MLE procedure. Monte Carlo simulation of 971 choice behavior (using the same number of trials and the same step-size for magnitude and probability as in the 972 measured data: 9 gamble probabilities, 11 safe magnitudes, 6 trials per gamble-safe pair) was repeated 1000 times, 973 producing the 95% confidence intervals on the parameter estimates (grey areas). Varying the utility function parameter 974 (p, 0.2 to 3) while keeping the probability distortion parameter constant (α =0.67) resulted in an unbiased estimate of 975 the utility shape (b). The probability distortion parameter (α), varying from 0.33 to 3 while keeping the utility shape fixed 976 (ρ =2), was recovered consistently and without bias (c). d, Modeled vs measured choice behavior. Comparison of 977 estimated (curves) and measured (circles) percentage of safe choices as a function of safe magnitude, for two example 978 gambles (probabilities 0.2 and 0.8); see Figure 3-1 for the full dataset. Estimated choice percentages were computed 979 using the discrete choice model with the MLE-recovered parameters (Eq. 3, using the Prelec-1 probability weighting 980 function). Estimated CEs are represented as red and blue points, EVs as vertical dashed lines. The estimated 981 psychometric functions closely approximated the measured data points, and differences in estimated CEs across 982 conditions are compatible with the observed data for both low and high probabilities (see Fig. 2b).

983

984 Extended Data Figure 3-1. Modeled vs measured choice behavior. Comparison of estimated (curves) and measured 985 (circles) percentage of safe choices as a function of safe magnitude. Conventions and symbols as in Fig. 3d. Thin lines 986 represent differences between estimated and experimental data percentages, with the horizontal line (at 0.5 on the y 987 axis) corresponding to perfect estimate (difference=0).

988

989 Figure 4. Utility and probability distortion functions in two elicitation conditions. a, Model parameter estimates (mean ± 990 SEM across sessions) in the MIXED (red) and REPEATED (blue) conditions. Asterisks indicate significant differences 991 across conditions (MANOVA). The probability distortion parameter (α) consistently varied across sequence structures 992 in both monkeys: negative log-values in the MIXED condition corresponded to inverse S-shaped probability distortion 993 (α <1), while positive log-values in the REPEATED condition implied S-shaped probability distortion (α >1). Numbers 994 below the bars represent effect sizes (Cohen's d). The utility (ρ) and softmax (λ) parameters significantly differed across 995 conditions only for one monkey, with a smaller effect size compared to the probability distortion parameter. b, Shapes 996 of the probability distortion function (left) and utility function (right) corresponding to the estimated parameters,

997 displaying the consistent difference in subjective probability evaluation across conditions for both monkeys. **c**, Two-998 dimensional representation of the utility and probability distortion parameter estimates. The dots represent the 999 simultaneously estimated utility (ρ) and probability distortion (α) parameters for single behavioral sessions, with 95% 1000 confidence ellipses.

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1002 Figure 5. Indifference lines in the Marshack-Machina triangle modeling different patterns of probability distortion. a, 1003 Representation of gambles in the Marshack-Machina triangle. Schematic representation of a three-outcome gamble 1004 (left): probabilistic combination (p1, p2, p3) of three fixed magnitudes (m1=0 ml, m2=0.25 ml, m3=0.50 ml) which can be 1005 represented in the Marshack-Machina triangle (right, with example gambles corresponding to points on the triangle 1006 edges). The grey line in the triangle connects points with equal expected value (EV=0.25 ml). b, Procedure for the 1007 psychometric measurement of one indifference line. An indifference point (top, blue dot) in choices between a fixed 1008 gamble A and different gambles B_i, circles) was defined as the point on the triangle hypotenuse for which a softmax 1009 function fitted on the ratio of A over Bi choices equated 0.5 (bottom). An indifference line was then constructed by 1010 connecting such indifference point on the hypotenuse to the fixed gamble A (blue line). c, Theoretical indifference lines. 1011 Indifference lines predicted by cumulative prospect theory, for different underlying shapes of utility (u(m), power1012 function) and probability distortion (w(p), Prelec-1 function). Each plot shows the indifference lines corresponding to a 1013 particular combination of u and w shapes, represented with orange and purple lines respectively. The shape of the 1014 utility function (linear in the first row of plots, concave and convex in the other two rows) changes the global orientation 1015 of the indifference lines, without affecting their fanning direction. On the contrary, a change in probability distortion 1016 shape corresponds to a change in the fanning direction of indifference lines: a linear probability distortion (first column) 1017 produces parallel indifference lines, while S-shaped (second column) and inverse S-shaped (third column) probability 1018 distortions correspond to indifference lines fanning-in and fanning-out respectively, regardless of the utility function 1019 shape.

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Figure 6. Effect of CE elicitation sequences on the Marshack-Machina triangle indifference lines. **a**, Modeled (left) and measured (right) patterns of indifference lines across conditions. The arrows indicate the direction and amount of shift for three sample indifference points between the MIXED (red) and REPEATED (blue) conditions, highlighting how the model correctly predicted the effect of condition change. The grey line connects points with the same expected value (EV=0.25 ml), representing an indifference line in case of risk-neutral behavior. Numbers define indices for the indifference lines, corresponding to fixed gambles on the triangle edges (black dots, also represented as visual cues).

1027 b, Fanning direction of the indifference lines. Points represent the slope of indifference lines (angle between each line 1028 and the horizontal axis) as a function of indifference line index (circles: model; dots: experimental data). Lines represent 1029 linear regressions, separately computed on the two task conditions for model (dashed lines) and data points (continuous 1030 lines). A regression line with negative slope corresponds to a decrease in indifference lines angle, indicating fanning-1031 out; conversely, a positive regression coefficient indicates fanning-in of indifference lines. c, Statistical comparison 1032 between model and experimental data. Shift in location of indifference points across elicitation sequences (average 1033 difference ± SEM). A linear regression between the modeled and measured shifts (inset) confirmed the match between 1034 model and data in terms of predicted shift in indifference points, corresponding to a correct prediction of the change in 1035 the fanning direction across conditions.

1036

1037 Figure 7. Sequence-dependent effects of trial history on probability distortion shape. a, Influence of past trials on 1038 current trial's choice. Standardized regression coefficients (mean ± SEM across sessions) for current trial's gamble EV, 1039 safe reward magnitude and previous trials' gamble EV (up to eight trials in the past). Asterisks represent coefficients 1040 significantly different from zero: for both monkeys, the choice behavior depended on at least one trial in the past. 1041 Positive regression coefficients indicated that an increase in the previous trial's gamble EV induced the monkeys to 1042 choose the current trial's gamble option more frequently. b, Effect of the past outcomes on gamble choices. 1043 Standardized regression coefficients (mean ± SEM across sessions) for gamble EV, safe magnitude, previous triai's 1044 gamble outcome (0 ml or 0.5 ml) and gamble position. A significant positive coefficient for the previous outcome 1045 indicated that monkeys chose the gamble more often when the previously chosen gamble was successful (0.5 ml) than 1046 when it was not successful (0 ml): the gamble was chosen more after a win than after a loss. In terms of BIC score this 1047 model (Eq. 15) was at least as good at describing the choice data when compared to the model with no past trials' 1048 influence (Eq. 2) (Monkey A: BIC2=84.2, BIC14=82.3, t-test: p=0.14; Monkey B: BIC2=221.4, BIC14=215.8, t-test: 1049 $p=5.8 \times 10^{-5}$). c, Effect of past outcomes on the utility and probability distortion functions. The utility function appeared 1050 more convex following a gamble-win trial (0.5 ml reward) than following a loss (no reward), suggesting that gamble 1051 outcomes had an influence on the relative value of gamble and safe options on the next trial. The utility parameter 1052 estimates followind win and loss trials are indicated as aW and aL respectively, while probability distortion parameter 1053 as pW and pL respectively. The arrows highlight the change in the utility parameter between loss and win trials. Error 1054 bars represent the 95% confidence intervals of the parameter estimates. d, Simulated effect of EV upgdate mechanism 1055 based on past outcomes. Mean ± SEM across simulated sessions (N=50) of the CE resulting from choices simulated 1056 using the learning model (Eq. 16) in MIXED and REPEATED conditions. The parameters used in the simulation were 1057 recovered from the MLE procedure with the same model separately for each monkey. Linear probability weighting and

- 1058 linear magnitude coding were used in the simulation, demonstrating that an EV update mechanism interacting with the
- 1059 local trial structure could explain the observed change in risk attitudes across conditions without explicitly introducing
- 1060 a non-linear probability distortion.















indifference lines

indifference lines

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