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Probability distortion depends on choice sequence in rhesus monkeys
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Abstract
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 probabilities non-linearly: overvaluing low probabilities of reward, and undervaluing high ones. A growing body of evidence, however, points to a more flexible pattern of distortion than the classical inverse-S one, highlighting the effect of experimental conditions in shifting the weight assigned to probabilities, such as task feedback, learning, and attention. Here we investigated the role of sequence structure – the order in which gambles are presented in a choice task – in shaping the 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 revealed that choices in each sequence type were guided by significantly different patterns of probability distortion. Whereas we elicited the classical inverse-S shaped probability distortion in pseudorandomly MIXED trial sequences of gamble-safe choices, we found the opposite pattern 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 of the sequence structure in which the animals make choices. Finally, we showed that the value 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 differences in choice sequence are sufficient to reverse the direction of probability distortion.

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.

Introduction

Choices between uncertain rewards require decision-makers to evaluate each option along 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 to other choice prospects. The von Neumann and Morgenstern utility theorem, commonly referred to as Expected Utility (EU) theory, was the first axiomatic model of rational behavior capable of describing people’s choices in these situations (Von Neumann & Morgenstern, 1944). EU theory rigorously introduced the concept of utility as a representation of a decision-maker’s subjective value for an objective reward quantity. Through the metric of utility, EU theory was able to describe different risk attitudes, like the risk-seeking behavior of a gambler or the risk aversion of an 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, 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 utility theory and cumulative prospect theory) incorporated the concept of probability distortion (Kahneman & Tversky, 1979; Quiggin, 1982; Tversky & Kahneman, 1992). While maintaining the 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 small probabilities tend to be overweighted by decision-makers, large probabilities are instead underweighted (Gonzalez & Wu, 1999; Kahneman & Tversky, 1979; W. R. Stauffer, Lak, 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 & 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 variability have yet to be identified, differences in probability distortions could relate to the way in which probability information is presented to decision-makers (Hertwig et al., 2004), or the way in which probability knowledge is acquired and stored by the decision-maker (Camilleri & Newell, 2013). Some studies suggested that prospect theory might, altogether, be incapable of explaining differences in risk attitudes across these contexts (Kellen, Pachur, & Hertwig, 2016).

Here we investigated the role of choice context, specifically sequential structures, as a possible source of probability distortion variability in rhesus macaques: animals known to show quantifiable and reproducible probability distortions (W. R. Stauffer et al., 2015). To achieve this, we first 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 the subjective value of the gamble in the ‘currency’ of the safe reward. We then simultaneously estimated the contributions of utility and probability distortion to these subjective values, allowing 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.

Materials and Methods

Animals and Experimental Setup

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 between rewarding stimuli presented on a computer monitor positioned 30cm in front of them. The animals reported their choices between options with a left-right motion joystick (Biotronix 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, Natick, MA) using Psychtoolbox (v3.0.11). All experimental protocols were assessed and approved by the Home Office of the United Kingdom.

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 side-preference.

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 pitted a safe reward against a gamble. All gambles consisted of two probabilistic rewards: the monkey could either get a fixed 0.5 ml of juice with probability \( p \), or 0 ml of juice with probability \( 1 - p \). 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 ml, 0.25 ml, 0.5 ml). In these trials, one of the gambles could have two non-zero outcomes (0.25 ml and 0.5 ml). In all cases, reward was delivered probabilistically, matching the probabilities cued 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 for a trial to begin. After successfully maintaining the cursor on the central cross for 0.5 to 1 s, two visual option cues appeared left and right of the central cross (Fig. 1a). In the case of imperative trials, only one option appeared while the other side remained dark. The animal had 3 seconds to 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 appearance and the beginning of the joystick movement, was collected for individual trials. Reward delivery occurred after the holding time (0.1 s to 0.2 s), and the selected option lingered 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. 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.

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.

\[
P_{\text{ChooseSafe}} = \frac{1}{1 + e^{-\frac{\text{SafeReward}_{\text{net}} - x_0}{\sigma}}}
\]  

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 \(\sigma\), 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 $x_0$ 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 risk-seeking 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 measured CEs in one of two elicitation conditions: MIXED or REPEATED trial sequences (Fig. 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 until each gamble-safe pair had been presented a minimum of 4 times each. In the case of 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 elicitation sequence. Other than these sequence designs, everything from visual cues to timescales was identical. The only difference between elicitation conditions was the number of 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 imperative training before their daily elicitation sessions. We collected on average $172.95 \pm 20.24$ (SEM) trials per daily session over 56 sessions for monkey A (22 REPEATED and 34 MIXED sessions, in consecutive days), and $414.63 \pm 27.87$ trials over 59 sessions for monkey B (31 REPEATED and 28 MIXED sessions, in consecutive days).

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:

\[ y = \beta_0 + \beta_1(V_{\text{gambles}}) + \beta_2(V_{\text{safe}}) + \beta_3(\text{Risk}) + \beta_4(\text{Position}_{LR}) + \varepsilon \]  (2)

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 independent variables: option values \( (V_{\text{gambles}}, V_{\text{safe}}) \) were defined as the EV of gamble and
safe rewards; gamble position \( (\text{Position}_{LR}) \) as 0 for left, 1 for right screen side; and the
outcome’s risk value was defined as \( \sqrt{p \times (1-p)} \), a proportional representation of probabilistic
variance. We fitted individual testing days separately, fully standardizing the \( \beta \)-coefficients and
then testing for statistical significance (one sample t-test, \( p < 0.05 \)) in order to identify relevant
decision variables. Positive regression coefficients indicated an increase in the likelihood of
choosing a gamble over a safe option with increasing independent variable value; negative
regression coefficients indicated a decrease in the likelihood of choosing the gamble.

Once the use of onscreen stimuli to guide choices had been confirmed, CEs were measured
using the aforementioned 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 ($V_S$).

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

(3)

The softmax parameter, $\lambda$, 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:

$$V(p, m) = w(p) \times u(m)$$

(4)

Utility was modeled through a power function

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

(5)

where $\rho>1$ captured risk-seeking choice behavior, $\rho<1$ captured risk-averse choice behavior ($\rho<1$), and $\rho=0$ implied risk neutrality (Hsu, Krajbich, Zhao, & Camerer, 2009). Magnitude values were divided by 0.5 ml ($m_{\text{max}}$), 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: $\alpha$) and the Kahneman and Tversky probability weighting function (Eq. 7, Tversky, parameter: $\varepsilon$); the others
had two fitting parameters: the two-parameter Prelec function (Eq. 8, Prelec-2, parameters: $\alpha, \beta$)

and the Gonzalez and Wu log-odds model (Eq. 9, Gonzalez, parameters: $\gamma, \delta$). Formally:

\[
\begin{align*}
    & w(p) = e^{-\ln(p)^2} \\
    \quad & w(p) = \frac{p^\epsilon}{(p^\epsilon + (1 - p)^\epsilon)^{1/\epsilon}} \\
    \quad & w(p) = e^{-\beta(-\ln(p))} \\
    \quad & w(p) = \frac{\delta p^\gamma}{\delta p^\gamma + (1 - p)^\gamma}
\end{align*}
\]

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

\[
LL(u(m), w(p) | y) = \sum_{i=1}^{n} y_i \cdot \log(P_{\text{Choose Gamble}}) + \sum_{i=1}^{n} y_i' \cdot \log(P_{\text{Choose Safe}})
\]

The log-likelihood function was defined on all trials in a session ($n$), the trial number ($i$) and the choice outcome parameter for the gambles and safe options ($y$ and $y'$ respectively). The outcome parameters took a value of 1 if their respective option was chosen; 0 otherwise. We used an unconstrained Nelder-Mead search algorithm (MATLAB: fminsearch) to compute the functional parameters that minimized the negative log-likelihood (-LL). This maximum likelihood estimation 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. 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).

We further validated the parameter estimation procedure by running 10 simulated choice datasets within the fitting algorithm. Datasets used for testing were generated by fixing the utility parameter (ρ) and varying the probability distortion parameter (α), or vice-versa. The softmax temperature parameter was kept constant (λ=10) as we specifically wanted to test the robustness of the 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 pair (safe magnitude levels: 0 ml to 0.5 ml in steps of 0.05 ml). Five datasets varied in terms of utility (ρ = 0.20, 0.50, 1.00, 1.50, 3.00), five in terms of probability distortion (α = 0.33, 0.67, 1.00, 1.50, 3.00). We measured estimation accuracy as the 95% confidence interval on estimated parameters from Monte Carlo simulations on the parameter-derived datasets.

The final estimated parameters were first log-transformed to account for the asymmetric distribution of the utility and probability distortion parameters (ranging from 0 to ∞, with a value of 1 defining the linear case). We then compared the parameter estimates via one-way MANOVA 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 parameters in capturing risk preference. More specifically, the MANOVA identified which model function parameters (choice softmax, utility, or probability distortion) differed significantly between 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:

\[ P_{\text{choose gamble}} = \frac{1}{1 + e^{-\lambda(1-k)\cdot V_G - k\cdot V_S}} \]  

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).

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.

The Marschak-Machina triangle defines a two-dimensional space where any probabilistic combination of three fixed reward magnitudes \( m_1 < m_2 < m_3 \) can be represented (see Results for 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 explicitly represented in the diagram, but it can be readily obtained as \( p_2 = 1 - (p_1 + p_3) \). Points on the horizontal axis therefore correspond to gambles with outcomes \( m_1 \) and \( m_2 \), while points on the vertical axis identify gambles with \( m_2 \) and \( m_3 \) as possible outcomes; the hypotenuse comprises 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.

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), resulting in 8 indifference lines.

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 triangle (three-outcome gambles). Nevertheless, the slopes of the indifference lines univocally 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 literature to characterize choice behavior, particularly in relation to the predictions of generalized expected utility theories. This property allowed us to quantify behavioral changes across elicitation conditions and to compare the observed data with predictions from the theoretical economic model.

Crucially, gambles resting on the two axes were never used in the elicitation of CEs, representing an out-of-sample test. As a consequence, the choice behavior observed in the Marschak-Machina 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

\[ V(\text{gamble}) = u(m_H) \cdot w(p_H) + u(m_L) \cdot (1 - w(p_H)) \]  

\[ V(\text{gamble}) = u(m_H) \cdot w(p_H) + u(m_L) \cdot (1 - w(p_H)) \]  

\[ (12) \]
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

$$u(m_3) \cdot w(p_3) = V(gamble):$$

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

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

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-out—much 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 pattern and 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 $p_3$ 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.

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:

$$y = \beta_0 + \beta_1(EV_{\text{gamble}}) + \beta_2(EV_{\text{safe}}) + \beta_3(EV_{\text{gamble}^{-1}}) + \cdots + \beta_n(EV_{\text{gamble}^{-n}}) + \varepsilon$$  (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 ($EV_{\text{gamble}}, EV_{\text{safe}}$), as well as the gamble EV of up to 8 trials in the past ($EV_{\text{gamble}^{-n}}$) 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:

\[ y = \beta_0 + \beta_1(EV_{gambles}) + \beta_2(EV_{safes}) + \beta_3(Outcome_{past}) + \beta_4(Position_{LR}) + \epsilon \quad (15) \]

If the previous choice had been that of a gamble, and that gamble had won (i.e. resulted in a 0.5 ml reward), the 3rd independent variable (Outcome\_past) took a value of 1; if the past chosen gamble had instead been unsuccessful, Outcome\_past was 0. By including current \( EV_{gambles}, \) \( EV_{safes}, \) and \( Position_{LR}, \) we could identify the relative effect of a previous gamble’s outcome on current choice. The logistic regression analysis was only applied to trials in which the previous trial’s gamble was 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 decrease in the likelihood of picking the gamble, whatever it may be, after a ‘loss’.

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:

$$V_G = V_G + \eta \cdot \text{preWin} - \eta \cdot \text{preLoss}$$

(16)

Where $\text{preWin}$ and $\text{preLoss}$ are variables encoding the last trial’s outcome, i.e. $\text{preWin}=1$ if a gamble was won in the previous trial, 0 otherwise, and vice versa for $\text{preLoss}$. The value-updating parameter $\eta$ 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 $\eta$ 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.

Statistical Analysis

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 corresponding independent variable’s standard deviation over the standard deviation of the predicted variable (Menard, 2011). Standardized regression coefficients were tested for statistical significance through one sample t-test. Two-factor ANOVA, one-factor MANOVA, linear regression, and t-test results were considered significant at $p<0.05$, while one-way repeated-measures ANOVAs were Greenhouse-Geisser corrected (degrees of freedom adjustment) to account for sphericity violations (Mauchly’s test $p<0.05$; Greenhouse & Geisser, 1959). Post-hoc analysis with Bonferroni-Holm correction for multiple comparisons were applied.
Results

Design

We tested whether the shape of the probability distortion would be influenced by the order in 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), we presented them with sequences of binary choices between different probabilistic rewards (or 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 equivalent to gambles, or a gamble’s certainty equivalent (CE). This procedure revealed the animals’ attitude towards risky choices: gamble CEs larger than said gamble’s objective expected value (EV) reflected risk-seeking behavior; risk-aversion was characterized instead by gamble CEs smaller than the gamble’s EV.

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.

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: $t(55)=-44.65$, $p=6.8 \times 10^{-45}$; Monkey B: $t(58)=-58.61$, $p=2.6 \times 10^{-53}$) 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: $t(55)=4.58$, $p=2.7 \times 10^{-5}$; Monkey B: $t(58)=7.79$, $p=1.4 \times 10^{-10}$). 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.

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
REPEATED gamble sequences (Fig. 2b). In the MIXED condition, we estimated CEs from
sequences of binary choices containing several different gambles pitted against safe rewards.
All 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 blocks of trials that contained a single, unique gamble versus different safe
rewards. In this way, we elicited a unique gamble’s CE for each given block. Importantly, the
two conditions used the same visual stimuli; any difference between estimated CEs would therefore be due to the elicitation sequence in which CEs were estimated.

We aggregated the daily CEs of individual monkeys, for both conditions, to determine the risk-preference pattern derived from the CEs measured in each elicitation sequence. The risk-preference pattern was therefore directly inferred from the relation between the CEs and the respective EVs, as opposed to being theoretically derived from the shape of utility and probability distortion functions. We found a significant difference between the distribution of CE values 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 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}). We also saw a main effect of elicitation conditions (Monkey A: F(1,237)=7.69, p=0.006; Monkey B: F(1,337)=20.21, p=9.6×10^{-6}), where CEs elicited in the MIXED condition were significantly different to those in the REPEATED condition. Adding to this effect, we observed a significant 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 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 pattern of the MIXED-condition CEs contrasts with the S-shaped distribution of the REPEATED-condition CEs.

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.

We defined the value of each reward option as the product of its subjective probability and utility, consistent with prospect theory and other modern decision theories (Kahneman & Tversky, 1979; 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-averse \((p<1)\), or risk neutral attitude \((p=1)\) for the range of reward magnitudes. We tested only one model 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 differed in terms of the order in which gamble probabilities were experienced. We tested four classical models of probability distortion to maximize the reliability of our model in capturing real 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 parameters for each decision function through maximum likelihood estimation (MLE) (see Materials and methods).

Across all testing sessions, the BIC scores of the Prelec curves were consistently lower than the 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 one-parameter Prelec showed had a marginally lower sum of squared errors (SSE) between predicted and average experimental CEs (one-factor ANOVA with repeated measures, Monkey A: \(F(3,144)=6.166, p_{GGc}=5.7\times10^{-4}\); Monkey B: \(F(3,168)=3.699, p_{GGc}=1.3\times10^{-2}\)). We ultimately selected the one-parameter Prelec due to this lower SSE, lower parameter count, and because
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 ones were underweighted. With an $\alpha=1$, probabilities were treated linearly. Monte Carlo simulations from predefined parameters confirmed the reliability of the MLE method for the selected model: we recovered accurate parameters for both the utility (Fig. 3b) and probability 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).

We compared daily estimated parameters across CE elicitation conditions for utility and probability distortion (Fig. 4a). Both animals exhibited convex utility ($\rho>1$) in the tested range of 0-0.5 ml accounting for risk-seeking behavior, with linearity only in the case of Monkey B's REPEATED condition. Importantly, probability distortions inverted across elicitation condition. In the MIXED elicitation condition, both animals overweighted low probabilities and underweighted high ones ($\alpha>1$), while they instead underweighted low probabilities and overweighted high ones within the REPEATED condition ($\alpha<1$) (Fig. 4b). MANOVA analysis confirmed the impact of the different elicitation sequences on both animals’ choice pattern (Monkey A: $F(1,54)=24.96$, Wilk’s $\lambda=0.41$, $p=3.85\times10^{-10}$, $\eta^2=0.59$; Monkey B: $F(1,57)=40.78$, Wilk’s $\lambda=0.31$, $p=5.2\times10^{-14}$, $\eta^2=0.69$) with only the probability distortion parameter ($\alpha$) consistently different across conditions (Fig. 4a,c). The change in risk-attitude between the two conditions could therefore, at least in the case 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=5.7×10^{-2} (t-test), Monkey B: t(30)=-1.25; p=2.2×10^{-1}), suggesting that both options were fully considered when making choices in the REPEATED condition.

Reversal of probability distortion in the Marschak-Machina triangle

To extend our findings past gamble-safe choices, we characterized the choice behavior of one monkey in a different set of gambles using the Marschak-Machina triangle. This diagram was first introduced as a way of "organizing" a series of anomalies observed in risky choices, most notably 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. Each theory predicted indifference curves with distinctive shapes in the Marschak-Machina triangle, making it an ideal framework to evaluate and compare the alternative theories (Machina, 1982).

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 extend our results to a wider range of problems. We did this to test the robustness of the 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 indifference lines, which connected points of the triangle edges for which the animal expressed choice indifference (Fig. 5b), we could quantify the effects of elicitation condition that were
specifically dependent on changes in probability distortion, and independent of changes in the shape of the utility function.

One of the theoretical consequences of probability distortions in the Marschak-Machina triangle is that indifference lines would not be parallel to each other, as in the case of linear probability weighting, but would instead fan-out or fan-in depending on the probability distortion (Fig. 5c): an inverse S-shaped probability distortion would induce fanning-out, while an S-shaped one would 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 outcomes. As steeper lines correlate with more risk-seeking behavior, fanning-out would imply an inverse S-shaped probability distortion. The opposite would happen with fanning-in indifference 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 fanning direction is independent of the utility function and is therefore solely determined by the shape of the probability distortion. In that sense, any observed change in the fanning direction of the indifference lines with a change in elicitation sequence could only be due to a change in the probability weighting function (Fig. 5c).

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 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 elicited parameters, showed a slight fanning-out pattern for the MIXED condition, where a weakly inverse S-shaped probability distortion was measured. Conversely, we saw a fanning-in pattern in the REPEATED condition, for which we had observed an S-shaped probability distortion (Fig. 6a, left).
The direct experimental measure of indifference lines was carried out by presenting the animals with binary choices between a gamble represented by a fixed point on the triangle edge and one of several points on the triangle’s hypotenuse. The indifference line was defined as the segment connecting the fixed point with the point corresponding to choice indifference on the hypotenuse. 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 condition, and clear fanning-in in the REPEATED condition (Fig. 6a, right). We quantified this directional pattern of indifference lines using a measure for the fanning direction. The fanning of 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 would produce fanning-out, whereas a decreasing slope would produce fanning-in. Following this 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 slope in the MIXED condition ($R^2=0.08$, $p=0.50$), indicating no fanning of indifference curves, while in the REPEATED condition a significant linear regression ($R^2=0.98$, $p=4.4 \times 10^{-6}$) indicated 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).

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 $r=0.78$, $p=4.0 \times 10^{-3}$) 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.
The Effect of Trials History on the Probability Distortion

Because the structure of elicitation sequences appeared to affect probability distortions specifically, we investigated whether the differences in choice behavior could be explained in 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).

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; 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 impact on the animals' decisions (Eq. 14). We found that, in the MIXED condition, both monkeys made use of at least one past gamble to make their decision (Fig. 7a). The monkeys appeared to bias their choices in favor of the gamble (positive regression coefficient) when the prior gamble's EV was higher. In game-theoretic terms, and taking the gamble’s EV as a proxy for its ‘win rate’, monkeys seemed to follow a win-stay/lose-shift (WSLS) strategy, whereby receiving a reward from a risky choice option increased the likelihood of choosing a similar option again; the opposite 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, looking at their propensity to choose a gamble over a safe outcome when they had previously chosen a gamble and won (Fig. 7b). As expected, we found a significant effect of both the current gamble’s EV (one-sample t-test,
Monkey A: $t(50)=29.41, p=3.19 \times 10^{-33}$; Monkey B: $t(58)=32.28, p=9.38 \times 10^{-39}$ and the current safe outcome's EV on the likelihood of choosing a gamble (one-sample t-test, Monkey A: $t(50)=-38.71, p=6.05 \times 10^{-39}$; Monkey B: $t(58)=-46.19, p=1.9 \times 10^{-47}$). Both monkeys had a small but significant side bias (one-sample t-test, Monkey A: $t(50)=-4.59, p=2.97 \times 10^{-5}$; Monkey B: $t(58)=-2.55, p=1.3 \times 10^{-2}$). More importantly, there was a significant 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: $t(50)=10.75, p=1.3 \times 10^{-14}$; Monkey B: $t(58)=8.32, p=1.76 \times 10^{-11}$).

In other words, receiving a reward from a risky gamble made the next gamble more attractive relative to the safe outcome.

We investigated this effect further, by estimating separate utility and probability distortion 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, 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. 7c). Probability distortions, however, were not consistently different between these two classes of trials, maintaining their respective inverse-S and S-shapes for MIXED and REPEATED conditions. Much like in the logistic regression, these results suggested a tendency to choose the 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, however, was a change in the relative value distribution between gambles and safe options - one that varies with past experience. In other words, gambles following a rewarded trial would be of higher relative value for the monkeys than those following unrewarded trials, at least in terms of safe rewards.

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 following lower past returns. This would drive down the CE value of high probability gambles. In the case of low probability gambles, high past returns would drive CEs up. From this, we would 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 driven down in value by repeated experience, whereas a high probability gamble would see its 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 choices in the Marschak-Machina triangle paradigm.

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 increased by a fixed amount after a win, and decreased by the same amount after a loss (Eq. 16). Importantly, in the choice model, the gambles’ starting values were the respective objective EVs, 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 distinction between parameters estimated in repeated or mixed sequences. We again estimated the model parameters through MLE on each session’s trial-by-trial choice data, and retrieved a significant, mean value-updating parameter for both monkeys (Monkey A: \( \eta = 4.5 \times 10^{-3} \pm 9.0 \times 10^{-4} \) SEM; \( t(55)=4.96, p=7.1 \times 10^{-6}; \) Monkey B: \( \eta = 4.1 \times 10^{-3} \pm 5.8 \times 10^{-4} \) SEM; \( t(58)=7.1, p=2.0 \times 10^{-9} \)). The value of \( \eta \) corresponded to the fixed amount of value being added to
or removed from the gamble’s subjective value estimate following “win” and “lose” trials respectively.

After running the estimation procedure on all sessions, we tested if the average observed value-updating 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^{-6}; 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.

Discussion

This study demonstrated that the shape of the probability weighting function guiding value-based choices in monkeys depended largely on the task’s sequence structure. When deriving CEs from sequences in which different probabilistic rewards pseudorandomly alternated (MIXED), we found that monkeys overweighted low probability rewards and underweighted high
probability ones. Conversely, the same CE elicitation method yielded the opposite choice pattern (underweighting of low probabilities and overweighting of high ones) when choice sequences consisted of trial 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 opposing choice patterns we observed could be explained by a reversal of the standard inverse 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 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.

Modern economic theories of choice under risk introduced distorted probability weightings to account for biases and departures from expected utility theory's predictions (Allais, 1953; Kahneman & Tversky, 1979; Von Neumann & Morgenstern, 1944). Since then, the typical finding has been that humans overweighted low probabilities all the while underweighting high ones (Abdellaoui, 2000; Gonzalez & Wu, 1999; Lattimore, Baker, & Witte, 1992; Tobler, Christopoulos, O’Doherty, Dolan, & Schultz, 2008), an inverse-S probability distortion (Kahneman & Tversky, 1979). This shape has also been replicated in monkeys (W. R. Stauffer et al., 2015), where human-ported tasks resulted in a reliable inverse-S probability distortion. The current study ties-in with these findings, using a coherent set of visual stimuli for both gambles and safe reward 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 choice theories, further characterize the effects of sequence
structure on utility and probability 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 of
probability distortion.

Other findings from human experiments suggest that the way in which probability information is
presented could account for the reported variability in subjects' risk attitudes. For example,
when reward probabilities are explicitly described (choice from description) to human subjects,
they act as if overweighting the probability of rare events, but when probabilities are learned
from experience (choice from experience), subjects choose as if underweighting the probability
of rare events. This effect has been aptly referred to as the description-experience (DE) gap
(Hertwig et 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-human primates (Heilbronner & Hayden, 2016). While some authors have called
for two separate theories explaining choices from description and choices from experience
(Abdellaoui, L'Haridon, & 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 distortion function between the two settings (Frey, Mata, & Hertwig,
2015; Ungemach, Chater, & Stewart, 2009).
While the dichotomous choice patterns we observed are comparable to those described in the 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 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 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, & Hertwig, 2018) echoes the repetitive structure of our REPEATED sequence; conversely, described prospects are typically presented in a less structured, randomized sequence, 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.

Sampling bias has been identified as a source of variability in probability distortions, particularly in relation to the DE gap. Indeed, sampling bias is particularly problematic in ‘experienced’ 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 prescribed by their nominal probability (Camilleri & Newell, 2013; Hertwig & Erev, 2009; Hertwig & 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 every gamble. Any bias would therefore affect the two conditions in a similar manner. With no obvious sampling biases, our data suggest that the DE gap could be modeled on the probability 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 - 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.

In conclusion, our results demonstrated the effect of a task's sequence structure on the shape of 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 through time: the patterns of indifference lines observed in the Marschak-Machina triangle after a session of MIXED or REPEATED sequences were compatible with the probability distortion 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 preceding the Marschak-Machina triangle paradigm might have driven and reinforced a gap between the subjective values of identical probabilities, one that influenced choices between gambles in the Marschak-Machina triangle. The reinforcement learning model we used supports 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 probabilistic information. More sophisticated models, such as the addition of a standard Rescorla-Wagner learning rule or a non-linear transformation of safe magnitudes to the current value 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 learning/association phase was not analyzed here in reinforcement learning terms, as it was 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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Legends

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

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 in the two different elicitation sequences: MIXED (red) and REPEATED (blue) sequences. The percentages of safe choices as a function of safe magnitude (circles) were fitted to softmax functions (curves). Vertical lines indicate the gambles EVs (dashed lines); filled circles indicate the CEs. In both monkeys, low probability gambles (top) had a lower CE in the REPEATED condition than in the MIXED condition, where the CEs were consistently higher than the EVs, indicating a risk seeking attitude. High probability gambles (bottom) showed the inverse pattern, indicating a risk seeking behavior only in the REPEATED condition. **c**, Pattern of CEs across the two elicitation sequences (MIXED vs. REPEATED). Single sessions’ CEs (small data points) and average CEs across sessions (large data points) plotted as a function of gamble EV, with cubic spline interpolated curves. The full pattern of CEs shows a smooth transition from low to high probability gambles in terms of CE difference across the two elicitation sequences. For low probability gambles, both monkeys showed higher CEs in the MIXED than in the REPEATED conditions; when increasing gamble probabilities, the CE difference across conditions gradually reduced and inverted, resulting in lower CEs in the MIXED than in the REPEATED condition for high reward probabilities. Single sessions’ data points were shifted horizontally (REPEATED condition: left; MIXED condition: right) for visualization purpose. **d**, Response times. Mean RT (± SEM across sessions) in the two elicitation conditions. RT for monkey A were similar in the two conditions (RT difference = 3.0 ms, t(9088)=-0.59 p=0.56); Monkey B showed faster response in the MIXED condition compared to the REPEATED 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’ EV.

**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.

**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^{-8}). Lower BIC values for the Prelec weighting functions (Tversky, Prelec-1) indicate a better fit of the data compared to...
the one-parameter Tversky or two-parameter Gonzalez functions. BIC values for all model pairs except for Prelec-1 vs Prelec-2, Prelec-1 vs Gonzalez, and Prelec-2 vs Gonzalez in Monkey A, and the Prelec-2 vs Gonzalez in monkey B, were significantly different (post-hoc analysis, p<0.05) for both monkeys. The sum of squared errors in CE estimation was the lowest in the Prelec models. b, c, Validation of the parameter estimation procedure using the Prelec-1 probability weighting function. Upper plots in b and c represent the utility (left) and probability distortion (right) functions used to simulate choices; lower plots represent the functions recovered with the MLE procedure. Monte Carlo simulation of choice behavior (using the same number of trials and the same step-size for magnitude and probability as in the measured data: 9 gamble probabilities, 11 safe magnitudes, 6 trials per gamble-safe pair) was repeated 1000 times, producing the 95% confidence intervals on the parameter estimates (grey areas). Varying the utility function parameter (p, 0.2 to 3) while keeping the probability distortion parameter constant (α=0.67) resulted in an unbiased estimate of the utility shape (b). The probability distortion parameter (α), varying from 0.33 to 3 while keeping the utility shape fixed (p=2), was recovered consistently and without bias (c). d, Modeled vs measured choice behavior. Comparison of estimated (curves) and measured (circles) percentage of safe choices as a function of safe magnitude, for two example gambles (probabilities 0.2 and 0.8); see Figure 3-1 for the full dataset. Estimated choice percentages were computed using the discrete choice model with the MLE-recovered parameters (Eq. 3, using the Prelec-1 probability weighting function). Estimated CEs are represented as red and blue points, EVs as vertical dashed lines. The estimated psychometric functions closely approximated the measured data points, and differences in estimated CEs across conditions are compatible with the observed data for both low and high probabilities (see Fig. 2b).

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

Figure 4. Utility and probability distortion functions in two elicitation conditions. a, Model parameter estimates (mean ± SEM across sessions) in the MIXED (red) and REPEATED (blue) conditions. Asterisks indicate significant differences across conditions (MANOVA). The probability distortion parameter (α) consistently varied across sequence structures in both monkeys: negative log-values in the MIXED condition corresponded to inverse S-shaped probability distortion (α<1), while positive log-values in the REPEATED condition implied S-shaped probability
distortion ($\alpha > 1$). Numbers below the bars represent effect sizes (Cohen’s $d$). The utility ($\rho$) and softmax ($\lambda$) parameters significantly differed across conditions only for one monkey, with a smaller effect size compared to the probability distortion parameter. b, Shapes of the probability distortion function (left) and utility function (right) corresponding to the estimated parameters, displaying the consistent difference in subjective probability evaluation across conditions for both monkeys. c, Two-dimensional representation of the utility and probability distortion parameter estimates. The dots represent the simultaneously estimated utility ($\rho$) and probability distortion ($\alpha$) parameters for single behavioral sessions, with 95% confidence ellipses.

**Figure 5.** Indifference lines in the Marshack-Machina triangle modeling different patterns of probability distortion. a, Representation of gambles in the Marshack-Machina triangle. Schematic representation of a three-outcome gamble (left): probabilistic combination ($p_1$, $p_2$, $p_3$) of three fixed magnitudes ($m_1=0$ ml, $m_2=0.25$ ml, $m_3=0.50$ ml) which can be represented in the Marshack-Machina triangle (right, with example gambles corresponding to points on the triangle edges). The grey line in the triangle connects points with equal expected value (EV=0.25 ml). b, Procedure for the psychometric measurement of one indifference line. An indifference point (top, blue dot) in choices between a fixed gamble A and different gambles $B_i$ (circles) was defined as the point on the triangle hypotenuse for which a softmax function fitted on the ratio of A over $B_i$ choices equated 0.5 (bottom). An indifference line was then constructed by connecting such indifference point on the hypotenuse to the fixed gamble A (blue line). c, Theoretical indifference lines. Indifference lines predicted by cumulative prospect theory, for different underlying shapes of utility ($u(m)$, power function) and probability distortion ($w(p)$, Prelec-1 function). Each plot shows the indifference lines corresponding to a particular combination of $u$ and $w$ shapes, represented with orange and purple lines respectively. The shape of the utility function (linear in the first row of plots, concave and convex in the other two rows) changes the global orientation of the indifference lines, without affecting their fanning direction. On the contrary, a change in probability distortion shape corresponds to a change in the fanning direction of indifference lines: a linear probability distortion (first column) produces parallel indifference lines, while S-shaped (second column) and inverse S-shaped (third column) probability distortions correspond to indifference lines fanning-in and fanning-out respectively, regardless of the utility function shape.

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

**Figure 7.** Sequence-dependent effects of trial history on probability distortion shape. a, Influence of past trials on current trial’s choice. Standardized regression coefficients (mean ± SEM across sessions) for current trial’s gamble EV, safe reward magnitude and previous trials’ gamble EV (up to eight trials in the past). Asterisks represent coefficients significantly different from zero: for both monkeys, the choice behavior depended on at least one trial in the past. Positive regression coefficients indicated that an increase in the previous trial’s gamble EV induced the monkeys to choose the current trial’s gamble option more frequently. b, Effect of the past outcomes on gamble choices. Standardized regression coefficients (mean ± SEM across sessions) for gamble EV, safe magnitude, previous trial’s gamble outcome (0 ml or 0.5 ml) and gamble position. A significant positive coefficient for the previous outcome indicated that monkeys chose the gamble more often when the previously chosen gamble was successful (0.5 ml) than 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 model (Eq. 15) was at least as good at describing the choice data when compared to the model with no past trials’ 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: p=5.8×10^{-5}). c, Effect of past outcomes on the utility and probability distortion functions. The utility function appeared more convex following a gamble-win trial (0.5 ml reward) than following a loss (no reward), suggesting that gamble outcomes had an influence on the relative value of gamble and safe options on the next trial. The utility parameter estimates followed win and loss trials are indicated as \( \alpha_W \) and \( \alpha_L \) respectively, while probability distortion parameter as \( \rho_W \) and \( \rho_L \) respectively. The arrows highlight the change in the utility parameter between loss and win trials. Error bars represent the 95% confidence intervals of the parameter estimates. d, Simulated effect of
EV update mechanism based on past outcomes. Mean ± SEM across simulated sessions (N=50) of the CE resulting from choices simulated using the learning model (Eq. 16) in MIXED and REPEATED conditions. The parameters used in the simulation were recovered from the MLE procedure with the same model separately for each monkey. Linear probability weighting and linear magnitude coding were used in the simulation, demonstrating that an EV update mechanism interacting with the local trial structure could explain the observed change in risk attitudes across conditions without explicitly introducing a non-linear probability distortion.
