Non-human primates use combined rules when deciding under ambiguity

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Decision outcomes in unpredictable environments may not have exact known probabilities. Yet the predictability level of outcomes matters in decisions, and animals, including humans, generally avoid ambiguous options. Managing ambiguity may be more challenging and requires stronger cognitive skills than decision-making under risk, where decisions involve known probabilities. Here we compare decision-making in capuchins, macaques, orangutans, gorillas, chimpanzees and bonobos in risky and ambiguous contexts. Subjects were shown lotteries (a tray of potential rewards, some large, some small) and could gamble a medium-sized food item to obtain one of the displayed rewards. The odds of winning and losing varied and were accessible in the risky context (all rewards were visible) or partially available in the ambiguous context (some rewards were covered). In the latter case, the level of information varied from fully ambiguous (individuals could not guess what was under the covers) to predictable (individuals could guess). None of the species avoided gambling in ambiguous lotteries and gambling rates were high if at least two large rewards were visible. Capuchins and bonobos ignored the covered items and gorillas and macaques took the presence of potential rewards into account, but only chimpanzees and orangutans could consistently build correct expectations about the size of the covered rewards. Chimpanzees and orangutans combined decision rules according to the number of large visible rewards and the level of predictability, a process resembling conditional probabilities assessment in humans. Despite a low sample size, this is the first evidence in non-human primates that a combination of several rules can underlie choices made in an unpredictable environment. Our finding that non-human primates can deal with the uncertainty of an outcome when exchanging one food item for another is a key element to the understanding of the evolutionary origins of economic behaviour.

This article is part of the theme issue 'Existence and prevalence of economic behaviours among non-human primates'.

1. Introduction

Although making decisions is a usual aspect of our life, making the right decision at the right time can sometimes be crucial for our future wellbeing, career development or even survival [1]. Given the ever-changing characteristics of their environment, animals including humans make most of their decisions in a context that economists would consider ambiguous as opposed to risky ([2,3], see also [4]). The most critical difference between these two

contexts is how much an individual knows about the likelihood of the outcomes of each possible choice. Indeed, under ambiguity, people have little or no information about these likelihoods. By contrast, people making decisions under risk know the likelihood of each alternative (for example, a one in six chance to win) before deciding.

Humans sometimes exhibit marked attitudes toward risk (i.e. they can be either risk seekers for small risks like gambling in a casino, or risk averse for high risks, leading most people to take out insurance contracts). They also subjectively evaluate outcomes, and are prone to errors of judgement [5,6]. The hot hand effect, for example, consists of continuing to take risks after a series of gains [7]. Humans are also generally more affected by losses than by equivalent gains (loss aversion, [8]). Some of these characteristics are shared with other species when choosing under risk, and especially our closest living relatives (loss aversion, [9,10], hot hand effect, [11]). This suggests that the determinants of our decisions could be inherited from naturally selected features in our ancestors [12–17].

The investigation of decision-making under ambiguity is a recent field in non-human primates. It has been studied less than decision-making under risk [14]. Ultimately, comparing decision-making under risk and under ambiguity in several primate species may enable us to decipher the cognitive, adaptive and/or ecological mechanisms that shape our choices. Humans value options differently under risk than they do in a context of ambiguity [3,4,18], and human attitudes and choices in one context do not always help to predict accurately choices in the other [19]. For example, a risk seeker is not necessarily an ambiguity seeker (see [20] for a review). There is a general consensus in the literature that humans show ambiguity aversion [6,20–22]. This is also true of non-human primates [23,24]. When given a choice between an ambiguous option and an option that is either risky or safe, bonobos (*Pan paniscus*), chimpanzees (*Pan troglodytes*, [24]) and rhesus macaques (*Macaca mulatta*, [23]) avoided the ambiguous option.

Given that most aspects of their environment have an element of unpredictability, this widespread aversion to ambiguity is quite intriguing [14]. It is unclear whether individuals reject ambiguity due to a lack of information or because dealing with ambiguity may be cognitively more challenging than dealing with risk. Indeed, in an ambiguous context, individuals may have to compute a range of probabilities to make the best possible decision, whereas under risk individuals have all information needed to evaluate the likelihood of options.

Earlier risk studies have revealed that several species of great apes, macaques and capuchins take the predictability of outcomes into account to maximize their benefits [11,23,25–28]. Other studies have shown intuitive probabilistic inferences in capuchins (*Sapajus apella*, [29]) and great apes [30,31]. Thus, non-human primates are equipped with the cognitive skills needed to process odds of outcome. However, there are some indications that the decision-making process may shift from odds evaluation to simpler decision rules when the cognitive load of a task increases. In a recent study, we presented great apes and monkeys with a risky food gambling task in which information about the odds of winning was displayed in front of them before each trial. To gamble in this game, subjects had to relinquish a food item that was already in their possession to obtain the contents of one out of six cups displayed in front of them. The cups contained different amounts of food, with rewards that were larger, smaller or the same size as the food item the subject already possessed. In the first version of the task, the chances of winning progressively decreased throughout the study, and individuals successfully used the odds associated with each outcome before gambling [11]. This gradual decrease in the chances of winning probably facilitated the extraction of information about odds. Odds were modified from one trial to the next in a second version of this task [32], thus requiring individuals to pay close attention to the odds displayed to them at each trial. Here, many individuals applied a Maximax heuristic, and were more likely to gamble when there was at least one chance of winning (disregarding potential losses). Heuristics are simplified decision rules that help individuals to deal with situations that require a high cognitive investment [33,34]. Thus, individuals apply heuristics when faced with an increased difficulty in extracting information about the odds. Under ambiguity, where information is partial, individuals may be more likely to make use of simple decision rules rather than attempting to evaluate the odds of winning or losing, but this has not been investigated to date.

This study investigated the role played by information about odds in decisions made under risk and ambiguity by capuchin monkeys, Tonkean macaques (*Macaca tonkeana*), orangutans (*Pongo abelii*), gorillas (*Gorilla gorilla*), chimpanzees and bonobos. We used a modified version of the risky gambling game mentioned above. In this task, subjects could bet a food item in their possession in exchange for the contents of one of the six cups displayed in front of them. Each cup contained either a larger or smaller amount of food than the amount possessed by the subject. The decision was made under risk when the subjects could visually assess the odds of winning and losing (for example, they had five chances out of six to receive more food if five cups contained a larger cracker and one cup contained a smaller cracker than the one they already possessed). Ambiguity was implemented by covering some of the cups. By changing the presence and location of the covers, we could vary the amount of information available so that subjects made their decision under four conditions: (i) risky lotteries, where subjects could see all the potential outcomes; (ii) predictably advantageous lotteries, where subjects could not see but could infer (according to how the lotteries were set up, see Material and methods) that the covered cups contained large rewards; (iii) predictably disadvantageous lotteries, where subjects could not see but could infer that the covered cups contained small rewards; and (iv) ambiguous lotteries, where subjects could not guess the exact probabilities associated with potential outcomes. The safe choice was therefore to keep the food they already possessed, while the risky or ambiguous choice was to gamble. This experimental set-up allowed us to investigate which elements subjects used to make their decision. We anticipated three decision-making scenarios. First, subjects may reject ambiguous lotteries altogether by only gambling in lotteries without covers (risky lotteries). Second, they may ignore ambiguity and gamble based on visible information through simple heuristics such as counting the number of large visible rewards. Third, subjects may consider the level of information about odds, thus responding differently to contexts in which they can predict their odds of gains and those where they cannot. Unlike the two previous alternatives, this third alternative is
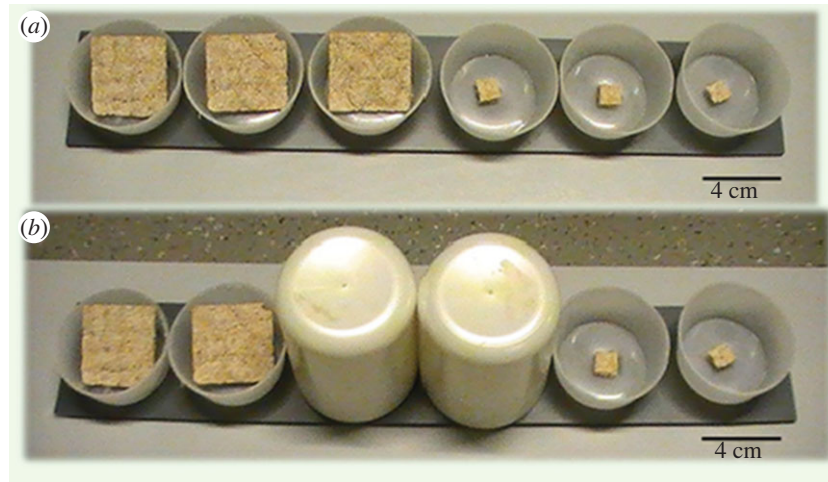
Figure 1. Example of two lotteries presented to the subjects. (*a*) A tray of six plastic cups containing pieces of crackers that are either larger or smaller than the food item they have already been given. In this risky lottery (#16), three cups contain a large cracker (cups 1–3, left) and three cups contain a small cracker (cups 4–6, right). There are no covers and individuals can see that there is a 50% chance of success. (*b*) In this ambiguous lottery (either lottery #10, #14 or #18), there are two covers in the middle that can each hide small or large crackers. Individuals cannot precisely estimate their chances of winning. Large crackers: $4 \times 4 \times 0.5$ cm. Small crackers: $1 \times 1 \times 0.5$ cm. (Online version in colour.)

more complex because it requires subjects to build correct expectations about the content of the covered cups in predictable lotteries. Great apes, macaques and capuchin monkeys can make inferences based on partial visual information [35–37], and may therefore have the cognitive skills to build correct expectations. However, we cannot exclude that the great apes might be more skilled in doing so. We know more about the inferential skills of great apes than those of other species [38]. Evaluating the odds of outcome in risky lotteries or the range of possible odds of outcome in the ambiguous one may be less demanding for them than for monkeys. Each species may also have its own decisional pathway, and choices could reflect a species' general sensitivity to risk or ambiguity. For example, macaques [11] and capuchins have sometimes been described as rather risk prone [39], and chimpanzees have been described as more risk prone than bonobos in some studies [27,40]. These species might be more likely to gamble in higher risk lotteries than others, and they may be less averse to the ambiguity of the task than the other species.

2. Material and methods

(a) Subjects

Thirty subjects were involved in the study: four brown capuchin monkeys, five Tonkean macaques, five orangutans, four gorillas, seven chimpanzees and five bonobos (electronic supplementary material, table S1). All subjects were socially housed in enclosures with access to indoor and outdoor areas. Water was available *ad libitum* and subjects were not food deprived. Procedures were non-invasive and subjects could choose to stop participating at any time. All individuals had previous experience in a food gambling task and were familiar with exchanging food items of different sizes with a human experimenter (see electronic supplementary material and table S2 for training and pre-analyses procedures).

(b) Apparatus and experimental procedure

The procedure was a food gambling task similar to that used by Pelé *et al.* [11]. Six cups were presented aligned in front of the

subject. Each cup contained one piece of cracker that could be large ($4 \times 4 \times 0.5$ cm) or small ($1 \times 1 \times 0.5$ cm) (figure 1). We manipulated the contents of the cups to offer lotteries with varying gain predictability (table 1). Crackers were always placed in the cups according to their size and were aligned in decreasing order of size from the left to the right. Lotteries were presented under four conditions (table 1): (a) *risky*: no cups were covered, thus all potential crackers were visible (figure 1*a*); (b) *predictably advantageous*: two of the six cups were covered, but the ranking of crackers by size enabled subjects to infer that two large crackers were hidden under the covers (see for example lottery 6, table 1); (c) *predictably disadvantageous*: two of the six cups were covered, and the individual could infer from their position that they contained small crackers (see for example lottery 22, table 1); and (d) *ambiguous*: two of the six cups were covered and subjects could not predict the size of the hidden crackers (figure 1*b*). Note that all subjects had already experienced the ordering of crackers by size in the lottery cups in a previous study on decision-making under risk [32].

In each trial, the experimenter sat in front of the subject's compartment holding an initial food item (always a medium-sized cracker measuring $2 \times 2 \times 0.5$ cm) in one hand, and the lottery in the other hand (i.e. the tray of six aligned plastic cups). The experimenter ensured that the subject had seen the six-cup tray, and then gave him or her the initial food item. The experimenter held out her empty hand and offered the subject the opportunity to gamble by giving the initial food item back. If the subject chose to keep the initial allocation, the trial ended. If the subject gambled, it received the contents of one of the six cups, randomly determined prior to testing. While the subject consumed the cracker (either the initial food item or the lottery cracker), the experimenter refilled the cups out of the subject's sight before starting the next trial with the next lottery. In the cases where the lottery contained covered cups, a subject who decided to keep the initial allocation would be shown the contents of the covered cups and the trial would end. If the subject chose to return the initial allocation, the experimenter removed the covers then gave the subject the contents of a randomly assigned cup which could sometimes be one of the covered cups. A total of 28 lotteries (table 1) were used, each presented once in a random order within a series of 28 trials (i.e. one lottery after the other), and each series was repeated 18 times (18 sessions). To prevent satiety, the great apes participated in 14 trials per day and the monkeys in seven trials per day.

Table 1. The 28 lotteries. LRv, number of large rewards visible; large square, large reward; small square, small reward; blue rectangle, position of cup with cover. (Online version in colour.)

lottery number (#)	lottery configuration	visible probability of gain	real probability of gain	no. LRv	level of information
1		1	1	6	risky
2		1	1	4	ambiguous
3		1	1	4	predictably advantageous
4		1	1	4	predictably advantageous
5		1	0.83	4	ambiguous
9		1	0.67	4	ambiguous
8		0.83	0.83	5	risky
6		0.75	0.83	3	predictably advantageous
7		0.75	0.83	3	predictably advantageous
13		0.75	0.5	3	predictably disadvantageous
12		0.67	0.67	4	risky
16		0.5	0.5	3	risky
11		0.5	0.67	2	predictably advantageous
10		0.5	0.67	2	ambiguous
14		0.5	0.5	2	ambiguous
18		0.5	0.33	2	ambiguous
17		0.5	0.33	2	predictably disadvantageous
20		0.33	0.33	2	risky
15		0.25	0.5	1	predictably advantageous
21		0.25	0.17	1	predictably disadvantageous
22		0.25	0.17	1	predictably disadvantageous
24		0.17	0.17	1	risky
19		0	0.33	0	ambiguous
23		0	0.17	0	ambiguous
27		0	0	0	ambiguous
25		0	0	0	predictably disadvantageous
26		0	0	0	predictably disadvantageous
28		0	0	0	risky

(c) Data analysis

We sought to identify which of the following variables best explained the responses of subjects: the species, the number of visible large rewards (#LRv, from 0 to 6), the level of information (risky, predictably advantageous, predictably disadvantageous or ambiguous), the point in the study duration (either during the first nine sessions from S1 to S9 or the last nine sessions, from S10 to S18), and the size of the outcome received at the previous trial (large-, medium- or small-sized rewards). We added subjects, study site (as a proxy for housing conditions) and age (juvenile or adult) as random factor (with the following nested structure: 1/age/subjects and 1/study site/subjects). We first ran a GLMM model (package *lme4*, in R) with a model selection procedure based on Akaike's second-order information criterion (function dredge in R, package MuMin, [41], AICc, [42]) in order to identify the variables contributing to the best model, all species included. Given that the best model was statistically equivalent in terms of data fit to the full model (Delta < 2), we chose the model with the highest explanatory power, i.e. the full model.

For each species, we then used the decision tree approach with these variables (except the variable 'species') to analyse the data because we (i) expected interactions between variables and nonlinear effects and (ii) wanted to capture the hierarchical decision pathway (order of variables, potential threshold of these variables) for each species. The random factors study site and age were not included in this analysis as each species had only one study site, and some species had only adult individual. Generalized linear mixed models (GLMMs) allow for the incorporation of within individual repetitions and the dependent variable (gambling) was binomial. We therefore used model-based recursive partitioning (a type of decision tree) based on GLMMs called generalized linear mixed effects models trees (GLMM trees). The algorithm identifies subgroups, i.e. the terminal nodes, which differ according to the gambling rate. To identify these subgroups, the observations in the dataset are partitioned with respect to defined splitting variables, like in any tree algorithms. The main interest of tree-based algorithms is that they can handle high-order interactions, which in our case correspond to the decision pathway. Unlike other tree algorithms, GLMM trees take into account the clustered structure of datasets by including a cluster random effect, which allows us to account for the pseudo replication of the same individual in the dataset. Since we wanted to identify subgroups differing from each other by their gambling rate, we specified the node-specific model that included only one intercept (i.e. the gambling rate mean per subgroup). Specifically, the tree algorithm proceeds via the following steps, all of which are adjusted for the random effects: at each node, the algorithm assumes that there is at least one splitting variable, which, at a certain threshold (i.e. optimal split point) divides the observations in two subsets, ultimately leading to more stable (i.e. with a lower variance) intercept coefficients (i.e. gambling rate values) than at the beginning. This stability is objectified via the parameter instability test. The algorithm estimates an optimal split point for each splitting variable and applies instability tests. If several instability tests show significant results ($p < 0.05$ for several splitting variables), the node observations are partitioned into two subsets with respect to the splitting variable associated with the highest instability (lowest p-value). This process is repeated recursively until no further significant instabilities are found (i.e. all $p > 0.05$) or the subgroups become too small. All tests are Bonferroni-adjusted to account for multiple testing across all covariates.

We used the function glmertree of the package glmertree [43]. For each species, we specified a model with only the intercept in order to identify subgroups differing on their gambling rate. To account for individual differences, we set individual identity as a random intercept. Finally, we specified the splitting
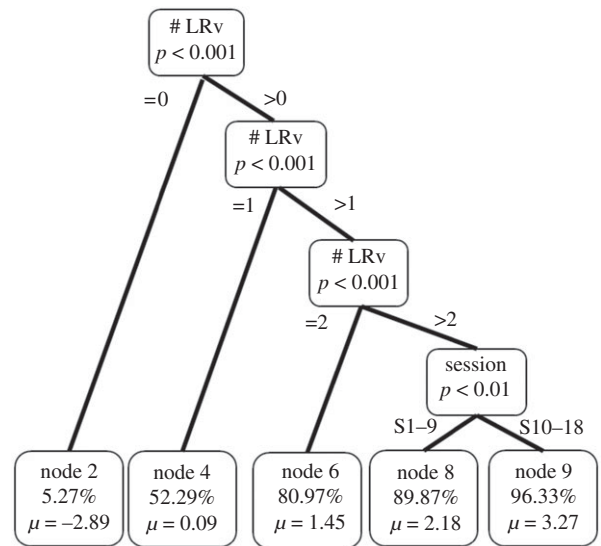

Figure 2. Decision tree for the capuchin monkeys showing the hierarchical organization of the variables structuring the decision. Capuchins gamble more than 50% of the time when at least one large reward is visible (from node 4). For 3 LRv lotteries (nodes 8 and 9), they also gamble more at the end of the study compared to the beginning. # LRv, number of large rewards visible; session, point in the study duration (S1–9, from session 1–9; S10–18, from session 10–18); p-value, node instability (unstable with a p-value < 0.05 in all intermediary nodes); μ, the intercept coefficient (i.e. the logit transformation of the gambling probability expressed in % and given above).

variables 'number of large visible rewards', 'level of information', 'point in the study duration', and 'previous outcome' as potential partitioning variables. Because the response variable is a binary variable, we specified 'binomial' as the model family whose link function is the function logit by default. Further details on the R code are given in the electronic supplementary material. Because of our initial specifications in the model (including only the intercept), we only obtained the intercept coefficient (μ) corresponding to the logit transformation of the gambling probability. These gambling probabilities were computed using the inverse of the logit function (2.1) to extract the mean of gambling rate per model.

$$\mathrm{logit}^{-1}(\mu) = \frac{1}{1 + e^{-\mu}}. \tag{2.1}$$

In the decision trees, we report the value of (μ) and the gambling probabilities as percentages (figures 2–7). We also calculated the intra-class correlation (ICC, see electronic supplementary material procedure for the R code) for each species to evaluate how much variance could be explained by inter-individual variations.

In addition, we ran a second analysis to evaluate if the previous choice and its outcome could influence the next decision (stay with or shift from the previous decision to exchange or not). To do so, we looked at all the lotteries where subjects received information that their choice had been right or wrong. This analysis was based on a subset of data involving 9934 decisions. The dataset was restricted to the following four cases: (1) trials where individuals exchanged and were right to do so (when they subsequently won, whatever the lottery). (2) Trials where they refrained from exchanging and were right to do so. But note that this 'rightness' could only be experienced by subjects in lotteries 25, 26 and 27, where they could see that they would have lost if they had exchanged, i.e. by seeing only small rewards when the covers of the cups were removed. In other lotteries, the subjects had no way to guess which cup
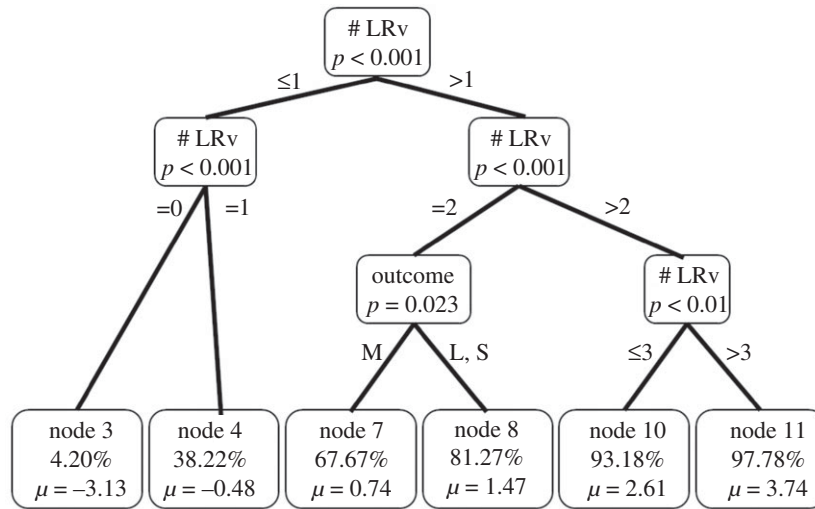
Figure 3. Decision tree for the bonobos. Bonobos gamble more than 50% of the time in lotteries with at least 2 LRv (from node 7). In lotteries with 2 LRv, they are less likely to gamble if the previous reward was medium sized. # LRv, number of large rewards visible; outcome, previous outcome (M, medium; L, large; S, small); p-value, node instability (unstable with a p-value < 0.05 in all intermediary nodes); μ, the intercept coefficient (i.e. the logit transformation of the gambling probability expressed in % and given above).
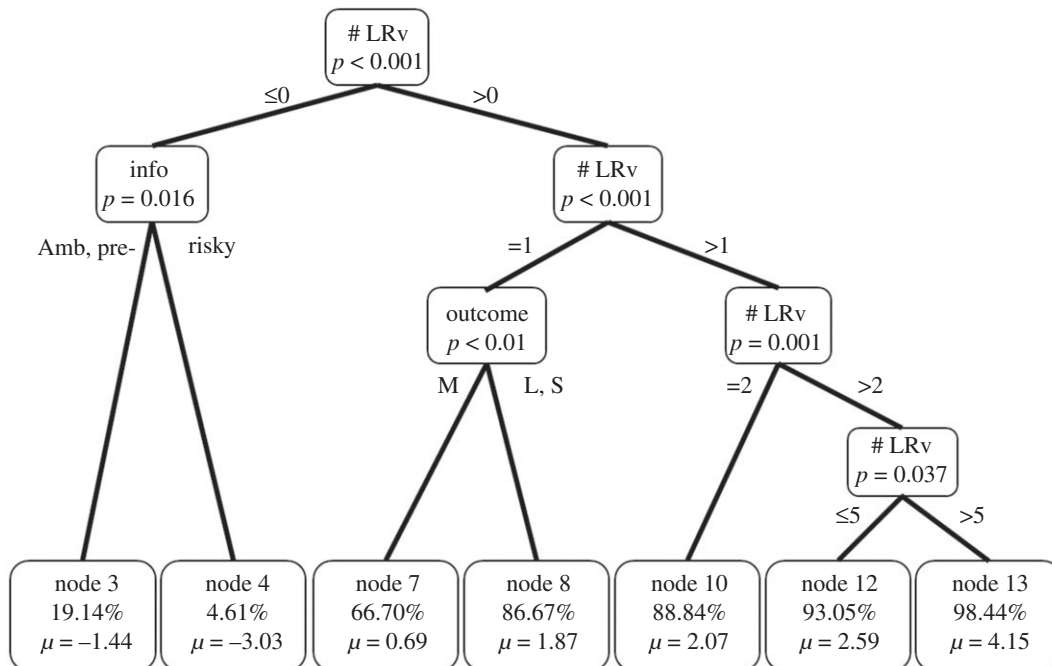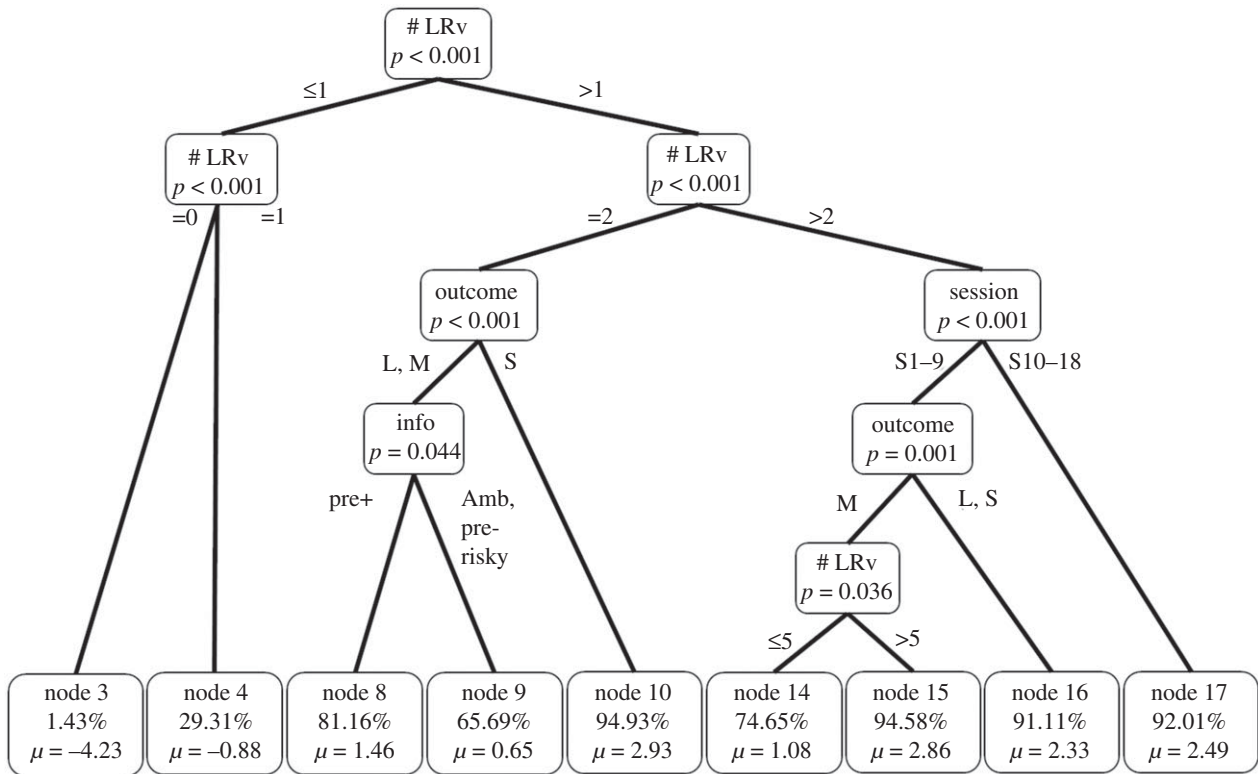

Figure 4. Decision tree for the gorillas. Gorillas gamble more than 50% of the time for lotteries with at least 1 LRv (from node 7). The level of information plays a role in 0 LRv lotteries: they are more likely to gamble in lotteries with covered cups (node 3) than in risky lotteries (node 4). Previous outcome can play a role for lotteries with 1 LRv (nodes 7 and 8). # LRv, number of large rewards visible; info, level of information (pre+, advantageous; pre−, disadvantageous; Amb, ambiguous, risky); outcome, previous outcome (M, medium; L, large; S, small); p-value, node instability (unstable with a p-value < 0.05 in all intermediary nodes); μ, the intercept coefficient (i.e. the logit transformation of the gambling probability expressed in % and given above).

they would have received. We cannot therefore make a judgement about whether or not individuals felt that their choice not to exchange had been wise. (3) Trials where they exchanged and were wrong to do so (when they subsequently lost, whatever the lottery). (4) Trials where they did not exchange and were wrong to do so. But note here also that this 'wrongness' could only be experienced by subjects in lotteries 2, 3 and 4, where they could see that they would have won if they had exchanged, i.e. seeing only large rewards when the covers of the cups were removed. In other lotteries, the subject had no

way to guess which cup they would have received. Thus, we could not evaluate whether individuals would have regretted their decision to not exchange. For each of these four cases, we then looked at whether they maintained the strategy in the following trial (right-keep, right-shift, wrong-keep, wrong-shift: an example of right-keep would be to see the individual refusing to exchange after having being right to not exchange in the previous trial).

If individuals were influenced by the result of the previous decision, we predicted that being right at a given trial should

Figure 5. Decision tree for the Tonkean macaques. Tonkean macaques gamble more than 50% of the time for lotteries with at least 2 LRv (from node 8). Level of information, point in the study duration, and previous outcomes are also splitting variables in various parts of the decision tree. They can distinguish between predictably advantageous lotteries and the other ones, but only for 2 LRv lotteries and only if the previous outcome was a medium-sized or large reward. # LRv, number of large reward visible; info, level of information (pre+, advantageous; pre−, disadvantageous; Amb, ambiguous, risky); outcome, previous outcome (M, medium; L, large; S, small); session, point in the study duration (S1–9, from session 1–9; S10–18, from session 10–18); p-value: node instability (unstable with a p-value < 0.05 in all intermediary nodes); μ, the intercept coefficient (i.e. the logit transformation of the gambling probability expressed in % and given above).

make subjects adopt the same strategy in the following trial (whatever the strategy, i.e. exchanging or not). We also predicted that subjects should shift strategy if they had been wrong in the previous trial (whatever the strategy). We conducted a GLMM analysis with a logit link function and binomial distribution to evaluate if the predictions were verified (1: prediction verified, 0: prediction unverified) according to the species and the type of decision (right or wrong), with individuals as random factor. We ran a model selection analysis to select the best model.

3. Results

(a) Identifying the main decisional variables and building the decision tree

The results of the best model selection procedure indicate that the full model including the five variables was the best model (see electronic supplementary material, table S3). The results of the decision tree analysis are shown for each species in figures 2–6 and summarized in table 2. As expected, the first splitting variable is the number of large visible rewards (#LRv) for all species. The scenarios then differ according to each species. Some trees remain 'simple' with five terminal nodes in capuchins, six in bonobos and seven in gorillas, while others are more complex with nine nodes in macaques, 11 nodes in chimpanzees and 13 nodes in orangutans. Species results are presented in increasing order of terminal nodes in the decision trees. For individual gambling rates, see electronic supplementary material, table S4 results section and

see table 2 for the proportion of total variance explained by ICC.

The simplest tree, i.e. the one with the fewest nodes, is that of capuchins (figure 2). They start gambling more than 50% of the time when at least one large reward is visible, as indicated by the probability of gambling shown below each terminal node of the figure (here, from node 4 in figure 2). The first splitting variable is the number of large visible rewards (LRv). They distinguish between lotteries with 0, 1, 2 and 3–6 LRv, gambling more as the number of LRv increases. For lotteries with at least 3 LRv, the probability that capuchins will gamble is higher by the end of the study (96.32%, node 9) compared to the beginning (89.87%, node 8). Previous outcomes do not play any role and the level of information is never a splitting variable, suggesting that capuchins do not consider the level of information provided by the different lotteries (i.e. the fact that the covers hide rewards).

For bonobos, the number of LRv is also the first splitting variable (figure 3). They start gambling more than 50% of the time in lotteries with at least 2 LRv (from node 7). They distinguish between 0, 1, 2, 3 and 4–6 LRv (gambling more as the number of LRv increases). In lotteries with 2 LRv, they are less likely to gamble at a given trial if the previous outcome was a medium-sized reward (i.e. if they had not exchanged; 67.67% of gambling, node 7) than a reward of any other size (81.27% of gambling, node 8). Like for the capuchins, the level of information is never a splitting variable, suggesting that they do not consider the level of information provided by the different lotteries.
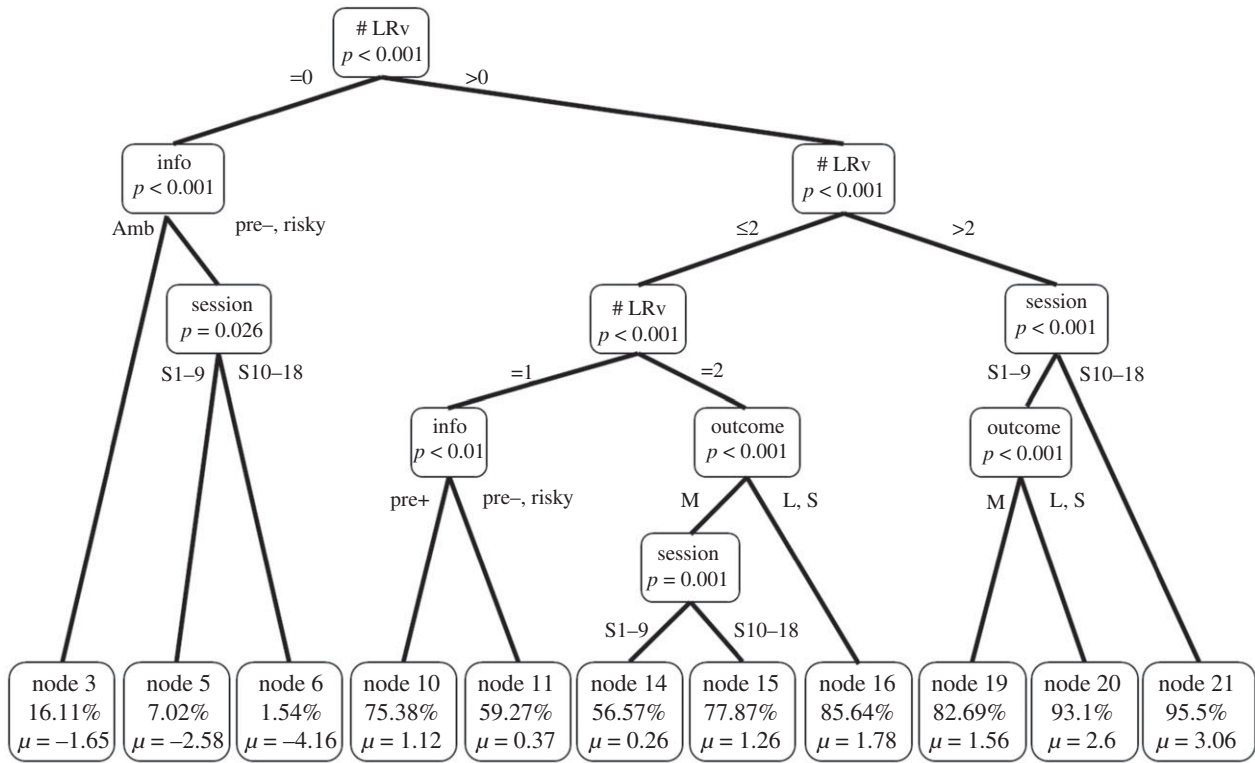
Figure 6. Decision tree for the chimpanzees. Chimpanzees gamble more than 50% of the time for lotteries with at least 1 LRv (from nodes 10 and 11). The level of information plays a role at 0 LRv and 1 LRv lotteries and chimpanzees gamble more at lotteries that are indeed more likely to provide large rewards under the covers (nodes 3 and 10). The point in the study duration and the size of the outcome can also play a role in the decision-making process (see the Results section). # LRv, number of large rewards visible; info, level of information (pre+, advantageous; pre−, disadvantageous; Amb, ambiguous, risky); outcome, previous outcome (M, medium; L, large; S, small); session, point in the study duration (S1–9, from session 1–9; S10–18, from session 10–18); p-value: node instability (unstable with a p-value < 0.05 in all intermediary nodes); μ, the intercept coefficient (i.e. the logit transformation of the gambling probability expressed in % and given above).
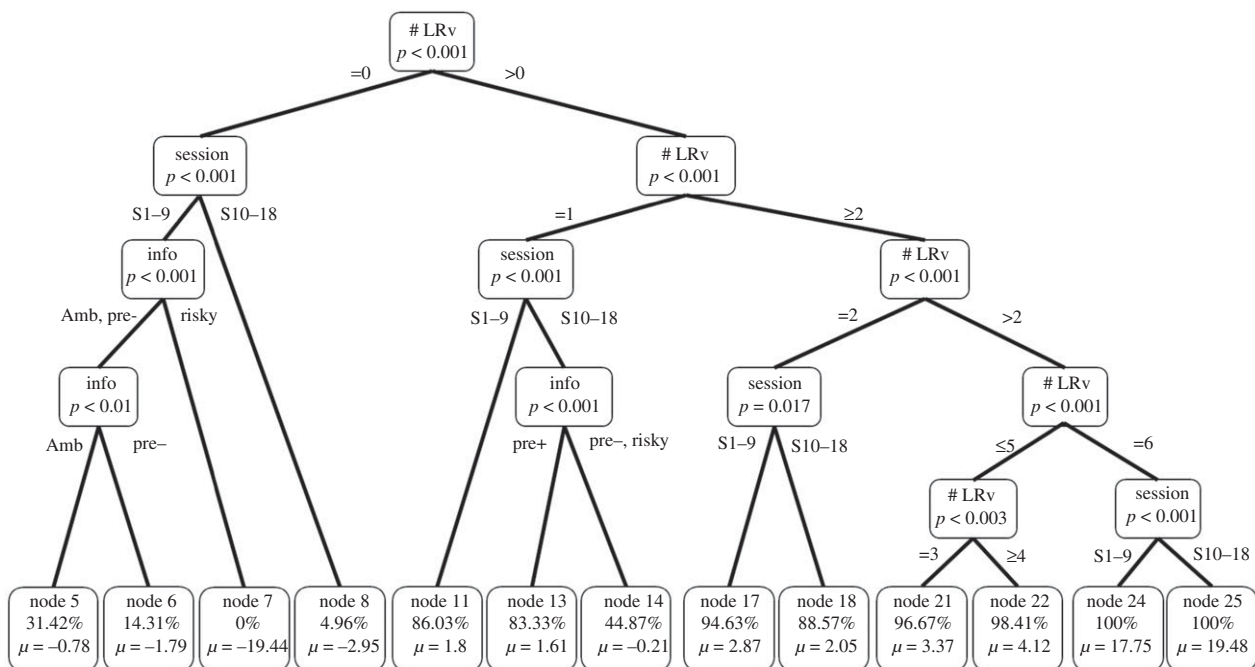
Figure 7. Decision tree for the orangutans. Orangutans gamble more than 50% of the time for lotteries with at least 1 LRv (from node 11, except for node 14). The level of information plays a role at 0 LRv (especially at the beginning of the study), and 1 LRv lotteries (especially at the end). Like chimpanzees, orangutans gamble more at lotteries that are more likely to provide large rewards under the covers (nodes 5 and 13). The point in the study duration can also play a role for 2LRv (see Results' section). # LRv, number of large rewards visible; info, level of information (pre+, advantageous; pre−, disadvantageous; Amb, ambiguous, risky); outcome, previous outcome (M, medium; L, large; S, small); session, point in the study duration (S1–9, from session 1–9; S10–18, from session 10–18); p-value, node instability (unstable with a p-value < 0.05 in all intermediary nodes); μ, the intercept coefficient (i.e. the logit transformation of the gambling probability expressed in % and given above).

Table 2. Summary of the main results of the study. *, Based on the response at risky lottery 24, significant difference between choices of the risky versus safe option; **, based on the analysis of the decision tree, when ambiguous lotteries are preferred to equivalent risky ones (for * and **, note that future studies should run econometric evaluations to confirm these attitudes); ICC, intra-class correlation: percentage of total variance explained by individual variance.

	significant variables in the decision trees	gambling > 50%	can make correct expectations	made correct expectations in more than one type of lottery	potential (*) attitude toward risk	potential (**) attitude toward ambiguity	ICC (%)
capuchins	# LRv	# LRv ≥ 1	no	no	risk seeking		41
bonobos	# LRv, outcome	# LRv ≥ 2	no	no			29
gorillas	# LRv, outcome, level of information	# LRv ≥ 1	no	no	risk seeking	ambiguity seeking	0.3
macaques	# LRv, outcome, level of information, point in the study duration	# LRv ≥ 2	yes	no			55
chimpanzees	# LRv, level of information, point in the study duration, outcome	# LRv ≥ 1	yes	yes	risk seeking		19
orangutans	# LRv, point in the study duration, level of information	# LRv ≥ 1	yes	yes	risk seeking		58

For gorillas, the first splitting variable is also the number of LRv (figure 4). They gamble more than 50% of the time for lotteries with at least 1 LRv (node 7) and they distinguish between lotteries with 0, 1, 2, 3–5 and 6 LRv. For lotteries with 0 LRv, the level of information is also a splitting variable. They are more likely to gamble in lotteries with covered cups (19.14% of the time, node 3) than in risky lotteries (4.61%, node 4). This evidence strongly suggests that the subjects knew that some of the covered cups can contain large rewards but do not make any distinction between the different levels of information. For lotteries with 1 LRv, the previous outcome can play a role on the decision as gorillas are more likely to gamble (86.67%, node 8) if they received a large or a small reward (i.e. if they had exchanged) at the previous trial than if they had received a medium-sized reward (66.70%, node 7), in other words, if they had not exchanged.

For Tonkean macaques, the first splitting variable is also the number of LRv (figure 5). They generally start gambling more than 50% of the time for lotteries with at least 2 LRv (from node 8) but the level of information, point in the study duration, and previous outcomes are also splitting variables. With 0 LRv, they almost never gamble (1.43%, node 3) and gamble more with 1 LRv (29.31%, node 4). With 2 LRv, they are more likely to gamble if they received a small reward at the previous trial (94.93%, node 10) than if they received any other size of reward (equal to or less than 81.16%, node 8 and 9). With 2 LRv, if the previous reward was large or medium sized they took into account the level of information, playing more in predictably advantageous lotteries (81.16%, node 8) than in the others (65.68%, node 9). For lotteries with 3 LRv or more, they generally gamble more at the end of the study (92.01%, node 17) than at the beginning (node 14–16, but not 15), and at the beginning of the study, they can be influenced by both previous outcomes and #LRv (nodes 14–16, see figure 5 for more details).

The first splitting variable for chimpanzees is also the number of LRv (figure 6). They gamble more than 50% of the time for lotteries with at least 1 LRv (from node 10 and 11). For lotteries with 0 LRv, the level of information is also a splitting variable. Chimpanzees rarely gamble, but they are more likely to gamble for ambiguous lotteries (16.11%, node 3) than predictably disadvantageous and risky lotteries (below 7.02%, node 5 and 6). In the last two types of lotteries, the point in the study duration is also a splitting variable, as the probability to gamble is lower at the end of the study (1.54%, node 6) compared to the beginning (7.02%, node 5). For lotteries with 1 LRv, the level of information is, again, a splitting variable. Chimpanzees gamble more at predictably advantageous lotteries (75.38%, node 10) than at the others (59.27%, node 11). For lotteries with 2 LRv, previous outcome and point in the study duration play a role. They are less likely to gamble after receiving a medium-sized reward at the beginning of the study (node 14) compared to the end (node 15). This outcome effect is also detected for 3–6 LRv lotteries, but only occurs at the beginning of the study (node 19).

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Orangutans distinguish between lotteries with 0, 1, 2, 3, 4–5 and 6 LRv (figure 7). They are more likely to gamble more than 50% of the time for lotteries with at least 1 LRv (node 11 and 13, but not 14). The level of information is a splitting variable in two cases. The first case is lotteries with 0 LRv. In the first nine sessions, the subjects never gamble for risky lotteries (node 7) and are more likely to gamble at ambiguous lotteries (node 5) compared to predictably disadvantageous lotteries (node 6). After the first nine sessions, they gamble from time to time but at very low rates, whatever the level of information (node 8). The second case concerns lotteries with 1 LRv. Here subjects are more likely to gamble more for predictably advantageous lotteries compared to others, but they only do so in the second half of the study (node 13 versus 14). They also gamble more for 2 LRv lotteries at the beginning of the study than they do at the end.

(b) Investigating the potential effects of previous decisions

In general, subjects followed the prediction (keep the strategy when right and shift when wrong) in 5142 trials (51.76%) and did not follow the prediction (shift when right, or keep when wrong) in 4792 trials (48.24%). However, the best model selection indicates that the variables species and type of decision (right or wrong), and the interaction between them, influenced the likelihood to follow the prediction (see electronic supplementary material, table S5).

A pairwise comparison with a Bonferroni correction indicated that capuchins, macaques and orangutans were more likely to not follow the 'right keep/wrong shift' strategy than to follow it (capuchins: estimates $= -0.32 \pm 0.11$, 95% CI $= -0.61$ to -0.03; macaques: estimates $= -0.36 \pm 0.09$, 95% CI $= -0.59$ to -0.13; orangutans: estimates $= -0.27 \pm 0.08$, 95% CI $= -0.5$ to -0.05). This effect was not detected in other species. The effect of the type of decision indicates that correct predictions (right keep/wrong shift) were more likely than incorrect predictions (right shift/wrong keep) after a right decision (mean correct predictions: 63%; GLMM: estimates $= 0.5 \pm 0.04$, 95% CI $= 0.42$–0.59), and that incorrect predictions were more likely than correct predictions after a wrong decision (mean incorrect prediction: 72.5%; GLMM: estimates $= -0.98 \pm 0.05$, 95% CI $= -1.09$ to -0.87).

The pairwise comparisons of the interaction between the variables 'type of decision' and 'species' indicate that for the right decisions, keeping the same strategy was more likely than shifting in all species except in the Tonkean macaques (macaques: estimates $= 0.13 \pm 0.09$, 95% CI $= -0.12$ to 0.39; capuchins: estimates $= 0.42 \pm 0.09$, 95% CI $= 0.14$–0.69; orangutans: estimates $= 0.75 \pm 0.09$, 95% CI $= 0.5$–0.99, chimpanzees: estimates $= 0.59 \pm 0.07$, 95% CI $= 0.39$–0.8, gorillas: estimates $= 0.72 \pm 0.09$, 95% CI $= 0.44$–0.99; bonobos: estimates $= 0.42 \pm 0.09$, 95% CI $= 0.14$–0.69). In the wrong decisions, all the species were also more likely to maintain their decision than to shift strategy (macaques: estimates $= -0.85 \pm 0.12$, 95% CI $= -1.19$ to -0.5; capuchins: estimates $= -1.05 \pm 0.15$, 95% CI $= -1.49$ to -0.61; orangutans: estimates $= -1.29 \pm 0.11$, 95% CI $= -1.63$ to -0.96, chimpanzees: estimates $= -0.88 \pm 0.09$, 95% CI $= -1.15$ to -0.61, gorillas: estimates $= -1.14 \pm 0.12$, 95% CI $= -1.5$ to -0.79; bonobos: estimates $= -0.67 \pm 0.12$, 95% CI $= -1.04$ to -0.31; see electronic supplementary material, figure S1). This analysis also indicated that chimpanzees, gorillas and orangutans were more likely to keep the same strategy after a right decision than Tonkean macaques (comparison chimpanzee–macaque: estimates: 0.46 ± 0.11, $z = 4.04$, $p < 0.01$; comparison gorilla–macaque: estimates: 0.59 ± 0.13, $z = 4.50$, $p < 0.001$; comparison macaque–orangutans: estimates: -0.61 ± 0.12, $z = -4.97$, $p < 0.001$). Finally, bonobos were more likely to shift strategy after a wrong decision than orangutans (estimates: 0.62 ± 0.17, $z = 2.75$, $p = 0.02$). Thus, while making the right decision may have slightly biased individuals' next decision, making the wrong decision did not affect the following choice.

4. Discussion

The main goal of this study was to comparatively evaluate the cognitive strategies involved in the resolution of an ambiguous gambling decision in several species of non-human primates. We summarized the results in table 2. Capuchins and bonobos did not consider the level of information, ignoring the fact that rewards could be hidden. Gorillas seemed to know that covers could hide large rewards, but they did not discriminate between predictable and ambiguous lotteries (figure 4, nodes 3 and 4). Tonkean macaques may have discriminated between predictably advantageous and other lotteries, but it occurred on a limited number of occasions (only for 2LRv lotteries, and only after receiving a large or a medium-sized reward, figure 5, node 8). Only orangutans and chimpanzees formed correct expectations about the contents of the cups in more than one instance in the decision tree. A potential ceiling effect (high rates of gambling as soon as more than one or two large rewards were visible) may have prevented the detection of marked attitudes towards ambiguity. Nonetheless, our results stand out from previous studies reporting strong aversion to ambiguity in most tested primate species [23,24]. Far from being unsettled by the ambiguity of this particular context, each species in this study resolved each trial with its own strategy.

One of our hypotheses was that heuristics could be used in this ambiguous context. Indeed, these simple decision rules could alleviate the cognitive load of each decision. Note that although humans can estimate probabilities, they often rely on heuristics to increase the speed of the decision or to avoid the cognitive cost/challenge [44]. In our study, capuchins and bonobos clearly used a simple strategy based solely on the number of large visible rewards. Capuchins gambled in 52% of the trials if at least one large reward was visible. This is reminiscent of the Maximax heuristic reported in a previous study testing decision under risk [32]. Similarly, bonobos used a simple decision rule and mostly gambled in lotteries with at least two large visible rewards. They may therefore have used the number of large visible rewards as a proxy to evaluate the odds, which is a heuristic in itself. We know that these species (like all the non-human primate species tested so far) can easily discriminate between different food quantities [45–47]. Focusing on the size and number of large crackers thus appears a good way to make a rapid decision. A focus on reward magnitude has also been shown to impact decision under risk in humans and non-human primates [48]. In a recent study, Farashahi et al. [49] showed that in an uncertain environment, decisions were more likely to follow an additive model of choice rather than a multiplicative one. When individuals have no exact

information about odds, they first compare what they already possess and what they may obtain, then evaluate reward probabilities separately and make their choice based on a combination of these two pieces of information. The heuristic detected in capuchins and bonobos is mostly based on the number of large visible rewards and could correspond to a model of this type.

Other species seem to understand that some information was missing and that the covers hid some rewards. Tonkean macaques might belong to this category, although the effect of the level of information was only detected in lotteries with 2 LRv and only when the previous outcome had been large or medium sized (figure 5, node 8), a result which we cannot explain. If Tonkean macaques had indeed considered that covers always hid large rewards in predictably advantageous lotteries, we would not have expected an effect of outcome. In addition, we would have expected to detect an effect of covers in other lotteries (0 LRV and 1 LRv lotteries), which was not observed. Thus, the evidence concerning the expectations of Tonkean macaques is inconclusive. Gorillas may also belong to the group of species understanding that some information was missing. They generally were very likely to gamble as soon as 1 LR was visible. We could therefore only detect an effect of the level of information in lotteries with no LRv, where they gambled as if they expected potential large rewards whatever the type of lotteries (ambiguous or predictably disadvantageous, figure 4, nodes 3 versus node 4). This response may be due to some attraction to ambiguity, but given that we did not detect it elsewhere, we cannot affirm this. Given that their expectations were not necessarily correct (they gambled similarly in node 3 in ambiguous lotteries, which could indeed yield a reward, and in predictably disadvantageous ones, which could not), they seem to have failed to grasp the 'predictable' component of the task.

Chimpanzees and orangutans displayed a more complex understanding than the other species that some information was missing and that covers hid some rewards. One of our predictions was that individuals would be able to guess what was underneath the covers in the predictable lotteries and would gamble more if they expected large rewards and less if they expected smaller rewards, or if they were faced with risky lotteries. The response of chimpanzees and orangutans confirmed this prediction for lotteries with 1 LRv. The visible odds of winning cannot explain this result. Note that this effect was not detected in lotteries with 2 LRv or more, as both species already gambled at high rates in these cases. These two species also distinguished between the different levels of information in lotteries with no LRv, seemingly forming the correct expectations that ambiguous lotteries were more likely to be advantageous than the others. Great apes are generally capable of dealing with visible and invisible information in tasks built around disjunctive syllogisms. They can make inferences and deduce that if no reward is visible in box A and no information is available about box B, then they are more likely to find food in box B than in box A [36]. Moreover, they can also make inferences about the location of food in invisible displacements [50–52] and two-item tasks [50,53]. There is also some evidence that great apes are capable of diagnostic and predictive inference (see [38] for a review). In economics, making inferences involves a computation of conditional probabilities using Bayes' rule, a cognitively demanding task. However, it is not clear what

kind of reasoning chimpanzees and orangutans used in our task. A more detailed evaluation of their decisional steps shows that individuals first used the number of LRv, which is a visual and real cue, followed by their own expectations about what was hidden by the covers. Here is an example of how chimpanzees may have psychologically apprehended lottery 15 compared to the other 1 LRv lotteries: 'If I see 1 LRv then I should not gamble, but I can guess that there are two large rewards underneath the two covers. Therefore, I will gamble'. In humans, such an attitude would be modelled as follows: 'If there is a 100% probability of having two large rewards under the covers, conditional on there being one large visible reward on the right of the cover, then one must rationally gamble in 100% of cases'. To our knowledge, this combination of factual and expected information has not been reported in gambling and decision-making studies in primates, and is surprising insofar that expectation pushes the individual into taking actions that are contrary to the facts (i.e. gambling despite the fact that there is no interesting reward visible).

Interestingly, the decisions made by orangutans changed throughout the study with the parallel occurrence of a simplification of the decision for 0 LRv lotteries and a complexification of the process for 1 LRv. It seems that the orangutans decided to invest less energy in the 0 LRv lotteries by the end of the study and focus more on the 1 LRv lotteries. This is a rather efficient strategy as they were highly likely to lose in 0 LRv lotteries whatever the condition. Experience with the set up and the different lotteries probably explain these adjustments in the decisional process. Indeed, we gave each subject the possibility to see what was underneath the covered cups after each trial. We did so to ensure that individuals received the correct information at each trial and would not progressively build erroneous beliefs based solely on their own outcomes. In a complementary analysis, we evaluated how seeing underneath the covers could affect individuals of each species. Indeed, the notions of regret (for example not gambling then realizing that large rewards had been hidden, [54–57]) or confirmation (having gambled and obtained a large reward, thus validating its choice, [58]) can impact the next decision. Our results show that confirmation about the rightness of a previous choice may have encouraged subjects to select the same choice in the next trial (albeit in about 60% of the cases, which is admittedly slightly more than a 50% random choice, see also [59], for a lack of win-stay/lose-shift strategy in rhesus macaques). However, regrets about a wrong choice did not lead individuals to shift their decisions in the next trial. We also showed that the size of the reward received in the previous trial could influence the decision for all species except capuchins and orangutans. In most of these cases but one (in macaques), individuals were less likely to gamble if they had just received a medium-sized reward rather than a small or large one. In other words, they were less likely to gamble if they had not gambled at the previous trials (retaining a medium-sized reward) compared to when they had gambled (and either lost or won). Thus, it was not really the previous outcome that influenced the decision, but rather the previous decision in itself. This suggests that individuals could sometimes make a decision that they would apply in at least two consecutive trials, whatever the lottery. This may indicate a decrease in their attention level after a correct decision. Few existing risk studies have considered how subjects are likely to change the way they

evaluate each option with time and experience, or explored the motivational factors involved [10]. Further studies with more in-depth econometrics measures are needed to investigate these questions in our set up.

The current results raise the difficult question of interspecies differences and whether the latter could be explained by different cognitive toolboxes and/or different socioecology [60]. The ability of chimpanzees and orangutans to combine facts and abstractions in this study contrasts with the simplicity of the responses of bonobos and capuchins, which used simpler decision rules. We expected the strategies of great apes to be more complex than those of monkeys, using more steps and more adjustments to various modalities of the task. However, the responses of gorillas and macaques are intermediate and not so clear-cut. The response of bonobos can also be considered surprising, i.e. a behaviour that is very much like that of capuchins. One possibility is that responses here are not connected to their cognitive abilities but rather to the more general difficulty bonobos have dealing with risk and ambiguity in comparison to chimpanzees, which could be linked to the feeding ecology of each species [24,40,60]. However, both species exhibited similar ambiguity aversion when compared in an ambiguous gambling game where they had no information about the odds [24]. This logically leads to the question of whether each species could be influenced by a specific attitude towards risk and ambiguity. The fact that capuchins, chimpanzees, orangutans and gorillas gambled above 50% of the time for the risky 1 LRv lottery may suggest risk-seeking behaviour (table 2). Several studies using standard risky choice tasks have reported marked attitudes towards risk in capuchins (risk seekers, [39]), macaques (risk seekers [61]), bonobos (risk avoiders [40]) and chimpanzees (risk seekers, [40]). However, these attitudes strongly depend on various parameters including the type of task (in macaques [59]), or experience with the set up (in macaques [62]). In a former study using a risky food gambling task very similar to the current one, we showed that capuchins, macaques, chimpanzees, gorillas and bonobos were mostly risk averse [10]. In the current study, we did not have sufficient statistical power to run an econometric analysis on attitudes towards risk, but the possibility that these attitudes could have influenced the responses of individuals whatever their species cannot be entirely excluded.

Another key future improvement to this study would be to test a larger number of subjects per species. Our sample size remains comparable to or larger than what is usually done in the field of primate cognition. However, our data have shown that in some cases, individual variations explained a large part of the variance, thus calling for a larger sample size. Our limitation lies in the small number of subjects available to take part in such studies. Although the diversity in the housing facilities of individuals could be considered another limitation, all individuals lived in a captive group setting with indoor-outdoor access, enrichment and frequent cognitive stimulations, which made their environments very similar. We nevertheless took this factor into account by implementing the study site as a random factor in the main model. It is also important to highlight that all the subjects here, except the chimpanzees, had already had extensive experience of cognitive studies, having been involved in dozens of them in the facilities in which they were housed. The skills detected in our study may therefore be potentially harder to detect in less trained

or wild individuals. Age can also impact decision-making strategies under risk and ambiguity in young and adolescent humans compared to adults [63–66], but this factor was taken into account as it was implemented as a random factor in the main model. Additional work is needed on the responses of these species under ambiguity and how this may be linked to both their socioecology and/or cognitive limitations.

Each species produced its own solution when faced with ambiguity. Some are based on facts and ignore invisible cues, while others are based on decision rules combining observable facts and expectations. More detailed analyses would be required to evaluate decisions at the individual level. Here, we used a new methodological approach that can detect the diversity of strategies at the species level while taking into account individual repetitions. All species successfully applied one strategy that would minimize the potentially disruptive role of ambiguity. Given that ambiguous situations are likely to be frequently met in the environment, this response is unsurprising. Interestingly, we did not find any evidence of strong ambiguity aversion (gambling solely for risky lotteries, for example) as the individuals could gamble regardless of the amount of information available. One possibility is that our set up was not ambiguous enough to elicit such a strong ambiguity aversion. Indeed, the lack of information could be overcome by various strategies such as guessing, ignoring or imagining the presence of a reward hidden in the cups. Further studies with increased levels of ambiguity may be needed to evaluate how these species cope in this context. Making a decision based on the amount of information (high under risk, low under ambiguity) rather than a purely automatic rejection of ambiguity appears to be less costly in terms of survival and was most probably promoted through natural selection.

It is still unclear whether the strategies observed in this study reflect those used by individuals in their everyday lives when dealing with ecological and social challenges in captivity, and whether these strategies reflect the decision-making profile of their wild counterparts. Nonetheless, showing that some great apes could use advanced reasoning processes like conditional inferences to decide whether to gamble and exchange food is a significant step in our understanding of the evolution of economics in humans.

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