

## **Are Monkeys Sensitive to the Regularity of Pay-off?**

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Animals commonly face fluctuations in their environment and resources. To maximize their benefits, they need to integrate the risks attached to potential pay-offs. We do not know, however, to what extent individuals account for irregularity in the latter. We tested the sensitivity of monkeys (*Cebus apella*, *Macaca tonkeana*, *M. fascicularis*) to the irregularity of pay-offs in two different tasks. In a first experiment, the subjects were given an exchange task where the reward probability varied between different conditions, but yielded the same average pay-off. There was no evidence of subjects favoring either condition, meaning that they behaved in accordance with the predictions of the classical decision theory (Expected Utility Theory). In a second experiment, we offered to subjects a choice between two options involving different pay-off regularity. In this case, a wide range of inter-individual variation was found in the choices of individuals. Whereas monkeys accepted irregular pay-off in a rational way, there were individual biases in their preferences. These results indicate that the preferences of animals in a risky situation were not unequivocally shaped by the environment in which species have evolved.

Individuals commonly face fluctuations in their environment and resources. As assumed by behavioral ecology theory, natural selection should favor decision mechanisms producing optimal strategies, that is, maximizing the net rate of energy intake while minimizing time investment (Schoener, 1971). In the foraging context, two main variables influence decision-making, namely the expected amount of food and the time needed to obtain it. Regarding delay, animals prefer the variable delay to the fixed delay when choosing between two options; however, they prefer a fixed amount of food to a variable amount (Kacelnik & Bateson, 1996).

In the context of the Expected Utility Theory (EUT), Von Neumann and Morgenstern (1944) argue that risky choices can be specified both in terms of outcomes and probabilities of these outcomes, and that how individuals pick one option rather than another is based on maximizing expected utility. This behavior is referred to rationality in classical economic decision-making. Thereafter, any rational, risk-neutral individual should be indifferent when faced with two options having identical expected outcomes. For example, in animals facing variable and fixed delays with identical expected delay for the two options, risk neutrality would prevail if animals do not exhibit preference for either option. In other words, as subjects prefer the variable option to the fixed one, they are risk-prone regarding delays and risk-averse regarding food amounts. These results are very interesting according to the EUT, because it is precisely because animals are risk-averse for food amounts that they care about risk when seeking food resources.

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A number of experimental studies have, however, demonstrated that human decision-making is not consistent with EUT predictions (Plott & Smith, 2008; Tversky & Kahneman, 1981). Among the well-observed deviations from rationality, it appears that individuals feel more pain from losses than satisfaction from equivalent gains; this behaviour is called loss-aversion. Moreover, risk-aversion in humans is different for upside and downside risk (Camerer, Issacharoff, Lowenstein, & O'Donoghue, 2003; Tversky & Kahneman, 1981). In other words, individuals are risk-averse in the domain of gains whereas they are generally risk-prone in the domain of losses. It has been shown that chimpanzees (*Pan troglodytes*) and tufted capuchin monkeys (*C. apella*) display similar loss aversion when having to give or receive the same goods (Brosnan et al., 2007; Chen, Lakshminaryanan, & Santos, 2006; Lakshminaryanan, Chen, & Santos, 2008). It is therefore interesting to study non-human primate behaviour when certain outcomes involve a loss. In the following study, we will avoid labeling individuals' attitudes as risk-sensitive if individuals can obtain a gain which is either equal to zero or superior to the initial investment, the focus will be put on the impact of the pay-off regularity.

To study economic decision in animals, subjects are typically offered a choice between two options, a first option with delay or food quantity which remains constant from one trial to another and a second option with delay or food quantity which varies from one trial to the next. The reward to be gained is not predictable at a given trial in the variable option, but as the two options are equivalent over the experiments, individuals can learn the general pattern of reward delivery (Bateson & Kacelnik, 1997; Hayden & Platt, 2007). In a visual gambling task, two rhesus macaques (*Macaca mulatta*) were seen to choose the less regular options but their preference declined with increasing delay between choices (Hayden & Platt, 2007; McCoy & Platt, 2005). In a foraging choice task, Heilbronner, Rosati, Stevens, Hare, and Hauser (2008) found that chimpanzees preferred an irregular option, whereas bonobos (*Pan paniscus*) favored the regular one; the authors therefore assumed that the level of uncertainty of the ecological environment surrounding a species shapes the economic preferences of individuals.

The ability of animals to compare costs and benefits may be also examined using a food-exchange task. Non-human primates can readily engage in exchanges of goods with humans. They attribute values to non-edible tokens and give them back for food (Brosnan & de Waal, 2004; Hyatt & Hopkins, 1998; Westergaard, Liv, Rocca, Cleveland, & Suomi, 2004). They exchange food to receive a quantitatively or qualitatively more desirable one (Drapier, Chauvin, Dufour, Uhlrich, & Thierry, 2005; Lefebvre & Hewitt, 1986; Steelandt, Dufour, Broihanne, & Thierry, 2011) and can wait significant periods of time in order to maximize pay-off (Dufour, Pelé, Sterck, & Thierry, 2007; Pelé, Dufour, Micheletta, & Thierry, 2009; Ramseyer, Pelé, Dufour, Chauvin, & Thierry, 2006).

We studied tufted capuchin monkeys (*Cebus apella*) and macaques (*Macaca tonkeana*, *Macaca fascicularis*) to assess whether they account for the regularity of pay-off. In a first experiment, subjects were tested in an exchange task where the reward probability and the reward rule varied between different conditions, albeit yielding the same average pay-off. If monkeys were rational decision makers, they were expected to accept exchanging at the same rate in any

condition; otherwise, they should behave differently according to conditions. In a second experiment, the subjects were tested in a choice task where they had to choose between two options for which the regularity of pay-off differed. If the sensitivity of animals to reward regularity is shaped by the ecological environment in which species have evolved, each group of individuals should display the same patterns of response; otherwise, inter-individual variations should be observed within groups.

## Method

### Subjects and Living Conditions

Subjects were maintained at the Primatology Center of the Strasbourg University (Table 1). Nine tufted capuchins belonged to a group of 18 individuals housed in a 78 m<sup>2</sup> indoor-outdoor enclosure composed of several compartments. Four Tonkean macaques belonged to a group of seven individuals housed in a 35 m<sup>2</sup> indoor-outdoor enclosure composed of several compartments. Two other Tonkean macaques belonged to a group of 16 individuals raised in a 1 acre wooded area including a shelter and a 40 m<sup>2</sup> wire-mesh fenced enclosure used for experiments. Three long-tailed macaques were housed together in an enclosure of 10 m<sup>2</sup> composed of several compartments and located in an indoor room. Three other long-tailed macaques were socially housed in individual cages of 125 x 80 x 80 cm allowing visual and physical contacts with others. Commercial monkey diet and water were available *ad libitum* and subjects were never deprived of food. For testing, group-living subjects were temporarily separated from their mates and placed in individual compartments using positive reinforcement. All research complied with animal care regulations, ASP Principles for the Ethical Treatment of Non-Human Primates and national laws.

### Experiment 1

**Testing procedure.** Subjects had been already involved in food exchange tasks with human experimenters during previous studies (Pelé et al., 2009; Pelé, Micheletta, Uhlrich, Thierry, & Dufour, 2011). We used Corinthian raisins for training and testing. The experimenter sat in front of the wire mesh and laid three cups containing three potential rewards on the ground in full view of the subject. The number of potential rewards shown depended on the experimenter running the trial. A test started when the experimenter showed the subject three raisins on a teaspoon for 2 s. She then gave them to the subject. After 3 s, the experimenter held out a hand, palm open, in front of the subject requesting them back. When the subject gave one or more raisins, the experimenter could reward the subject by supplying him/her with raisins taken from one of the three cups. If the subject did not return raisins, the trial ended. The experimenter waited 1 min after food consumption before starting another trial.

**Experimental design.** Subjects were submitted to three different testing conditions. The subjects could recognize these conditions from different cues. First, the cups containing potential rewards were laid in full view of subjects. Second, a different experimenter conducted the tests in each condition. The three experimenters rewarded subjects with different degrees of regularity, the probability to be rewarded differing between experimenters. A first experimenter regularly gave back double the number of raisins returned by subjects in every trial; potential rewards in the cups numbered two, four or six. A second experimenter gave back three rewards for each returned raisin but only in two trials out of three; in this irregular condition, the subjects did not receive anything in one test out of three. Potential rewards in the cups numbered three, six or nine. A third experimenter gave back six rewards for each returned raisin but only in one trial out of three; in this very irregular condition the subjects did not receive anything in two tests out of three. Potential rewards in the cups numbered six, 12, or 18 raisins.

Table 1  
*Information about subjects.*

Subjects	Age (yrs)	Sex	Rearing conditions
Tufted capuchins			
Ass*	19	female	group-living, indoor-outdoor
Kin	17	female	group-living, indoor-outdoor
Ali	10	female	group-living, indoor-outdoor
Pao	8	female	group-living, indoor-outdoor
Arn	11	male	group-living, indoor-outdoor
Pis	8	male	group-living, indoor-outdoor
Pop	8	male	group-living, indoor-outdoor
Rav	7	male	group-living, indoor-outdoor
Sam	6	male	group-living, indoor-outdoor
Tonkean macaques			
Syb	6	female	group-living, indoor-outdoor
Rim	7	male	group-living, indoor-outdoor
She	6	male	group-living, indoor-outdoor
Sim	6	male	group-living, indoor-outdoor
Lad*	12	female	group-living, semifree-ranging
Sha	6	male	group-living, semifree-ranging
Longtailed macaques			
Lou	12	male	group-living, indoor
Ram	17	male	group-living, indoor
Sad	13	male	group-living, indoor
Cas	13	male	separated, indoor
Jac	16	male	separated, indoor
Joe	12	male	separated, indoor

\* For reasons irrelevant to the study, Ass (died) and Lad (gave birth) were not tested in Experiment 2. All other subjects were tested both in Experiments 1 and 2.

**Training phase.** Prior to testing, subjects were run in several training periods carried out by an experimenter different from the three experimenters involved in testing. In a first training period, the experimenter gave two raisins and requested the subjects to return them both to obtain six raisins. Sessions of twelve trials were run until subjects succeeded in at least 80% of trials; they needed between one and four sessions to reach this criterion. They were then run in two sessions of twelve trials in which the experimenter gave three raisins and requested the subjects to return them all to obtain six raisins. We required subjects to succeed in at least 80% of trials in two consecutive sessions; they needed between three and eight sessions to reach this criterion. In another 2 day training period, subjects were submitted to one daily session of nine trials. The experimenter gave one, two or three raisins and requested subjects to return them to obtain twice the returned number, i.e., two, four or six raisins. Three trials were run in a random order in each condition. The aim was to show subjects that they could receive a reward amount proportional to the returned number of raisins; no learning criterion was required. In a further 2 day training period, subjects were habituated to the three testing experimenters. Subjects were exposed in a single trial to each of the three experimenters. Subjects had to give back at least one raisin to each experimenter. If they failed, a second trial was run; subjects needed between two and seven trials to succeed with all experimenters. In the last training period, subjects were run in daily sessions of nine trials. There were four successive sets of

three sessions with each session corresponding to one of the three experimental conditions selected in a random order. This training aimed to lead subjects to learn that the three experimental conditions were rewarded in different ways. An examination of individual results showed that several subjects followed a learning curve during these first sets of sessions, but that all displayed stable performances during the testing phase (Fig. 1).

**Testing phase.** The testing phase was the continuation of the last training phase in which subjects were run in daily sessions of nine trials. They were tested in four other successive sets of three sessions with each session corresponding to one of the three experimental conditions selected in a random order. The experimenter's offers in each session were the same in the three conditions, i.e., between 0 and 54 rewards depending of the number of raisins returned by subjects. The subjects could get the same final number of raisins, i.e., between 27 and 54 raisins depending of the number of raisins returned. The order of trials was randomized in each session for irregular and very irregular conditions. The role of experimenters was also counterbalanced across subjects; each experimenter intervened regularly, irregularly or very irregularly with two or three subjects in each species.

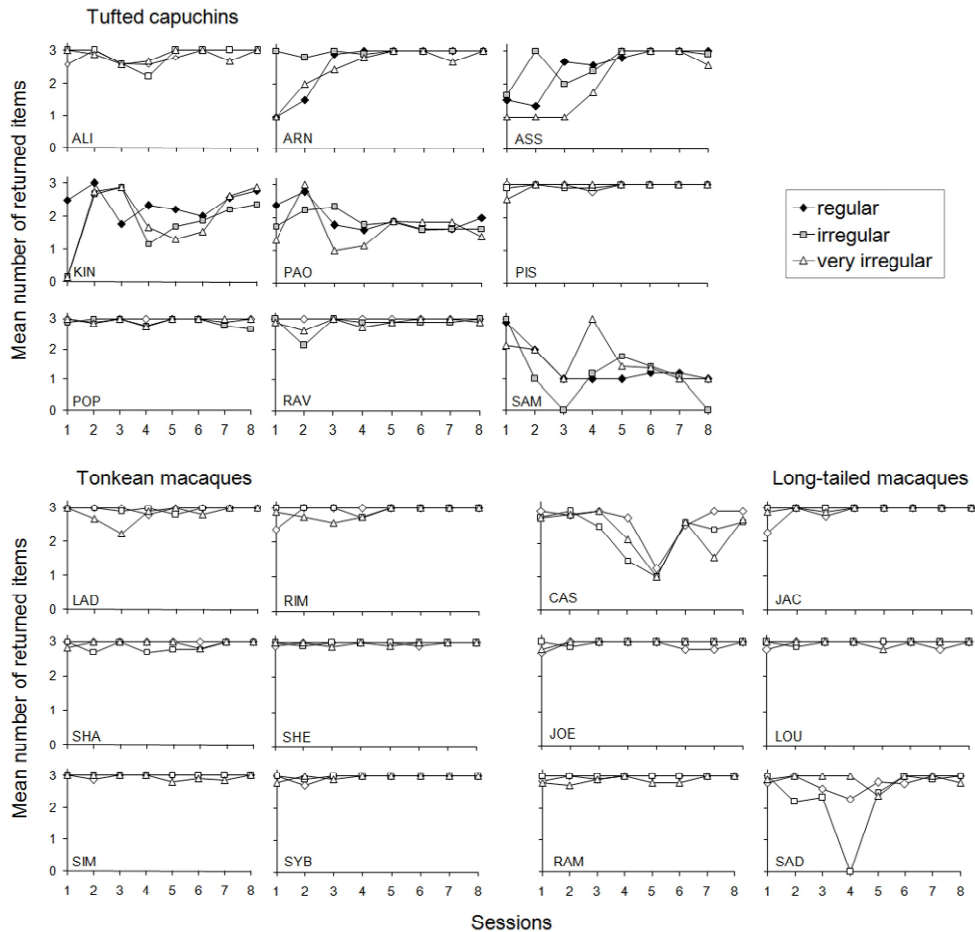


Figure 1. Number of raisins returned by monkeys. Each plot represents the mean number of raisins returned in one session of nine trials, along with standard errors. Several subjects followed a learning curve during the first sets of sessions. All subjects displayed quite stable performances during the testing phase (sessions 5 to 8).

## Experiment 2

**Apparatus.** Subjects faced the experimenter through a wire mesh. Food rewards were placed on a plastic support (55 cm x 38 cm). Rewards could be obscured by plastic bowls of different colors and shapes (red bowl: diameter 12 cm, height 8 cm; grey bowl: diameter 12 cm, height 6 cm; white bowl: diameter 9 cm, height 9 cm). We used an occluder (height 10 cm, length 40 cm) to cover the bowls during baiting and prevent subjects seeing how many items were available beneath the bowls. During sessions, the experimenter placed the options on the support hold-off individuals so that they could be slid forward within the subject's reach.

**Testing procedure.** The experimenter sat in front of the wire mesh and laid two bowls and two cups on the support. The occluder prevented the subjects from seeing how many items were loaded on the cups beneath the bowls. The experimenter loaded the cups with the appropriate number of raisins and covered each side with the corresponding colored bowl. She always loaded the cups from left to right, in case subjects attempted to infer amounts from body placement. Then, the occluder was lifted and the experimenter pushed the two bowls forward to allow the subject to make a choice. The subject then had 10 s to make a choice by touching or jabbing in the direction of one of the two bowls. The experimenter then moved back the two bowls, uncovered the food amount, and rewarded the subject with the cup of raisins beneath the chosen bowl. The experimenter waited for 1 min after the end of food consumption before starting another trial.

**Experimental design.** There were three options for reward. The first option was regular; it always yielded six raisins. The second was irregular as it yielded nine raisins in two trials out of three. The third was very irregular as it yielded 18 raisins in one trial out of three. Subjects were submitted to binary choices between options: regular vs. very irregular, regular vs. irregular, irregular vs. very irregular. They could choose between a less regular option and a more regular option based on the shape and color of the bowl since each bowl was associated with a given option for each subject. The assignment of bowl color to each option was counterbalanced across subjects. The side assignments for the options were counterbalanced within sessions. For the two irregular options, rewarded trials were randomized within each session.

**Training phase.** Prior to testing, subjects completed two training periods. A first period aimed at teaching subjects to jab in the direction of one of the bowls. We performed two sessions of nine trials where we placed four raisins beneath one bowl and 1 raisin beneath the other bowl. The side assignments for the options were counterbalanced within sessions. There was no learning criterion for this period. The second period aimed to train subjects to discriminate between options. The procedure was the same as in testing except that the occluder was not used. Subjects saw the actual reward quantities for 4 s before the experimenter covered them with the appropriate bowls in full view of the subject. We performed four daily sessions of nine trials with each choice. For each training session, subjects were required to succeed in at least 80% of trials. Subjects needed between four and eight sessions to succeed.

**Testing phase.** In the testing phase, we run subjects in one set of four sessions of nine trials for each binary choice. There was no more than one session per half-day. The order of sets of sessions was counterbalanced across subjects. Each set of sessions was run straight after the four sessions of the corresponding second training period. The subjects' total pay-off could vary as follows within one session: from 18 to 90 raisins in the regular/very irregular choice, from 36 to 72 in the regular/irregular choice, and from 27 to 81 in the irregular/very irregular choice. Note that each option provided an average pay-off of 54 raisins in each session regardless of the option.

If a subject did not make a choice (i.e., did not jab in the direction of one bowl or did not touch one of the two bowls) within 10 s of being given access the two bowls, the trial was considered aborted. If a subject failed to consume all the food, the trial was aborted. If three trials were aborted in one session, the entire session was ended and the data discarded. Only two sessions were aborted in this way. Moreover, to eliminate side-biased data, if a subject chose a single side eight or more times out of nine trials, the data from that session were discarded and the session repeated. Based on this criterion, 19 sessions were consequently deemed biased.

## Statistical Analysis

Data were analyzed using non-parametric statistics with SPSS 17.0 (SPSS Inc., Chicago, IL, U.S.A.). The significance level was fixed at 0.05.

Table 2

*Experiment 1: comparison of the number of raisins returned by subjects in exchanges differing by the regularity of pay-off (mean number  $\pm$  SD).*

Subjects	Conditions			<i>p</i> *
	regular	irregular	very irregular	
Tufted capuchins				
Ali	2.94 $\pm$ 0.04	2.33 $\pm$ 0.21	2.47 $\pm$ 0.19	0.09
Arn	2.92 $\pm$ 0.08	2.92 $\pm$ 0.08	2.92 $\pm$ 0.06	0.72
Ass	2.94 $\pm$ 0.06	2.81 $\pm$ 0.12	2.33 $\pm$ 0.20	0.80
Kin	2.39 $\pm$ 0.15	1.89 $\pm$ 0.16	1.81 $\pm$ 0.19	0.12
Pao	1.81 $\pm$ 0.08	1.56 $\pm$ 0.12	1.61 $\pm$ 0.12	0.27
Pis	3.00 $\pm$ 0	3.00 $\pm$ 0	3.00 $\pm$ 0	1
Pop	2.97 $\pm$ 0.03	2.78 $\pm$ 0.11	2.92 $\pm$ 0.08	0.10
Rav	3.00 $\pm$ 0	2.92 $\pm$ 0.05	2.94 $\pm$ 0.04	0.25
Sam	0.92 $\pm$ 0.09	1.08 $\pm$ 0.14	1.31 $\pm$ 0.15	0.10
Tonkean macaques				
Lad	3.00 $\pm$ 0	2.86 $\pm$ 0.09	2.86 $\pm$ 0.10	0.25
Rim	2.92 $\pm$ 0.08	2.83 $\pm$ 0.12	2.83 $\pm$ 0.12	0.78
Sha	2.50 $\pm$ 0.19	2.56 $\pm$ 0.17	1.67 $\pm$ 0.24	0.60
She	2.97 $\pm$ 0.03	3.00 $\pm$ 0	2.97 $\pm$ 0.03	0.61
Sim	3.00 $\pm$ 0	2.92 $\pm$ 0.08	2.39 $\pm$ 0.19	0.10
Syb	3.00 $\pm$ 0	3.00 $\pm$ 0	3.00 $\pm$ 0	1
Long-tailed macaques				
Cas	2.42 $\pm$ 0.16	2.11 $\pm$ 0.18	1.58 $\pm$ 0.22	0.10
Jac	3.00 $\pm$ 0	3.00 $\pm$ 0	3.00 $\pm$ 0	1
Joe	2.89 $\pm$ 0.07	2.92 $\pm$ 0.08	2.92 $\pm$ 0.08	0.61
Lou	2.86 $\pm$ 0.10	3.00 $\pm$ 0	2.94 $\pm$ 0.06	0.37
Ram	3.00 $\pm$ 0	3.00 $\pm$ 0	2.64 $\pm$ 0.16	0.20
Sad	2.11 $\pm$ 0.22	2.06 $\pm$ 0.22	2.11 $\pm$ 0.22	1

\*Friedman test (N = 36)

## Results

### Experiment 1

We compared the number of returned rewards in the three experimental conditions for each subject. The Friedman test did not yield statistically significant differences between conditions for any subjects (Table 2). We then compared the mean performances of all subjects in the three experimental conditions. Although individuals tended to return a larger number of rewards in more regular conditions, the trend was not statistically significant (regular mean  $\pm$  standard deviation = 2.69  $\pm$  0.07, irregular 2.60  $\pm$  0.09, very irregular 2.49  $\pm$  0.12; Friedman test:  $p$  = 0.064, N = 21).

## Experiment 2

For every subject we compared the number of options chosen in each binary choice using binomial tests (Table 3). Eight subjects displayed a significant preference in the regular/very irregular choice, three favoring the regular option and five the very irregular. Seven subjects displayed a significant preference in the regular/irregular choice, five favoring the regular option and two the irregular. Ten subjects displayed a significant preference in the irregular/very irregular choice, two favoring the very irregular option and eight the irregular. It must be stressed that only four subjects were consistent in their choices, two always favoring the more regular option and two the more irregular. Three other subjects were inconsistent, favoring either the more regular or the more irregular depending on choices. These various strategies were quite uniformly distributed among the three species studied. It may be noted however that long-tailed macaques generally tended to favor the less regular option (Table 3).

Table 3  
*Experiment 2: preferences of subjects in binary choices between options differing in the regularity of pay-off.*

Subjects	Ratio of number of choices for more regular options by number of choices for less regular options		
	regular/ very irregular	regular/ irregular	irregular/ very irregular
Tufted capuchins			
Ali	0.83***	0.94***	0.36
Arn	0.64	1.00***	0.00***
Kin	0.28*	0.83***	0.22***
Pao	0.69*	0.50	0.58
Pis	0.33	0.47	0.31*
Pop	0.44	0.39	0.19***
Rav	0.39	0.00***	0.67
Sam	0.53	0.50	0.92***
Tonkean macaques			
Rim	0.22***	1.00***	0.00***
Sha	0.75**	0.58	0.86***
She	0.61	0.56	0.58
Sim	0.64	0.53	0.33
Syb	0.64	0.86***	0.33
Long-tailed macaques			
Cas	0.47	0.47	0.06***
Jac	0.31*	0.56	0.17***
Joe	0.11***	0.19***	0.39
Lou	0.33	0.53	0.33
Ram	0.19***	0.47	0.36
Sad	0.42	0.44	0.31*

Values above 0.5 indicate a preference for the more regular option, values below 0.5 indicate a preference for the less regular option. Binomial test:  $N = 36$ , \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$

## Discussion

In a first experiment we found no evidence that subjects were sensitive to the regularity of pay-off, whereas in a second experiment many of them displayed a preference, albeit in different directions, when they had to choose between two conditions differing by the regularity of pay-off.

In Experiment 1, individuals returned a similar number of raisins in three conditions differing by the probability and quantity of reward in each trial, but not by the average pay-off in a session. It could be argued that subjects failed to distinguish between conditions despite the different cues attached to them, i.e. cups and experimenters. This explanation appears unlikely, however, since there is ample evidence that macaques and capuchin monkeys can readily learn to discriminate cues and recognize experimenters (e.g., Kuroshima, Fujita, & Adachi, 2003; Mitchell & Anderson, 1997; Paukner, Anderson, Borelli, Visalberghi, & Ferrari, 2005). In particular, they can differentiate magnitudes and make “more” or “less” judgments about discrete quantities (Addressi, Crescimbeni, & Visalberghi, 2007; Beran, Evans, Leighty, Harris, & Rice, 2008; Hauser, Carey, & Hauser, 2000; Wood, Glynn, Hauser, & Barner, 2008). In a study requiring monkeys to trade tokens for rewards with two different experimenters, tufted capuchins selected the one providing the higher pay-off (Chen et al., 2006). Besides it is possible that monkeys met difficulties distinguishing between the three different conditions; future research should check whether they would show the same responses when tested with two opposite conditions of pay-off regularity.

Previous works have shown that monkeys display loss aversion. In an exchange task with two experimenters, capuchin monkeys preferred trading with a first experimenter who presented and gave a reward rather than a second one who presented two rewards but gave only one (Chen et al., 2006; Lakshminaryanan et al., 2008). Yet when important gains are at stake, macaques and capuchin monkeys can significantly delay gratification; they are able to tolerate loss by giving back a piece of cookie and can then wait dozens of minutes to obtain a cookie 40 times larger (Pelé et al., 2009, 2011). The results of Experiment 1 were consistent with the prediction of the expected utility theory, which states that rational decision makers should be indifferent between options of same expected pay-off (Von Neumann & Morgenstern, 1944). The subjects’ maximal expected satisfaction corresponded to the same utility function in the three conditions, making understandable that their performances did not differ in a significant way in the three conditions. The subjects of the three species studied optimized pay-off by investing comparable amounts in all conditions. It is noteworthy that they continued investing despite suffering a full loss in one or two trials out of three. Whereas the expected utility theory was built to account for the decisions of human beings, the present results show that it is also applicable to monkeys.

Whereas in Experiment 1 subjects could only accept an exchange or not, they had to choose between two options differing by the regularity of rewards in Experiment 2. A main finding of this second experiment is the large amount of variation observed between subjects. A majority of them displayed some significant preference, albeit in different directions. Several subjects exhibited inconsistent preferences, selecting either the more regular or the less regular option

depending on proposed options. Moreover, two individuals consistently selected the more regular option while two others consistently selected the less regular one. Although long-tailed macaques tended to favor the less regular option, the results showed that there was no single decision-making pattern among subjects. Such individual biases contrast with the experiment of Heilbronner et al. (2008) who found that five bonobos favored the regular option, whereas five chimpanzees favored the irregular option, leading the authors to suggest that the preferences displayed by individuals depended on fluctuations typical of the environment in which the species evolved. On the other hand, it is worth noting that large individual differences remain a major finding from economic experiments in humans, e.g. in the trust game, the ultimatum game and the dictator game (Scheres & Sanfey, 2006). The absence of specific patterns in monkeys indicates that individual sensitivity to the regularity of pay-offs cannot simply be related to the habitat in which a species has evolved.

Inter-individual variations in patterns of decision-making in risky situations may be related to the differences in temperament arising from the influence of factors such as sex, age and rearing history (Clarke & Boinski, 1995; Coleman, Anntully, & McMillan, 2005; Suomi, 1991). Considering the limited sample size and the fact that study groups were not balanced for these factors, their possible significance could not be assessed here. So far, few studies have experimentally addressed how risks affect economical choices in animals. Future research should investigate the factors underlying decision-making, and in particular how chance and the amount of expected losses or gains can shape the strategies of individuals under various conditions of food income.

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