

Thirst-dependent risk preferences in monkeys identify a primitive form of wealth

Hiroshi Yamada^{a,b,1,2}, Agnieszka Tymula^{c,1}, Kenway Louie^a, and Paul W. Glimcher^a

^aCenter for Neural Science, New York University, New York, NY 10003; ^bDepartment of Neurophysiology, National Institute of Neuroscience, National Center of Neurology and Psychiatry, Tokyo 187-8502, Japan; and ^cSchool of Economics, University of Sydney, Sydney, NSW 2006, Australia

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Experimental economic techniques have been widely used to evaluate human risk attitudes, but how these measured attitudes relate to overall individual wealth levels is unclear. Previous noneconomic work has addressed this uncertainty in animals by asking the following: (i) Do our close evolutionary relatives share both our risk attitudes and our degree of economic rationality? And (ii) how does the amount of food or water one holds (a non-pecuniary form of “wealth”) alter risk attitudes in these choosers? Unfortunately, existing noneconomic studies have provided conflicting insights from an economic point of view. We therefore used standard techniques from human experimental economics to measure monkey risk attitudes for water rewards as a function of blood osmolality (an objective measure of how much water the subjects possess). Early in training, monkeys behaved randomly, consistently violating first-order stochastic dominance and monotonicity. After training, they behaved like human choosers—technically consistent in their choices and weakly risk averse (i.e., risk averse or risk neutral on average)—suggesting that well-trained monkeys can serve as a model for human choice behavior. As with attitudes about money in humans, these risk attitudes were strongly wealth dependent; as the animals became “poorer,” risk aversion increased, a finding incompatible with some models of wealth and risk in human decision making.

utility | satiety

What We Know About Humans. Significant headway has been made toward understanding human choice behavior under risk. At a theoretical level, any logically consistent chooser behaves as if he consults a continuous monotonic internal representation of utility. Choice is then the process of maximizing utility (see ref. 1 for a review). At an empirical level, consistent human choosers are typically somewhat risk averse, maximizing a weakly compressive utility function. Logically inconsistent choosers do not reflect such a maximization process (2–5), in principle.

Less headway has been made in understanding how wealth level affects risk attitudes. Although a consensus view is that choosers should become less risk averse as wealth levels increase (6–8), solid empirical data have been difficult to obtain because wealth levels are hard to systematically manipulate in humans.

What We Know About Animals. The risk attitudes of many species have been assessed, both with and without confirmation that choosers are logically consistent (9–11), with variable and sometimes controversial results (12). Caraco and colleagues (13), for example, found that sparrows were risk averse over food choices in a manner similar to that of humans, but that this depended on how many calories the subjects had already stored internally—a form of primitive consumption-related “wealth” shared by all animals and premonetary humans. When the birds were heavily food deprived (low caloric stores for future consumption or wealth), they became risk seeking. However, later studies in starlings challenged this conclusion, suggesting persistent risk aversion across a broad range of food “wealth levels” (14).

Studies in laboratory monkeys, a standard neurobiological model for human choice, have been equally confusing. Some

widely cited studies even suggest that rhesus monkeys are hugely and consistently risk seeking under typical experimental conditions (11, 15), preferences that lie far outside the range observed in humans and have been used to challenge the notion that monkeys are an appropriate model for the study of human choice behavior.

The Present Study. To engage these issues we tested three sequential hypotheses: (i) Are trained rhesus macaques consistent in their behavioral choices in the technical economic sense? (ii) If they are consistent, are they risk averse or risk neutral like humans or are they necessarily massively risk seeking? And (iii) if they are consistent and risk averse or risk neutral, can we assess how nonmonetary wealth (how much water they have stored internally, measured as hydration state) affects risk preference?

We therefore examined choice behavior in monkeys performing a gambling task for fluid rewards. After significant training, our monkeys began to show consistent maximization behavior, allowing meaningful assessment of risk preferences, using both non-parametric and model-based methods. Like humans, our animals were weakly risk averse (following economic definition we define weak risk aversion as preferences that cannot be statistically differentiated from risk aversion or risk neutrality). Examined as a function of the amount of water the subjects possessed before choice trials [quantified by measuring blood osmolality (16)], subjects “richer” in terms of water were less risk averse over identically sized rewards. They showed diminishing absolute risk aversion over a consumable reward.

Summary. Our results differ from earlier studies suggesting that rhesus monkeys cannot show human-like preferences and support the hypothesis that trained rhesus monkeys can be consistent weakly risk-averse choosers like their human counterparts. Our empirical study of wealth levels with regard to a consumable

Significance

We show that monkeys display similar risk preferences and rationality to those of humans, suggesting that despite concerns raised by earlier reports, they can serve as a model for human behavior. Standard experimental economic techniques have long allowed us to evaluate human risk attitudes, but we do not know how they relate to wealth levels, a critical variable in economic models. We find thirsty monkeys to be more risk averse and discuss implications for the role of wealth in human decision making.

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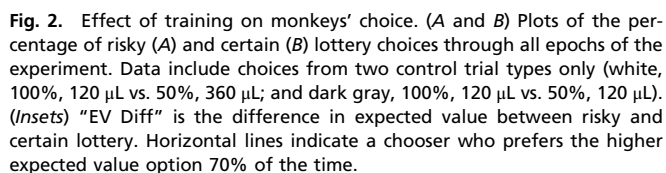
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¹H.Y. and A.T. contributed equally to this work.

²To whom correspondence should be addressed. E-mail: h-yamada@ncnp.go.jp.

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subject, the percentage of trials in which the risky option was chosen. Although precise definitions of risk attitude require a parametric model, all such models identify a subject who always chooses the risky option in our choice set as more risk seeking than one who chooses the risky option rarely. As a benchmark, we use the number of times a risk-neutral chooser would select the risky option. We adopt here the standard definition of risk-neutral chooser who is indifferent between risky and riskless options that have equal expected value. Fig. 3*A* plots daily risk attitude in this manner for the two monkey subjects, with the dotted line showing the behavior of a risk-neutral chooser (50% risky choice). Comparing Figs. 2*B* and 3*A* (which share a common x axis), we can see that as monkey choosers become consistent, as indexed by obeying first-order stochastic dominance, they approach risk neutrality and even weak risk aversion. Thus, monkey subjects, at least in this task, serve as reasonable models of human decision makers with regard to both their consistency and their risk attitudes. Further, compliance with first-order stochastic dominance means that, in principle, this observed behavior can be adequately modeled with a utility-function style analysis (4, 7, 22, 23). Utility-function analyses are, of course, controversial. Many have pointed out (e.g., refs. 22–24) that these analyses can be highly misleading when choosers show inconsistent behavior. It is essential to note, however, that once our monkeys show consistent behavior after training, their behavior is specifically of the type utility theory was designed to describe. One can, of course, argue that these parametric analyses are of no interest but one cannot in this case argue that these analyses are misleading or inaccurate. That they are accurate under these conditions is a matter of mathematical proof (4).

Parametric Risk Attitude Assessment. To parametrically quantify risk attitude, we estimated each monkey’s risk attitude on a daily basis, using a simple model common to expected utility theory and prospect theory: $Eu = p \times v^\alpha$ with a logistic function for choice (see *Methods* and Fig. 4A for model fitting). In this model, an exponent (α) greater than 1 indicates risk seeking, an $\alpha = 1$ indicates risk neutrality, and an $\alpha < 1$ indicates risk aversion. We found that monkeys were risk seeking early in training, but this risk-seeking behavior ($\alpha > 1$) became risk neutral (α statistically indiscriminable from 1.0) and then slightly risk averse ($\alpha < 1$) as the monkeys gained experience (Fig. 3B). Notably, this shift to a risk-neutral or a risk-averse estimate closely paralleled the

monkey's shift toward consistency as indexed by obeying first-order stochastic dominance (Fig. 2*B*). This suggests that when choice behavior is technically inconsistent (and utility models assuming monotonicity should not be applied), behavior erroneously appears risk seeking, using such analyses. When, however, monkeys shifted to effective maximization behavior and expected utility theory can be properly applied, the monkeys showed risk-neutral or risk-averse utility functions (Fig. 3*B*). Overall choice stochasticity (β : logistic choice function slope) (*SI Methods*) also changed through training; perhaps unsurprisingly, the choices of the monkeys became less stochastic as training continued (Fig. 3*C*).

Aggregate Choice Data After Training. After our subjects had experienced all 20 lottery pairs and completed training (Figs. 2 and 3), we collected 10,517 and 7,501 free-choice trials in monkeys HU and DE, respectively, over the course of 34 d distributed over two nonsequential months (first and second epochs) (*Methods*). To assess risk attitudes, we first pooled data across conditions, yielding four datasets for each monkey corresponding to the four payoff conditions depicted in Fig. 1*B*. Each payoff condition thus yielded a single choice curve with a single indifference point (Fig. 4*A*). Five red points depict the average choices of monkeys HU and DE in payoff condition 1: a certain reward of 60 μ L of water or a 50% chance of gaining 5, 60, 120, 180, or 240 μ L of water. The dark blue points plot choices in payoff condition 2: a certain reward of 120 μ L and a range of risky rewards (120–360 μ L); similarly, the green and turquoise points plot choices in payoff conditions 3 and 4. Well-trained monkeys, like humans, lawfully transitioned to selecting the risky lottery as the value of the risky lottery grew. Additionally, as the magnitude of the certain reward grew, choice curves lawfully shifted to the right.

The solid lines in Fig. 4A plot the choices of the parametric utility model fitted simultaneously to the entire aggregate dataset. When the risky and certain options offer identical expected value, a risk-neutral chooser would be indifferent (vertical dashed lines).

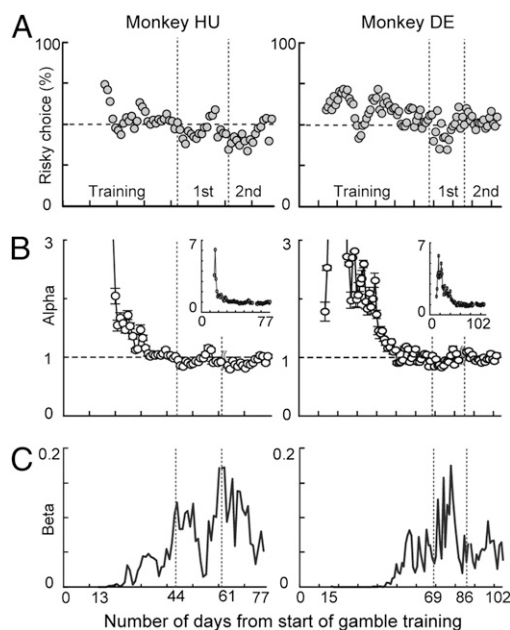


Fig. 3. Day-by-day risk sensitivity throughout training and first and second epochs. (A) Nonparametric analysis, percentage of risky choices. (B) Parametric analysis, daily values of α . Large plots exclude days with $\alpha > 3$ (all data presented in *Insets*). Error bars show SEM. Dashed lines in A and B indicate risk neutrality. (C) Values of β (stochasticity in choice) estimated for each day. In A–C, the values were estimated after monkeys had experienced at least three different types of trials (100%, 120 μL vs. 50%, 120 μL , 240 μL , and 360 μL in payoff condition 2; days 13 and 15 for monkeys HU and DE, respectively).

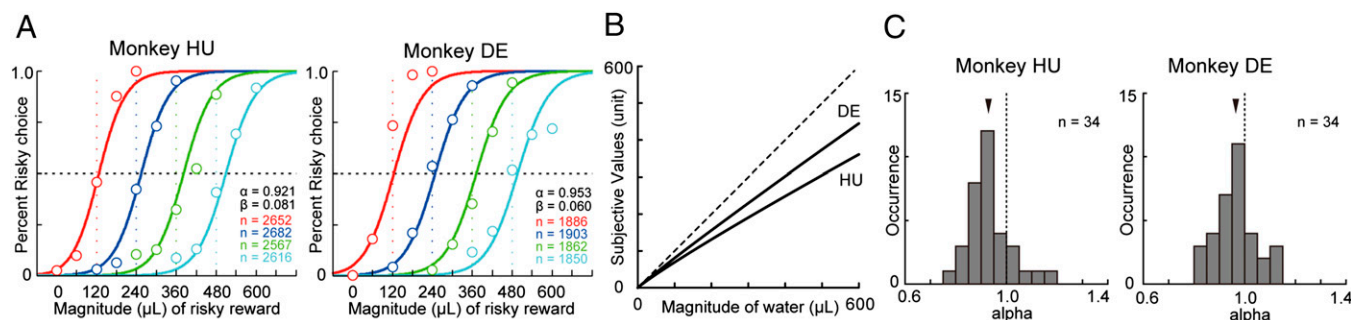


Fig. 4. Well-trained rhesus monkeys were slightly risk averse for fluid rewards. (A) Probability of risky choice plotted against reward magnitude in each payoff condition (indicated by color). Solid, colored choice curves were fitted using maximum-likelihood estimates of α and β . Dashed colored lines indicate where risky and certain options have equal expected value. (B) Plot of the estimated utility function for each monkey. (C) Estimated α in each of 34 d during the first and second epochs. Black arrowheads indicate means. Dashed black lines indicate risk neutrality.

If the fitted curves are shifted to the left of the points where the $P = 0.5$ line crosses the colored dashed lines, the subject can be defined as risk seeking. Curves shifted to the right indicate risk aversion. The corresponding fitted utility functions are plotted in Fig. 4B.

Overall, the power utility function fitted the data well (Fig. 4A, maximal log-likelihoods = $-4,354.1$ and $-3,314.5$ in monkeys HU and DE, respectively), confirming that subjects behaved in a globally rational, or consistent, manner. Monkeys were slightly, but significantly, risk averse as assessed with this tool (log-likelihood-ratio test, $P < 0.001$, mean \pm SEM: monkey HU, $\alpha = 0.921 \pm 0.004$, $\beta = 0.081 \pm 0.003$, log-likelihood = $-4,354.1$; monkey DE, $\alpha = 0.953 \pm 0.005$, $\beta = 0.060 \pm 0.002$, log-likelihood = $-3,314.5$).

Daily Choice Data After Training. We also examined the risk attitudes of each monkey on each day to determine the degree of variability in risk preferences. The dataset for each of 34 d consisted of 200–600 free-choice trials collected in one to three repetitions of the four payoff condition blocks. A histogram of daily α -values for each subject (Fig. 4C) showed, on average, weak but significant risk aversion across days (one-sample t test: monkey HU, $\alpha = 0.929 \pm 0.014$, $P < 0.001$; monkey DE, $\alpha = 0.965 \pm 0.013$, $P < 0.001$).

Effect of Thirst on Risk Attitudes. Unlike several previous studies, our monkeys were risk averse or risk neutral, like human subjects in similar tasks (17, 24). Could this discrepancy reflect a disparity between the metabolic state (the water wealth) of our subjects and the metabolic states of subjects in other studies? The controversial observation that birds become risk seeking as they get hungrier (13) might suggest that as our subjects become thirstier they should also become more risk seeking. To examine this prediction, we measured the relationship between daily blood serum osmolality [a physical index of water wealth (16)] and risk attitude for 17 d during the second epoch of our data collection. Blood was collected from each monkey each day about 30 min before testing began.

We found, perhaps surprisingly, that the level of risk aversion increased significantly as the total water that the monkey possessed decreased. As shown in Fig. 5A, the frequency of risky option selection (our nonparametric estimate of risk attitude) declined as water-wealth levels fell (linear regression in each monkey: monkey HU, $b_1 = -0.012 \pm 0.02$, $P < 0.001$; monkey DE, $b_1 = -0.004 \pm 0.001$, $P = 0.007$). Parametric analysis yielded an identical result (Fig. 5B). As animals became more thirsty, they became more risk averse (linear regression in each monkey: monkey HU, $b_1 = -0.013 \pm 0.002$, $P < 0.001$; monkey DE, $b_1 = -0.007 \pm 0.002$, $P = 0.001$). To additionally characterize risk sensitivity as a function of water wealth, we fitted all of the data with a utility function of the form $Eu = p * v^{a_0 + a_1 \text{Osmo}}$ and a choice function of the form $P_{\text{chooses risky}} = 1 / (1 + e^{-(Eu_{\text{risky}} - Eu_{\text{certain}}) * (\beta_0 + \beta_1 \text{Osmo})})$, which

model risk attitude and choice stochasticity as comprising a constant component and an osmolality-dependent level. We found that risk attitude was negatively correlated with osmolality level ($\alpha_1 = -0.0061 \pm 0.0027$, $P = 0.024$) whereas choice stochasticity was independent of osmolality level ($\beta_1 = -0.0018 \pm 0.0017$, $P = 0.312$). These data suggest that not only were our subjects weakly risk averse, but also thirstier monkeys are more risk averse. In the language of economics, our monkeys showed diminishing absolute risk aversion over water reward.

This effect of thirst level on risk attitude was also evident in behavioral changes observed within single days (Fig. S1). We determined this by dividing each daily dataset from the first and second epochs in half, obtaining beginning-of-the-day and end-of-the-day halves. First and second half datasets (Fig. S1A and B) produced significantly different estimates of α at $P < 0.001$ (two-sample t test, Fig. S1C). Monkeys were less risk averse when they were more hydrated within a day (less thirsty) (see ref. 16 for time course of hydration). Over the range of osmolalities we explored, increasing thirst (decreasing water wealth) made our animals more risk averse rather than more risk seeking.

Discussion

Risk Preferences of Monkeys. Risk preferences have been measured previously in different species, using a variety of procedures and designs. The two most widely cited studies suggest that monkeys are, unlike humans, always quite risk seeking (11, 15). The degree of risk seeking proposed for these animals would, in fact, place them well outside the range ever observed in human decision makers [see, for example, Holt and Laury (17)] and might suggest that monkeys are a poor model for human choice behavior.

In one of these studies, McCoy and Platt (11) offered monkeys choices between a certain gain of 150 μL and a 50% chance of

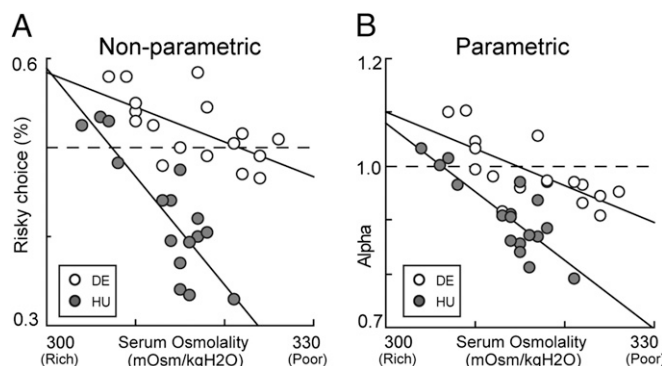


Fig. 5. Hydration state correlated with risk attitude in each monkey. (A) Proportion of risky choices and (B) risk estimate (α) in each day of the second epoch are plotted against serum osmolality. Solid lines indicate regression lines.

winning either more or less in a variable option, with the constraint that the high-variance option always had an expected value of 150 μ L. Their monkeys preferred the variable option even when high variances were used. All trials offered to the monkeys, however, had equal expected values and all choices were offered many times. Thus, the choices of the animals had no significant impact on fluid consumed averaged over tens of trials. One might hypothesize that the animals in that study were thus under little pressure to behave consistently, in the economic sense, and we do not know if these animals obeyed the first-order stochastic dominance or monotonicity assumptions required for a utility-theoretic analysis. In the other study, O'Neill and Schultz (15), using a similar strategy while recording from orbitofrontal neurons, drew a similar conclusion.

In contrast to these two classic studies of monkey risk attitudes, classic estimates of human utility function curvature (17, 25) nearly always show weak to moderate risk aversion or at most risk neutrality, under conditions like ours where multiple choices are sequentially realized. Related studies of humans by our group have never observed a consistent chooser with an α greater than 1.2, with average choosers exhibiting an α of 0.7 (26). It is important to note that even human risk attitudes vary from study to study; Hayden and Platt (27) found that human choosers can show risk-seeking behavior for both juice and monetary rewards under some conditions.

One possible source of this discrepancy between our monkey data and the data in previous studies may be the larger range of payoff conditions we used. In McCoy and Platt (27), the largest reward ever offered was 250 μ L. It may be the case that if the reward amount for the certain option is held to this specific range, subjects may be less interested in all certain options. Indeed, in a recent study, So and Stuphorn (28) found that monkeys appeared to prefer the risky option only when the certain outcome was small (less than 120 μ L), a hypothesis for which there may be some evidence in the behavior of monkey DE (Fig. S2).

Risk-seeking behavior in rats has also been suggested both to occur and to disappear as the number of food pellets associated with a certain reward increases (29). These findings suggest that the range of reward magnitudes being offered may be a factor in determining risk attitude, but direct measurements of choice consistency are not available for these studies, making unambiguous interpretation with regard to economic risk attitudes difficult.

Effect of Satiety State on Risk Attitudes. In this study, both monkeys showed weakly risk-averse behavior for water rewards that varied as a lawful function of hydration state. Day-to-day and within-day changes in risk attitudes were tightly correlated with blood osmolality, with thirstier (poorer) monkeys more risk averse and more satiated (richer) monkeys closer to risk neutral. This observation is inconsistent with the Caraco et al. study in birds (13). Although they did not estimate the overall form of the utility function for their subjects, Bateson and Kacelnik (30), studying starlings under similar conditions, showed a pattern of risk attitudes broadly similar to the one we observed.

Economic Models of Risk Attitudes as a Function of Wealth. In the economics literature, the appropriate modeling assumptions for the study of decision making under risk have been a subject of ongoing debate, especially with regard to the relationship between financial wealth and risk attitude (8, 31–33), as well as the relationship between factors like satiety and risk attitude. Some of the unresolved issues are the following: Do people integrate their financial decisions with their current wealth level? If yes, to what extent? Do risk attitudes change as a function of wealth, as most normative theories require? Can biological stores of resources be treated as an evolutionarily primitive form of wealth in the economic sense or only as a form of state dependence? Answering these questions can inform our understanding of functional forms for the relationship between risk attitude and wealth in humans.

One reason these questions remain unanswered is that very few within-subject data on the relationship between wealth level and risk attitude are available in humans. Instead, existing studies usually rely on self-reported wealth measures compared across subjects (e.g., survey data), and these two constraints limit the accuracy and reliability of many existing datasets. Animal studies may thus shed light on the interaction between wealth and risk attitude at a level of detail that has not previously been possible in human subjects—if we can use the amount of a valuable resource, in this case water, possessed by a monkey as model for thinking about wealth.

Traditionally, satiety effects have been viewed in terms of state-dependent utility functions, and our results can be interpreted equally validly in this framework. However, we suggest that viewing physiological quantities such as energetic state or hydration status as forms of wealth may allow a broader understanding of wealth-related effects in both humans and animals. Like monetary wealth, total water level—even when it is stored within the interstitial spaces of the body rather than an external container—can be accumulated, can be consumed (in the form of sweat or urine), and can affect the valuation of further acquisitions. If wealth is defined as a stock of resource that can be stored and used to fund present or future consumption, then a human who possesses water in an arid climate, whether or not she can trade it, and whether or not she drinks it, can be considered wealthy. To put this more apocryphally, a desert camel who possess 10 L of water in a clay jar should probably be considered just as rich as one who stores that water in his hump.

Critically, if human sensitivity to wealth levels evolved in the primate line before the advent of fiat currencies, it may be that the neurobiological mechanisms that mediate the relationship between consumption wealth and risk attitudes in monkeys are related to the human mechanisms that play a similar role in other domains. It seems likely that the biological mechanisms that mediate changes in risk attitudes with wealth evolved around satiety mechanisms rather than around mortgages. If that is true, then these findings provide unique insights into how the desirability of rewards quantitatively varies with the most primitive form of wealth—satiety.

Our monkeys exhibited a lawful relationship between risk aversion and water wealth, suggesting that decision making under risk has to incorporate the water-wealth level. In this study, monkeys paid a higher premium to avoid a risky lottery when their water-wealth level was low. Consider a monkey given the choice between getting 240 μ L for sure and getting 480 μ L or nothing with equal probability. When satiated monkey HU had an $\alpha = 0.965$ at osmolality 308, he was willing to give up 1.9% of the expected value (EV) of the lottery (4.8 μ L) to avoid the risky option. The same monkey was on average more risk averse when he was thirstier ($\alpha = 0.792$ at osmolality 321), and the required risk premium was more than twice as large (4.3% EV). This wealth-dependent change in risk aversion occurs in absolute terms (change in risk premium, measured in microliters or in percentage of EV) as well as in relative terms (change in risk premium normalized by wealth level): As monkeys grow wealthier in terms of water, they become less risk averse in both absolute and relative terms.

The decreasing absolute risk aversion as wealth level grows in this study is in line with the economic intuition that the utility function flattens as wealth increases, but the theoretical details here are more complex. Relative risk aversion, a change in one's risk attitude when making decisions about a constant fraction of one's total wealth, is more controversial: Economists argue about whether it increases or decreases with wealth (8, 32). This is a matter of some importance in the economic domains of development and institutional design, where poor countries with hungry populations must develop economic systems that maximize the accumulation of wealth. There is already some evidence that hungry people make financial decisions differently from sated people (34–36). And it is widely acknowledged that poor people make different decisions about whether to accept a particular

risk than do their more wealthy peers (37–39). In our data, the richer monkeys become, the less risk averse they become, even in relative terms, consistent with decreasing relative risk aversion with increasing wealth. If this is a more global feature of how risk attitudes change with wealth in the developing world, it may be of broad economic significance.

Summary. Recent developments in neuroeconomics have begun to reveal the neural basis of decision making under risk and uncertainty (40–43). Our data, unlike those in previous studies, suggest that at least under some conditions monkeys can be good behavioral models for humans in this regard. It is also clear, however, that most of the brain regions related to value-based decision making are affected by satiety state (44, 45), although this has not been widely examined. If our results generalize to other forms of wealth, they suggest that risk attitudes decline as both absolute and relative functions of wealth. Our results suggest the importance of a quantitative understanding of how satiety for food and fluid rewards affects the neural processes that produce risk preferences in each individual.

Methods

Subjects and Surgical Procedures. Two rhesus monkeys were used (DE, 7.5 kg, 6 y; HU, 8.0 kg, 6 y). All experimental procedures were approved by the New York University Institutional Animal Care and Use Committee and performed in compliance with the Public Health Service's Guide for the Care and Use of Animals. Before training, each animal was implanted with a head-restraint prosthesis and a scleral eye coil (46), using standard techniques (47).

Experimental Procedure. Eye movements were measured using a scleral coil at 500 Hz. Visual stimuli were generated by cathode ray tube 30 cm from the

monkey's face. Monkeys were seated using standard methods (47). During the first 3 mo, the "training epoch," subjects practiced the lottery task. After animals were proficient and estimates of risk attitudes had stabilized, a 1-mo "first epoch" began. Data were gathered 4–5 d/wk. A second month of data collection followed, the "second epoch," during which blood osmolality was sampled immediately before each daily session (16).

Water Access Control. In the approved protocol we used, monkeys received a fixed minimal daily allocation of water determined independently for each individual and based on our prior studies of blood osmolality and controlled water access (16). Monkeys HU and DE obtained daily water of at least 150 mL and 140 mL, delivered in at least two separate daily rations, through all of these experiments, respectively. The monkeys usually obtained ~50–80% of the allocation during the task. During the training and the first epochs, monkeys usually obtained ~100–150 mL (monkey HU) or ~50–120 mL (monkey DE) of water during the task. During the second epoch, they obtained about 50 mL of water reward during the task. Additional water was delivered such that no animal was without water for 16 h.

Blood Osmolality Measurements. Blood was drawn from monkeys ~30 min before behavioral testing during the second epoch. At least 0.5 mL serum was extracted from the 1.5-mL blood sample by centrifugation, and 0.2-mL samples of the extracted serum were measured using a freezing-point method (16).

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Supporting Information

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SI Methods

Lottery Task: Forced-Choice Trials. Animals performed one of two visually cued saccadic choice tasks: forced-choice lottery task and free-choice lottery task (Fig. 1A). Each trial of the forced-choice lottery task started with a 300-ms 500-Hz tone, after which the monkey had 1,000 ms to align its gaze to within 2° of a 1°-diameter central fixation target (yellow or red). After fixating for 400 ms, two peripheral 8° stimuli (pie charts) providing information about reward magnitude were presented for 500 ms, 8° to the left and right of fixation. One hundred milliseconds after cue offset, red and yellow 1° choice targets appeared at these same locations. Three hundred milliseconds later, the fixation point disappeared, cueing saccade initiation; a correct saccade that shifted gaze to within 3.5° of the choice target matching the color of the fixation target could yield a water reward. Red and yellow colors were randomly assigned to fixation and peripheral targets on each trial.

On trials in which the central fixation point cued a certain reward (example in Fig. 1A), animals received the reward indicated by the pie chart if they shifted gaze to the correct target (at right in this example). When the fixation color cued a choice to the risky target (no example shown), animals received the reward indicated by the pie chart with a probability of 0.5. The locations of the certain and risky targets were learned from experience during a block. A 1-kHz or 0.1-kHz 300-ms acoustic tone was then presented if the saccade had been correctly performed. A high tone preceded a reward by 200 ms. A low tone indicated that no reward would be delivered, but that the task had been performed correctly. A 2-s intertrial interval followed. Aborted and error trials were presented again.

Lottery Task: Free-Choice Trials. Free-choice trials began with the onset of a gray central target. As in forced-choice trials, pie charts indicated the magnitude of certain and risky rewards (Fig. 1A). After offset of the fixation target, animals were free to choose by shifting gaze to either target.

Payoff and Block Structure. Pie charts indicated reward magnitudes from 60 μ L to 600 μ L in 60- μ L increments (Fig. 1B). A 5- μ L reward was signaled by a blank pie chart. During data collection, blocks of 86 trials were presented, in random order, built from one of the four payoff conditions (Fig. 1C). The first 36 trials in a block were forced-choice trials. During a block the certain option was fixed and the magnitude of the risky option varied randomly across its five possible values (Fig. 1B). The middle-valued risky target always offered a reward of the same expected value as the certain target in that block. Then, 50 free-choice trials (10 of each type) followed in random order. A new block with a new payoff condition was then presented. After all four payoff conditions had been presented in random order without replacement, the sampling procedure was repeated up to a maximum of three times in 1 d.

Behavioral Training and Data Collection. During training, monkeys were required to learn (i) the association of pie chart with reward magnitude, (ii) that certain and risky rewards existed, and (iii) that there was a 50% chance of gaining risky rewards. Initially monkeys encountered only 2 of our 20 choice conditions (Fig. 1B). These 2 conditions offered a certain reward of 120 μ L and a risky reward ($P = 0.5$) of either 120 μ L or 360 μ L (Fig. 2A and B, Insets).

After monkeys demonstrated a preference for the certain option in the first case and for the risky option in the second case >70% of the time, additional payoffs from condition 2 were gradually introduced. Once monkeys showed consistent behavior in all five of these payoff options, monkeys were sequentially introduced to payoff conditions 1, 3, and 4. See Table S1 for details.

After each monkey had experienced all possible conditions, the first epoch began. Choice data were collected during 17 d over 1 mo. When these were complete, a break of ~6 mo ensued. The second epoch also lasted for 17 d of data collection (during which blood osmolality data were gathered) distributed over 1 mo. During the second epoch, monkeys performed a constant number of trials in each daily session (344 trials: 86 trials in each of four payoff condition blocks).

Model Fitting and Parameter Estimation. We used stochastic utility theory to model the subject-specific expected utility. We fitted the monkey choice data, using a standard one-parameter utility function with a one-parameter logistic choice function. We estimated the expected utility of each offered reward as

$$Eu(p, v) = p \times v^\alpha,$$

where p is the probability of obtaining the offered reward, v is the magnitude of the offered reward in microliters, and the parameter α indicates risk attitude. An α of 1 indicates that the subject is risk neutral (utility thus equals expected value); an α less than 1 and an α greater than 1 indicate risk-averse and risk-seeking behaviors, respectively. The monkey's choices were estimated as a logistic function

$$P_{\text{chooses risky}} = \frac{1}{1 + e^{-(Eu_{\text{risky}} - Eu_{\text{certain}}) * \beta}},$$

where the parameter β indicates the degree of stochasticity observed in choice. Values of α and β were estimated by maximizing the log-likelihood.

Testing First-Order Stochastic Dominance. Estimating a utility function from choice requires that subjects be maximizing utility or benefit. To test this assumption, we analyzed behavior in the two lottery conditions: (i) certain 120 μ L against risky 120 μ L and (ii) certain 120 μ L against risky 360 μ L.

Statistical Analysis. Whether risk preferences (α) were significantly different from risk neutral (1.0) was determined by likelihood-ratio test at $P < 0.05$. Within-day changes of risk attitude were estimated by dividing the data into a first and a second half. The changes of α within day were regarded as significant by a two-sample t test at $P < 0.05$.

The influence of the serum osmolality on risk attitude, measured before the monkeys engaged in the lottery task, was analyzed separately in each monkey, using a general linear model. The risk attitude was fitted using $Y = b_0 + b_1 * \text{Osmolality} + \varepsilon$, where b_0 and ε are the intercept and residual, respectively. Osmolality is the serum osmolality. If the coefficient b_1 differs from 0 at $P < 0.05$, we concluded that the risk attitude was significantly affected by the serum osmolality.

