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Reward value revealed by auction in rhesus monkeys

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Abstract

Economic choice is thought to involve the elicitation of the private and subjective values of various choice options. Thus far, the estimation of subjective values in animals has relied upon repeated choices and was expressed as an average from dozens of stochastic decisions. However, decisions are made moment-to-moment, and their consequences are usually felt immediately. Here we describe a Becker-DeGroot-Marschak (BDM) auction-like mechanism that encourages animals to truthfully reveal their subjective value in individual choices. The monkeys reliably placed well-ranked BDM bids for up to five juice volumes while paying from a water budget. The bids closely approximated the average subjective values estimated with conventional binary choices, thus demonstrating procedural invariance and aligning with the wealth of knowledge acquired with these less direct estimates. The feasibility of BDM bidding in monkeys encourages single-trial neuronal studies and bridges the gap to the widely used BDM method in human neuroeconomics.

Keywords: BDM, second-price auction, bidding, ranking, choice

Introduction

In economic choice between commodities, decision makers aim to maximise their rewards. The underlying decisions are thought to involve the elicitation of private and subjectively held values for the choice options and the subsequent comparison between such values (Montague and Berns 2002; Camerer 2008). Thus, the elicitation of subjective value is a fundamental process in economic choice and an object of neuroeconomic research. In all such research on animals, subjective value has been estimated in repeated choices (Platt and Glimcher 1999; Padoa-Schioppa and Assad 2006; Kobayashi and Schultz 2008), inferring an average, single subjective value from dozens of decisions that are performed with some amount of stochasticity (in the decision process and/or the underlying neuronal mechanisms). However, decisions are made in single instances, on a moment-to-moment basis, and have immediately tangible consequences. Repeated choices may be adequate for many scientific investigations, but daily behavior often consists of single decisions. Therefore, to better understand the underlying processes, we need methods that elicit values in single choices.

Typical human experimental economics research considers the single-shot nature of economic decisions and assesses subjective value in individual trials. One of the most commonly used assessments of subjective value in humans is the Becker-DeGroot-Marschak auction-like mechanism (BDM; Becker et al. 1964). This method represents an experimental formalization of a conventional auction in which several bidders compete for a single item, trying to obtain it at a price that is no greater than its subjective worth to them. An equivalent method was first used by Johann Wolfgang von Goethe who in 1797 wanted to sell his epic poem 'Hermann und Dorothea' to a publisher (Moldovanu & Tietzel 1998). Goethe set a secret reserve price below which he would not sell the poem, and then asked the publisher for an offer. If the offer was above Goethe's secret reserve price, Goethe would sell it for the reserve price; otherwise, he would try later. This is an example of what is now referred to a second-price auction.

In the experimental BDM, a single bidder competes with a computer. The computer sets a random bid that is unknown to the bidder. Then the participant places her bid for the desired item. If her bid equals or exceeds the computer bid, she wins the auction and pays a price equal to the computer's competing, second-highest bid and receives the item. If, however, the bid is below the computer bid, the participant loses the auction, does not receive the item, and pays nothing. Thus, the BDM is equivalent to a second-price sealed-bid auction with two bidders (Vickrey 1961). Importantly, the optimal BDM strategy is to bid one's true subjective value for the desired commodity (Milgrom and Weber 1982). By bidding higher, the participant would sometimes pay a higher price for the commodity than it is worth to her. By bidding lower, she may lose to a competing bid that is lower than her value for the commodity, and thus forego a profitable trade. Thus, the optimal strategy in the BDM encourages agents to truthfully report the subjective value with each bid that is made (incentive compatibility; Karni and Safra 1987). For these reasons, the BDM is widely used in human experimental economics for understanding the psychology behind economic choice (Shogren & Lusk 2007) and the underlying neural mechanisms (Plassmann et al. 2007; Chib et al. 2009; Linder et al. 2010; Harris et al. 2011; Tang et al. 2014; Tyson-Carr et al. 2018).

The current study. Our objective was to obtain single-trial behavioral estimates of subjective reward value of monkeys in the laboratory. We implemented the well conceptualized Becker-DeGroot-Marschak (BDM) auction like mechanism in which an animal bids for specific volumes of fruit juice against a random computer opponent and paid from a water budget. This mechanism has been shown to reveal the true, internal value of the bidder (incentive compatibility; Karni and Safra 1987): if the bid is too high, the bidder may pay too much; if the bid is too low, the bidder may not obtain the object that is being bid for. So, the bidder should state the true, internal, subjective value for the item that is being bid for.

We aimed to estimate the true subjective value of rewards in monkeys in single trials in a way that reflects the moment-by-moment nature of economic decisions. Monkeys are particularly suitable for behavioral and neuronal economic studies due to their size and sophisticated behavioral repertoire that is well understandable due to their closeness to humans. Further, this species has, at this basic level of reward function, a globally similar brain organisation as humans; the feasibility of a behavioral task used frequently in humans could provide unprecedented information about the role of single reward and decision neurons in auction-like mechanisms. We trained rhesus monkeys to move a joystick cursor on a computer monitor in order to place a bid for juice reward, paying from a water budget to obtain it. We chose these commodities because our animals are highly familiar with them and express meaningful, ordered preferences across them (Kobayashi and Schultz 2008; Stauffer et al. 2014; Pastor-Bernier et al. 2019). We found that the animals reliably expressed well-ranked, trial-by-trial estimates of subjective economic value for up to five juice volumes. The order of these subjective values paralleled the animals' preferences in conventional binary, repeated, stochastic choice between the same rewards, thus demonstrating procedural invariance and linking the BDM to the wealth of economic choice studies in monkeys. These results should pave the way for future single-trial neuronal investigations of subjective reward value in primates.

Method

Animals. Two purpose-bred and group-housed male rhesus monkeys (Macaca mulatta), A (weighing 10.8kg) and B (weighing 7.9kg), were used for this study. Monkeys A and B were trained, via a number of training tasks, on the BDM and a closely related binary choice (BC) task over a period of 24 and 36 months respectively. The animals participated in experiments for 1-2 hours every weekday.

This research has been approved and supervised by the UK Home Office, UK Animals in Science Committee and UK National Centre for Replacement, Refinement and Reduction of Animal Experiments (NC3Rs), and locally at the University of Cambridge by its Animal Welfare and Ethical Review Body (AWERB), Governance and Strategy Committee, Biomedical Service (UBS) Certificate Holder, Welfare Officer, Named Veterinary Surgeon (NVS), and Named Animal Care and Welfare Officer (NACWO).

During experimental sessions animals sat in a primate chair (Crist Instruments) positioned 60cm from a computer monitor. They made choices in the BDM and BC tasks using a custom-built joystick (Biotronix Workshop, University of Cambridge). The joystick allowed for both forward/backward movement to move the bid cursor up/down in the BDM task, and left/right movement to choose between the options in the BC task. The joystick also had a touch sensor that detected whether the animal was holding it.

Becker-DeGroot-Marschak (BDM) procedure. The beginning of each BDM trial was signaled to the animal by a yellow cross at the center of the screen during a 0.5s Preparation epoch. This was followed by an Offer epoch with presentation of the juice volume to bid for, represented by a specific fractal image, and a rectangular bar stimulus (budget bar) whose total grey area indicated 1.2ml of water. A dark-red horizontal bar (bid cursor) also appeared within the limits of the budget bar. The Offer epoch was presented for a variable time, mean 2s±1s with a flat hazard rate, as such temporal uncertainty is known to encourage attention to stimulus changes.

After the Offer epoch, animals used the joystick to move the bid cursor up/down within the confines of the budget bar. The beginning of this Bidding epoch was indicated by a color change of the bid cursor. Animals had 6s to place a bid and did so by maintaining a given bid cursor position for >0.25s. Following stabilization of the bid cursor's position, it could no longer be moved. The animal waited until the end of the 6s bidding period regardless of when it had finalized its bid. Thus, the animal could not manipulate reward rate or temporal reward discounting by making bids more/less quickly. Failure to stabilize their bid cursor within the 6s Bidding epoch resulted in abortion of the trial.

Bidding was followed by a Computer Bid epoch in which a green horizontal bar (computer bid cursor) appeared within the budget bar at a position corresponding to the randomly generated computer-bid for that trial. Computer bids were generated from a pseudo-normal beta distribution, with support [0,1] and parameters ($\alpha = 4$, $\beta = 4$); the random number thus generated was simply multiplied by the maximum bid of 1.2 to generate a bid between 0ml and 1.2ml. Presentation of the computer bid was followed by a 1.5s Budget epoch: if the animal's bid was higher than the computer's, then the water budget to be paid was represented by occluding the area between the bottom of the budget bar and the computer's bid cursor; otherwise, there was no change in the display as no payment was required. In either case the remaining volume of water was delivered at the end of the Budget epoch.

Finally, trials ended with a 0.5s Juice epoch which followed the onset of water delivery by 0.5s. If the animal had made a winning bid, then the fractal was surrounded by a red border and the indicated volume of juice was delivered. Otherwise, the fractal disappeared, and no juice was delivered at the end of the Juice epoch.

Trials were interleaved with inter-trial intervals of random duration (4s±1s, conforming to a truncated exponential function). Animals were required to maintain hold of the joystick from the Preparation epoch to the end of the Bidding epoch, and to maintain the joystick in a central position at all times, except during the Bidding epoch. Failure to comply with these restrictions led to abortion of the trial as an error trial. All errors resulted in the same blue error screen, error sound, and a delay of 3s plus the remaining trial time with no further liquid delivery.

Joystick position data and digital task event signals were sampled at 2 kHz and stored at 200 Hz (joystick) or 1 kHz (task events). Liquid reward was delivered by a computer-controlled solenoid liquid valve (~0.006ml/ms opening time), with a standard deviation of droplet size approximately equal to 0.06ml. Behavioral tasks were controlled by custom-made software (MATLAB; The MathWorks) running in conjunction with the Psychophysics toolbox (Brainard, 1997) on a Microsoft Windows 7 computer.

Across the 30 sessions of BDM testing, Monkey A made 433 errors out of 6433 trials (6.73%), and Monkey B made 2692 errors out of 8692 trials (30.97%). However, most of Monkey B's errors consisted of long strings of consecutive trials during which the animal did not hold or did not center the joystick, with the remaining errors due to not successfully making a bid. Observation of the animal during these periods indicated that they were not attending to the task as they were free to move their head/gaze away from the screen.

Binary Choice (BC) procedure. The most important factor motivating the design of our stochastic BC task was the elicitation of subjective values for comparison with BDM bids while maintaining a perceptual and economic equivalence between the tasks. Thus, the same stimuli and payouts were used in both tasks, and the timings of analogous stimulus changes, choice periods, behavioral requirements, and reward events were the same between them.

The beginning of each BC trial was signaled by a white cross at the center of the screen during a 0.5s Preparation epoch. This was followed by an Offer epoch with presentation of two options on either side of the screen: one of the options consisted of a bundle formed of a specific juice volume (indicated by a specific fractal) together with a variable volume of water budget (quantitatively indicated by the grey area above the green line), and the other option consisted of the fixed full water budget (indicated by the full grey rectangle). The side on which each of these options appeared was randomized on each trial. A dark-red circle (choice cursor) also appeared at the center of the screen. The Offer epoch was presented for a variable time, with mean 2s±1s with a flat hazard rate.

After the Offer epoch, the animal used the joystick to move the choice cursor left/right within the confines of the screen. The beginning of this Choice epoch was indicated by a color change of the choice cursor. The animal had 6s to make a choice and did so by maintaining a given choice cursor position for >0.25s, choices also had to fall within the rightmost/leftmost third of the screen, where the choice cursor changed color from red to blue. Following stabilization of the choice cursor's position, it could no longer be moved. The animal had to wait until the end of the 6s choice period regardless of when they had stabilized the choice cursor, and so could not alter reward rate or temporal reward discounting by making choices more/less quickly. Failure to stabilize their choice cursor within the 6s Choice epoch resulted in abortion of the trial with an error.

The Choice epoch was followed by a 1s Outcome epoch, which began with the unchosen option disappearing from the screen. After this, the 1.5s Budget epoch began: if the bundle was chosen then the water budget difference between the bundle and B_T was occluded at the beginning of this epoch, otherwise, if the animal had chosen B_T, then no further stimulus changes took place. In either case the volume of water indicated by the chosen option was delivered at the end of the Budget epoch.

Finally, trials ended with a 0.5s Juice epoch which immediately followed water delivery. If the animal had chosen the bundle, then the fractal was surrounded by a red border and the indicated volume of juice was delivered. Otherwise, no stimulus change took place, and no juice was delivered at the end of the Juice epoch.

Trials were interleaved with inter-trial intervals of random duration (4s ± 1s, conforming to a truncated exponential function). The animals were required to maintain hold of the joystick from the Preparation epoch to the end of the Choice epoch, and always had to maintain the joystick in a central position, except during the Choice epoch, else trials were aborted with an error. All errors resulted in the same blue error screen, error sound, and a delay of 3s plus the remaining trial time with no further liquid delivery.

Monkey A made 378 errors in 2378 BC trials (15.90%) and Monkey B made 721 errors in 2721 trials (26.50%). For both animals most errors were due to long strings of consecutive trials during which they did not attend to the task.

Optimal BDM Strategy. The optimal strategy in the BDM is the same as that in a second-price sealed-bid, or Vickrey, auction. Here, we present the optimal strategy for a second-price sealed-bid auction, as adapted from Milgrom and Weber's (1982) more comprehensive proof.

To find the optimal strategy for bidder $\boldsymbol{i}$, assuming they have a smooth, continuous and differentiable utility function increasing in income, $\boldsymbol{U_i}$, let $\boldsymbol{v_i}$ represent the value placed on the good by bidder $\boldsymbol{i}$, who places a bid, $\boldsymbol{b_i}$, to obtain the good against other bidders. If bidder $\boldsymbol{i}$ wins the auction, they will derive utility from the difference between the second highest bid - the price, $\boldsymbol{p}$ - and their valuation; this is given by $\boldsymbol{U_i(v_i - p)}$. If bidder $\boldsymbol{i}$ loses, their monetary value from participation is taken as zero. At the time of bidding, the price, $\boldsymbol{p}$, is effectively a random variable. Suppose that bidder $\boldsymbol{i}$ has an expectation of the price characterised by the cumulative distribution function $\boldsymbol{F_i(p)}$, with support $[\underline{\boldsymbol{p_i}}, \overline{\boldsymbol{p_i}}]$ and probability density function $\boldsymbol{f_i(p)}$. Expected utility $(\boldsymbol{E[U_i]})$ is therefore expressed by the following equation:

$$\boldsymbol{E[U_i] = \int_{\underline{p_i}}^{b_i} U_i(v_i - p)\, dF_i(p) + \int_{b_i}^{\overline{p_i}} U_i(0)}$$

$$= \int_{\underline{p_i}}^{b_i} U_i(v_i - p) f_i(p) dp + \int_{b_i}^{\overline{p_i}} U_i(0)$$

We normalize the utility of zero money to zero, such that $U(0) = 0$:

$$E[U_i] = \int_{\underline{p_i}}^{b_i} U_i(v_i - p) f_i(p) dp$$

The maximum of this function is found when its first derivative with respect to the bid, b_i, is set equal to zero:

$$\frac{\partial E[U_i]}{\partial b_i} = U_i(v_i - b_i) f_i(b_i) = 0$$

It is apparent that this equation is satisfied when $b_i = v_i$, i.e. when player i's bid is set equal to their value.

Stimulus training. We trained each animal to associate fractal visual cues with different volumes of the same juice over a period of 2 months of daily training. At this stage, the animals were also trained to maintain hold of the joystick for each trial to progress to juice delivery. This hold requirement was used in all subsequent training procedures and both the BDM and BC tasks.

The animals then learnt to associate the grey area of a rectangular bar (budget bar) with a corresponding volume of water over another month of training. On each trial, the green cursor stimulus used to indicate computer bids in the BDM task appeared at a random location on the budget bar, and the area of the bar below this was occluded. The animals received a volume of water proportional to the remaining grey budget area, with the full area predicting 1.2ml of water.

We then trained the animals in sessions in which both the juice and water budget appeared concurrently over a period of approximately 1 month. The indicated volumes of water and juice were then delivered in the same order and with the same delay that would be used in the BDM task.

Joystick training. After the animals had learned the stimulus-reward associations, they were trained to operate the joystick in both forward/backward and left/right directions, over a period of 3 months.

For left/right movement, animals were first trained on a very simple binary choice task, with budget bars presented on either side of the screen. On each trial, animals had to move a red circular cursor from the center of the screen to their preferred side within a 6s choice epoch. The cursor changed color from red to blue at the rightmost or leftmost third of the screen to indicate that the cursor had been moved far enough to choose the offer on that side. The animals then had to stabilize the cursor in a given position to indicate that a choice had been made, else the trial would end with an error. We started by presenting budget bars offering large differences in water volume and gradually reduced the difference in volume between the two offers as the animals came to reliably choose the budget bar with the most water.

The animals also performed a version of the left/right training task which used fractals indicating juice on either side of the screen. Thus, both versions of this training task acted not only to teach the animals left/right movement of the joystick for the final BC task, but also confirmed that animals understood the relative values of the juice predicting fractals and the significance of the grey area of the budget bar.

Finally, animals were trained to make vertical movements of their bid cursor by moving the joystick forwards/backwards. The animals performed a target-training task in which there were both juice and budget bar cues, like the final BDM task, however, in this case animals had 6s to move the red bid-cursor into a blue target area which appeared at a random location on the budget bar. The bid cursor had to be stabilized within the target area, else the trial would end due to failure to meet the stabilization requirement. This would then act as a forced bid, and the rest of the trial proceeded as in the BDM task, with the appearance of a green cursor at a random height and receipt of either some water and juice or the full volume of water, depending on the relative locations of the animal's red cursor and the randomly generated green cursor. As animals' performance improved, we gradually decreased the size of the blue target's height, until animals could reliably perform the task with a target that was $1/10^{th}$ of the total budget bar height.

Joystick control. Voltage outputs for joystick movement in both axes were separate, and in the central position the voltage output was 0v. A maximal forward or rightward movement produced an output of 5v, and a maximal backward or leftward movement produced an output of -5v. The positions of on-screen cursors were modulated by the following equations, where $\boldsymbol{G}$ is the gain or amplification applied to the voltage modulation, $\boldsymbol{V}$, and $\boldsymbol{P}$ is the pixel position of the center of the cursor at time $\boldsymbol{T}$:

$$\Delta_{\boldsymbol{T}} = \boldsymbol{GV}$$
$$\boldsymbol{P_T} = \boldsymbol{P_{T-1}} + \Delta_{\boldsymbol{T}}$$

Thus, the value of $\boldsymbol{P}$ changes more quickly with greater deflections of the joystick. In the BDM, forward and backward deflections of the joystick move the bid cursor up and down the budget bar, with the maximum and minimum values of $\boldsymbol{P}$ being limited to the top and bottom pixel positions of the budget bar. In the BDM, the value of $\boldsymbol{G}$ was the same for movements in both directions.

In the BC task, the value of $\boldsymbol{G}$ depended on whether $\boldsymbol{V}$ took a positive or negative value, thus the gain could be set differently for rightward/leftward joystick movements. This feature counteracted the effects of side-bias on the animal's choices. Values of $\boldsymbol{G}$ were set for each direction such that the animals made choices without a statistically significant side-bias when both the left and right-hand-side offers were the same.

The animals found it difficult to hold the joystick perfectly still in the central position, so a window of tolerance for slight movements was necessary to prevent small erratic deflections of on-screen cursors during choice/bidding epochs. A minimum threshold of 2% of the maximal voltage displacement was applied in every direction, such that any output with an absolute magnitude of 0.1v or less was treated as a 0v modulation and did not produce any deflection of on-screen cursors.
For tight control of animals' movements, we enforced three behavioral requirements relating to joystick control, failure of which led to a blue error screen for a duration equal to the remaining trial time plus 3s, and no reward for that trial:
- Hold requirement: The animals had to maintain hold of the joystick throughout choice/bidding epochs and in all epochs preceding them, as detected by a built-in touch sensor.
- Centre requirement: The animals had to maintain the joystick in a central position outside of the choice/bidding epochs, such that only deflections leading to voltage outputs less than or equal to 0.1v were tolerated in all other epochs.
- Stabilization requirement: The animals had to stabilize on-screen bid and choice cursors in their desired final position for 250ms, such that the voltage output was less than or equal to 0.1v for 500 consecutive samples at 2kHz. This indicated a purposeful choice and had to be completed within the 6s allocated to the choice/bidding epochs.

Statistical Analysis. To evaluate how well animals' bids reflected increasing juice volumes on individual days, or sessions, of BDM testing we used Spearman rank correlation (MATLAB: corr) between bids and juice volumes as it assumes a monotonic, but not necessarily linear, relationship between the two variables (Table S1).

We also wanted to assess how distinct animals' mean bids were for different juice volumes in individual sessions. We used 1-way ANOVAs (MATLAB: anova1) to test whether mean bids for different juice volumes were different to one another in each of the 30 BDM sessions (Table S1). For these and all other ANOVAs, we also present the omega-squared (ω^2) measure of effect size for different factors. Post-hoc Bonferroni tests for multiple pairwise comparisons (MATLAB: multcompare) were performed to find which juice volumes received mean bids that were significantly different to one another, thus reflecting how well animals' bids discriminated different juice volumes.

Within those sessions in which animals' mean bids reliably discriminated all five juice volumes (i.e. all sessions for Monkey A and 21/30 sessions for Monkey B), we identified how quickly animals achieved this. We found the first trial, T_n, for which a 1-way ANOVA and Bonferroni-corrected multiple comparisons tests over mean bids were significantly different for all juice volumes, and, were also significant for the 10 trials which followed, T_{n+1} - T_{n+10}; such that from trial T_n discrimination of juice volumes by bidding was reliable and consistent.

We performed an unbalanced two-way ANOVA (MATLAB: anovan) on animals' bids with main factors of juice volume and bid starting position condition to explore the relative influence of motor contingencies, which vary with starting position (Table S2). To more closely interrogate the effects of the starting location of the bid cursor on animals' final bids, we performed a multiple regression analysis (MATLAB: fitlm) on bids, with regressors for the juice volume (JV) and the interaction between each juice volume and the bid cursor's exact starting position ($SP_{JV=Xml}$), according Eq. 1. For each animal, this regression analysis was conducted separately for each of the 10 random starting position sessions, finding the mean value of the coefficient for each regressor across sessions. As bid cursor position was expressed in terms of the corresponding bid volume, all regressors had the same units and scale and could therefore be compared directly (see main text). For Monkey A, $B_0 = 0.05 \pm 0.1$ (mean ± SD); $B_1 = 1.38 \pm 0.14$; $B_2 = -0.11 \pm 0.12$; $B_3 = -0.17 \pm 0.1$; $B_4 = -0.04 \pm 0.06$; $B_5 = 0.02 \pm 0.05$; $B_6 = -0.02 \pm 0.04$. For Monkey B, $B_0 = -0.03 \pm 0.07$; $B_1 = 1.42 \pm 0.24$; $B_2 = 0.04 \pm 0.07$; $B_3 = -0.02 \pm 0.05$; $B_4 = 0 \pm 0.05$; $B_5 = 0.02 \pm 0.1$; $B_6 = 0 \pm 0.16$.

Value estimation during Binary Choice (BC). We used choices the BC task to estimate the water equivalents of different apple and mango juice volumes. Using a logistic regression model, we estimated regression by fitting the probability of choosing the full 1.2ml water budget, *P(B choice)*, for each of the bundles, which contained variable water volumes, B_X. Each bundle in this analysis was expressed in terms of the difference in water volume between it and the full budget option, $\Delta B = B - B_X$.

For each of the 5 volumes of juice, we fitted the logistic function (MATLAB: fitglm) of the following form onto the choice data from the BC task:

$$P(B\ choice) = 1 / (1 + e^{-(\alpha+\beta(\Delta B))})$$

The value of ΔB at which *P(B choice)* is equal to 0.5 is an estimate of the animal's water-value for the volume of juice which appeared in that set of bundles. In this case, α is a measure of choice bias and β is a measure of the animal's sensitivity to changes in the volume of water available in the budget options. Note, even if ΔB is replaced by the ratio of water volumes in the bundle and full budget option, as is the case in some binary choice analyses, we arrive at the same estimates of water-value; because the volume of water in the budget-only option is constant in this task.

We conducted this analysis on each of the 10 BC sessions for each animal (Fig. S6A, B), but choices were too variable and trials too few to attain reliable value estimates using individual sessions.

Animals were tested in five BC sessions preceding BDM testing and five BC sessions after BDM testing to detect any change in the values of the juice volumes across the period of BDM testing. No significant change in mean value estimates was detected. We therefore pooled all 10 BC sessions for each animal to acquire better estimates of their average values for these five juice volumes, using the method described above. These acted as our best estimates of the animals' values.

If BC value estimates are taken as the animals' true values for each juice volume, then the optimal bid should be equal to the BC value estimate, except where the estimated value is greater than the maximum bid of 1.2ml, in which case the optimal bid is equal to this maximal volume. This was only the case for Monkey A's value for the 0.75ml apple and mango juice.

How well animals' bids reflected the BC value estimates was determined using a simple linear regression (MATLAB: fitlm) on bids with the BC value estimates for each juice volume as the sole predictor (see main text).

The BC value estimates were also used to compute each animal's total payoff in terms of water for each trial, as well as the payoffs of optimal and random simulated bidders (see main text and following section on simulation methods). This was not possible for the 0.75ml juice volume, for which Monkey A's value could not be identified and as such trials for that juice were excluded from those analyses.

Simulated Bidding. We simulated two types of decision-maker for the BDM task, either an optimal decision-maker who always bid the animal's exact BC value for each juice volume, or, a random decision-maker who always made a completely random bid drawn from a uniform distribution with support [0, 1.2].

These two simulated bidders were presented with the same juice presentations that each animal faced over 30 BDM sessions of 200 trials each (though trials in which the 0.75ml juice was presented were excluded for Monkey A as his value for that juice volume and therefore the payoffs, could not be computed - see above). The computer bids for each juice volume were also the same as those that each animal actually faced. BC values were substituted for juice volumes so that payoffs were always expressed in terms of the equivalent volume of water. The mean per-trial payoff was then calculated for each juice volume by dividing the total payoff for that reward by the number of times that reward was presented. This process was repeated separately for each animal.

These simple simulations provided an idea of how each animal performed in terms of behaviorally relevant outcomes, on a spectrum from completely random behavior to mechanically perfect rational bidding (i.e. with no motor or decision noise).

Juice-delivery error. To deliver juice and water in our tasks we used a solenoid delivery system, with opening time controlled by voltage pulses. There was an approximately linear relationship between solenoid opening time and the volume of water/juice delivered, and we tested and calibrated the opening times so that we could deliver the appropriate volumes of the different liquids in the task. Calibration of the solenoid systems showed a mean standard deviation of 0.06ml at any given opening time.

This degree of variability in the volume of liquid delivered at a given solenoid opening time could limit the animal's ability to discriminate the small differences in expected payoffs that result from different bids in the BDM, as these variations in liquid volume may be indistinguishable from the variability of the solenoid itself.

Increasing water budget volume and juice volume reduces the relative magnitude of the solenoid's variability in liquid delivery, as the standard deviation of the delivered volume is the same regardless of the mean volume delivered.

These considerations motivated the use of larger liquid volumes in the BDM task. With a larger water budget volume, expected losses are greater for the same pixel distance displacement of the bid cursor from the optimal bid, and the relative contribution of variability in the solenoid delivery is reduced. Thus, animals should be able to discriminate differences in expected payoff at smaller relative distances between the actual and optimal bids.

Results

Designing a monkey BDM. Two monkeys, A and B, were taught to perform a BDM task against a computer in which they placed bids for specific volumes of juice and paid a price from a budget of water (Fig. 1; see Fig. S1A for task epochs and behavioral requirements). Thus, both the juice and the water were commodities with similar characteristics (liquid) that were ecologically relevant for the animals, with which they were familiar, and which they would conceivably be able to evaluate reliably. On each trial the animal bid for one of five randomly selected volumes of the same apple or mango juice, each volume being represented by a specific fractal image (Fig. 1A). A fresh budget of 1.2ml of water was available on each trial, represented by the full grey budget rectangle. The animal used a joystick to move a red cursor within the budget bar on a computer monitor, indicating its bid by stabilising the cursor at the chosen position for > 0.25s. The randomly generated computer bid was then shown by a green line on the budget bar. If the animal's bid was higher than the computer bid, the animal won the auction and paid a volume of water equal to the computer bid (second price) (Fig. 1B, C top). The animal first received the water remaining from the budget and then the juice (0.5s after water onset). Alternatively, if the animal's bid was lower than the computer's, it received the full water budget of 1.2ml but no juice (Fig. 1B, C bottom). Each animal completed 30 daily sessions of BDM testing, each consisting of 200 trials.

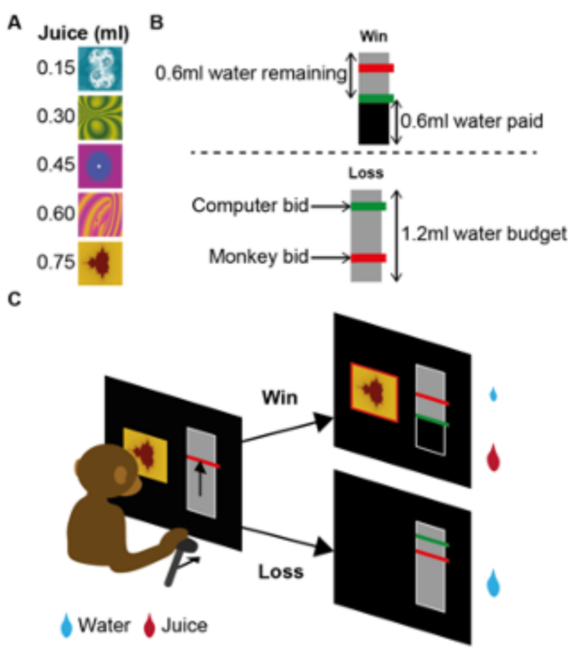

Fig. 1. A BDM task for monkeys.
(A) Five fractals indicating five specific volumes of same fruit juice.
(B) A fresh water budget of 1.2ml was available on each trial and was represented by the full area of the grey rectangle. Monkey bids and computer bids were indicated by heights of red and green lines, respectively. The water to be paid in case of a winning bid was represented by occlusion of an equivalent area below the green line at the bottom of the grey budget

rectangle (computer bid = second price); the remaining grey area above represented the remaining volume of water that is paid out to the animal together with the gained juice.
(C) Bidding task. The monkey placed a bid by moving the red cursor up-down via pushing-pulling a joystick. The computer bid was then shown (green line). When winning the BDM (top), the water remaining above the green line was delivered first, followed 0.5s by the juice; thus, the water volume lost below the green line (corresponding to the computer price) was the price paid for the gained juice. When losing (bottom), only the full water budget was delivered.

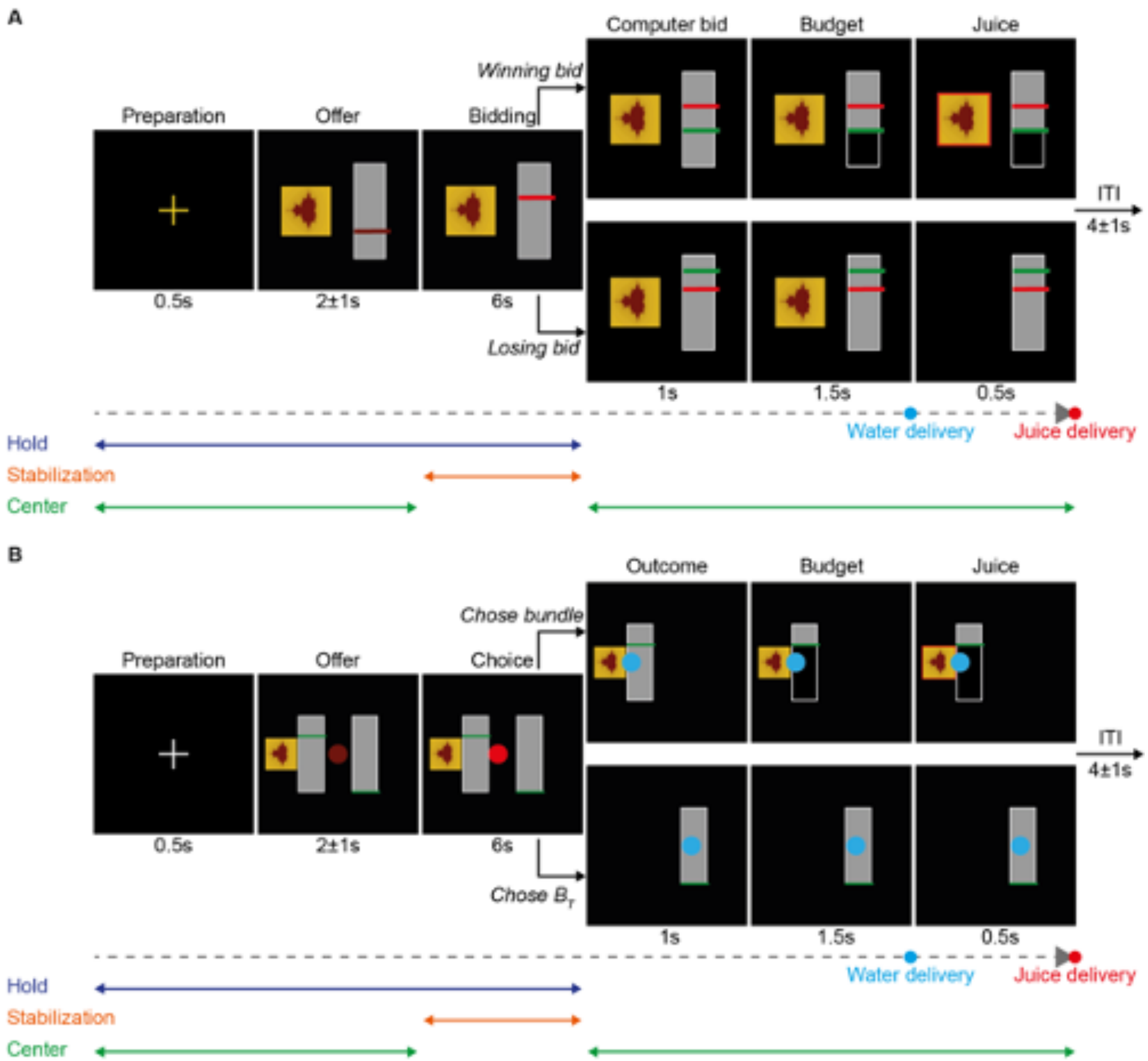

Fig. S1. BDM and Binary Choice (BC) tasks.
(A) BDM task. A cross during the Preparation epoch prompts the monkey had to maintain grasp of a joystick (blue line, 'Hold') and keep it in a central position (left green line, 'Center'). In the subsequent Offer epoch, the animal was presented with a fractal image indicating the volume of juice to bid for; the full water budget; and the bid cursor's starting position. The Bidding epoch began after a variable delay governed by a flat hazard function. Now the animal was free to move the red bidding cursor via the joystick within the grey vertical rectangle. Each bid was made by the animal stabilizing the cursor at the desired position for >250ms after it had moved it there to place a bid (orange line, 'Stabilization'). Failure to make a bid within the 6s Bidding period, or joystick release before the end of this period, resulted in trial termination and constituted an error. Joystick movement outside the Bidding epoch also constituted an error. The computer bid was displayed after the Bidding epoch (and the animal turned the joystick-cursor back to the central position and held it there without moving the cursor, right green line, 'Center'). If the monkey's bid was higher than the computer's (win), the budget

bar below the computer bid was occluded and the animal received the remaining water budget at the end of the Budget epoch, and the juice at the end of the Juice epoch. Otherwise (loss), the full 1.2ml water budget was delivered at the end of the Budget epoch, but no juice was delivered. Trials were separated by a variable inter-trial interval (ITI) of 4 ± 1s.
(B) BC control task. Stimuli, rewards, delays after stimuli and movements were the same as in the BDM. The same behavioral requirements applied at equivalent epochs (blue, orange and green lines): centring of joystick in the Offer epoch; stabilising of bid cursor position in the Bidding epoch; and no joystick movement allowed outside of the Bidding epoch.

We used several successive steps to train both animals in the BDM task. First, they learned to associate different fractals on a computer monitor with different juice volumes (Fig. S2A; Materials and Methods: Stimulus training). Then they learned to associate the budget bar on the computer monitor with different volumes of water (Fig. S2B). We also accustomed them to the sequential delivery of the water budget and the offered juice (Fig. S2C). Then they learned to use a joystick in order to move the bid cursor and receive the different outcomes (win/loss) depending on the position of the computer bids relative to their own (Fig. S3) (Materials and Methods: Joystick training). Then we introduced the animals to various preliminary BDM task versions, using essentially similar types of fractal stimuli for juices but different volumes of juice reward and different volumes of water budget. We limited initially the reward volume in a given trial so that the animals completed as many trials as possible on a test day. In earlier, reduced versions of the task with only three juice volumes and low budget volume, the animals ordered their bids according to their preferences, but their bids were inconsistent and poorly differentiated (Fig. S4). We reasoned that while the relative cost of deviating from the optimal bid is unchanged by changing the budget volume, the absolute cost of a given deviation in terms of distance on the screen, or movement of the joystick, is increased when larger rewards are on offer (Fig. S5). With successively larger volumes of juice and water, bidding behavior improved, both in terms of correlation strength between bids and juice magnitude, as measured by Spearman rank correlation, and in terms of separation of bids for different juice volumes. For example, in an earlier task version with 0.6 ml of water as budget, Monkey A's mean Spearman Rho for the correlation between bids and juice magnitude was 0.46 ± 0.085, compared to 0.91 ± 0.02 in the final task. Similarly, for Monkey B, using 0.9 ml of water as the budget resulted in a mean Spearman Rho of 0.31 ± 0.26 for this correlation, compared to 0.81 ± 0.05 in the final BDM version. The larger volume limited the daily total trial numbers to 200. Due to time constraints in testing earlier versions of the task, we changed several parameters at once (including juice type, magnitude and timing of stimulus presentation and reward delivery) and were unable to implement each change alone followed by a significant period of testing. This made it difficult to attribute any improvement in performance to a single parameter change or manipulation of the task structure. Nevertheless, the improvements we observed using larger budget volumes in these unstructured preliminary tests guided our approach in using a larger budget volume for the final BDM task.

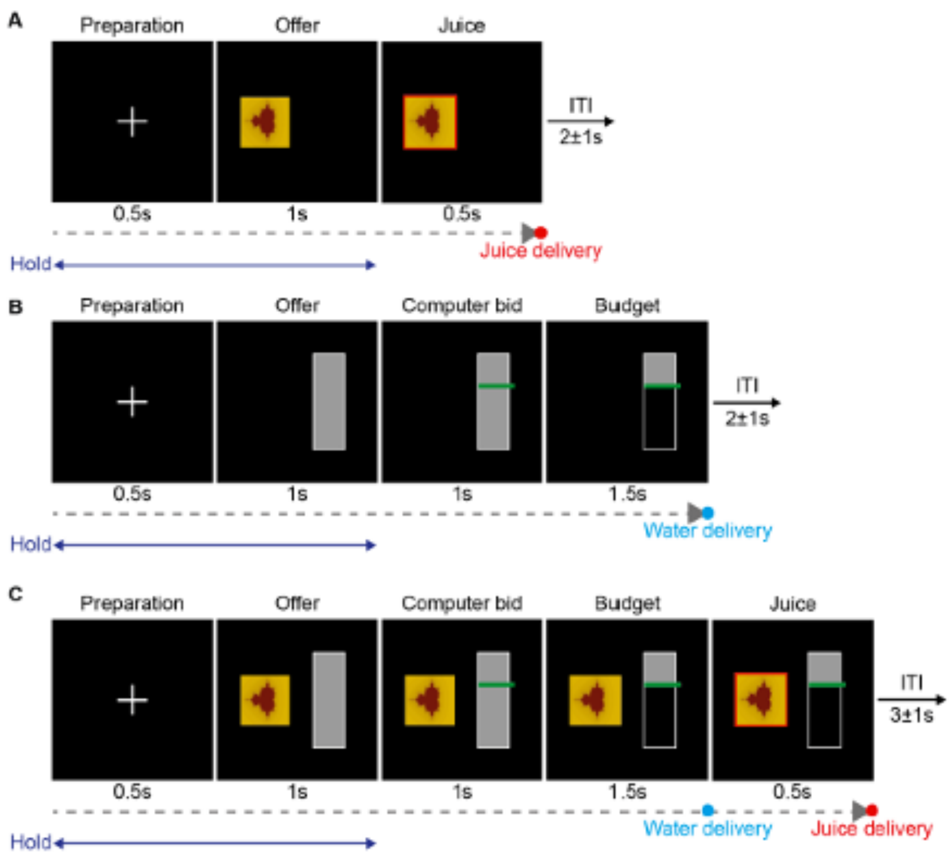

Fig. S2. Stepwise learning of stimulus-juice associations.
(A) Initial learning to associate each of 5 unique fractal images with 5 specific juice volumes. Fractals were surrounded by a red border 0.5s before juice delivery, as in the final BDM and BC tasks. At this point, the monkey was also taught to maintain hold of the joystick throughout Preparation and Offer epochs (blue line, 'Hold'); else trials were considered erroneous and aborted.
(B) Subsequent learning to associate the budget bar with water budget volumes. The monkey was presented with a grey bar stimulus whose full area represented 1.2ml of water. Then a green cursor, as later used to indicate the computer bid in the BDM, appeared at a random location on the vertical rectangle, and the area of the rectangle below was occluded. The animals received the remaining volume of water (% of remaining grey area × 1.2ml) at 1.5s after occlusion of the rectangle below the computer bid cursor, as in the final BDM and BC tasks.
(C) Learning the relative timing of delivery of water budget and juice. The monkey was presented with both stimuli concurrently. Both the BDM and BC tasks had identical timing of water delivery (from the point at which the budget bar was occluded below the green cursor) and juice delivery (0.5s later).

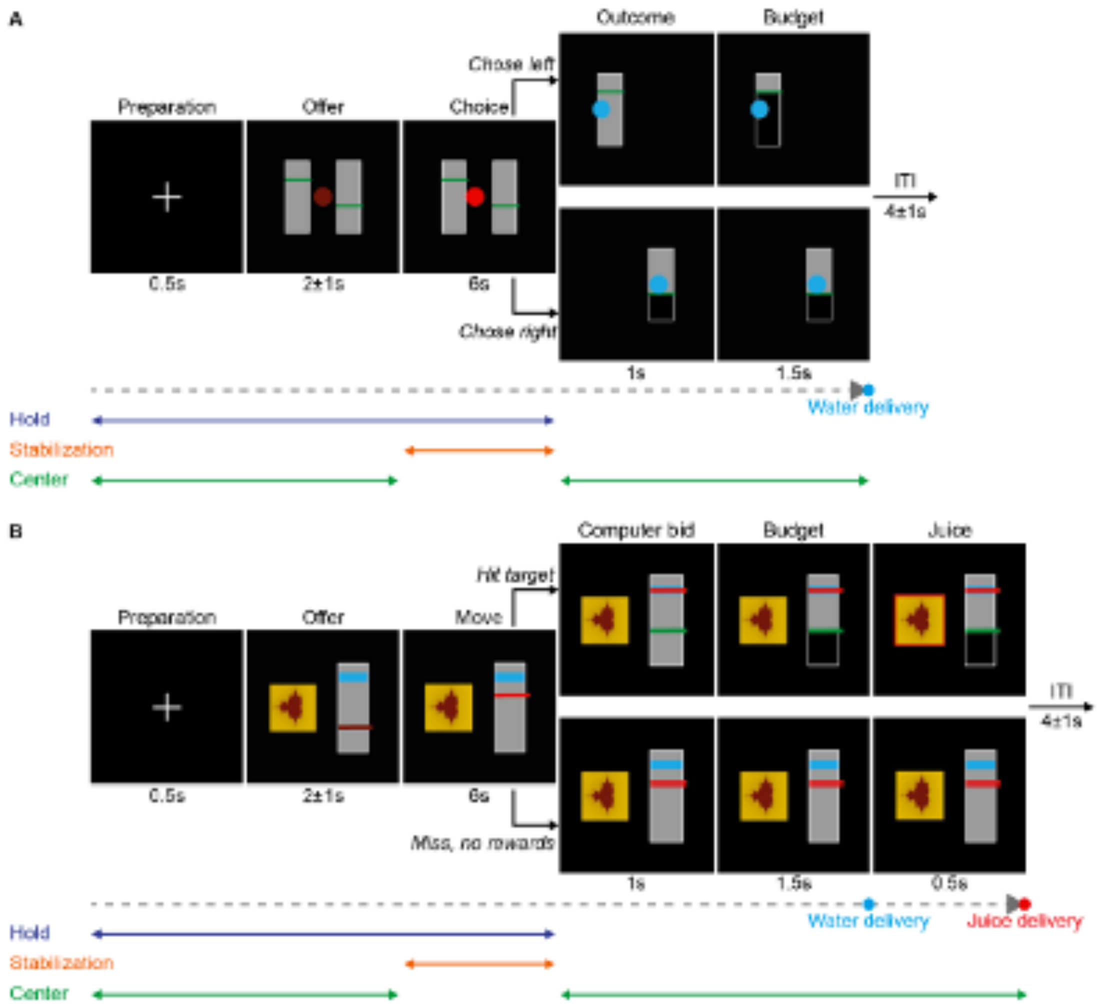

Fig. S3. Learning joystick control.
(A) Initial choice task. To confirm the animal's understanding of the stimuli, each animal was trained to choose between different volumes of the same juice. To do so, the animal moved a red circle with a joystick from a central holding position into the left or right third of the screen and stabilised its location for 250ms to state its choice (blue, orange and left green lines); it re-centered the joystick after bidding (right green line). Each animal performed this task with two different fractals on either side. On a subset of these trials, we eliminated any possible choice bias by adjusting the gain of joystick movement on either side until identical juice volumes were chosen with equal probability.
(B) BDM training, with similar task epochs as initial choice task (blue, orange and green lines). The animal was taught to control a cursor vertically on the monitor with forward/backward movements of the joystick. The animal had to move a red cursor into a randomly positioned blue target area. If it placed the cursor successfully into the target area, the computer bid appeared, and the animal received the juice and water after the same delay as in the BDM task, and according to whether the animal's bid was greater/less than the computer's. If the cursor was not secured within the target area in the Move epoch, then no further stimulus change took place until trial end, and reward was withheld. The height of the blue target area was progressively reduced as the animal's performance improved.

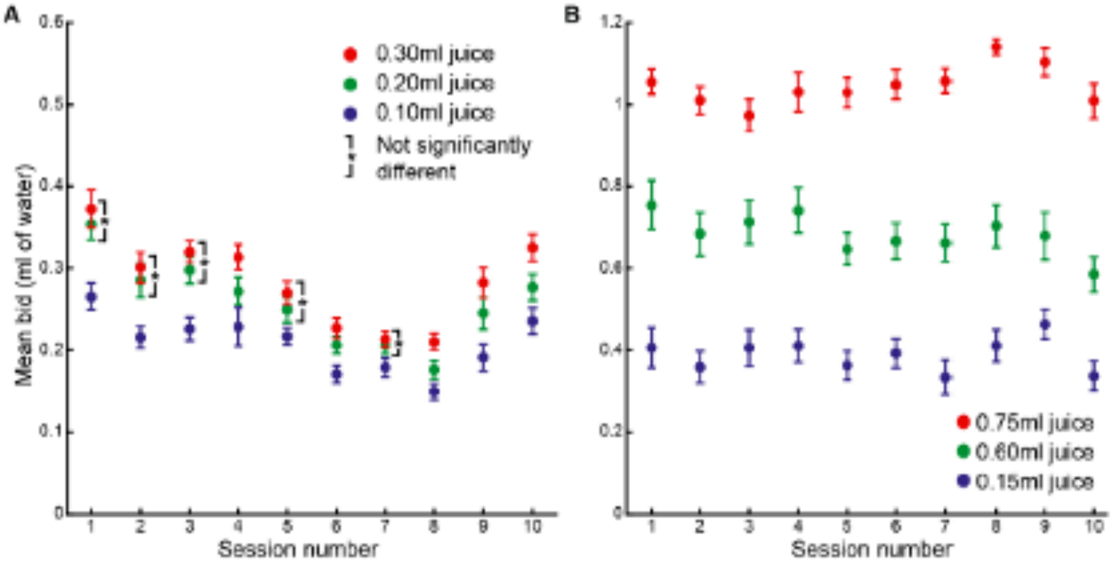

Fig. S4. Performance in early BDM task versions. Juice volumes were selected from performance in a preceding binary choice task such that their subjective values covered a wide range of possible bids. All bids started at the bottom. Error bars show 95% confidence intervals of the mean. Monkey A.

(A) Early version of BDM task with small water budget volume (0.6ml) and 3 small juice volumes to be bid for. Small volumes maximised the number of trials in each session before satiety set in; however, bids were not well differentiated, and the correlation between juice volumes and bids was weaker than in later task versions (mean Spearman Rho = 0.45±0.25). Asterisks indicate insignificantly varying mean bids after Bonferroni correction for multiple comparisons ($\alpha = 0.05$).

(B) We hypothesised that an increase in the water budget and juice volumes would lead to more careful bidding as the absolute losses for a given deviation in terms of distance from the optimal bid would be increased. We therefore doubled the water budget volume to 1.2ml and used larger juice volumes, such that the range of juice reward values covered this wider range of possible bids. This led to a marked performance improvement, with mean bids for all juice volumes being significantly different to one another in every session. Moreover, the correlation between juice volumes and bids was markedly and consistently stronger than in the lower budget volume version of the task shown in A (mean Spearman Rho = 0.80 ± 0.03).

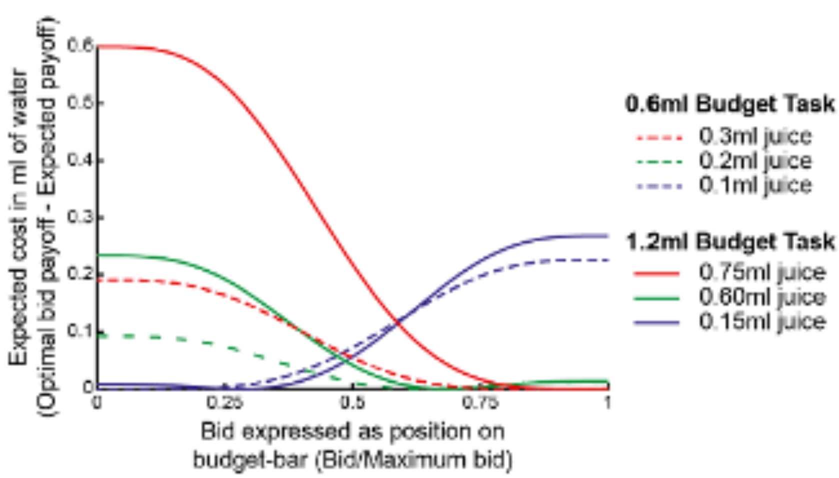

Fig. S5. Increasing expected suboptimal bidding cost with increasing juice and water budget. The optimal BDM bid is equal to the value of the juice volume being bid for and will lead to the highest expected payoff compared to all other bids. The lower expected payoff of other bids constitutes an expected cost relative to the optimal bid. In the two BDM payoff settings shown in Fig. S4, the 0.3ml and 0.75ml, 0.2ml and 0.6ml, and 0.1ml and 0.15ml juice volumes elicited optimal bids that were similarly positioned on the 0.6ml and 1.2ml budget bars used in each task, respectively. This can be seen by the fact that the minimum costs for these pairs of juice volumes are at similar positions on the budget bar. For a given deviation of the final bid in terms of distance on the budget bar, the cost is higher in the 1.2ml budget task than in the 0.6ml budget task. This effect is more pronounced the further bids are away from the centre of the bidding range, because the mean computer bid was at the centre of this range. Moreover, the effect is exaggerated for lower bids for higher juice volumes, as the cost of losing a higher juice volume by bidding less than its value is greater.

Rank-ordered bidding. Once BDM training was concluded, we advanced to testing the animals' performance in the BDM task. For both animals, there were significant differences between bids for the five juice volumes (one-way ANOVA in each of the 30 sessions, $P < 0.05$: Monkey A: F = 176.42 to 392.36; Monkey B: F = 40.17 to 166.76; Table S1). Post-hoc t-tests (Bonferroni-corrected for multiple comparisons) confirmed significant differences in all pairwise comparisons of mean bids for the five juice volumes in each of the 30 BDM sessions for Monkey A (all $P < 0.05$), and in 21 of the 30 sessions for Monkey B ($P < 0.05$). With Monkey B, bids differed significantly with all but one pair of juice volumes in eight sessions and two pairs in one session. Fig. S6 shows mean bids from all sessions in both monkeys and post-hoc comparisons of means. Thus, the animals made distinct but noisy bids for different rewards.

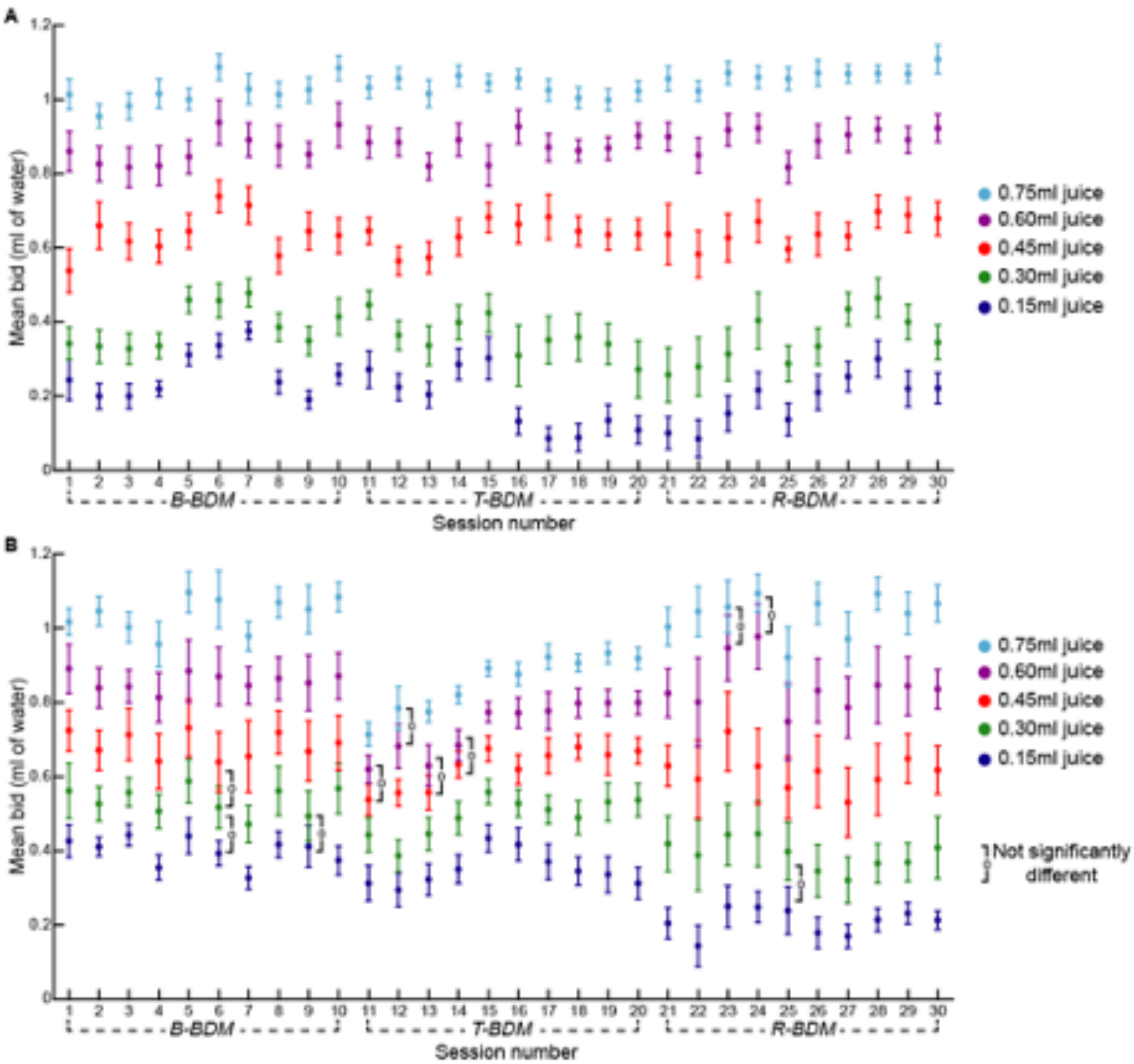

Fig. S6. BDM bids in individual sessions.
(A) Monkey A. All mean bids for each of the five juice volumes differed significantly in all 30 sessions. Error bars are 95% confidence intervals of the mean. In sessions 1-10 the bid cursor started at the bottom of the budget bar (B-BDM); for

sessions 11-20 the cursor started at the top of the budget bar (T-BDM); and for sessions 21-30 the cursor started at a random position on the budget bar (R-BDM). Each session was composed of 200 correct trials.
(B) Monkey B. Mean bids differed significantly in 21 of the 30 sessions. In 8 sessions (1 B-BDM; 4 T-BDM; 3-RBDM) the mean bids for two juice volumes were not significantly different. In session 6 (B-BDM), the mean bid for the 0.30ml juice was not significantly different to those of either the 0.15ml or 0.45ml juice volumes. 0 in brackets indicates lack of significant difference of mean bids after Bonferroni correction for multiple comparisons ($\alpha = 0.05$).

Moreover, both animals consistently placed monotonically increasing bids for larger juice volumes (Fig. 2A, B). This positive monotonic relationship between bids and five juice volumes was significant in each of the 30 BDM sessions for both animals (Monkey A, Spearman Rho = 0.91±0.02; mean ± SD; Monkey B, Spearman Rho = 0.81±0.05; all $P < 0.05$; Table 1). Thus, Rho is a measure of how well the animals' bids ranked the five juice volumes.

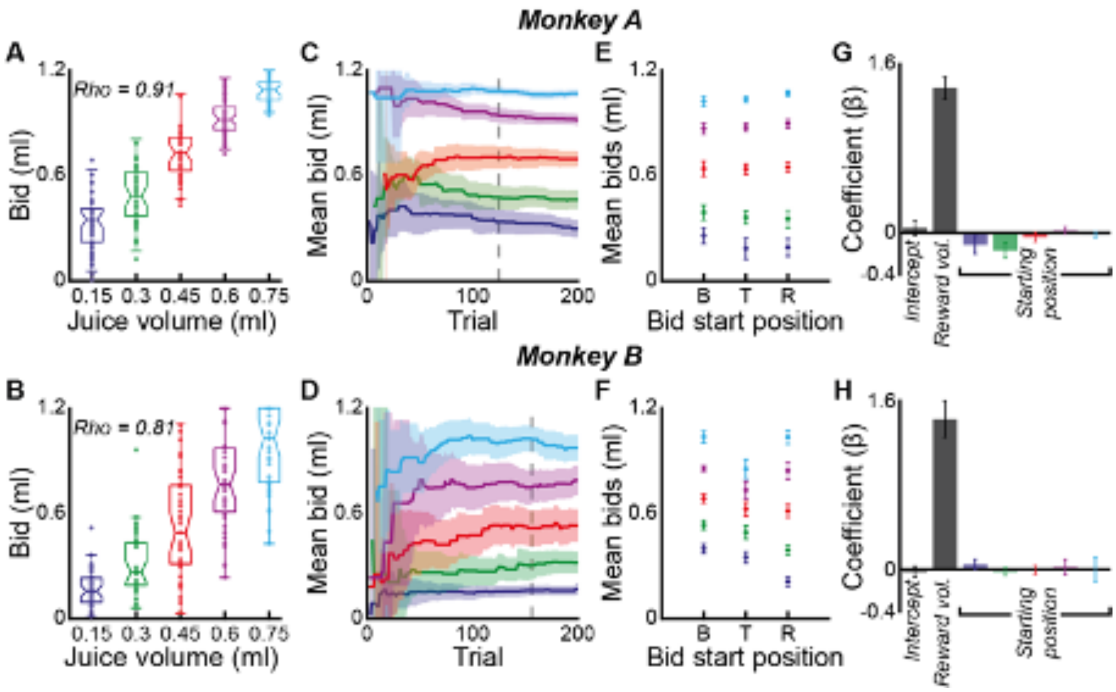

Fig. 2. Increasing BDM bids with increasing juice volume, irrespective of bid cursor starting position.
(A, B) Monotonic increase of bids with juice volume in single sessions. Boxplots center lines show the median and notches show 95% confidence intervals of the median, boxplot edges mark interquartile range. Colors for juice volumes apply to all panels.
(C, D) Development of differential bidding across consecutive trials (same sessions as shown in A and B). Mean bids for all juice volumes became significantly different by trial 114 (Monkey A) and 170 (Monkey B) ($P < 0.05$, Bonferroni corrected t-test; grey dashed lines). Solid lines show mean bids, shaded areas show 95% confidence intervals.
(E, F) Similar discrimination of juice volumes by bids irrespective of bottom (B), top (T) or random (R) starting position (means of mean bids across all 10 sessions ($N = 2{,}000$ trials in each animal) for each starting position).
(G, H) Mean beta coefficients from regression on juice volume and random starting position of bid cursor, for all five juice volumes (all 10 sessions in each animal; $N = 2{,}000$ trials in each animal) (Eq. 2). Bids varied significantly with cursor starting position only for the two smallest juice volumes with Monkey A (**G**: maroon, green). Error bars: 95% confidence intervals of the mean.

Within each session, the animals' bids ranked all 5 rewards according to their reward volumes long before the end of the session. For Monkey A, this was typically achieved by trial 18.5 ± 11.8, with a significantly positive correlation between bids and reward volumes at this point (Spearman's Rho =

0.87 ± 0.08). Similarly, Monkey B typically required only 19.6 ± 12.4 trials to achieve this (Spearman's Rho = 0.74 ± 0.14). Moreover, whenever the animals achieved complete separation of all bids, they also achieved this before the end of the 200 correct trials that constituted a single testing session. On average, Monkey A needed 105.7 ± 38.4 trials (n = 30 sessions), and Monkey B needed 148 ± 30.1 trials (n = 21 sessions) to achieve complete separation of bids (Fig. 2C, D).

Thus, the animals were both consistent in their ranking of rewards and in the precision of their bidding such that bids reliably reflected preferences and distinct subjective values for different rewards relatively early in each session, and within a single session of testing. These results demonstrate that monkeys were able to use the BDM to truthfully express their subjective value for rewards.

Control for action effects. The animals' bidding behavior might be explained by motor vigor or simple conditioned motor responses. To assess the potential impact of such reasonable confounds, we used three different starting positions for the bid cursor in 10 sessions each, for the total of the 30 BDM sessions with each animal; the bid cursor started either at the bottom (B), top (T), or, at a random position (R) on the budget bar. Both animals' bids discriminated all juice volumes regardless of initial cursor position (Fig. 2E, F). Two-way unbalanced ANOVAs with factors of juice volume, bid cursor starting condition and their interaction demonstrated a highly significant effect of juice volume on the animals' bids (Monkey A: $F_{4,5985} = 6889.46$, $P = 0.0$, $\omega^2 = 0.82$; Monkey B: $F_{4,5985} = 2353.17$, $P = 0.0$, $\omega^2 = 0.58$) (Table S2). Bid cursor starting position had a smaller but still significant effect (Monkey A: $F_{2,5985} = 7.18$, $P = 8 \times 10^{-4}$, $\omega^2 = 3.67 \times 10^{-4}$; Monkey B: $F_{2,5985} = 148.94$, $P = 7.49 \times 10^{-64}$, $\omega^2 = 0.018$). The interaction between juice volume and starting position was also significant (Monkey A: $F_{8,5985} = 13.55$, $P = 1.24 \times 10^{-19}$, $\omega^2 = 3 \times 10^{-3}$; Monkey B: $F_{8,5985} = 55.86$, $P = 3.94 \times 10^{-88}$, $\omega^2 = 0.027$). Thus, while the starting position of the bidding cursor affected bidding to some extent, differential bidding for juice volume remained significant irrespective of the starting position.

To more closely interrogate the influence of motor contingencies on bidding, we further analysed the bids from the 10 sessions in which the cursor's starting position varied randomly. As the cursor came up at any vertical position, bidding required joystick movement that varied in up-down direction and amplitude. We regressed the animals' bids on both juice volume (JV) and cursor starting position (SP), such that:

$$Bid = \beta_0 + \beta_1 * JV + \beta_2 * SP \quad \text{(Eq. 1)}$$

Across these 10 sessions, we found that the animals' bids varied significantly with the juice volume (Monkey A: $\beta_1 = 1.53 \pm 0.12$; Monkey B: $\beta_1 = 1.40 \pm 0.10$), with a far smaller effect of the cursor's starting position for monkey A (β_2 was significantly smaller than zero; $\beta_2 = -0.06 \pm 0.05$) but with no effect of starting position for monkey B ($\beta_2 = 0.01 \pm 0.05$). To investigate for any variable effect of starting position with different juice volumes, we then performed a regression of the animals' bids on both juice volume (JV) and cursor starting position separately for each of the five juice volumes ($SP_{JV=Xml}$), such that:

$$Bid = \beta_0 + \beta_1 * JV + \beta_2 * SP_{JV=0.15} + \beta_3 * SP_{JV=0.30} + \beta_4 * SP_{JV=0.45} + \beta_5 * SP_{JV=0.60} + \beta_6 * SP_{JV=0.75} \quad \text{(Eq. 2)}$$

The results from this analysis confirmed the small but significant effect of starting position for the two smallest juice volumes for Monkey A ($\beta_2 = -0.11 \pm 0.12$; $\beta_3 = -0.17 \pm 0.10$), but none of the position coefficients differed significantly from zero for Monkey B (Fig. 2G, H). For Monkey A this may have reflected reduced motivation to bid precisely on trials that promised lower juice volumes. Nevertheless, juice volume had a far greater influence on the final bid than cursor starting position, for both animals (Monkey A: $\beta_1 = 1.38 \pm 0.14$; Monkey B: $\beta_1 = 1.42 \pm 0.24$).

These results suggest that the animals were not merely responding with greater vigor to larger juice volumes, or just learning conditioned motor responses. Their bids seemed to reflect their subjective economic value irrespective of the specifics of the required joystick movement.

Mechanism independence. While the positive monotonic relationship of BDM bids to juice volumes in both animals suggests systematic value estimation, it is important to know whether these results were specific for the BDM mechanism or were independent of the eliciting mechanism. A different eliciting mechanism would also provide independent estimates for assessing optimality in BDM bidding. Therefore, we compared the subjective values inferred from BDM bids with estimates from a conventional value eliciting method commonly used in animals. (Note that while the study's goal was to assess subjective juice value in single BDM trials, comparison with value estimation by conventional binary choice required repeated measures.)

We implemented a binary choice (BC) task with repeated trials that used the same options, visual stimuli and juice and water outcomes as the BDM task and differed only in the choice aspect (Fig. 3A; Fig. S1B). Option 1 contained a bundle comprised of one of the five juice volumes and a varying, partial water amount, equivalent to the outcome when winning the BDM. Option 2 contained the full water budget, equivalent to the outcome when losing the BDM. Thus, when choosing the juice-water bundle, the animal forewent some of the full water budget to obtain the juice (like when winning the BDM); when choosing the other option, the animal received the full water budget but no juice, like when losing the BDM. We performed 10 of these BC sessions, and each session consisted of 200 trials. In each session every reward volume appeared in one of 10 possible bundles (i.e. with 10 different possible volumes of water in the bundle), and each of these combinations was repeated 4 times per session, such that there were 40 trials per reward volume in each session, for a total of 200 trials.

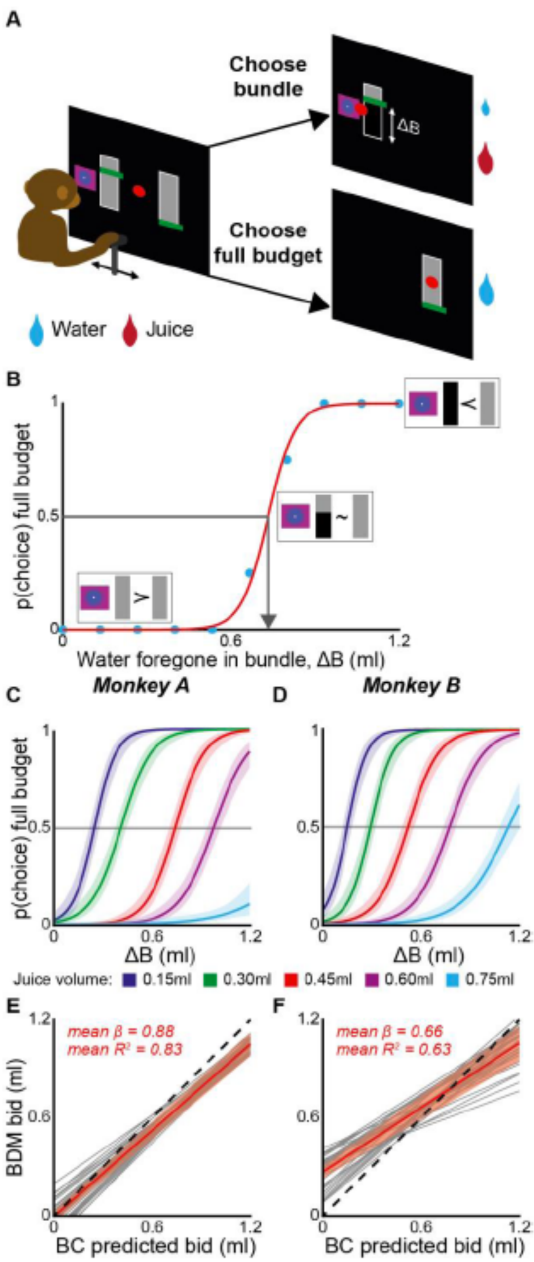

Fig. 3. Mechanism independence: comparison with value estimation in Binary Choice (BC) task.
(A) BC task. Choice between [bundle of specific juice volume (fractal) combined with a specific water volume (grey area above green line) (option 1)] and [full water budget (full grey vertical rectangle) (option 2)]. The animal indicates its choice by moving a horizontal joystick-driven red dot onto the preferred option. At left, the grey rectangle below the green line (bundle, option 1) represents the water foregone (ΔB) from the full budget and is blackened after the animal's choice (see 'Choose bundle' at right). Left and right option positions alternate pseudorandomly.
(B) Psychophysical value estimation of juice value in the currency of water during BC. Decrease of water in option 1 increased the choice probability of option 2. At choice indifference (P (choice) = 0.5, grey line), the water foregone in the bundle (ΔB) indicated the

subjective value of the juice volume in units of ml of water. A logistic regression (red) was fitted to the monkey's choices (blue). More preferred (≻); indifferent (~); less preferred (≺).
(C, D) BC value estimates for each of the five juice volumes used in the BDM. Choices are pooled across all 10 BC sessions (n = 2000 trials) for each animal. Shaded areas are 95% confidence intervals of the fitted logistic function.
(E, F) Regression of monkeys' bids on the best bid as predicted by the BC task. The best bid is equal to the BC task value estimate, or, the maximum bid of 1.2ml, whichever is smaller. The identity line is dashed; the mean fit across all sessions is shown in red and the red shaded area shows the 95% confidence interval; fits for individual sessions are shown in grey.

Choice preference among the two options varied systematically (Fig. 3B). The animals showed little choice of the full water budget (option 2) when the alternative juice-water bundle (option 1) contained substantial water amounts in addition to the juice; apparently the slight loss in water volume was overcompensated in value by the added juice (Fig. 3B left). Choice of the full water budget increased gradually with more water foregone in the juice-water bundle (ΔB against the full water budget). At some specific volume of water foregone, the animal preferred the full water budget as much as the juice-water bundle (Fig. 3B centre; P (choice) = 0.5; choice indifference). At this point, the juice together with the remaining water was valued as much as the full water budget alone; hence the juice compensated fully for the water foregone and was valued as much as that water volume (ΔB). Thus, the subjective value of the juice can be expressed on a common currency basis in ml of water volume foregone at choice indifference (ΔB). In this way, psychophysics allowed us to estimate the subjective value for each specific juice volume being tested.

In both animals, the choice indifference points in the BC task followed the same rank order as the BDM bids for the five juice volumes (Fig. 3C, D; see Fig. S7A-C for individual sessions and Table S3 for BDM and BC values). We performed 5 BC sessions before and 5 after the 30 BDM sessions, and found the BC estimates of value were stable across this period of BDM testing (Fig. S7E, F). We therefore pooled choices across all 10 sessions of the BC task to infer an estimate of value for each juice reward in terms of water volume across sessions. Thus, each value estimate we used in subsequent analyses was inferred from 400 pooled trials of the BC task (10 sessions, with each reward presented 40 times per session). Accordingly, Pearson correlation coefficients between the bids elicited across all 30 BDM sessions and the value estimates from all 10 BC sessions were high (Monkey A: 0.91 ± 0.02; Monkey B: 0.79 ± 0.05). To confirm these results and provide more detail, we performed a least-squares regression of BDM bids on the values estimated by the BC task, such that:

$$Bid = B_0 + B_1 * BC\ PredictedBestBid \qquad \text{(Eq. 3)}$$

The PredictedBestBid inferred from performance in the BC task is equal to the water value of the chosen option in the BC task, except when the BC value is greater than the maximum possible bid of 1.2 ml of water, in which case the best possible bid is equal to 1.2 ml, as was the case for the 0.75ml reward for Monkey A. An optimal bidder's BDM bids should perfectly reflect the subjective value for the commodity ($B_1 = 1$) without any bias in bidding ($B_0 = 0$) (the subjective value may, for example, be modulated by the mental and/or motor effort of placing a bid). BDM bids correlated closely with the BC estimates for both Monkey A (mean $B_1 = 0.88 \pm 0.09$, and mean $R^2 = 0.83 \pm 0.03$) and Monkey B (mean $B_1 = 0.66 \pm 0.15$, mean $R^2 = 0.63 \pm 0.08$) (Fig. 3E, F). Monkey A did not have any significant bidding bias ($B_0 = 0 \pm 0.09$), but monkey B had a significant bias which accounted for overbidding for low juice volumes ($B_0 = 0.27 \pm 0.10$).

In showing good correlations between single BDM bids and conventional binary stochastic choices with both numerical methods, these data suggest that value estimation by BDM is not due to its specific elicitation method. Thus, the BDM provides a valid mechanism for estimating subjective economic value in monkeys.

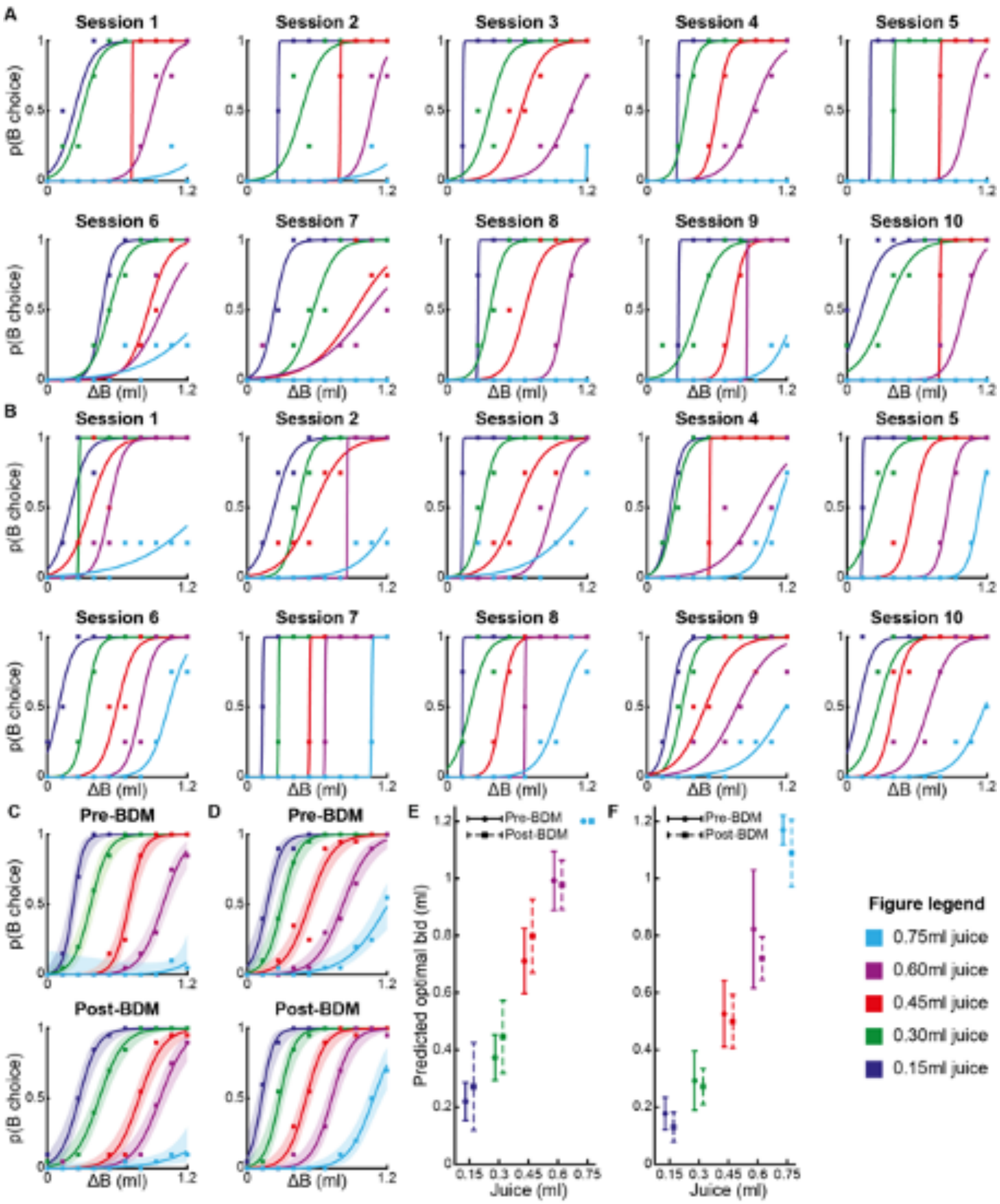

Fig. S7. Choice probabilities in Binary Choice task, and pre- and post-BDM comparison.
(A) Lines of best fit for logistic regression of choice probability of full budget, p(B choice), on water volume foregone in each bundle (ΔB). Monkey A.
(B) as A, but Monkey B.
(C, D) As A and B, respectively, but pooled from 5 session before BDM (Pre-BDM) and 5 sessions after all 30 BDM sessions (Post-BDM).
(E, F) Comparison of mean predicted optimal bids for each juice volume from 5 Binary Choice task sessions before BDM (Pre-BDM; solid lines) and 5 sessions after BDM (Post-BDM; dotted lines), for Monkeys A and B, respectively. Changes in predicted optimal bid for any of the juice volumes was insignificant for either monkey (two-tailed Student t-tests, all $P > 0.05$). Error bars are 95% confidence intervals of the mean.

Optimality in bidding. The incentive compatibility of the BDM rests on the notion that bidders benefit most by stating their accurate subjective value for a given item (Material and Methods: Optimal BDM Strategy). However, unlike human subjects in the BDM, animals cannot be made explicitly aware of the optimal strategy for maximising their utility. Instead, they adjust their bidding behavior according to the experienced outcome. Further, performance in the BDM provides less intuitive assessments due to its second-price nature, and BDM outcomes are risky because they depend on the computer bid drawn from a fully specified probability distribution. By contrast, stimuli in the BC task display the options in a direct and explicit manner, and the animal gets exactly what it has chosen. Therefore, we used the economic values estimated in the BC task to assess optimal bidding for each juice volume. Specifically, the optimal bid is equal to the PredictedBestBid stated above and is derived from the combined value of both the juice and the water budget, as expressed in common currency units of ml of water.

To assess the optimality of BDM bidding, we compared each animal's payoffs to those of two hypothetical bidders: those of an optimal bidder who always bids the BC value for each juice volume according to the best BDM strategy, and those of a random bidder whose bids are drawn from the same uniform distribution for all juice volumes (Material and Methods: Simulated Bidding). These simulated optimal and random bidders faced the same 6,000 juice presentations and computer bids as the animals did across 30 sessions of BDM testing (200 trials each).

For Monkey A, the average per-trial payoff if the bids were optimal across the four juice volumes for which this could be calculated would have been 1.34 ± 0.20ml (payoffs could not be computed for the 0.75ml juice for this animal as the value for this volume was above the possible bidding range). This animal received only 0.02 ± 0.05ml less than the optimal 1.34 ± 0.20ml on a typical trial, whereas the random bidder received 0.11 ± 0.17ml less than the optimal bidder. For Monkey B, the average per-trial payoff across all juice volumes if the bids were optimal would have been 1.36 ± 0.24ml of water, and it received 0.03 ± 0.08ml less than the optimal 1.36 ± 0.24ml, whereas the random bidder received 0.14ml ± 0.20ml less than the optimal bidder. Thus, both animals' bids were insignificantly lower than those of their respective optimal bidder; in fact, their small differences were comparable to the juice delivery system's error due to the variability of droplet size (and therefore may have been even too small to be perceived by the animals; standard deviation of 0.06ml per trial; Material and Methods: Juice-delivery error). By contrast, the differences to the respective random bidders were significant in both animals for all juice volumes (Monkey A: $F_{2,14316} = 716.97$, $P = 0.0$; Monkey B: $F_{2,17993} = 931.61$, $P = 0.0$; two-way ANOVA; Fig. 4A, B).

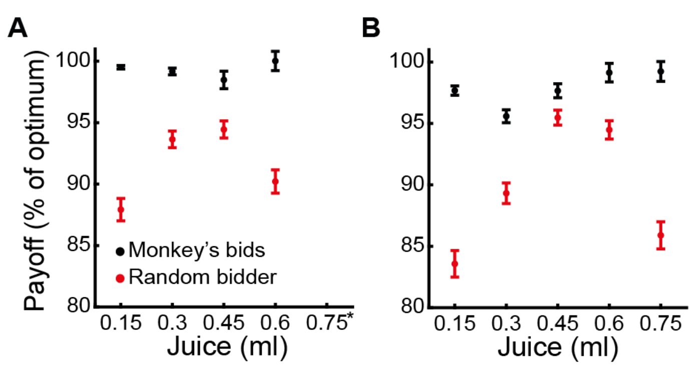

Fig. 4. Optimality of BDM bids. For each juice volume, the monkey's (black) and a simulated random bidder's (red) average per trial payoff is shown as a percentage of the simulated optimal bidder's payoff. Both monkeys (shown in **A** and **B**) lost significantly less than the random bidder drawing bids from a uniform distribution. *Payoffs could not be calculated for the 0.75ml juice volume for Monkey A.

A comparison of the hypothetical 'optimal' and 'random' bidder's performance shows a perhaps surprisingly small difference in outcomes, with the 'random' bidder on average acquiring more than 80% of the reward that an 'optimal' bidder would (Fig. 4A, B). This is a result of the second-price nature of the BDM (Lusk et al. 2007); take for example over-bidding, in the BDM the subject only stands to lose from over-bidding when the computer bids an amount between the subject's value and their bid, such they have to pay an amount greater than their value, however, the subject would still pay less than their value if the computer had bid any amount lower than this. This is not the case in the more familiar 'first-price' auction, in which case the payable amount is equal to the highest bid. Thus, while the BDM is incentive compatible, it imposes low costs on deviations from optimality (rewards/costs drive learning by forming a reward/cost gradient across the range of possible bids).

Nevertheless, these data suggest that the animals did learn to bid in a meaningful manner and that even though they could not be informed of the best bidding strategy, they performed significantly better than a random bidder and close to an optimal bidder in terms of maximising their reward on a given trial. However, this observation of relatively low costs of deviation from optimality in the BDM remains an important limitation of the method as higher costs would likely incentivise more precise bidding (albeit not incentive compatible bidding in the case of first-price auctions), and the lower costs of the method may contribute to the extensive training required to teach the task to new subjects, especially when the optimal strategy cannot be made explicit and the subjects must rely on feedback in the form of variable reward outcomes on each trial.

Discussion

This study shows that monkeys can truthfully report their internal, subjective economic value of rewards in individual trials by placing bids in a BDM auction-like mechanism. The animals reliably and systematically ranked their preferences over five juice volumes. Their BDM bidding correlated with their choices in the BC task, indicating that their value estimation was not due to any particular BDM feature. The animals achieved a level of performance that approximated that of a simulated optimal bidder and well exceeded that of a random bidder. Besides reporting the capacity of monkeys to perform auction-like bidding in resemblance to human behavior, these experiments contribute a novel method of value assessment for behavioral and neurophysiological work on reward processing in monkeys.

The current finding of meaningful BDM performance in monkeys was obtained with substantial experimental constraints. The animals were seated for a few hours in a primate chair, which is a standard situation that capitalizes on the monkeys' ability to adapt to controlled experimental conditions. This experimental situation focuses the behavior onto the task at hand and may have encouraged performance in this rather abstract valuation. Natural wildlife does not prepare monkeys for explicitly stating their values against some odds, even though animals always need to make some form of commitment to satisfy their needs. The fact that the monkeys did so well speaks in favor of their adaptive cognitive abilities. A factor that may have contributed to their performance may have been our use of tangible and ecologically relevant liquids with which the animals were very familiar. It is unclear how the animals would have performed if bidding for more abstract items, such as tokens used in neurophysiological experiments (Seo & Lee 2009). Thus, future work may help to delineate the conditions in which rhesus monkeys are able to successfully perform a BDM task.

It is not enough to interrogate the activity of neurons in the presence of rewards; rather, for understanding reward processing, animals should reveal their preferences by making choices (Platt and Glimcher, 1999; Stauffer et al., 2014). Besides these conventional BC tasks, experimenters may now benefit from eliciting truthful valuation when examining neuronal processes underlying economic choice. It would also be interesting to see the extent to which the existing data from conventional BC tasks depend on their specific eliciting mechanism. For example, neurons encoding action-specific reward values have been identified in the striatum (Samejima et al. 2005), but it is not known whether these reward values were specific to the decision rules and contexts in which they were elicited.

The current BDM bidding mechanism for monkeys has a close temporal relationship to the activity of neurons measured during on-going behavior in single-unit recordings. Unlike current methods that employ multiple trials of stochastic choices, the animals in the BDM reported subjective values on a trial-by-trial basis. The close temporal relationship would facilitate trial-by-trial statistical regressions of neuronal activity on subjective value, rather than relying on multi-trial averages. The suitability of BDM bidding for neuronal recordings in monkeys is further supported by the current finding that action only affects reward valuation to a very limited extent. In particular, different actions, as required by different bidding start positions, did not substantially affect reward valuation. Thus, the ready distinction between reward value and movement is another advantage when using BDM.

The primate BDM makes the link to human studies in several ways. Apparently, the relative closeness in cognitive functions between human and monkey would not only explain their successful BDM bidding but also allow for more direct comparisons with human neuroimaging studies, as BDM is commonly used in experimental work (Plassmann et al. 2007; Chib et al. 2009; Harris et al. 2011; Tang et al. 2014; Tyson-Carr et al. 2018) and consumer economics (Linder et al. 2010). Whereas human neuroimaging provides a larger overview of brain processes, single-neuron electrophysiology provides better cellular resolution for distinction of valuation functions in different neuron types. In this way, the current BDM data provide both an evolutionary and methodological link between the two primate species.

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Table 1. Spearman rank correlation between bids and juice volume.

		Monkey A		Monkey B	
Condition	Session	Rho	p	Rho	p
Bottom Start BDM	1	0.87	1.44×10^{-63}	0.81	3.26×10^{-47}
	2	0.91	1.27×10^{-75}	0.84	6.30×10^{-55}
	3	0.90	6.00×10^{-74}	0.84	1.88×10^{-55}
	4	0.91	2.77×10^{-77}	0.77	8.62×10^{-41}
	5	0.92	3.55×10^{-80}	0.73	6.65×10^{-34}
	6	0.90	2.31×10^{-71}	0.74	1.57×10^{-36}
	7	0.89	1.15×10^{-69}	0.82	6.52×10^{-51}
	8	0.91	1.24×10^{-76}	0.80	3.90×10^{-45}
	9	0.93	5.42×10^{-91}	0.72	5.84×10^{-33}
	10	0.91	8.48×10^{-76}	0.77	4.62×10^{-41}
Top Start BDM	11	0.91	4.98×10^{-79}	0.72	6.99×10^{-33}
	12	0.93	2.79×10^{-88}	0.76	2.45×10^{-39}
	13	0.92	2.24×10^{-82}	0.77	3.69×10^{-41}
	14	0.91	1.54×10^{-76}	0.81	3.31×10^{-47}
	15	0.89	4.89×10^{-69}	0.86	1.98×10^{-58}
	16	0.92	2.95×10^{-83}	0.80	1.60×10^{-45}
	17	0.93	1.17×10^{-89}	0.83	8.79×10^{-52}
	18	0.92	7.82×10^{-83}	0.87	3.79×10^{-62}
	19	0.92	4.56×10^{-85}	0.83	1.39×10^{-52}
	20	0.93	2.29×10^{-85}	0.87	4.72×10^{-63}
Random Start BDM	21	0.89	6.81×10^{-68}	0.85	1.32×10^{-57}
	22	0.89	2.68×10^{-71}	0.75	4.49×10^{-38}
	23	0.89	6.28×10^{-70}	0.74	1.87×10^{-36}
	24	0.89	3.26×10^{-68}	0.81	1.59×10^{-47}
	25	0.94	2.55×10^{-94}	0.67	1.25×10^{-27}
	26	0.90	3.18×10^{-72}	0.81	3.30×10^{-47}
	27	0.93	5.74×10^{-88}	0.80	1.02×10^{-45}
	28	0.91	1.25×10^{-76}	0.85	6.03×10^{-57}
	29	0.93	3.82×10^{-87}	0.86	5.06×10^{-59}
	30	0.92	1.73×10^{-83}	0.88	1.12×10^{-65}

Juice volume was measured in ml. Each of the 30 sessions in each animal is comprised of 200 trials.

Supplementary Material

Table S1. Effect of juice volume on BDM bids in individual sessions.

Monkey-Session	Factor	d.f.	SS	MS	F	p	ω^2
A-1	JV	4	17.80	4.45	176.42	1.25×10^{-63}	0.78
	Error	195	4.92	0.03			
	Total	199	22.71				
A-2	JV	4	18.09	4.52	251.01	1.02×10^{-75}	0.83
	Error	195	3.51	0.02			
	Total	199	21.61				
A-3	JV	4	17.26	4.31	226.28	4.44×10^{-72}	0.82
	Error	195	3.72	0.02			
	Total	199	20.98				
A-4	JV	4	16.93	4.23	247.28	3.46×10^{-75}	0.83
	Error	195	3.34	0.02			
	Total	199	20.27				
A-5	JV	4	13.64	3.41	255.32	2.55×10^{-76}	0.84
	Error	195	2.60	0.01			
	Total	199	16.24				
A-6	JV	4	15.62	3.90	210.78	1.26×10^{-69}	0.81
	Error	195	3.61	0.02			
	Total	199	19.23				
A-7	JV	4	12.11	3.03	198.25	1.54×10^{-67}	0.80
	Error	195	2.98	0.02			
	Total	199	15.09				
A-8	JV	4	16.91	4.23	247.64	3.07×10^{-75}	0.83
	Error	195	3.33	0.02			
	Total	199	20.24				
A-9	JV	4	19.16	4.79	364.38	2.81×10^{-89}	0.88
	Error	195	2.56	0.01			
	Total	199	21.72				
A-10	JV	4	18.73	4.68	238.52	6.43×10^{-74}	0.83
	Error	195	3.83	0.02			
	Total	199	22.56				
A-11	JV	4	15.13	3.78	250.72	1.12×10^{-75}	0.83
	Error	195	2.94	0.02			
	Total	199	18.07				
A-12	JV	4	19.17	4.79	360.57	6.93×10^{-89}	0.88
	Error	195	2.59	0.01			
	Total	199	21.76				
A-13	JV	4	18.07	4.52	282.65	5.86×10^{-80}	0.85
	Error	195	3.12	0.02			
	Total	199	21.19				

A-14	JV	4	17.16	4.29	245.79	5.64×10^{-75}	0.83
	Error	195	3.40	0.02			
	Total	199	20.56				
A-15	JV	4	14.52	3.63	192.60	1.47×10^{-66}	0.79
	Error	195	3.67	0.02			
	Total	199	18.19				
A-16	JV	4	26.13	6.53	309.90	2.68×10^{-83}	0.86
	Error	195	4.11	0.02			
	Total	199	30.24				
A-17	JV	4	27.18	6.79	370.95	6.05×10^{-90}	0.88
	Error	195	3.57	0.02			
	Total	199	30.75				
A-18	JV	4	21.22	5.30	303.17	1.69×10^{-82}	0.86
	Error	195	3.41	0.02			
	Total	199	24.63				
A-19	JV	4	20.09	5.02	320.28	1.67×10^{-84}	0.86
	Error	195	3.06	0.02			
	Total	199	23.14				
A-20	JV	4	25.51	6.38	344.15	3.73×10^{-87}	0.87
	Error	195	3.61	0.02			
	Total	199	29.12				
A-21	JV	4	26.59	6.65	196.55	3.03×10^{-67}	0.80
	Error	195	6.60	0.03			
	Total	199	33.19				
A-22	JV	4	23.30	5.82	203.59	1.93×10^{-68}	0.80
	Error	195	5.58	0.03			
	Total	199	28.88				
A-23	JV	4	24.27	6.07	200.55	6.26×10^{-68}	0.80
	Error	195	5.90	0.03			
	Total	199	30.17				
A-24	JV	4	19.85	4.96	186.57	1.72×10^{-65}	0.79
	Error	195	5.19	0.03			
	Total	199	25.03				
A-25	JV	4	23.45	5.86	392.36	4.75×10^{-92}	0.89
	Error	195	2.91	0.01			
	Total	199	26.36				
A-26	JV	4	19.97	4.99	218.65	6.86×10^{-71}	0.81
	Error	195	4.45	0.02			
	Total	199	24.42				
A-27	JV	4	17.98	4.49	324.26	5.86×10^{-85}	0.87
	Error	195	2.70	0.01			
	Total	199	20.68				
A-28	JV	4	15.97	3.99	235.20	1.99×10^{-73}	0.82
	Error	195	3.31	0.02			
	Total	199	19.28				

A-29	JV	4	18.96	4.74	320.52	1.56×10^{-84}	0.86
	Error	195	2.88	0.01			
	Total	199	21.85				
A-30	JV	4	21.71	5.43	311.62	1.68×10^{-83}	0.86
	Error	195	3.40	0.02			
	Total	199	25.10				
B-1	JV	4	10.19	2.55	91.59	1.09×10^{-43}	0.64
	Error	195	5.42	0.03			
	Total	199	15.61				
B-2	JV	4	9.86	2.46	123.97	1.94×10^{-52}	0.71
	Error	195	3.88	0.02			
	Total	199	13.74				
B-3	JV	4	8.56	2.14	121.78	6.69×10^{-52}	0.71
	Error	195	3.43	0.02			
	Total	199	11.99				
B-4	JV	4	9.21	2.30	71.98	2.35×10^{-37}	0.59
	Error	195	6.24	0.03			
	Total	199	15.45				
B-5	JV	4	9.87	2.47	54.84	6.40×10^{-31}	0.52
	Error	195	8.77	0.05			
	Total	199	18.64				
B-6	JV	4	11.77	2.94	63.48	2.76×10^{-34}	0.56
	Error	195	9.04	0.05			
	Total	199	20.80				
B-7	JV	4	11.53	2.88	104.87	1.70×10^{-47}	0.68
	Error	195	5.36	0.03			
	Total	199	16.89				
B-8	JV	4	9.90	2.47	85.74	6.79×10^{-42}	0.63
	Error	195	5.63	0.03			
	Total	199	15.53				
B-9	JV	4	10.69	2.67	53.70	1.86×10^{-30}	0.51
	Error	195	9.71	0.05			
	Total	199	20.40				
B-10	JV	4	10.81	2.70	73.97	4.84×10^{-38}	0.59
	Error	195	7.13	0.04			
	Total	199	17.94				
B-11	JV	4	3.56	0.89	52.46	6.00×10^{-30}	0.51
	Error	195	3.31	0.02			
	Total	199	6.87				
B-12	JV	4	5.90	1.47	69.41	1.89×10^{-36}	0.58
	Error	195	4.14	0.02			
	Total	199	10.04				
B-13	JV	4	5.29	1.32	74.08	4.43×10^{-38}	0.59
	Error	195	3.48	0.02			
	Total	199	8.77				

B-14	JV	4	5.31	1.33	95.93	5.69×10^{-45}	0.66
	Error	195	2.70	0.01			
	Total	199	8.01				
B-15	JV	4	5.26	1.31	133.42	1.10×10^{-54}	0.73
	Error	195	1.92	0.01			
	Total	199	7.18				
B-16	JV	4	5.50	1.37	87.12	2.51×10^{-42}	0.63
	Error	195	3.08	0.02			
	Total	199	8.57				
B-17	JV	4	7.81	1.95	107.05	4.30×10^{-48}	0.68
	Error	195	3.55	0.02			
	Total	199	11.36				
B-18	JV	4	8.30	2.07	156.08	1.24×10^{-59}	0.76
	Error	195	2.59	0.01			
	Total	199	10.89				
B-19	JV	4	8.63	2.16	111.98	2.09×10^{-48}	0.69
	Error	195	3.76	0.02			
	Total	199	12.38				
B-20	JV	4	8.82	2.21	165.31	1.71×10^{-61}	0.77
	Error	195	2.60	0.01			
	Total	199	11.42				
B-21	JV	4	16.51	4.13	129.99	6.97×10^{-54}	0.72
	Error	195	6.19	0.03			
	Total	199	22.70				
B-22	JV	4	20.33	5.08	64.62	1.04×10^{-34}	0.56
	Error	195	15.33	0.08			
	Total	199	35.66				
B-23	JV	4	17.55	4.39	62.63	5.77×10^{-34}	0.55
	Error	195	13.66	0.07			
	Total	199	31.20				
B-24	JV	4	21.14	5.28	96.96	2.85×10^{-45}	0.66
	Error	195	10.63	0.05			
	Total	199	31.76				
B-25	JV	4	10.99	2.75	40.17	1.59×10^{-24}	0.44
	Error	195	13.33	0.07			
	Total	199	24.32				
B-26	JV	4	20.14	5.04	92.11	7.64×10^{-44}	0.65
	Error	195	10.66	0.05			
	Total	199	30.80				
B-27	JV	4	17.58	4.39	87.94	1.41×10^{-42}	0.63
	Error	195	9.74	0.05			
	Total	199	27.32				
B-28	JV	4	22.38	5.60	130.02	6.86×10^{-54}	0.72
	Error	195	8.39	0.04			
	Total	199	30.78				

B-29	JV	4	17.60	4.40	139.44	4.68×10^{-56}	0.73
	Error	195	6.15	0.03			
	Total	199	23.76				
B-30	JV	4	18.60	4.65	166.76	8.89×10^{-62}	0.77
	Error	195	5.44	0.03			
	Total	199	24.04				

Statistical test: one-way ANOVA. Abbreviations: JV: juice volume, d.f.: degree of freedom, SS: sum of squares, MS: mean square, F: F-statistic, p: p-value, ω^2: omega-squared effect size.

Table S2. Effects of starting bid position and juice volume on BDM bids.

	Factor	SS	d.f.	MS	F	p	ω^2
Monkey A	Start	0.3	2	0.15	7.18	8×10^{-4}	3.67×10^{-4}
	JV	576.38	4	144.09	6889.46	0	0.82
	Start*JV	2.268	8	0.28	13.55	1.24×10^{-19}	3×10^{-3}
	Error	125.177	5985	0.021			
	Total	703.84	5999				
Monkey B	Start	10.41	2	5.21	148.94	7.49×10^{-64}	0.018
	JV	329.01	4	82.25	2353.17	0	0.58
	Start*JV	15.62	8	1.95	55.86	3.94×10^{-88}	0.027
	Error	209.2	5985	0.035			
	Total	566.41	5999				

Starting bid position was at bottom, top or random on budget bar. For Monkey A, overall, bids were significantly lower in the top-start BDM than in either the bottom-start ($P = 6.35 \times 10^{-4}$; unbalanced two-way ANOVA). or random-start versions of the task ($P = 0.034$); for Monkey B, bids were significantly greater in the bottom-start BDM than in either the top-start ($P = 2.1 \times 10^{-53}$) or random-start versions of the task ($P = 1.95 \times 10^{-44}$). However, a comparison of effect sizes (ω^2) reveals that for both monkeys the size of any effect due to starting position, or the interaction of starting position and juice volume, was negligible when compared to that of juice volume alone. Abbreviations: Start: starting bid position, JV: juice bolume, d.f.: degree of freedom, SS: sum of squares, MS: mean square, F: F-statistic, p: p-value, ω^2: omega-squared effect size.

Table S3. BDM bids in common currency of ml of water assessed in the binary choice task.

		B-BDM	T-BDM	R-BDM	All BDM	All BC
Monkey A	0.15ml	0.26 ± 0.12 (433)	0.18 ± 0.15 (413)	0.19 ± 0.16 (394)	0.21 ± 0.15 (1240)	0.25 ± 0.11 (400)
	0.30ml	0.37 ± 0.14 (400)	0.36 ± 0.18 (376)	0.35 ± 0.20 (392)	0.36 ± 0.17 (1168)	0.41 ± 0.16 (400)
	0.45ml	0.64 ± 0.16 (373)	0.63 ± 0.14 (403)	0.64 ± 0.18 (412)	0.64 ± 0.16 (1188)	0.74 ± 0.15 (400)
	0.60ml	0.86 ± 0.16 (405)	0.87 ± 0.12 (378)	0.89 ± 0.13 (395)	0.88 ± 0.14 (1178)	0.98 ± 0.18 (400)
	0.75ml	1.02 ± 0.12 (389)	1.03 ± 0.09 (430)	1.07 ± 0.09 (407)	1.04 ± 0.10 (1226)	1.64 ± 0.34 (400)
Monkey B	0.15ml	0.40 ± 0.12 (398)	0.35 ± 0.14 (406)	0.21 ± 0.13 (422)	0.32 ± 0.16 (1226)	0.15 ± 0.10 (400)
	0.30ml	0.53 ± 0.18 (407)	0.49 ± 0.14 (418)	0.39 ± 0.24 (388)	0.47 ± 0.20 (1213)	0.29 ± 0.12 (400)
	0.45ml	0.69 ± 0.22 (381)	0.62 ± 0.14 (401)	0.61 ± 0.27 (396)	0.64 ± 0.22 (1178)	0.52 ± 0.16 (400)
	0.60ml	0.86 ± 0.21 (417)	0.73 ± 0.15 (379)	0.84 ± 0.27 (390)	0.81 ± 0.22 (1186)	0.77 ± 0.18 (400)
	0.75ml	1.04 ± 0.16 (397)	0.86 ± 0.12 (396)	1.04 ± 0.20 (404)	0.98 ± 0.18 (1197)	1.14 ± 0.24 (400)

Each table data cell shows ml of water equivalent (mean ± standard deviation) from 200 trials, with number of trails in brackets underneath. B-BDM, T-BDM and R-BDM refer to bid cursor start at bottom, top or random position on the budget bar, respectively.