Supporting Information

Lak et al. 10.1073/pnas.1321596111

SI Methods

Subjects, Surgery, Setup, and Behavioral Training. The Home Office of the United Kingdom approved all experimental procedures. Two male rhesus macaque monkeys (*Macaca mulatta*) weighing 13.4 and 13.1 kg, respectively, were used in the experiment. Neither animal had been used in any prior study. Animals were implanted with titanium head-restraint devices (DAHP; Gray Matter Research and custom-made for monkeys A and B, respectively) and stainless steel recording chambers (6-IAC-X0F; Crist Instruments and custom-made) under general anesthesia. During experiments, animals sat in a chair (Crist Instruments) positioned 30 cm from a computer monitor. Their eye position was monitored using infrared eye tracking (ETL200; ISCAN). Licking was monitored with an infrared optosensor positioned before the juice spout (V6AP; STM Sensors). Eye and lick signals were sampled at 200 Hz. Custom-made software (Matlab; MathWorks) running on a Microsoft Windows XP computer controlled the behavior. Liquid and food delivery were controlled via solenoid valve (SCB262C068; ASCO) and peristaltic pump (Crist Instruments), respectively, both controlled by a Windows XP computer.

The animals were habituated to sitting in the chair and fixing their gaze on the monitor to earn juice rewards. Before the experiment we measured the monkeys' relative preferences in binary choices among and between juice rewards (black currant juice, orange juice, prune juice, strawberry juice, and lemon juice) and mashed food rewards (banana, chocolate + hazelnut (Nutella), or banana + chocolate + hazelnut). The rewards used in the experiment were chosen to maximize the subjective value difference between them. For monkey A juice 1 was black currant juice and juice 2 was strawberry juice. For monkey B juice 1 was black currant juice, juice 2 was orange juice, and the food reward was mashed mixture of banana + chocolate + hazelnut.

The animals were trained to associate visual cues with the respective rewards (Figs. 1*B* and 4*A*). An additional "currency cue" used in the parameter estimation by sequential testing (PEST) procedure explicitly predicted the amount of black currant juice by the height of a bar within a rectangle (Fig. 1*G* and Fig. S2).

Behavioral Testing. A binary choice task served to assess the animals' preferences for the different rewards (Figs. 1*A* and 4*A* and Fig. S1*A*). A central fixation spot indicated onset of each trial. Animals were required to direct their gaze toward the fixation spot within 1 s of spot appearance and hold it there for 0.5 s. Subsequently, two cues (randomly drawn) appeared to the left and right on the monitor. The animal had 1 s to indicate its choice by shifting its gaze to the center of the chosen cue and holding it there for another 0.5 s. Then the unchosen cue disappeared and the chosen cue remained on the screen for additional 1 s. The chosen reward was delivered at offset of the chosen cue. Trials were interleaved with intertrial intervals of random durations (2.5 ± 1.5 s exponentially distributed). Unsuccessful fixation during any task epoch resulted in a 6-s timeout. For the juice-only experiment, we collected 1,440 and 1,510 binary choice trials from monkeys A and B, respectively, over 4 d of testing. For the juice–food experiment, we collected 580 trials over 7 d of testing.

PEST was used to measure the amount of black currant juice that was subjectively equivalent to the subjective value associated with each reward. The rules governing the PEST procedure were adapted from Luce (1). Each PEST sequence consisted of several consecutive trials during which one of the cues was presented as a choice option against the currency cue. The currency cue consisted of a horizontal bar on a vertical axis (Fig. 1*G* and Fig. S2*A*). The height of the bar was a safe (riskless) and explicit indicator of the volume of the black currant juice. On the initial trial of a PEST sequence, the height of the bar in the currency cue (and thus the volume of black currant juice predicted by the cue) was chosen at random. Based on the animal's choice between the two cues, the value of the currency cue was adjusted on the following trial (Fig. S2*B*). If the animal chose the alternate cue on trial t, then the volume offered by the currency cue was increased by ε on trial $t + 1$. However, if the animal chose the alternate cue on trial t, the volume offered by the currency cue was reduced by ε on trial $t + 1$. Initially, ε was large. After the third trial of a PEST sequence, ε was adjusted according to the doubling rule and the halving rule. Specifically, every time two consecutive choices were the same, the size of ε was doubled, and every time the animal switched from one option to the other, the size of ε was halved. Thus, the procedure converged by locating subsequent currency offers on either side of the true indifference value and reducing ε until the interval containing the indifference value was small (Fig. S2*C*). The size of this interval is a parameter set by the experimenter, called the exit rule. For our study, the exit rule was 20 μL. When ε fell below the exit rule, the PEST procedure terminated, and the indifference value was calculated by taking the mean of the final two currency cues. A typical PEST session lasted 15–20 trials. We repeated the PEST procedure several times for each of reward over several days of testing (for the juice-only experiment, 25 and 40 times per cue for monkeys A and B, respectively; for the juice–food experiment, 10 times per cue for monkey B). This allowed us to compare the distribution of indifference values acquired for each cue (Fig. S2*D*) and measure the area under the receiver operating characteristic curve (auROC, Fig. 3).

Identification and Recording of Dopamine Neurons. Custom-made, movable, glass-insulated, platinum-plated tungsten microelectrodes were positioned inside a stainless steel guide cannula and advanced by an oil-driven micromanipulator (Narishige). Action potentials from single neurons were amplified, filtered (band-pass 100 Hz to 3 kHz), and converted into digital pulses when passing an adjustable time–amplitude threshold (Bak Electronics). We stored both analog and digitized data on a computer using custom-made data collection software (Matlab).

We recorded the extracellular activity of single dopamine neurons within the substantia nigra and in the ventral tegmental area (A8, A9, and A10). We localized the positions relative to the recording chamber using X-ray imaging and functional properties of surrounding cell groups (Fig. S3). Postmortem histology was postponed owing to ongoing experiments with these animals. Dopamine neurons were functionally localized with respect to (*i*) the trigeminal somatosensory thalamus explored in awake animals and under general anesthesia (very small perioral and intraoral receptive fields, high proportion of tonic responses, 2- to 3-mm dorsoventral extent), (*ii*) tonic, position coding ocular motor neurons, and (*iii*) phasic direction coding ocular premotor neurons in awake animals (Fig. S3). We identified discharges from putative dopamine neurons using the following classical criteria: (*i*) polyphasic initially positive or negative waveforms followed by a prolonged positive component, (*ii*), relatively long durations (>2.5 ms measured at 100-Hz high-pass filter), and (*iii*) irregular firing at low baseline frequencies (fewer than eight

spikes per second). Most neurons that met these criteria showed the typical phasic activation after unexpected reward (Fig. S4), which was used as a fourth criterion for inclusion. We rejected all neuronal recordings with <10 trials per experimental conditions. In total, we recorded 100 neurons (80 in the juice-only experiment and 20 in the juice–food experiment) and 96 (77 in the juice-only experiment and 19 in the juice–food experiment) met the criteria listed above and were used in our data analysis. During our initial recording sessions in the juice-only experiment ($n = 11$) the task did not include a fixation spot. The theoretical prediction error at the time of the cue depends on the presence or absence of a fixation spot, but the theoretical prediction error at the time of the reward does not. The fixation spot predicted the average value of all cues. Therefore, when the task contains the fixation spot, the prediction errors and the dopamine prediction error responses are both positive and negative (Fig. 2), as

$$\mathrm{PE}_{\mathrm{cue}} = \mathrm{Cue}_{\mathrm{value}} - \mathrm{Fixation\ spot}_{\mathrm{value}}.$$

Without a fixation spot, the animals could not predict when the cue would appear. Therefore, their prediction of future value was close to zero before cue onset, and the prediction error was always positive, as

$$\mathrm{PE}_{\mathrm{cue}} = \mathrm{Cue}_{\mathrm{value}} - 0.$$

Because of the difference between these two conditions, we removed these neurons recorded without a fixation spot ($n = 11$) from the analysis of the cue responses.

In contrast, prediction errors caused by rewards were identical in both cases. The prediction error at the time of the reward depended only on the preceding cue. The dopamine neurons reflected this, and for this reason we included in our reward response analysis all collected data (i.e., with and without a fixation spot).

During neuronal recordings, each trial began when a fixation spot appeared at the center of the screen (Fig. 2*A*). The animal directed its gaze to it and held it there for 0.5 s. The fixation spot disappeared, and then one of the cues occurred in pseudorandom order. The cue remained on the screen for 1.5 s and reward was delivered at cue offset. Unsuccessful central fixation resulted in a 6-s time-out. There was no behavioral requirement after the central fixation time had ended.

Analysis of Behavioral Data. By "choice probability" we refer to its definition used in the economy literature (2), rather than the concept used in sensory neurophysiology to relate neuronal response and behavioral judgment (3).

If an individual prefers cue *a* over cue *b* and cue *b* over cue *c*, then the weak axiom of stochastic transitivity requires the probability of choosing cue *a* over cue *c* to be ≥50% (4). The strong axiom of stochastic transitivity requires the probability of choosing cue *a* over cue *c* to be greater than or equal to the maximum observed choice probability between the two other choice conditions (4).

A binomial test on the choice probabilities from each cue pairing served to detect significant preferences (Figs. 1*E* and 4*A*). Two cues were considered to have different subjective values if the monkey chose one cue over another in significantly more than 50% of trials. We used Bonferroni correction to adjust significance for multiple comparisons.

We used the response strength theory to predict the choice probabilities for pairs of cues from the observed choice probabilities of other cues (2). Let $P(a,b)$ denote the probability that *a* is chosen over *b* when they are presented together to an agent. Likewise, let $P(b,c)$ denote the probability that *b* is chosen over *c*. We predicted $P(a,c)$ from the observation of $P(a,b)$ and $P(b,c)$, when $0 < P < 1$, using the following equation:

$$P(a,c) = \frac{P(a,b) \times P(b,c)}{P(a,b) \times P(b,c) + ((1 - P(a,b)) \times (1 - P(b,c)))}.$$

Pearson correlation related the observed and predicted choice probabilities (Fig. 1*F*).

To measure the effect of juice type and risk on behavioral measures of economic value, we calculated the auROC (Fig. 3).

Analysis of Neuronal Data. We constructed peristimulus time histograms (PSTHs) by aligning the neuronal impulses to task events and then averaging across multiple trials. The impulse rates were calculated in nonoverlapping time bins of 10 ms. PSTHs were smoothed using a moving average of 70 ms for display purposes.

The analysis of neuronal data used defined time windows that included the major positive and negative response components following fixation spot onset (100–400 ms), cue onset (80–340 ms and 150–500 ms in animals A and B, respectively), and juice delivery (200–550 ms). Analysis of responses to unpredicted juice outside of the task used a time window of 100-400 ms after juice onset. The longer durations of juice delivery within compared with outside the task required analysis windows of different durations. Control time windows had identical durations and preceded immediately each respective task event. For normalization, in each neuron we divided the neuronal activity in each time window by the ensemble average activity of the neuron in the control window. Thus, a neuronal response that was not modulated by a task event had a normalized activity equal to 1 for that task event.

To assess basic reward sensitivity of neurons, a Wilcoxon signed-rank test compared responses to unpredicted reward with control activity preceding the reward. Comparisons between different experimental situations used a Wilcoxon rank-sum test on the normalized neuronal data in the respective time windows. We used normalized responses from each neuron and from the population and regressed them (single linear regression) on the subjective value prediction errors of the cues and rewards assessed by the PEST procedure (Figs. 2 *F* and *G*, 4*C*, and 5*C*). We used one-way ANOVAs to test the effect of different trial types on the dopamine responses to the fixation spot (Fig. S5) and single linear regression to explore the effect of accumulated reward on responses to fixation spot (Fig. S7*E*). We used separate multiple linear regressions to explore the effects of the past six cues and the past six rewards on the neuronal responses to cues and fixation spot (Fig. S7 *A–D*).

To measure the individual effects of the two reward attributes (juice type and risk) on neuronal responses, we calculated the auROC in neurons whose responses showed a significant regression on subjective value (Fig. 3). We used an identical analysis to measure and compare the neuronal responses at the time of juice delivery (Fig. S9*A*). A bootstrap test (with 200,000 resamples) served to compute the confidence intervals and statistical significances ($P < 0.05$) of the single-neuron auROC as well as population averages of single-neuron auROC (Fig. 3*C* and Fig. S9*A*).

SI Results

Analysis of Saccadic Response Time in the Binary Choice Task and in the Nonchoice Recording Task. We sought to determine whether animals' saccadic response time (i.e., interval between cue onset and saccade arrival to the chosen cue) in the binary choice task could reflect the subjective ranking of cues. To perform this analysis we only included trials in which there was a clear difference between the average values of the presented cues (i.e., overall choice probability >70%) and the monkey correctly chose the cue with the higher average value. Response times measured in these trials showed weak but significant inverse correlation with the subjective value of the chosen cue (Fig. S1*D*, $P < 0.05$, linear regression).

We analyzed saccadic response times (i.e., interval between fixation spot onset and saccade arrival) in the nonchoice recording task. Response times were 480 ± 12 ms and 470 ± 22 ms in monkeys A and B, respectively (mean ± SEM across sessions). Saccadic response times were not significantly different following trials with different cues ($P > 0.5$ and $P > 0.3$ in monkeys A and B, respectively, one-way ANOVA) or different outcomes ($P > 0.5$ and $P > 0.2$ in monkeys A and B, respectively, one-way ANOVA).

Effect of Different Behavioral Variables on the Neuronal Response to Reward-Predicting Cues and Fixation Spot. The single linear regression analysis (Fig. 2 *F* and *G*) showed that subjective value of cues could significantly account for the variance in the dopamine responses with $R^2 = 0.27$ and 0.28 in monkeys A and B, respectively. This analysis, when performed on averaged responses of single neurons (rather than trial-by-trial responses) and on averaged population responses (rather than neuron-by-neuron responses) resulted in a higher coefficient of determination. Done this way, the R^2 for the highlighted neuron in Fig. 2 is 0.92 and average R^2 across significant and nonsignificant single neurons was 0.43 and 0.41 in monkeys A and B, respectively. The population R^2 was 0.78 and 0.84 in monkeys A and B, respectively.

To explore whether variables other than the subjective value of the reward-predicting cue could explain the trial-by-trial dopamine responses, we examined the effect of trial history and accumulated trials over a session. We first performed a multiple linear regression of the cue responses from individual neurons on the current subjective value plus the previous six cues' subjective value and a second multiple linear regression of the cue response on the subjective value of the six previous rewards. Consistent with our single linear regression analysis (Fig. 2), multiple linear regressions confirmed that the subjective value of the current cue had a highly significant effect on the neuronal responses (multiple linear regression, $P < 0.00001$), whereas other tested variables had smaller effects (Fig. S7 *A* and *B*). Only the subjective value of the cue presented in the previous trial reached significance, and only in monkey B (multiple linear regression, $P = 0.005$, Fig. S7*A*, *Right*). We performed the same analyses on the neuronal response to the fixation spot and found no effect (multiple linear regression, $P > 0.1$, Fig. S7 *C* and *D*). Next, we performed single linear regression of the neuronal responses to fixation spot on the accumulated number of trials during a recording session. This variable had a weak effect on the dopamine responses to fixation spot that reached significance in monkey B (Fig. S7*E*, $P = 0.001$). Consistent with the behavioral performance, the negative regression coefficient indicated that neuronal responses to the fixation spot were stronger during the early trials of the session compared with later trials. The accumulated number of trials had no significant effect on the responses to cues ($P > 0.1$).

1. Luce RD (2000) *Utility of Gains and Losses: Measurement-Theoretic and Experimental Approaches* (Lawrence Erlbaum Assoc, Mahwah, NJ).
2. Luce RD (1959) *Individual Choice Behavior: A Theoretical Analysis* (Wiley, New York).
3. Britten KH, Newsome WT, Shadlen MN, Celebrini S, Movshon JA (1996) A relationship between behavioral choice and the visual responses of neurons in macaque MT. *Vis Neurosci* 13(1):87–100.
4. Luce RD, Suppes P (1965) Preference, utility, and subjective probability. *Handbook of Mathematical Psychology*, eds Luce RD, Bush EE, Galanter E (Wiley, New York), Vol 3, pp 252–410.

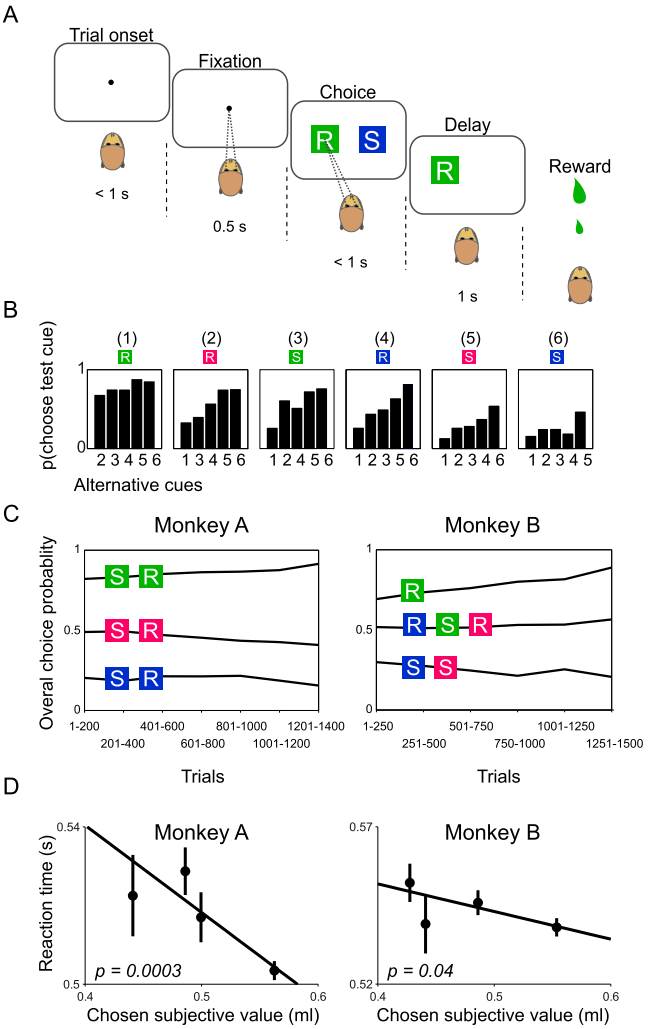

Fig. S1. Binary choice task. (*A*) Task sequence. From left to right: each trial started with presentation of a fixation spot on the center of the screen. The animal directed its gaze to the fixation spot within 1 s of its appearance and held it there for 0.5 s. Subsequently, two cues (randomly drawn) appeared on the screen. The animal indicated its choice within 1 s. After fixating on the chosen cue for an additional 0.5 s, the unchosen option cue disappeared. The chosen option cue remained on the screen for an additional 1 s, and reward was delivered at cue offset. Trials were separated by randomly varying intertrial intervals of 2.5 ± 1.5 s. Unsuccessful fixation during any task epoch resulted in a 6-s time-out. (*B*) Choice probabilities in monkey B. Each plot indicates the probability of choosing the test cue (shown on the top of the plot) over alternative cues (other five cues used in the experiment). For display reasons, the cues are ordered based on the overall probability that they have been chosen. The animal showed clear bias in selecting among cues. (*C*) Choice probabilities at the given value rank were stable over multiple days of testing. The choice probabilities of cues that animals were indifferent to were averaged between them. The probabilities were estimated across 200 and 250 consecutive trials with monkeys A and B, respectively. (*D*) Saccadic response time reflected the subjective value of the chosen cue in trials in which animals correctly chose the option with higher average subjective value.

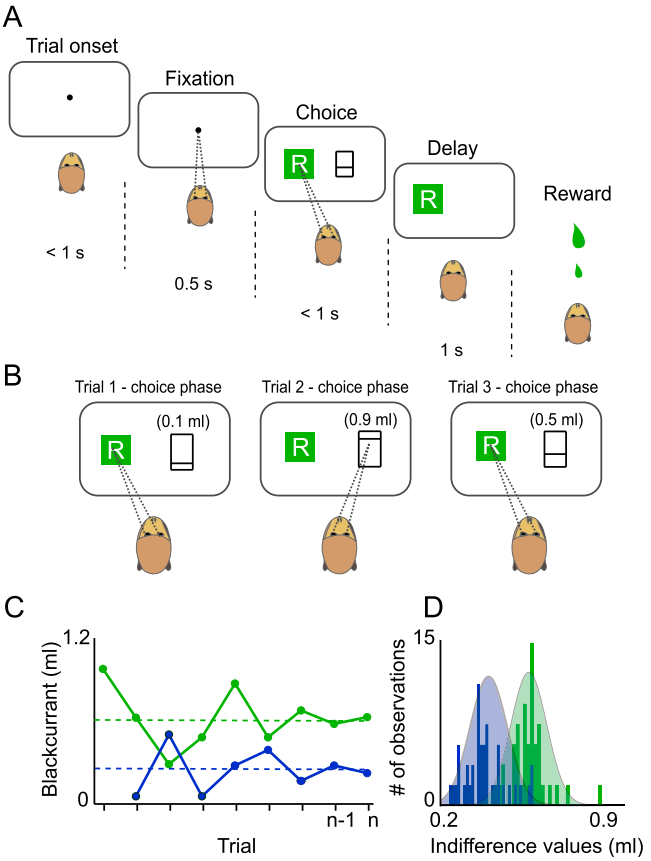

Fig. S2. Behavioral assessment using the method of PEST. (*A*) A PEST sequence. From right to left: the animal directed its gaze to the central fixation spot within 1 s of its appearance and held it there for 0.5 s. Then two option cues were presented simultaneously: One option was drawn from the cues and the other option was the currency cue. The animal indicated its choice within 1 s. After fixating the chosen cue for an additional 0.5 s, the unchosen option cue disappeared. The chosen cue remained on the screen for an additional 1 s, and reward was delivered at cue offset. Trials were separated by randomly varying intertrial intervals of 2.5 ± 1.5 s. Unsuccessful fixation during any task epoch resulted in a 6-s time-out. (*B*) The choice phase in three consecutive trials of a PEST sequence. The currency cue was adjusted based on the animal's previous choice. (*C*) Two PEST sequences. The *y* axis indicates the amount of black currant juice offered by the currency cue on each trial for a highly valued and a less valued cue (green and blue, respectively). The sequence terminated when the trial-to-trial adjustment in the currency cue fell below a predefined exit rule (20 μL). (*D*) Distributions of indifference values for highly valued and less valued cues (green and blue, respectively) in monkey B. For display purposes, the superimposed transparent areas show Gaussian fits on the value distributions.

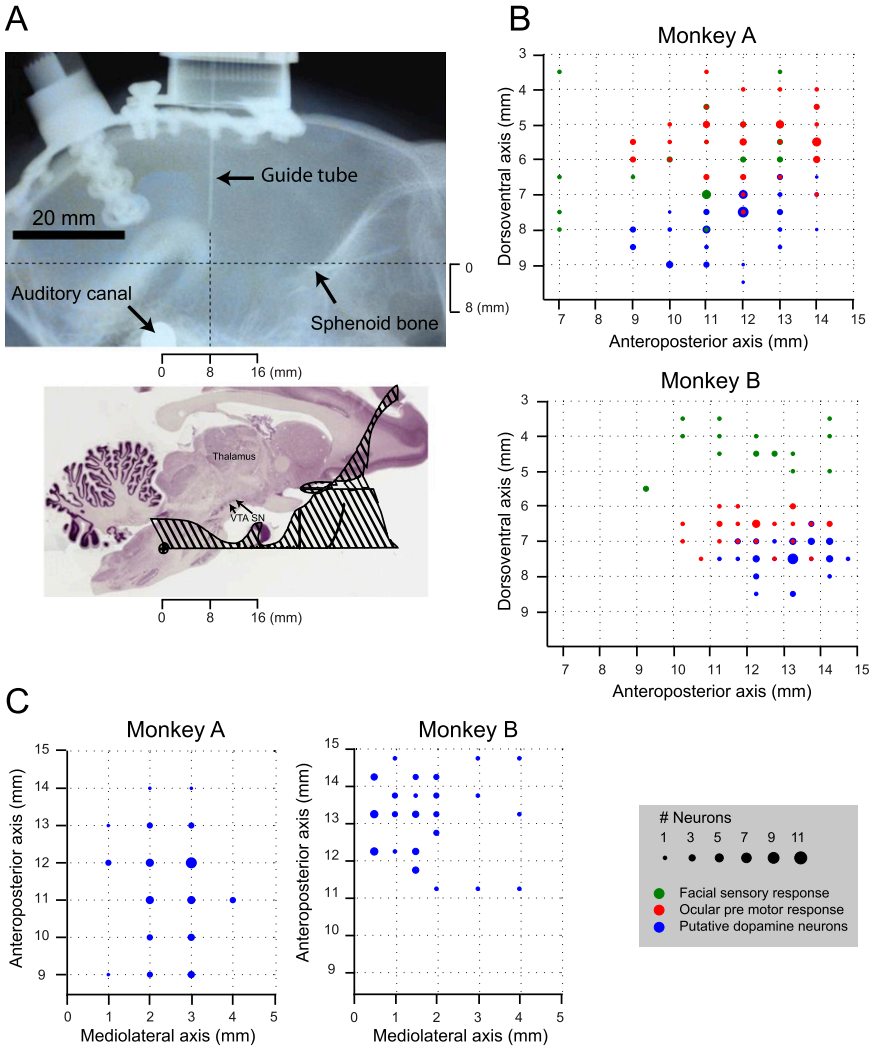

Fig. S3. Localization of dopamine recording sites. (*A*, *Upper*) X-ray of lateral view of monkey A's skull with a guide tube directed toward the midbrain area. (*A*, *Lower*) Composite figure of recording area in midbrain. The schematic drawing of the base of the skull was obtained from Aggleton and Passingham (1). Nissl-stained standard sagittal histological section from *Macaca mulatta* was obtained from www.brainmaps.org (slide 64/295). All figure components are displayed at the same scale as the X-ray shown in *A*, *Upper*. (*B*) Anteroposterior (relative to interaural line) and dorsoventral (relative to midline) view of the recording track in monkey A (*Upper*) and monkey B (*Lower*). Symbol sizes indicate numbers of neurons recorded in each track (right hemisphere in both animals). (*C*) Surface view of recording locations in monkey A (*Left*) and monkey B (*Right*) in mediolateral and anteroposterior axes. Image reprinted with kind permission of Springer Science+Business Media from ref. 1.

1. Aggleton JP, Passingham RE (1981) Stereotaxic surgery under X-ray guidance in the rhesus monkey, with special reference to the amygdala. *Exp Brain Res* 44(3):271–276.

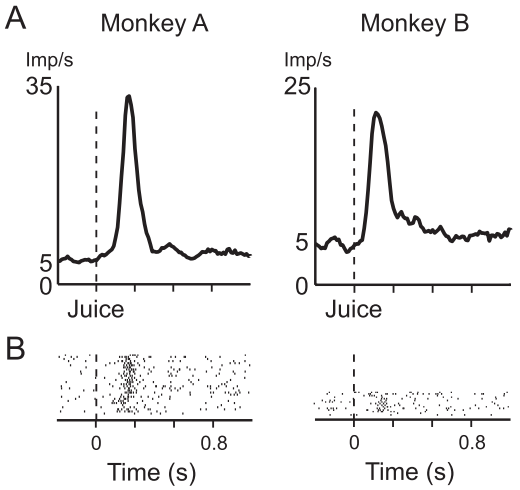

Fig. S4. Dopamine responses to unpredicted juice delivery. Dopamine neurons responded to free rewards (0.4 mL of juice) delivered randomly during intertrial intervals. (*A*) The PSTH averaged across all neurons recorded in juice-only experiment (40 and 37 neurons in monkeys A and B, respectively). (*B*) The response to unpredicted juice from the example neuron shown in Figs. 2 and 5 (*Left*) and an example neuron from monkey B (*Right*).

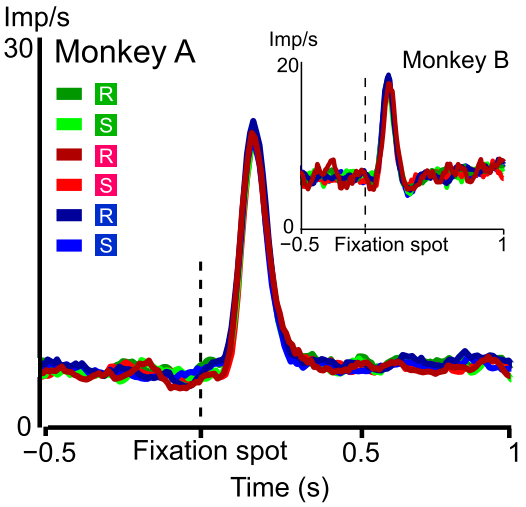

Fig. S5. Dopamine responses to fixation spot. Identical dopamine population response to fixation spot onset in different trial types (monkey A, main graph; monkey B, *Inset*).

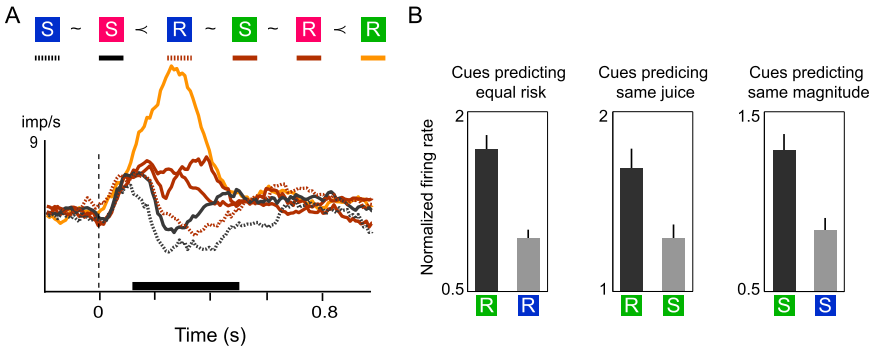

Fig. S6. Dopamine neuronal activity in monkey B in response to cues. (*A*) Population neuronal response to cues in monkey B (line conventions demonstrated below the corresponding cues). The horizontal black bar shows the temporal time window used for the statistical analysis of the neuronal data shown in Figs. 2 and 3. (*B*) The population neuronal response for singular reward attributes in monkey B.

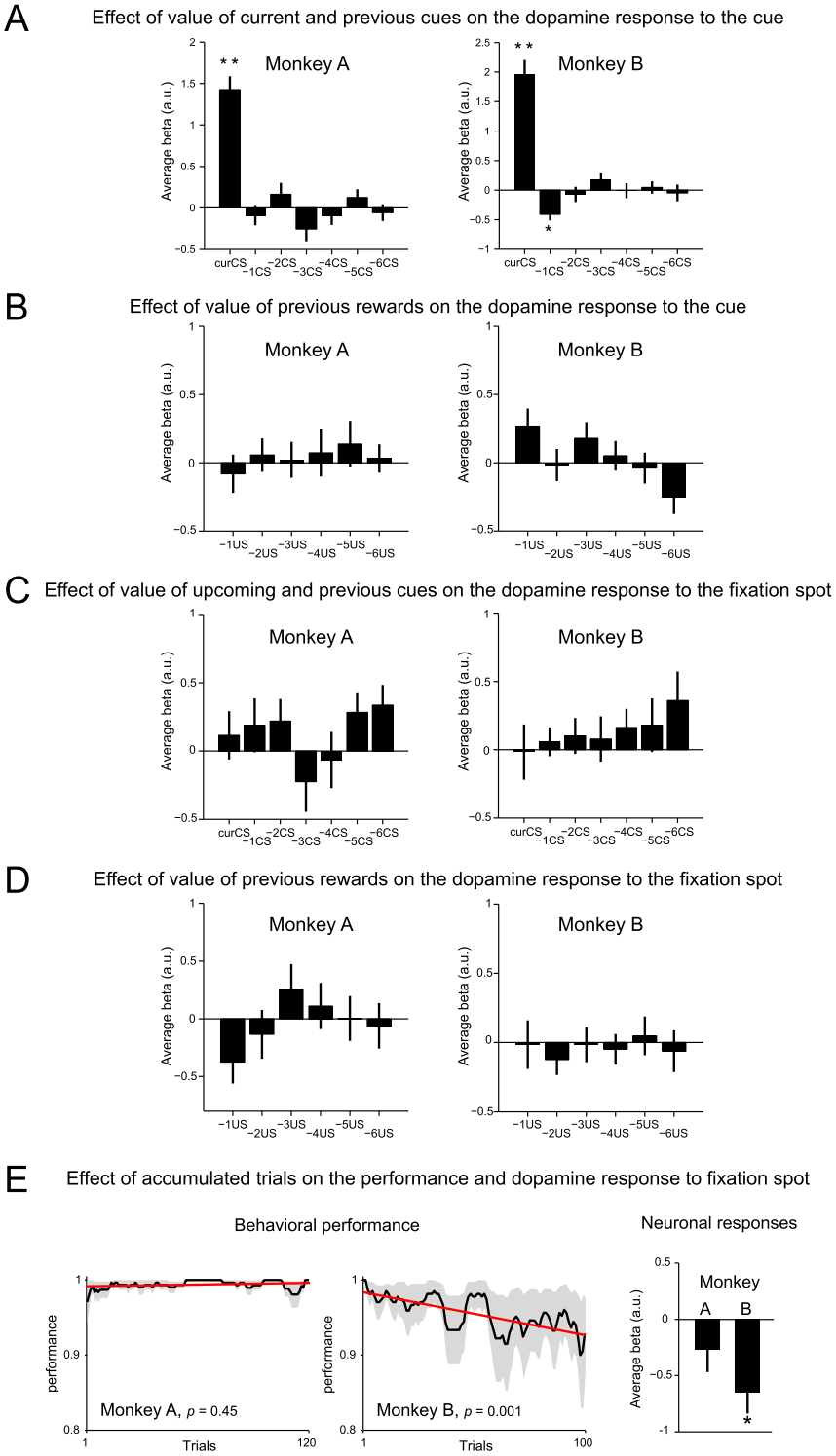

Fig. S7. Effect of different behavioral variables on the neuronal response to cues and fixation spot. (*A*) Effect of value of current and previous cues on the dopamine response to the cue. In each panel multiple regression betas have been plotted. Error bars are SEM. $^{**}P < 0.001$; $^{*}P < 0.01$. (*B*) Effect of value of previous rewards on the dopamine response to the cue. (*C*) Effect of value of upcoming and previous cues on the dopamine response to the fixation spot. (*D*) Effect of value of previous rewards on the dopamine response to the fixation spot. (*E*) Effect of accumulated trials on the behavioral performance (i.e., successful ocular fixation) and the dopamine response to the fixation spot.

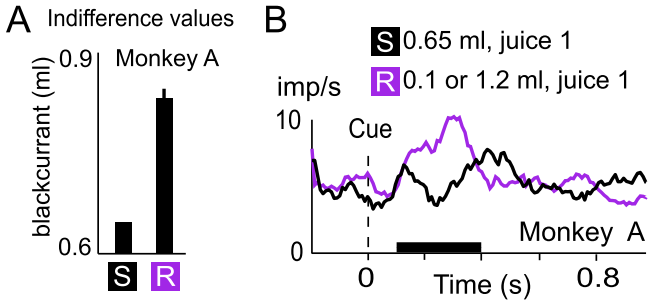

Fig. S8. Dopamine responses in monkey A to cues with large difference in risk. (*A*) Subjective value of a cue, predicting a equiprobable gamble between 0.1 and 1.2 mL, in monkey A. Measurements were done using PEST ($n = 29$). Although this animal was risk-neutral for gambles tested in the main experiments (Fig. 1), it showed clear risk-seeking behavior when tested with a gamble containing large risk. (*B*) Dopamine responses (monkey A) to the risky and safe cues. Consistent with the behavioral data, the neuronal responses ($n = 5$) are larger in response to the risky cue.

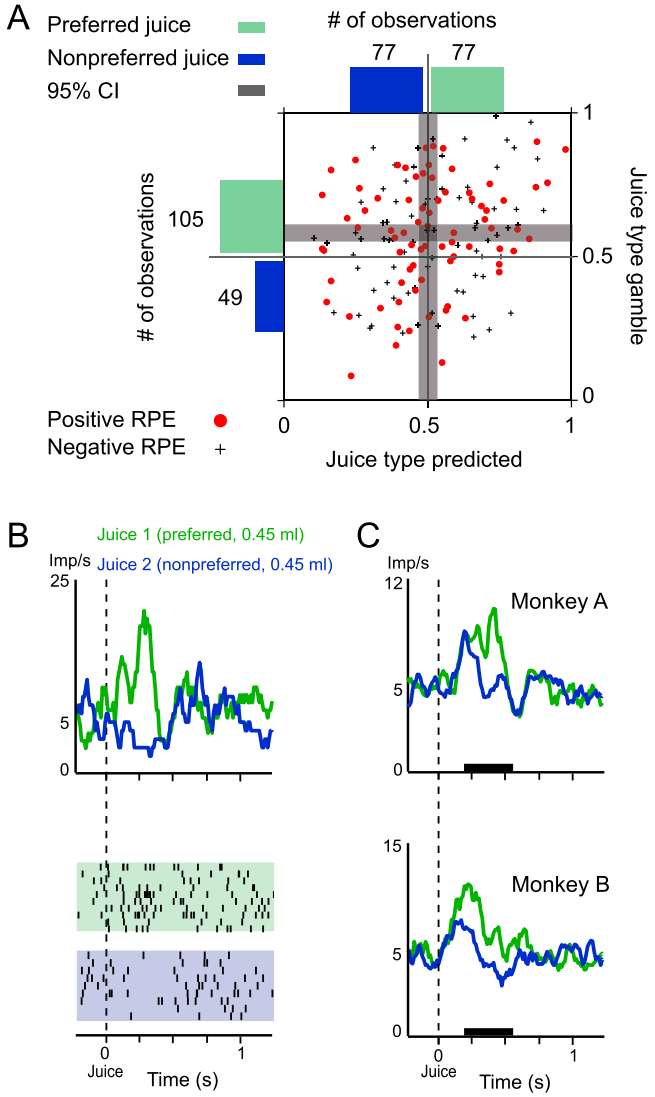

Fig. S9. Dopamine prediction error responses to different juice types. (*A*) Scatter plot of neuronal auROC measures when juice type was predicted (horizontal axis) and when juice type was not fully predicted (vertical axis). An auROC >0.5 indicates higher neuronal activity in response to preferred juice compared with nonpreferred juice. The auROC measures for each neuron are shown separately for positive (red) and negative (black) prediction error responses. Gray bars indicate the 95% bootstrapped confidence interval of auROC. The responses differed significantly between the two juices only when the type of juice was not fully predicted ($P < 0.0001$, bootstrap test). (*B*) Differential prediction error responses of an individual dopamine neuron to more preferred juice compared with less preferred juice. Juice magnitude was fully predicted (*Upper*, PSTH; *Lower*, rastergram). (*C*) As in *B*, *Upper* but for the neuronal populations recorded in each animal. The horizontal black bar indicates the time window used for statistical data analysis.

Table S1. Transitivity of choices in the binary choice task

Monkey A			Monkey B		
P (a > b)	*P (b > c)*	*P (a > c)*	*P (a > b)*	*P (b > c)*	*P (a > c)*
0.57	**0.89**	**0.97**	**0.67**	**0.56**	**0.74**
0.57	**0.81**	**1.00**	**0.67**	**0.74**	**0.87**
0.57	**0.85**	**0.96**	**0.67**	**0.75**	**0.85**
0.57	**0.91**	**1.00**	**0.74**	**0.51**	**0.74**
0.97	**0.59**	**1.00**	**0.74**	**0.72**	**0.87**
0.97	0.81	0.96	**0.74**	**0.76**	**0.85**
0.97	**0.81**	**1.00**	**0.74**	**0.63**	**0.87**
1.00	0.70	0.96	**0.74**	**0.81**	**0.85**
1.00	**0.84**	**1.00**	0.87	0.81	0.85
0.96	**0.58**	**1.00**	**0.56**	**0.63**	**0.74**
0.89	0.59	0.81	0.56	0.81	0.75
0.89	0.81	0.85	**0.74**	**0.54**	**0.75**
0.89	**0.81**	**0.91**	**0.51**	**0.63**	**0.76**
0.81	**0.70**	**0.85**	0.51	0.81	0.76
0.81	**0.84**	**0.91**	**0.72**	**0.54**	**0.76**
0.85	**0.84**	**0.91**	**0.63**	**0.54**	**0.81**
0.59	**0.70**	**0.81**	0.60	0.56	0.51
0.59	0.84	0.81	0.60	0.74	0.72
0.81	**0.58**	**0.81**	**0.60**	**0.75**	**0.76**
0.70	**0.58**	**0.84**	0.74	0.60	0.67

If an individual prefers cue *a* over cue *b* and cue *b* over cue *c*, then the weak axiom of stochastic transitivity requires the probability of choosing cue *a* over cue *c* to be ≥50%. For every combination of three cues, the choice probabilities in each animal satisfied the weak axiom of stochastic transitivity. The strong axiom of stochastic transitivity requires the probability of choosing cue *a* over cue *c* to be greater than or equal to the maximum observed choice probability between the two other choice conditions. This requirement was satisfied in 29 out of 40 combinations, as highlighted by boldface type in the table.