A computational and neural model of momentary subjective well-being

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The subjective well-being or happiness of individuals is an important metric for societies. Although happiness is influenced by life circumstances and population demographics such as wealth, we know little about how the cumulative influence of daily life events are aggregated into subjective feelings. Using computational modeling, we show that emotional reactivity in the form of momentary happiness in response to outcomes of a probabilistic reward task is explained not by current task earnings, but by the combined influence of recent reward expectations and prediction errors arising from those expectations. The robustness of this account was evident in a large-scale replication involving 18,420 participants. Using functional MRI, we show that the very same influences account for task-dependent striatal activity in a manner akin to the influences underpinning changes in happiness.

much is now known about how the brain responds to rewards. For example, midbrain dopamine neurons represent reward prediction error (RPE) signals in animals (17–19) and humans (20). Neuroimaging studies report correlates of RPEs in the ventral striatum, an area that is a target for dopamine projections, in tasks from reinforcement learning (21, 22) to gambling (23). Many studies have also related subjective feelings about discrete events to neural activity (24–26). However, it remains unknown how these events cumulatively influence happiness.

We modeled behavioral data using a computational model inspired by models of dopamine function. Here we show that momentary subjective well-being is explained not by task earnings but by the cumulative influence of recent reward expectations and prediction errors resulting from those expectations. We note that the temporal difference errors that dopamine neurons are thought to represent are closely related to these quantities. Our model explained momentary subjective well-being better than a model that accounts for the influence of rewards but does not include a role for expectations. Furthermore, we replicated these behavioral findings in two laboratory-based behavioral experiments as well as a large-scale smartphone-based experiment. Using fMRI we probed the relationship between reward-related task events, neural responses to those events, and subjective well-being. Task-dependent neural activity in the ventral striatum, a major projection site for dopamine neurons, correlated with subsequent reports of subjective well-being, consistent with this area playing a role in changes in happiness.

We scanned 26 subjects while they made choices between certain and risky monetary options (Fig. 1A). Chosen gambles

Significance

A common question in the social science of well-being asks, “How happy do you feel on a scale of 0 to 10?” Responses are often related to life circumstances, including wealth. By asking people about their feelings as they go about their lives, ongoing happiness and life events have been linked, but the neural mechanisms underlying this relationship are unknown. To investigate it, we presented subjects with a decision-making task involving monetary gains and losses and repeatedly asked them to report their momentary happiness. We built a computational model in which happiness reports were construed as an emotional reactivity to recent rewards and expectations. Using functional MRI, we demonstrated that neural signals during task events account for changes in happiness.

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Subjects earned £28.51 ± 7.60 (mean ± SD) in 150 trials, a significant increase in wealth from an initial £20 endowment \( t(25) = 5.7, P < 0.0001 \). Prizes up to £3 were sufficient to elicit changes in happiness with root-mean-square differences between successive ratings of 17 ± 8 (mean ± SD, range 6–43). However, self-reported overall happiness did not increase between the initial and final happiness ratings. Note that these quantities including EVs and RPEs (the difference between experienced and predicted rewards) and happiness. Happiness ratings across subjects \( (n = 26) \) in Fig. 1B. The relationship between task earnings and the difference between initial and final happiness was not significant \((P = 0.16, r^2 = 0.079)\).

**Computational Model of Momentary Subjective Well-Being**

We next examined the relationship between chosen certain rewards (CRs), the expected values (EVs) of chosen gambles, and RPEs (the difference between experienced and predicted rewards) and happiness. Note that these quantities including EVs and RPEs are linked to dopamine activity (17) and we hypothesized that these dopamine-related quantities might explain momentary happiness. We considered influences that decay exponentially in time (SI Methods):

\[
\text{Happiness}(t) = w_0 + \sum_{j=1}^{t} \gamma^t \cdot CR_j + w_2 \sum_{j=1}^{t} \gamma^t \cdot EV_j + w_3 \sum_{j=1}^{t} \gamma^t \cdot RPE_j,
\]

where \( t \) is the trial number, \( w_0 \) is a constant term, other weights \( w \) capture the influence of different event types, \( 0 \leq \gamma \leq 1 \) is a forgetting factor that makes events in more recent trials more influential than those in earlier trials, \( CR_j \) is the CR if chosen instead of a gamble on trial \( j \), \( EV_j \) is the EV of a gamble (average reward for the gamble) if chosen on trial \( j \), and \( RPE_j \) is the RPE on trial \( j \) contingent on choice of the gamble. If the CR was chosen, then \( EV_j = 0 \) and \( RPE_j = 0 \); if the gamble was chosen, then \( CR_j = 0 \). Parameters were fit to happiness ratings in individual subjects. We found that CR, EV, and RPE weights were on average positive \( (all t(25) > 4.6, P < 0.0001) \) with EV weights lower than RPE weights \( t(25) = 4.3, P < 0.001 \); Fig. 2A). The forgetting factor \( \gamma \) was 0.61 ± 0.30 (mean ± SD). This model explained moment-to-moment fluctuations in happiness well with \( r^2 = 0.47 \pm 0.21 \) (mean ± SD; Fig. 1) and, when judged according to complexity, explained this reactive happiness better than a range of alternative models, including models without exponential constraints, parameters for unchosen options, and utility-based models (SI Methods, Tables S1 and S2, and Fig. S1).

A prediction arising out of our model is that the final happiness rating should depend only on the final task events and not on earlier events. Consider the effect of just receiving £1 versus receiving £1 five trials ago. For a subject with the group average forgetting factor of 0.61, the latter would have only 8% of the impact of the former. For subjects with larger (0.8) or smaller (0.4) forgetting factors, this relative impact would be 33% or 1%, respectively. For most subjects, rewards received more than 10 trials in the past should have little effect on current happiness (Fig. S1). Therefore, any relationship between task earnings and change in happiness from the initial to the final rating should be accounted for by the final trials of the task. We used only the final 10 trials to predict the final happiness rating based on parameters estimated from a model fit to the first 140 trials. Residual errors of the predicted final happiness were uncorrelated with task earnings \((P = 0.81, r^2 = 0.003)\), suggesting that our model accounts for any relation between task earnings and happiness.

![Fig. 1](image-url) Effect of previous rewards and expectations on happiness ratings. (A) Experimental design. In each trial, subjects chose between a certain option and a gamble. Chosen gambles were resolved after a 6-s-delay period. Every two to three trials, subjects were asked to indicate “How happy are you at this moment?” by using button presses to move a cursor. (B–D) Cumulative task earnings and happiness ratings across subjects \((n = 26)\) in B and in example subjects in C and D. Happiness model fits are displayed for the model in Fig. 2A \([r^2 = 0.47 ± 0.21 \text{ (mean ± SD)}; \text{example subjects} r^2 = 0.79 \text{ in } C \text{ and } r^2 = 0.41 \text{ in } D]\).
choices and outcomes. When the RPE term (reward minus EV) was split into experimental design allowed the separation of expectation effects related to experiment, gamble choices had a 50% probability of ending with the text "outcome added to total" instead of the outcome being revealed. (2) This experimental design allowed the separation of expectation effects related to choices and outcomes. When the RPE term (reward minus EV) was split into separate GR and gamble EV terms, happiness ratings were positively correlated with GRs and negatively correlated with gamble EV at outcome.

We ran three additional behavioral experiments to validate our model (Fig. S2). Because subjects may be poor at estimating their current earnings, we conducted a behavioral experiment ("current earnings always shown") in which current task earnings were always displayed, including at the time when happiness ratings were made (SI Methods). If subjects are not reporting their momentary happiness but instead their belief about their current success or earnings, we should see a strong relationship between ratings and earnings in this experiment. Instead, we replicated our previous findings with positive CR, EV, and RPE weights, and EV weights lower than RPE weights for all $t(21) > 3.0$, $P < 0.01, n = 22$ [Fig. 2B]. The relationship between earnings and change in happiness was stronger than in the scanning experiment ($P = 0.042, r^2 = 0.19$). However, when we again used only the final 10 trials of the task to predict the final happiness rating, the residual errors of the predicted final happiness were uncorrelated with task earnings ($P = 0.17, r^2 = 0.094$), suggesting that even when subjects always know their exact earnings, the model still accounts for any relation between task earnings and happiness.

To verify a role for both reward expectations and RPEs in happiness, we also conducted an additional behavioral experiment in which the actual outcomes were only presented in randomly selected trials ("only some gamble outcomes shown"). Otherwise, the text "outcome added to total" was displayed when the outcome would normally be revealed (SI Methods). We again replicated our previous findings showing that CR, EV, and RPE weights are all positive and EV weights are lower than RPE weights [all $t(20) > 3.5$, $P < 0.005, n = 21$; Fig. 2C]. This model fits the data better (median $r^2 = 0.43$) than an alternative model with a gamble reward (GR) outcome term (median $r^2 = 0.39$) instead of an RPE term (SI Methods). There was again no relationship between task earnings and change in happiness ($P = 0.24, r^2 = 0.07$). When we fit a model with separate EV weights depending on whether the gamble outcome was revealed, we found that expectations had a positive effect on happiness even when outcomes were not revealed ($t(20) = 2.8, P = 0.011$). This task version allowed us to dissociate the effects of expectations at choice and outcome as well as to apply a more stringent test for a relationship between a signal and RPEs (27) in which the RPE term is split into its separate components: rewards and expectations (SI Methods). If happiness is positively affected by RPEs, then because RPE is equal to the reward minus EV, the weight for EV should be negative and subjects with larger negative EV weights should have larger positive reward weights to balance the two RPE components. As predicted, happiness was positively modulated by reward ($t(20) = 6.6, P < 0.0001$) and negatively modulated by EV ($t(20) = -4.3, P < 0.001$) and weights were anticorrelated ($r = -0.58, P = 0.006$; Fig. 2D).

Finally, laboratory experiments are necessarily based on relatively small numbers of subjects, raising issues of generalizability and demand characteristics. We were able to address these potential shortcomings by using a smartphone-based platform (The Great Brain Experiment, www.thegreatbrainexperiment.com) for iOS (Apple) and Android (Google) systems (SI Methods) that enabled us to run a 30-trial 12-rating version of the task. Here our sample comprised 18,420 anonymous unpaid participants who made over 200,000 happiness ratings. We divided the data into 92 subsets of 200 consecutive participants and fit our model in individual participants. CR, EV, and RPE weights were positive in all 92 data subsets ($t(199) > 2.0, P < 0.05$; Fig. 3). EV weights were lower than RPE weights in all but one data subset ($t(199) > 2.0, P < 0.05$). To test whether the model still applied when participants had minimal familiarity with the experimental context, we analyzed the first happiness rating preceded by a choice trial from each participant. CR, EV, and RPE weights were again positive with EV weights lower than RPE weights for a single happiness rating from each of 18,420 participants (all $P < 0.005$; SI Methods and Fig. 3C and Fig. S1C). Consistent with previous results, earnings increased on average when, but happiness did not (Fig. S2C). Because the cursor always started at the midpoint on the rating scale in all experiments, this starting point might act as an anchor to counteract increases in happiness due to task earnings. In this case, happiness should increase in subjects who both increased their earnings and had an average happiness below the midpoint, but there was only a modest increase in these subjects [$n = 2,211$, initial happiness: $42 \pm 18$, final happiness: $43 \pm 19$ (mean $\pm$ SD)], suggesting that this potential influence does not explain why happiness does not increase with earnings (Fig. S3). We also verified the out-of-sample validity of our model by using parameter weights from the fMRI experiment to predict happiness ratings in the other experiments (median $r^2 = 0.23$ for the three experiments; Table S3).

**Momentary Subjective Well-Being in Striatum and Insula**

To test the relationship between neural activity in the fMRI experiment and the current level of happiness, we regressed blood-oxygen-level-dependent (BOLD) activity at task events from trials preceding happiness ratings (option and outcome onsets) on those subsequent ratings. BOLD activity in the ventral striatum was significantly correlated with z-scored future happiness ratings (Fig. 4; left coordinates $-9, 8, -8; t(23) = 5.1$; right coordinates $18, 8, -5, t(23) = 3.9$; both $P < 0.05$, small-volume corrected). We then tested whether this activity was related to parameters of our behavioral model, regressing event-related activity in this region of interest (ROI) on parametric task
variables (SI Methods). The striatal weights associated with these factors were all significantly positive (all $P < 0.001$; Fig. 4B), as was the case in our behavioral model (Fig. 2A). As for the behavioral analysis, we again applied the higher standard of splitting the RPE term into separate components (27) and verified the finding that individuals adapt to long-lasting changes in life circumstances (34, 35).

Across four separate studies we obtained qualitatively similar parameter estimates for model fits, including for a large-scale smartphone-based replication. Participants in the smartphone experiment were unpaid and anonymous, thus minimizing demand characteristics that may exist in the laboratory. However, even in this context we saw little change in the results, even when considering only a single happiness rating from each of the 18,420 participants, suggesting that the intrinsic rewards in smartphone games are sufficient to affect momentary happiness in the absence of monetary incentives.

The observation that recent rewards affected ongoing reactive happiness ratings is to be expected. More surprising, and a key finding across each of our studies, was the important role for expectations in determining happiness. This role balanced the influence of reward in a manner consistent with prediction errors playing a key determining role in momentary happiness. Because RPEs capture the difference between rewards and expectations, the effect of an outcome on happiness depends on what the alternatives are. For example, a £0 prize decreases happiness if the alternative was winning £2, but increases happiness if the alternative was losing £2. Expectations also affect happiness before outcomes are revealed and we show that choosing a gamble with a positive EV makes subjects happier even if the outcome is never revealed. In fact in the real world, rewards associated with life decisions are often not realized for a long time (e.g., jobs, marriage) and our results suggest that expectations

**Discussion**

Conscious emotional feelings, such as momentary happiness, are core to the ebb and flow of human mental experience. Our computational model suggests momentary happiness is a state that reflects not how well things are going but instead whether things are going better than expected. This includes positive and negative expectations, even in the absence of outcomes. Our results are in accord with well-being studies suggesting that the ongoing state of happiness varies around a hedonic set point (33). Indeed, an average forgetting factor of 0.61 in our fMRI experiment indicates that rewards received more than 10 trials ago have essentially no influence on current happiness in the task. Although we used a stationary environment, value estimates in a dynamic environment could be continually updated, allowing agents to adapt to persistent changes in reward rates. This prediction would be consistent with the “hedonic treadmill,” the finding that individuals adapt to long-lasting changes in life circumstances (34, 35).

Fig. 3. Smartphone-based large-scale replication. (A) A screenshot from the smartphone experiment. In each trial, participants chose between a certain option and a gamble. Here the choice is between a certain 30 points and a gamble to gain 72 points or 0 points. Every two to three trials, participants were asked to indicate, “How happy are you at this moment?” (B) The computational model that best explained happiness in the first 200 participants had positive CR, gamble EV, and gamble RPE weights. Error bars represent SEM. (C) This model also explained the happiness rating after the first two to three trials from each participant, with similar model fits for a single happiness rating from each participant ($n = 18,420$). Error bars represent SE computed from the covariance matrix of the single model fit.

Fig. 4. Relationship between happiness and neural responses during preceding events. (A) Striatal activity during task events preceding subjective state ratings correlated with later self-reported happiness ($P < 0.05$, small-volume corrected). (B) Neural responses in ventral striatum were explained by the same parametric task variables as the variables that explained happiness. Error bars represent SEM.
related to those decisions, both good and bad, do have an impact on happiness. In all our experiments, we found that EV weights were significantly lower than RPE weights, indicating that the overall effect of expectations on happiness is negative: a positive weight for EV in choices combines with a larger negative weight for EV in outcomes (because RPE is equal to reward minus EV) for an overall negative expectation effect. As a result, positive expectations effectively reduce the overall emotional impact of trials with positive outcomes and negative expectations effectively reduce the overall emotional impact of trials with negative outcomes. A role for expectations, independent of outcomes, also ensures that subjects are happier on average after choosing gambles with positive rather than negative EV.

The well-described peak–end rule (36) suggests that remembered feelings depend most on how experiences were at the peak and end, explaining for example why painful medical procedures are remembered as less unpleasant when extended to end with a less painful period (37, 38). Our model does not give extra weight to peak events because task outcomes are relatively homogeneous. However, in common with the rule, we found that recent events have relatively greater impact on mood, extending findings of previous studies to the “experiencing” and not just the “remembering” self. Pleasant and unpleasant feelings during medical procedures could be modeled using experience-sampling techniques and the role we highlight for expectations could potentially be used to leverage better outcomes. Our results also have potential policy implications. Lowering expectations increase the probability of positive outcomes (something routinely observed). However, lower expectations reduce well-being before an outcome arrives, limiting the beneficial scope of this manipulation. One intriguing notion would be to use a sufficiently negative expectation to create an overall positive emotional impact from a negative event. For example, news of a 1-h delay should, by our model, have a net positive impact for the average passenger. However, floating the extreme possibility of a 6-h delay might well have other negative consequences for the airline.

Our key finding is that happiness is related to quantities associated with temporal difference errors that phasic dopamine release is thought to represent, errors that signal changes in long-term expected reward (17–19, 39–41). We also found that happiness relates to BOLD activity in the striatum, a prominent target for ascending dopamine projections. At the very least, this hints at a link between dopamine and emotional state, consistent with suggestions that this neuromodulator plays a role in mood regulation in healthy and depressed subjects (42). The potential importance of this link is bolstered by observations that stress engages depression-like behavior via a modulation of striatal dopamine responses (43). A dopamine manipulation alone does not impact on overall mood (44) but, based on our model, we suggest that dopamine may act to modulate changes in emotional state in response to discrete events. However, one caveat is that we did not find that striatal activity significantly mediates the relationship between RPEs and happiness in our task. Although our results suggest that the ventral striatum is the best candidate region for mediating this relationship, this mediation may be sensitive to task demands and may be absent in tasks like ours where RPEs do not modify behavior. Striatal RPEs are notably absent in subjects that fail to learn in a reinforcement-learning task (45). Therefore, we predict that striatal activity in reinforcement-learning tasks will mediate the relationship between RPEs and happiness only in subjects who learn the reward associations.

Aberrant responses to daily life events are a defining characteristic of mood disorders. Our findings show that conscious emotional states can be precisely manipulated and characterized using computational models in a similar manner to studies of conscious perception (46). Our approach offers a rich quantitative means of relating emotional state to brain and behavior and, in doing so provides a framework for the development of model-based assays of mood disorders that can be exploited so as to probe the underlying neurobiological mechanisms.

**Methods**

**Subjects.** Twenty-six healthy right-handed subjects took part in the fMRI experiment (age range 20–40 y, seven male). Twenty-one of these 26 subjects agreed on invitation to participate in an additional behavioral experiment (median 53 d apart; range, 3–162 d). Eleven of the 26 subjects agreed on invitation to participate in a second behavioral experiment (14–17 mo later). An additional 11 subjects were recruited for this second behavioral experiment (age range 20–34, four male). Subjects were endowed with £20 at the beginning of each experiment and paid according to performance. Two subjects were excluded from fMRI analysis due to excessive head movement.

In a smartphone-based experiment we tested 18,420 unpaid participants (age 18 y and over; 8,557 male). All subjects gave informed consent and the Research Ethics Committee of University College London approved all studies.

**Laboratory-Based Experimental Tasks.** During each of the 150 trials of the tasks, subjects chose between a certain option and a gamble, with equal probabilities of two outcomes (Fig. 1A and SI Methods). There were three trial types: mixed trials (a certain amount of £0 or a gamble with a gain and loss amount), gain trials (a certain gain or a gamble with £0 and a larger gain), and loss trials (a certain loss or a gamble with £0 and a larger loss). Gamble choices remained on the screen for 6 s before gamble outcomes were revealed for 1 s. Subjects were presented with the question, “How happy are you at this moment?” after every two to three trials. After a 5-s delay period, a rating line appeared with endpoints labeled “very unhappy” and “very happy.” Subjects had 4 s to move the cursor along the scale with button presses, making a total of 63 happiness ratings. Current earnings were displayed after each of the three blocks of 50 trials. In the only-some-gamble-outcomes—shown behavioral experiment, although all choices counted for real money, only some gamble outcomes were revealed, enabling us to dissociate expectation effects at choice and outcome (SI Methods). After half of gamble choices, the delay period would end with the text “outcome added to total.” In the current-earnings-always—shown behavioral experiment, the current task earnings were displayed at all times, including during happiness ratings. Before each experiment, before the task instructions, we measured life happiness by asking subjects, “Taken all together, how happy are you with your life these days?”

**Smartphone-Based Experimental Task.** Researchers at the Wellcome Trust Centre for Neuroimaging at University College London worked with White Bat Games to develop The Great Brain Experiment, available as a free download on iOS and Android systems. One of these games was based on the task we used for the fMRI experiment. Subjects started the game with 500 points and made 30 choices in each play. In each trial, subjects chose between a certain option and a gamble. Chosen gambles, represented as spinners, were resolved after a brief delay. Subjects were presented with the question, “How happy are you at this moment?” after every two to three trials.
Subjects completed 30 choice trials and answered the happiness question 12 times in each play.

Happiness Computational Models. We modeled moment-to-moment happiness for all ratings preceded by choices using models that assume an exponential decay of previous event influences and terms for CRs, gamble EVs, and RPs. Models were fit using nonlinear least squares using the optimization toolbox in MATLAB (MathWorks, Inc.). To verify the appropriateness of our model, we tested a wide variety of alternative models (SI Methods and Tables S1 and S3). We included several models following established procedures for estimating utilities (47). We evaluated the models using Bayesian model comparison techniques (48, 49).

fMRI Data Acquisition and Analysis. All scanning was performed on a 3-Tesla Siemens Allegra scanner with a Siemens head coil with an echo-planar sequence (SI Methods). We used standard preprocessing in SPM8 (Wellcome Trust Centre for Neuroimaging) and estimated three general linear models for each subject which included regressors related to option and gamble values and happiness ratings (SI Methods). Statistical significance was determined at the group level using a random-effects analysis. All analyses used a voxel-wise significance threshold of \( P < 0.001 \) and a corrected significance threshold of \( P < 0.05 \) based on a family-wise error cluster-level small-volume correction centered on coordinates from previous studies (SI Methods). We used the Multilevel Mediation and Moderation Toolbox (50, 51) to perform the mediation analysis (SI Methods and Fig. S5).

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Supporting Information

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SI Methods

Laboratory-Based Experimental Tasks. Stimuli were presented in MATLAB (MathWorks, Inc.) usingCogent 2000 (Wellcome Trust Centre for Neuroimaging). Subjects made 150 choices in each task. During each trial of the functional MRI (fMRI) task, subjects chose between a certain option and a gamble, with equal probabilities of two outcomes (Fig. L). There were three trial types: mixed trials (a certain amount of £0 or a gamble with a gain and loss amount), gain trials (a certain gain or a gamble with £0 and a larger gain), and loss trials (a certain loss or a gamble with £0 and a larger loss). If subjects failed to respond within the 3-s time limit, they received the worst outcome. Unchosen options disappeared immediately following a choice. Certain choices remained on the screen for 7 s. Gamble choices remained for 6 s before the outcome was revealed for 1 s. Each trial was followed by a 3 to 11-s jittered intertrial interval. The intervals followed a gamma distribution with a shape parameter of 6 and a scale parameter of 1 with values exceeding the boundary values of 3 s and 11 s set to those values.

The 50 mixed trials consisted of a choice between a certain £0 and a gamble with equal probabilities of a monetary gain or loss. There were five gamble gain amounts in pence (30, 50, 80, 110, 150) and gamble loss amounts were determined by 10 multipliers on the gain amount (0.2, 0.3, 0.4, 0.52, 0.66, 0.82, 1, 1.2, 1.5, 2) chosen to accommodate a range of loss sensitivity. The 50 gain trials consisted of a choice between a certain gain and a gamble with equal probabilities of a larger gain or £0. There were five certain amounts (20, 30, 40, 50, 60) and the gamble gain amount was determined using 10 multipliers on the certain amount (1.68, 1.82, 2, 2.22, 2.48, 2.8, 3.16, 3.6, 4.2, 5). The 50 loss trials used the same monetary amounts as the gain trials with five certain amounts (−20, −30, −40, −50, −60) and the same 10 multipliers as used for gain trials. The maximum gamble gain or loss for a single trial was £3.

Subjects were presented with the question, “How happy are you at this moment?” after every two to three trials. After a 5-s-delay period, a rating line appeared and subjects had 4 s to move the cursor along the scale with button presses. The left end of the line was labeled “very unhappy” and the right end of the line was labeled “very happy.” The cursor always started at the midpoint. Because the largest movements were required when reporting being very happy or very unhappy, there was no relationship between the amount of movement made and happiness ratings [r(25) = 0.54, P = 0.59]. Therefore, any neural activity correlated with happiness ratings is not explained by any trivial motor confound. Furthermore, there was no difference in the percentage of trials where the rating was greater than or less than 50 [50.8% versus 47.9%, r(25) = 0.29, P = 0.78; the remaining ratings were equal to 50] and no difference in the average movement from the midpoint for those ratings [14.0 versus 15.0, r(25) = −0.57, P = 0.57].

Each rating was followed by a 3 to 11-s jittered intertrial interval. Subjects completed 150 choice trials and answered the happiness question 63 times. Subjects rarely failed to respond and the median number of missed choice trials in both fMRI and behavioral experiments was 1 (range of 0 to 5 for both). Missed trials were excluded from further analysis. Trials were divided into three 50-trial blocks of ~19 min each. Subjects were informed of their current task earnings after each block. Each block started and ended with a happiness question. We refer to the rating at the start of the first block as the “initial happiness” and at the end of the third block as the “final happiness.” Model fits included all ratings that were preceded by trials (20 per block).

Twenty-one of 26 participants in a behavioral experiment (“only some gamble outcomes shown”). This experiment was identical to the fMRI experiment except that, although all choices counted for real money, only some gamble outcomes were revealed, enabling us to dissociate expectation effects at choice and outcome. After gamble choices there was a 50% probability that the delay period would end with the text “outcome added to total” appearing alongside the chosen gamble for 1 s. The current task earnings were reported at the end of each block as before.

Twenty-two subjects participated in an additional behavioral experiment (“current earnings always shown”) including 11 subjects from the fMRI experiment. The behavioral experiment was identical to the fMRI experiment except that the current task earnings were displayed at all times, including when subjects were asked the happiness question.

Before each experiment, before the task instructions, we measured life happiness by asking subjects, “Taken all together, how happy are you with your life these days?” Subjects marked a point on a line to indicate their response, with the endpoints labeled “very unhappy” and “very happy.” Subjects answered the question three times and we used the median response as their life happiness rating (mean = 66, range = 2–100). For some analyses, we split subjects from the fMRI experiment (after excluding two subjects for excessive head movement) into high (mean = 82, n = 12) and low (mean = 53, n = 12) life happiness groups. Subjects also completed the Beck Depression Inventory to quantify depression symptom severity (mean ± SD, 6.9 ± 5.9).

Smartphone-Based Experimental Task. Researchers at the Wellcome Trust Centre for Neuroimaging at University College London worked with White Bat Games to develop The Great Brain Experiment (www.thegreatbrainexperiment.com), available as a free download on iOS (Apple) and Android (Google) systems. One of these games was based on the task we used for the fMRI experiment. Subjects started the game with 500 points and made 30 choices in each play. In each trial, subjects chose between a certain option and a gamble with equal probabilities of two outcomes with the same three trial types as the laboratory-based experiments. Chosen gambles, represented as spinners, were resolved after a brief delay. Subjects were presented with the question, “How happy are you at this moment?” after every two to three trials. Subjects indicated their responses on a rating line and pressed a button labeled “continue” to proceed to the next trial. Subjects completed 30 choice trials and answered the happiness question 12 times in each play. Subjects were informed of their current earnings during all choice trials. Each play started and ended with a happiness question.

Each trial of the smartphone-based experiment was randomly drawn from a list of 30 mixed trials, 60 gain trials, and 60 loss trials. The 30 mixed trials used 3 certain amounts in points (40, 55, 75) and 10 multipliers (0.2, 0.34, 0.5, 0.64, 0.77, 0.89, 1, 1.1, 1.35, 2). The 60 gain trials used 4 certain amounts (30, 35, 45, 55) and 15 multipliers (1.64, 1.7, 1.76, 1.82, 1.88, 1.94, 2, 2.06, 2.12, 2.18, 2.26, 2.4, 2.7, 3.2, 4). The 60 loss trials used the same amounts as the gain trials with 4 certain amounts (−30, −35, −45, −55) and the same 15 multipliers as used for loss trials. The maximum gain or loss for a single trial was 220 points.

fMRI Data Acquisition. All scanning was performed on a 3-Tesla Siemens Allegra scanner with a Siemens head coil at the Wellcome Trust Centre for Neuroimaging at University College London.
London. Functional images were taken with a gradient echo T2*-weighted echo-planar sequence [repetition time = 2.40 s, echo time (TE) = 30 ms, flip angle = 90°, 64 × 64 matrix, field of view = 192 mm, slice thickness = 2 mm with 1-mm gap]. A total of 40 axial slices were acquired in ascending order (in-plane resolution 3 × 3 mm). Four hundred seventy-five volumes were acquired in each of three sessions and the initial five volumes of each session were discarded to allow for steady-state magnetization. Slices were tilted at an orientation of −30° to minimize signal dropout in ventral frontal cortex. Anatomical images were T1-weighted (1 × 1 × 1 mm resolution). We also acquired a field map [double-echo FLASH, short TE = 10 ms, long TE = 12.46 ms, 3 × 3 × 3 mm resolution with 1 mm gap] for distortion correction of functional images. We used a pulse oximeter and breathing belt to collect physiological data during scanning.

**Happiness Computational Models.** We modeled moment-to-moment happiness for all ratings preceded by choices (20 per block) using models that assume an exponential decay of previous event influences and terms for certain rewards (CRs, in £), gamble expected values (EVs, average of the two possible outcomes), and reward prediction errors (RPEs, the difference between gamble outcome and EV). Alternative models included models without gamble expectations, with separate forgetting factors for different event types, with decay in prior trial influence modeled as the sum of two exponential functions, or with parameters related to the value of unchosen options. To verify that decay in previous event influence was best explained by an exponential function, happiness ratings were also regressed on separate elements of trial history. Data were modeled using events from up to seven prior trials. Our model (model 1) contained separate terms for CR, gamble EV, and gamble RPE with influences that decay exponentially over trials. Thus, writing $t$ as trial number, $w_0$ as a constant term, weights $w_1$, $w_2$, and $w_3$ to capture the influence of the three event types respectively, $0 \leq \gamma \leq 1$ as a forgetting factor that makes events in more recent trials more influential than those in earlier trials, $\text{CR}_j$ as the CR if chosen instead of a gamble on trial $j$, $\text{EV}_j$ as the EV of a gamble (average of the two possible outcomes) if chosen on trial $j$, and $\text{RPE}_j$ as the RPE [difference between the gamble reward (GR) and the gamble EV] on trial $j$ if the gamble was chosen, we get

\[
\text{Happiness}(t) = w_0 + w_1 \sum_{j=1}^{t} \gamma^{j-1} \text{CR}_j + w_2 \sum_{j=1}^{t} \gamma^{j-1} \text{EV}_j + w_3 \sum_{j=1}^{t} \gamma^{j-1} \text{RPE}_j.
\]

Models with exponential constraints were fit using nonlinear least squares using the optimization toolbox in MATLAB (MathWorks, Inc.). The forgetting factor $\gamma$ is closely related to the time constant estimated when fitting an exponential function to weights for individual trials estimated using linear regression (Fig. S1). We used one-sample $t$ tests to determine whether parameter weights were different from zero on average and we used paired $t$ tests to compare different parameter weights. In the case of the weights estimated from a single rating from each subject in the smartphone data (Fig. 3C), we used a permutation test and fit 10,000 random shuffles of the happiness ratings to generate the null distributions.

To verify that happiness depends not only on rewards but also on expectations, we fit an alternative model (model 2) in which expectation terms were omitted and $\text{GR}_j$ is the GR received on trial $j$ if the gamble was chosen:

\[
\text{Happiness}(t) = w_0 + w_1 \sum_{j=1}^{t} \gamma^{j-1} \text{CR}_j + w_2 \sum_{j=1}^{t} \gamma^{j-1} \text{EV}_j.
\]

To verify that happiness is best explained by influences that decay exponentially in time with a single forgetting factor for all event types, we fit alternative models in which influences decayed according to the sum of two exponential functions with different forgetting factors (model 3) or with separate forgetting factors for each event type (model 4).

There was a broad variability in the forgetting factor estimated in model 1 across subjects [$\gamma = 0.61 \pm 0.30$ (mean ± SD), range 0-0.97]. Thus, we also fit linear regression models to estimate the influences of previous rewards and expectations without constraining the decay in influences to take any particular functional form. We fit linear regression models with the same event types as in model 1 and with terms for one, two, or seven previous trials (models 5, 6, and 7, respectively). Average parameter estimates from models 1 and 7 are shown in Fig. S1.

The quality of fits for nine behavioral models is summarized in Table S1. There was considerable variability in how subjects used the rating scale (mean ratings SD was 16, range = 6–29). To prevent subjects with higher rating variability from having a disproportionate effect on the model comparison, we z-scored ratings before performing model fits. Because we used z-scored ratings, we also omitted the constant term $w_0$ from these fits. We evaluated the models using Bayesian model comparison techniques (1, 2). We computed Bayesian Information Criterion (BIC) values for each model fit in individual subjects and summed BIC across subjects. BIC penalizes for parameter number and the model with the lowest BIC is the preferred model. Because the relative BIC value of different models is important and not the absolute size, we also computed BIC values for each model relative to the BIC value for model 1 to simplify comparison. Model 1, with influences decaying according to a single exponential function and weights for CR, EV, and RPE, was the overall preferred model according to BIC.

The only-some-gamble-outcomes-shown behavioral experiment allowed us to verify the role of both reward expectations and RPEs in determining happiness. In this experiment, expectations can affect happiness whenever gambles are chosen but RPEs can affect happiness only when gamble outcomes are revealed. To verify that happiness depends on RPEs, we fit an alternative model that includes a term for the EV of all chosen gambles but omits the RPE term. Instead the model includes a term $\text{GR}_j$ equal to the GR received on trial $j$ if the gamble was chosen and the outcome revealed and equal to zero otherwise:

\[
\text{Happiness}(t) = w_0 + w_1 \sum_{j=1}^{t} \gamma^{j-1} \text{CR}_j + w_2 \sum_{j=1}^{t} \gamma^{j-1} \text{EV}_j^{\text{choice}} + w_3 \sum_{j=1}^{t} \gamma^{j-1} \text{GR}_j.
\]

We used an additional model to dissociate expectation effects at choice and outcome that included an additional term equal to the gamble EV when the gamble outcome was revealed and zero otherwise:

\[
\text{Happiness}(t) = w_0 + w_1 \sum_{j=1}^{t} \gamma^{j-1} \text{CR}_j + w_2 \sum_{j=1}^{t} \gamma^{j-1} \text{EV}_j^{\text{choice}} + w_3 \sum_{j=1}^{t} \gamma^{j-1} \text{GR}_j + w_4 \sum_{j=1}^{t} \gamma^{j-1} \text{EV}_j^{\text{outcome}}.
\]

If happiness is positively affected by RPEs, then because RPE is equal to $\text{GR}$ minus $\text{EV}$, the weight $w_4$ will be negative and anticorrelated with $w_3$ across subjects.
We fit two additional models that included terms related to the value of unchosen options that might capture influences on happiness of the decision difficulty or regret for not obtaining the best available outcome. Model 8 included a term for the difference between the values of the chosen and unchosen options with the EV as the gambe value. If the weight for this term is positive it might capture the relief of having an easy decision or the regret of having possibly made a poor decision. Model 9 included a term for how much better the outcome could have been if the other option had been chosen. When the certain option was chosen, this term was equal to the gamble gain amount minus the certain amount. When the gamble was chosen and lost, this term was equal to the certain amount minus the gamble loss amount. The term was zero when the subject won the gamble. This quantity relates to the potential regret that could be felt due to a decision. If regret decreases happiness, the weight for this term would be negative.

We also fit an additional four utility-based behavioral models, using established procedures (3) to estimate utilities (Table S2). Each model contained a loss aversion coefficient $\lambda$, and curvature parameters of $\alpha$ for the gain domain and $\beta$ for the loss domain assuming a power function transformation. We fit a model in which $\alpha$ and $\beta$ were constrained to be identical and a model in which they could be different. We used the following equations to transform objective gain and loss magnitudes into utilities:

$$\text{utility(gain)} = \text{gain}^\alpha$$
$$\text{utility(loss)} = -\lambda(-\text{loss})^\beta.$$  

We then fit the following model of happiness using utilities rather than objective magnitudes:

$$\text{Happiness}(t) = w_0 + \sum_{j=1}^t \gamma_j \text{CR}^{\text{utility}}_j + w_2 \sum_{j=1}^t \gamma_j \text{EV}^{\text{utility}}_j + w_3 \sum_{j=1}^t \gamma_j (\text{GR}^{\text{utility}}_j - \text{EV}^{\text{utility}}_j).$$

In the first two models, we used individual choice data to estimate the best parameters in accounting for economic preferences. Parameters $\alpha$ and $\beta$ were constrained to be identical in model 10 and were allowed to differ in model 11. The probability of gamble acceptance was computed using a noise parameter $\mu$ and the softmax equation. Parameters were fit by the method of maximum likelihood. We then applied those parameter estimates to transform objective amounts into utilities before fitting the happiness model.

We fit two additional utility-based models in which we simultaneously estimated happiness model parameter weights and utility parameters $\lambda$, $\alpha$, and $\beta$ without reference to choice data. Parameters $\alpha$ and $\beta$ were constrained to be identical in model 12 and were allowed to differ in model 13. Results including model comparisons are shown in Table S2.

**fMRI Data Analysis.** We used SPM8 (Wellcome Trust Centre for Neuroimaging) for fMRI data analysis. Images were preprocessed using standard procedures [echo planar image unwarping using field maps, slice-time correction to the first volume, motion correction, spatial transformation to the Montreal Neurological Institute (MNI) template, spatial smoothing with a Gaussian kernel (8-mm full-width at half-maximum)].

We estimated parameters of three general linear models (GLMs) using regressors for option presentation, button press, gamble outcome, happiness question, and initial button press to register a happiness response. Six additional regressors captured residual movement-related artifacts and 18 additional cardiac and respiratory regressors corrected for physiological noise. In all GLMs, the regressor for the happiness question was parametrically modulated by the z-scored happiness rating.

In the first GLM, separate regressors at option presentation and gamble outcome for the two to three trials preceding each rating were parametrically modulated by the z-scored happiness rating subsequently given at the next probe question. In the second-level analysis these two regressors were weighted equally in computing the total effect. In the second GLM, the option presentation regressor was instead parametrically modulated by chosen CR magnitude and chosen gamble EV. The gamble outcome regressor was parametrically modulated by the RPE. These parametric regressors replaced the parametric happiness rating regressors at option and outcome onset in the first GLM. In the third GLM, the RPE term was split into separate parametric regressors for GR and gamble EV, but the GLM was otherwise the same as the second GLM. Parametric regressors were not orthogonalized in the design matrix, ensuring that parameter estimates were not confounded by spurious correlations due to signals related to other regressors (4). Statistical significance was determined at the group level using a random-effects analysis. All analyses used a voxel-wise significance threshold of $P < 0.001$ and a corrected significance threshold of $P < 0.05$ based on a family-wise error (FWE) cluster-level small-volume correction centered on coordinates from previous studies. Images were thresholded at $P < 0.005$ for display purposes only.

Because previous studies indicate that the ventral striatum represents reward-related signals and the right anterior insula plays a role in interoception and emotion, our a priori hypothesis was that these areas would be involved in our study. We performed a small-volume correction using 8-mm spheres at MNI coordinates from prior studies (5, 6) (left ventral striatum: $-10, 12, -8$; right ventral striatum: $10, 12, -8$; right anterior insula: $39, 5, -14$). Further analysis was performed on regions of interest (ROIs) defined as all voxels significant in the group-level analyses at $P < 0.001$, uncorrected. Striatal parameter estimates were also extracted from an independent bilateral ROI of 6-mm spheres at the ventral striatum coordinates used for small-volume correction. In addition to using cluster-level corrections, we also computed the FWE-corrected $P$ value for peak voxels. For the relationship between happiness and neural responses during preceding events, we extracted voxels in left and right ventral striatum and performed a small-volume correction after FWE correction (left ventral striatum: $P = 0.002$; right ventral striatum: $P = 0.022$) and the effect of the happiness question was also significant in the peak voxel in the right anterior insula ($P = 0.008$).

We used the Multilevel Mediation and Moderation Toolbox in SPM (7, 8) to perform the mediation analysis. We first estimated parameters for z-scored happiness ratings for the only-gamble-outcomes-shown behavioral experiment and used the median parameter weights ($w_1, w_2, w_3, \gamma$) to make happiness predictions from behavioral data for the fMRI experiment. In each individual, we calculated the first eigenvariate for the ventral striatum ROI defined in the group-level analysis at $P < 0.001$ from the first GLM. We deconvolved this time course to estimate neural activity for each task event, and used the out-of-sample forgetting factor $\gamma$ to weight neural activity to make happiness predictions. Neural predictions were mean subtracted for each block and the predictions concatenated. The multilevel mediation analysis analyzed each of the 24 subjects (after excluding 2 subjects for excessive motion), 60 behavioral predictions, 60 neural predictions (the mediator), and 60 happiness ratings. We tested whether the neural predictions from either ventral striatum ROI mediated the relationship between the behavioral predictions and the happiness ratings (see the mediation path diagram in Fig. S5). The relation between behavioral predictions and happiness ratings controlling for the mediator (neural predictions) is referred to as path “c’’ (the
direct effect). We estimated the relationship between happiness predictions and neural predictions (path “a”) and the relationship between neural predictions and happiness ratings (path “b”) controlling for happiness predictions. Thus, path a and b identify two separable processes that contribute to happiness ratings. A mediation test (path “ab”) examines whether the inclusion of the mediator (neural predictions) explains a significant amount of the covariance between happiness predictions and happiness ratings. We used multilevel path analysis with bootstrap significance testing to determine two-tailed uncorrected P values from the bootstrap confidence intervals for the path coefficients (see ref. 8 for details on the method).


Fig. S1. Effect of previous trials on happiness ratings. (A) Mean weighting function across subjects (n = 26 subjects, 1,560 ratings) in the fMRI experiment for model 1 with influences constrained to decay exponentially. (B) Mean parameter estimates across subjects in the fMRI experiment for model 7, a linear regression with weights for seven previous trials. The time constant of an exponential function fit to parameter weights at the group or individual level is closely related to the forgetting factor γ estimated in exponential models. (C) Parameter estimates from a single happiness rating following the first two to three trials ever played by a subject (n = 18,420 subjects, 18,420 ratings) in the smartphone experiment for a linear regression with weights for three previous trials. The maximum SEM for all means is indicated for the fMRI experiment. The SEs for all parameters are indicated for the smartphone experiment.

Fig. S2. Effect of previous rewards and expectations on happiness ratings in two behavioral experiments. (A) Cumulative task earnings, happiness ratings, and happiness model fits across subjects (n = 22) in the current-earnings-always-shown behavioral experiment. (B) Cumulative task earnings, happiness ratings, and happiness model fits across subjects (n = 21) in the only-some-gamble-outcomes-shown behavioral experiment. (C) Average cumulative task earnings, happiness ratings, and happiness model fits from the first 30-trial 12-rating play from the first 200 participants to complete the smartphone experiment. Overall, participants (n = 18,420) earned 564 ± 246 points (mean ± SD), a significant increase in wealth from an initial 500 point endowment [t(18,419) = 35.2, P < 0.0001], but happiness decreased over the experiment (initial happiness: 62 ± 20, final happiness: 57 ± 23 (mean ± SD), t(18,419) = −26.2, P < 0.0001).

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Fig. S3. Happiness in subjects in the smartphone experiment with mean happiness above or below the midpoint. (A) Average cumulative task earnings and happiness ratings in participants in the smartphone experiment who both increased their wealth from an initial 500-point endowment and had a mean happiness above the midpoint \([n = 8,674, \text{happiness: } 66 \pm 13, \text{earnings: } 727 \pm 163 \text{ points (mean } \pm \text{ SD)}]\). (B) Average cumulative task earnings and happiness ratings in participants who both increased their wealth from an initial 500-point endowment and had a mean happiness below the midpoint \([n = 2,211, \text{happiness: } 42 \pm 9, \text{earnings: } 687 \pm 149 \text{ points (mean } \pm \text{ SD)}]\). Despite a very significant increase in wealth \([t(2,210) = 59.3, P < 0.0001]\), there was only a modest increase in happiness (initial happiness: \(42 \pm 17\), final happiness: \(43 \pm 19\) \([\text{mean } \pm \text{ SD})], t(2,210) = 1.9, P = 0.051\).

Fig. S4. Neural responses in an independent ROI in the ventral striatum. (A) Blood-oxygen-level-dependent (BOLD) activity in the ventral striatum at the time of task events was correlated with the same parametric task variables that explained changes in happiness (all \(P < 0.005\); Fig. 2A). (B) When the gamble RPE term was separated into its components (GR and gamble EV at outcome), BOLD was positively correlated with GR and negatively correlated with gamble EV at outcome in the same way that those variables were related to changes in happiness (all \(P < 0.05\); Fig. 2D). Error bars represent SEM.

Fig. S5. Mediation path diagram for happiness predictions from striatal activity. Happiness predictions from behavioral data were made using out-of-sample median parameter weights \((w_1 = 0.52, w_2 = 0.35, w_3 = 0.80, \gamma = 0.72)\) for subjects \((n = 21)\) in the only-some-gamble-outcomes-shown behavioral experiment. Reported happiness ratings were highly correlated with behavioral predictions \((P < 0.001; \text{median } r^2 = 0.43)\). Happiness predictions were made from the neural data in the nonindependent happiness ventral striatum ROI by weighting striatal activity by the out-of-sample forgetting factor \((\gamma = 0.72)\). Reported happiness ratings were correlated with neural predictions \((P < 0.001)\). Striatal activity showed a positive path “a” effect \((P < 0.01)\), indicating higher neural predictions when behavioral predictions were higher. Striatal activity also showed a positive path “b” effect \((P < 0.01)\) controlling for behavioral predictions, and a positive path “c’’ effect \((P < 0.001)\). There was no significant mediation (path “ab,” \(P = 0.25\)). We repeated the mediation analysis for the independent ventral striatum ROI and obtained a similar result (path a, \(P < 0.05\); path b, \(P < 0.05\); path c, \(P < 0.001\); path ab, \(P = 0.97\)). Reported happiness ratings for the independent ROI were also correlated with neural predictions \((P < 0.003)\). Mean standardized path coefficients are shown with SEs. **\(P < 0.01\), ***\(P < 0.001\).
Life happiness across sessions. Life happiness ratings were collected before the fMRI experiment and the only-some-gamble-outcomes-shown behavioral experiment (median 53 d apart; range, 3–162 d). The two measures were correlated ($r = 0.68$, $P < 0.001$, $n = 21$) and this correlation remained significant in subjects with at least 30 d between sessions ($r = 0.60$, $P < 0.05$, $n = 12$). Life happiness ratings were also correlated between the fMRI experiment and the current-earnings-always-shown behavioral experiment 14–17 mo later ($r = 0.70$, $P < 0.05$, $n = 11$). There was a weak positive relationship between life happiness and average momentary subjective well-being in the task ($r = 0.32$, $P = 0.11$, $n = 26$). Life happiness ratings from the fMRI experiment were inversely correlated with Beck Depression Inventory (BDI) scores that quantify depression-related symptoms (Spearman’s $ρ = −0.54$, $P = 0.005$, $n = 26$). There was no relationship between BDI scores and right anterior insula parameter estimates for happiness ratings ($r = −0.062$, $P = 0.77$).

Table S1. Quality of behavioral fits for happiness models for the fMRI experiment

<table>
<thead>
<tr>
<th>Model no.</th>
<th>Parameters per subject</th>
<th>Mean $r^2$</th>
<th>Median $r^2$</th>
<th>Model BIC</th>
<th>BIC – BIC$_{\text{model}_1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>4</td>
<td>0.46</td>
<td>0.49</td>
<td>−671.6</td>
<td>0.0</td>
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<tr>
<td>2</td>
<td>3</td>
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<tr>
<td>4</td>
<td>6</td>
<td>0.48</td>
<td>0.50</td>
<td>−553.4</td>
<td>118.2</td>
</tr>
<tr>
<td>5</td>
<td>3</td>
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<td>0.24</td>
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</tr>
<tr>
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<td>6</td>
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<td>0.33</td>
<td>−141.3</td>
<td>530.4</td>
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<tr>
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<td>767.1</td>
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</tr>
<tr>
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<td>0.50</td>
<td>−632.3</td>
<td>39.3</td>
</tr>
<tr>
<td>9</td>
<td>5</td>
<td>0.48</td>
<td>0.51</td>
<td>−624.0</td>
<td>47.6</td>
</tr>
</tbody>
</table>

BIC measures are summed across the 26 subjects. Model fits for model comparison were performed with z-scored happiness ratings to prevent subjects with greater rating variability from having a disproportionate impact on the results. Our model (model 1) contains separate terms for CRs, gamble EVs, and gamble RPEs with influences that decay exponentially. Model 2 omits expectations and has terms for CRs and GRs. In model 3, influences decay according to the sum of two exponential functions. In model 4, each of the three event types has a separate forgetting factor. Linear regression models with the same event types as model 1 with terms for 1, 2, or 7 previous trials (models 5, 6, and 7, respectively) were also fit. Model 8 includes a term for the difference between the value of the chosen and unchosen options using the gamble EV as the gamble option value. This parameter was not different from zero on average ($P = 0.43$). Model 9 includes a term for how much better the outcome could have been by choosing the other option (equal to zero when the outcome was the gamble gain). This quantity relates to the potential regret that could be felt due to a decision. This parameter was no different from zero on average ($P = 0.31$).
Table S2. Quality of behavioral fits for utility-based happiness models for the fMRI experiment

<table>
<thead>
<tr>
<th>Model no.</th>
<th>Parameters per subject</th>
<th>Mean $r^2$</th>
<th>Median $r^2$</th>
<th>Model BIC</th>
<th>BIC – BIC$_{\text{model}_1}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>4</td>
<td>0.46</td>
<td>0.49</td>
<td>$-671.6$</td>
<td>0.0</td>
</tr>
<tr>
<td>10</td>
<td>4*</td>
<td>0.46</td>
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</tr>
<tr>
<td>13</td>
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<td>0.49</td>
<td>0.53</td>
<td>$-439.0$</td>
<td>232.6</td>
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</tbody>
</table>

BIC measures are summed across the 26 subjects. Model fits for model comparison were performed with z-scored happiness ratings, to prevent subjects with greater rating variability from having a disproportionate impact on the results. Model 1 is identical to model 1 in Table S1. For models 10 and 11, choice data were used to estimate the best parameters for explaining economic preferences. Parameters $\alpha$ and $\beta$ were constrained to be identical in model 10 and were allowed to differ in model 11. The average model fit for model 1 was pseudo-$r^2 = 0.43$ and the mean $\pm$ SEM parameters were $\mu = 0.30 \pm 0.18$, $\lambda = 1.43 \pm 0.22$, and $\alpha = 1.02 \pm 0.06$. The average model fit for model 2 was pseudo-$r^2 = 0.47$ and the mean $\pm$ SEM parameters were $\mu = 0.25 \pm 0.11$, $\lambda = 1.70 \pm 0.27$, $\alpha = 1.05 \pm 0.05$, and $\beta = 1.01 \pm 0.06$. The quality of these fits suggests that subjects chose in a manner consistent with standard economic models. Average loss aversion coefficients greater than 1 are consistent with loss aversion in our population. We used the model parameter estimates for the individual subjects in the fMRI study to fit the utility-based happiness model.

*There were three and four additional parameters per subject for models 10 and 11, respectively, but these parameters were fit on the choice data separately and so the BIC values for computing happiness do not penalize for these additional parameters. Compared with model 1, the fit was better for 13 of the 26 subjects for model 11 and better for 12 of 26 subjects for model 12, suggesting that the extra complexity of the utility-based approach did not improve fits in the majority of subjects. Models 12 and 13, which incorporated utility parameters into the happiness model, similarly resulted in only modest improvements not justified by the increase in parameter number.

Table S3. Out-of-sample happiness model predictions

<table>
<thead>
<tr>
<th>Dataset</th>
<th>No. of subjects</th>
<th>RPE model median $r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>fMRI experiment (individual model fits)</td>
<td>26</td>
<td>0.49</td>
</tr>
<tr>
<td>Behavior: only some gamble outcomes shown (median fMRI experiment parameters)</td>
<td>21</td>
<td>0.29</td>
</tr>
<tr>
<td>Behavior: current earnings always shown (median fMRI experiment parameters)</td>
<td>22</td>
<td>0.33</td>
</tr>
<tr>
<td>The Great Brain Experiment (median fMRI experiment parameters)</td>
<td>18,420</td>
<td>0.24</td>
</tr>
</tbody>
</table>

Model fits and predictions were performed with z-scored happiness ratings. Individual model fits were estimated for data from the fMRI experiment. Median parameter weights from the fMRI experiment model fits were used to make out-of-sample predictions for the two laboratory-based behavioral experiments and the smartphone-based experiment. The results demonstrate a high degree of out-of-sample validity.