Matching mental and neural representations of value during intertemporal choice

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Humans and animals make choices every day that reflect their inherently subjective preferences. One person may prefer 20 dollars today to as much as 100 dollars in a month while another may prefer as little as 21 dollars in a month over 20 dollars today. However, despite widespread acknowledgement that the values we place on objects or actions are inherently subjective, studies of the neural mechanisms of decision-making have generally focused on relating neural activity to objective measures such as the magnitude, probability or delay associated with rewards. Here we seek to relate behaviorally derived measurements of the subjective value of future gains, a mental state, to brain activity, a neural state, in humans using functional magnetic resonance imaging. We find that activity in multiple brain regions—including ventral striatum, medial prefrontal cortex and posterior cingulate cortex—precisely tracks the subjective value of the delayed gains to individual subjects. This close similarity between the behavioral and neural responses to delayed rewards provides the first unambiguous evidence for an explicit representation of subjective value in the human brain during choice. These findings further suggest that the neural mechanism involved in choosing between rewards at different delays shows striking parallels to the purely theoretical processes posited by revealed preference theories in economics.

Since its inception in the nineteenth century, perceptual psychophysics has rested on the notion that the objective intensity of a stimulus is distinct from the subjective intensity that guides behavior.\(^1,2\) If, for example, the number of photons emitted by a light source is doubled, the perceived intensity only increases by a factor of about 0.3.\(^3\) Since the eighteenth century, economics has rested on a similar insight.\(^4\) If the gain earned for an action is doubled, human
choosers behave as if the desirability of this action has been increased by a much smaller fraction. Economic theory refers to the functions that relate objective values and subject desirabilities as revealed preferences, since perceptual value is not observed directly but rather inferred from or “revealed” by a person’s choices. While the notion that choices reflect subjective desirability is central to nearly all economic theories of decision-making, studies of the neurobiological basis of decision-making have usually focused on relating neural activity to more objective measures5-17 (but see18-24). Thus while perceptual neurobiologists have accumulated evidence that subjective sensory percepts are encoded by the nervous system, there is less evidence to suggest that subjective valuations, or revealed preferences, are anything more than useful theoretical constructs. In the current study, we set out to find evidence that the subjective value of a monetary reward as perceived by an individual human chooser is explicitly represented in the human brain. Using functional magnetic resonance imaging, we measured neural activity in conjunction with choice behavior and found a clear match between the revealed preferences of our subjects and neural activity in the ventral striatum, medial prefrontal and posterior cingulate cortex. These data provide the first unambiguous evidence for preferences as a physical mechanism for choice in the human brain, as opposed to a purely descriptive (“as if”) theoretical construct as widely proposed in economics.25,26 From an economic perspective, these findings provide evidence for a neural process strikingly similar to the purely theoretical processes employed by revealed preference theories that rest on a continuous underlying scale for subjective value (a concept often referred to as cardinal utility). From a neurobiological perspective, these findings implicate particular neural structures in the subjective valuation of outcomes during decision-making.
For a clear example of how the construct of subjective value, or revealed preference, is required to account for the choice behavior of individuals, consider decisions involving monetary gains that become available after different delays. A subject who possesses a $20 check cashable in one week might be willing to trade that check for an immediately cashable check worth as little as $18. If the $20 check is payable in one month, she might accept as little as $15 now in return for forgoing that future gain. Such behavior suggests that the immediate subjective value of the $20 gain declines quite rapidly as the imposed delay increases, a widely-studied phenomenon referred to as **temporal discounting**.\(^{27-33}\) This decline in subjective value can also differ across individuals; a second person might accept as little as $10 immediately in lieu of $20 in a month. Additionally, this decline can differ for the same individual across different magnitudes of gains.\(^{32}\) Therefore simply knowing the objective value and objective time of delivery associated with each rewards does not predict choice; amongst other things, an idiosyncratic function relating delay to subjective value is required. This person-specific function, describing the decline in subjective value with increasing delays, is called a **discount function**. While temporal discounting has been widely studied behaviorally, there have been only a few investigations of the neural mechanisms of intertemporal choice in humans.\(^{24,34}\)

Despite evidence like this that human choice can only be explained on the basis of subjective value, studies of the neural basis of decision-making have usually focused on correlations between neural activity and objective quantities in the outside world such as the magnitude, probability, or delay associated with a gain\(^5-17\) (but see\(^18-24\)). In large part, this focus on externally quantifiable decision variables has been due to a methodological problem. How can
we relate neural activity to the subjective or perceived value of an outcome, given that we can only manipulate the objective properties of any given outcome?

**Psychometric-Neurometric Comparisons**

One of the most fruitful neurobiological approaches to the study of subjective experience has been to make *psychometric-neurometric comparisons*.\(^{35,36}\) This approach, which has been used most widely in sensory neurophysiology, tests the hypothesis that a particular externally quantifiable variable influences both psychophysical and neurobiological measurements in a similar, or identical, manner. In a widely influential example of this approach, monkey subjects were trained to make a series of perceptual judgments about the motion of a visual stimulus while the activity of single neurons in cortical area MT was measured.\(^{37}\) A close match was observed between the choices made by the monkey and those predicted by a mathematically defined ideal observer of the neural activity, providing evidence that the activity of MT neurons underlay decisions about the direction of the perceived motion. Of course, this approach need not be restricted to the study of directly observable phenomena like the choices made by a subject; it can also be used to relate indirectly revealed perceptual experiences or mental states, like those postulated by psychophysical theory, to neural activity.\(^{3,35}\) Indeed, some of the earliest psychometric-neurometric experiments applied this method to show that the subjective intensity of a somatosensory stimulus and the activity in peripheral somatosensory nerves were both similar power functions of objective stimulus intensity.\(^{38,39}\) When used in this manner, a psychometric-neurometric comparison does something different from predicting behavior—it is
a test of a specific relationship between psychological and physiological states (or linking proposition, after Teller and Pugh\textsuperscript{40}). More specifically, it tests that the rate of neural activity (or some other candidate code) is linearly related to, and thus can serve as a representation of, the magnitude of the subjective experience.

Despite their successful application to a range of issues in sensory neurophysiology,\textsuperscript{35,36} psychometric-neurometric comparisons have rarely been employed in cognitive neuroscience generally, or in the study of human decision-making. Studies of human decision-making, however, seem ideally suited for employing the psychometric-neurometric approach, particularly because well-established techniques allow the measurement of both revealed preferences (in the form of utility or discount functions) and neural activity in humans. Indeed, application of this technique would seem to unlock a key point of synergy between neuroscience and economics. Economics provides quantitative models of choice behavior which posit, at a purely theoretical level, the existence of hidden or internal preferences; looking for a representation of these subjective variables in the nervous system then provides a test of both the applicability of these economic models to physiological studies of behavior, as well as of the function of different brain regions in decision-making.

In the current study, we used the psychometric-neurometric approach to determine which brain areas, if any, represent the inferred subjective value of monetary rewards to human decision-makers. Subjects made repeated choices between immediate and delayed rewards while we measured neural activity using functional magnetic resonance imaging (fMRI). We used the behavioral choice data to infer how the subjective value of monetary gains changed as a function
of delay for each individual we studied. We then used these individualized discount functions to search for brain areas where activity was correlated with the subjective value of monetary gains.

**Psychometric Results**

An initial behavioral study characterized the discount function for each of our subjects prior to obtaining any neural measurements. We used a well established procedure to reveal the inter-temporal preference curve of each subject. In essence, we performed a variant of the simple discounting experiment described above, for real monetary gains, across a range of delays. On each trial, subjects made a choice, indicating whether they preferred a fixed immediate reward or a larger reward at a delay (see Figure 1). The immediate reward was always $20, and the amount and delay of the larger reward varied randomly from trial to trial. In a single session, the amount of the larger reward was drawn from six values between $20.25- $110, and the delay from six values between 6 hours-180 days. Subjects typically made 144 choices in a single session lasting between one and two hours, and completed 4-5 of these sessions over the course of 1-6 months, the last one or two of which were performed in the MRI scanner. At the end of each session, four trials were randomly chosen and the subject was paid the amount and delay combination they preferred on those trials. Payments were made using commercially available pre-paid debit cards that could automatically be incremented at the time of the payment.

We then used this series of choices to estimate the discount function *individually* for each subject (Figure 2). Sorting the trials by the delay to the larger reward, we constructed plots indicating the fraction of trials on which the subject preferred the larger reward at that delay, as a function of
the objective value of the larger reward (Figure 2a), and fit these data with a logistic function. This allowed us to estimate the point of subjective equality, also known as the isopreference point, for each delay duration. This was the monetary amount at which the increased size of the delayed reward exactly compensated for the imposed delay, rendering it equivalent in subjective value to an immediately available $20. When the delayed reward was less than this amount, subjects chose the immediate gain of $20, and when the delayed reward was more, they chose the larger delayed reward. The objective value of these indifference points rose, of course, as the imposed delays increased (Figure 2b). To compute from these indifference points the fraction by which subjective gains decline as a function of delay, we divided each indifference point into $20. The resulting plot (Figure 2c) is a discount curve for each subject, which describes how the subjective value of monetary rewards decreases as a function of delay for that subject over these amounts. These individual preference curves, which reveal in the monetary domain how a subjective quantity (in this case value) changes as a function of an objective variable (in this case delay), are directly analogous to perceptual functions in the sensory domain.

Consistent with previous behavioral findings in a range of species, the shape of the discount function for all subjects was well-characterized by a hyperbolic function (for behavioral data acquired during scanning sessions ranged from .84 to .98, with a median of .95) of the form:

\[ SV = \frac{1}{1 + kD} \]

where SV is the subjective value (expressed as the proportion of its immediate value), D is delay (in days), and k is a subject-specific constant. (While other functional forms, which include
additional parameters, may also fit these data well, we use the above single-parameter model for simplicity. Figure S1 shows that this hyperbolic model fits the data better than an alternative single-parameter exponential model.) The best fitting k parameter, or discount rate, varied widely across subjects, from a minimum of 0.0005 to a maximum of 0.1189 (Figure 2d). To give a sense of this range, a k of 0.0005 implies that for our most patient subject an immediate gain of $20 was less preferrable than a gain of $20.50 in a month. In contrast, a k of 0.1189 implies that for our most impulsive subject an immediate gain of $20 was more preferrable than a gain of $90 in a month. We thus observed significant heterogeneity in the discount rates of our subjects.

**Neurometric Results**

For ten subjects whose discount functions remained stable across three preliminary sessions, we also gathered neural data during an additional one or two sessions in which they performed this task. We then used the behaviorally-derived preference curve of each individual subject, which estimates how subjective value declines with delay, to find areas where neural activity was correlated with subjective value in each subject. For each trial, we calculated the subjective value of the delayed reward presented on that trial by multiplying the objective value of the delayed reward offered on that trial by the discount fraction inferred behaviorally for that delay. We then fit a regression model to our neural data that computed the correlation, across all of the trials presented to a subject, between the neural activation at each voxel in the brain and the revealed subjective value of the delayed reward offered on each trial. Since the immediate reward was held constant on all trials, this analysis would be sensitive to areas where average regional neural
activity, as measured by fMRI, tracked either the sum of the subjective values of both rewards, the difference in subjective value of the two rewards, or the ratio of subjective values of the two rewards.

Figure 3 shows the results of this analysis for three individual subjects. The top row shows the discount functions for these three subjects, which vary from one of our most patient subjects ($k = 0.0042$) to our most impulsive subject ($k = 0.1189$). Even though the subjective value of delayed rewards differs dramatically between these three subjects, the same regions exhibit activity correlated with subjective value in each subject. As can be seen in the second row, early in the trial (timepoints 4-6, roughly corresponding to the visual presentation of the delayed reward option), we found a correlation between the subjective value of the delayed reward and activity in the ventral striatum, medial prefrontal cortex, and posterior cingulate cortex. Critically, this analysis identified the same regions in different subjects because these regions exhibited a different pattern of activity across subjects, with the idiosyncratic pattern of neural activity in each subject being predicted by the idiosyncratic revealed preferences of that subject. This can be seen more clearly by looking at activity in the correlated regions as a function of the imposed delay associated with the larger-later reward, as shown in the third and fourth rows of Figure 3 for the same three subjects. For the most impulsive subject (right hand panels) these regions were identified because both the subjective value of the delayed gains and the neural activity associated with those delayed gains decreased sharply, and in a similar manner, as a function of delay. For the less impulsive subject (shown on the left), these measurements remained correlated but decreased much more gradually in both the neural and behavioral domains.
As shown in Figure 4a, the correlation between neural activity and subjective value observed in single subjects was also present at the group level. This correlation between subject-specific subjective value and brain activation reached our significance threshold (voxel-wise p < 0.005, with a spatial extent > 150 mm$^3$) in the ventral striatum, medial prefrontal cortex, and posterior cingulate cortex (as well as other areas, see Table S1). Subjective value also accounted for activity in these regions better than the objective reward characteristics or the subjects’ choices. As shown in Figure 4b, neural activity in these areas was correlated to a lesser extent with the amount of the larger-later reward, the inverse of the imposed delay to the larger-later reward, or the subject’s choice (with increased activity when the subject chose the delayed reward). However, the strength and spatial extent of the correlation with subjective value was much larger than that of any of these other variables. Finally, activity in these regions could not be better explained by any systematic deviation from the subjects’ behavioral discount rates. We took the averaged timecourse from the correlated regions in each individual subject, and refit the regression model while allowing the discount rate parameter (k) to vary. As shown in Figure S2, there is a close correspondence between the discount rate estimated from the neural data in this way and the discount rate estimated behaviorally, confirming that the voxels identified through the correlation analysis do indeed show a precise psychometric-neurometric match.

These results suggest that the ventral striatum, medial prefrontal cortex and posterior cingulate cortex represent the subjective value of different outcomes early in each trial, while subjects are making their decision after the delayed option is revealed. One remaining concern, however, is that these regions might also contain additional voxels correlated with a variety of discount rates in each subject (for example, see $^{24}$), which would have been missed by the previous analysis.
Thus it would be even more compelling to show that a psychometric-neurometric match existed across all value-sensitive voxels in these regions. In order to define value-sensitive ROIs in these areas in an unbiased manner, we selected voxels within each region which either demonstrated increased activity for (1) trials involving the largest amount of the delayed reward, compared to those involving the smallest amount (collapsed across all delays) or (2) trials involving the most immediate delay to the delayed reward, compared to those involving the longest delay (collapsed across all amounts). Example ROIs from a single subject are shown in Figure 5a. Figure 5b-d shows the fit of the neurometric function for each of the three ROIs in this subject, as determined by allowing the discount rate parameter (k) in the model of the neural data to vary. In an analagous manner to the psychometric analysis, this fit determines the tradeoffs between amount and delay that lead to equivalent neural activities. For this subject, the neurometric function in the ventral striatum shows a close match to psychometric function measured behaviorally. In medial prefrontal cortex, the neurometric function for this subject is somewhat less steep than the psychometric function, while in posterior cingulate cortex, the neurometric function is somewhat steeper than the psychometric function. Figure 5e-f plots the discount rate estimated from the neurometric function against the discount rate estimated behaviorally for each subject. While these data are expectedly noisier than those shown above, on average, the discount rate estimated from neurometric function tracks the discount rate estimated behaviorally. The $R^2$ of the model assuming a perfect psychometric-neurometric match, $\log(\text{neural } k) = \log(\text{behavioral } k)$—which has no free parameters—was .06, .34 and .05, respectively, in each ROI. In all cases the slope and intercept of the best-fit line were not significantly different from one and zero, respectively, the values predicted by a psychometric-neurometric match.
Discussion

Revealed preference theories in economics posit that individuals making choices behave as if different options have different subjective values.\textsuperscript{4,25,26} To date, there has been little evidence that subjective or perceived value is anything more than a useful construct in explaining choice behavior. In this study, we have demonstrated that neural activity in several brain regions—particularly the ventral striatum, medial prefrontal cortex and posterior cingulate cortex—precisely tracks the revealed subjective value of delayed monetary rewards. Our results suggest that choosing between immediate and delayed monetary rewards actually involves, at a physical level, comparing the neurally encoded subjective values of available rewards. Our data further suggest that a common neural currency metrically encodes the values of these revealed preferences.

The fact that the ventral striatum, medial prefrontal cortex and posterior cingulate cortex encode the subjective value of delayed monetary rewards, whether those rewards are selected by pressing a button (on half of the trials we studied) or by taking no action (on the other half of the trials we studied) suggests a role for these regions in the valuation of reward outcomes rather than in the generation of action. If this is correct, then it seems likely that these areas serve as functional inputs to structures that represent the subjective value of particular actions like the movement-related areas of the posterior parietal cortex.\textsuperscript{5,20} Indeed, when a motor action is required to select the delayed reward, we found additional regions in parietal cortex and motor
areas of frontal cortex where activity later in the trial was correlated with the subjective value of the delayed reward.

Our suggestion that the ventral striatum, medial prefrontal cortex and posterior cingulate cortex play a role in the valuation of outcomes is consistent with previous findings. Medial prefrontal and posterior cingulate cortex have been implicated in a “baseline” cortical system important for behavior mediated by internal or self-referential goals.\textsuperscript{41,42} Furthermore, all three regions, and particularly the ventral striatum, play a role in reward processing. Both functional imaging and single unit recording studies have demonstrated increased activity in these regions after subjects receive a reward or immediately preceding an expected reward, and this activity correlates with the reward size or probability.\textsuperscript{6-15,17} This reward-related activity is also greater for more preferred rewards, compared to less preferred rewards.\textsuperscript{18,19,21,43} While fewer studies have looked at reward sensitivity while subjects are freely choosing between different options, in the absence of immediate reward feedback, these three areas have previously been shown to exhibit greater activity during choices involving large gains than during choices involving smaller gains.\textsuperscript{13,16,44,45} Our results extend these findings by showing that the ventral striatum, medial prefrontal, and posterior cingulate cortex exhibit differential activity while subjects are making choices, and that this activity precisely tracks the subjective value of possible rewards.

We should note that these same three regions have previously been implicated in intertemporal choice by McClure and colleagues\textsuperscript{34}; however, our data suggest a very different conclusion regarding the role of these regions in intertemporal choice. Those authors hypothesized that these regions form an impulsive neural system that exclusively values immediate rewards and which
does not encode long-delayed rewards. Following an earlier proposal from the economic
literature, they proposed that the hyperbolic-like form of the human discount function was
produced by the action of this impulsive system working in concert with a more patient system,
based in lateral prefrontal cortex and posterior parietal cortex, that values both immediate and
delayed rewards. Their conclusion was based principally on the finding that the ventral striatum,
medial prefrontal cortex and posterior cingulate cortex show greater activity for choices
involving an immediate reward than for choices involving only delayed rewards. However, this
empirical finding (which our observations confirm) is also compatible with the hypothesis that
activity in these regions represents the subjective value of rewards at all delays, since the
subjective value of immediate rewards is greater than that of delayed rewards for all subjects.
Thus our minimal observation that activity in these regions varies as the delayed reward changes
(and the immediate reward remains constant) falsifies the hypothesis that the ventral striatum,
medial prefrontal cortex, and posterior cingulate cortex are exclusively involved in valuing
immediate rewards. Furthermore, the close correspondence seen in our complete dataset
between changes in neural activity and changes in the subjective value of the delayed reward, as
determined by subject-specific discount functions reconstructed for each subject from the
behavioral data, provides strong support for the alternative hypothesis that activity in these
regions represents the subjective value of rewards at all delays.

In the current study we adapted the method of psychometric-neurometric comparisons for use
with fMRI. This approach has been widely used in neurophysiological studies of perceptual
systems in animals, but has been used less often in more cognitive paradigms or in human
neurophysiological studies. Our results suggest that psychometric-neurometric comparisons
should prove fruitful in these other arenas, and particularly in studies of the neural mechanisms of decision-making. Such an approach holds promise for contributing to the fields of both neuroscience and economics. On the neuroscience side, this method provides a means to link the function of different neural systems with the hidden variables and processes posited in models of decision-making. On the economic side, this method provides preliminary evidence that the physical mechanism underlying intertemporal choice is strikingly similar to the class of revealed preference models resting on cardinal utility that have been proposed by many economic theorists over the last half century. This similarity cannot, of course, be used to prove or disprove theoretical economic models that make no predictions about the physical mechanisms of choice, nor does it speak to the logical status of such models. However, these data raise the possibility that theoretical models which do rest on demonstrable physiological foundations may prove more robust and extensible than those that lack such a foundation.

**Methods**

*Subjects.* Twelve paid volunteers participated in the experiment (7 women, 5 men, all right-handed, mean age = 21.7 years). Ten of these volunteers (6 women, 4 men, mean age = 21.2 years) participated in both the behavioral and scanning portions of the experiment. The two remaining volunteers participated only in the behavioral sessions; these participants were not scanned because their inter-temporal preferences were not stable within and across sessions. One subject’s choices occasionally reversed more than once as the delayed amount increased, thus precluding estimation of an indifference point; the other subject had significantly different
discount rates across the last two behavioral sessions. All subjects gave informed consent in accordance with the procedures of the Institutional Review Board of the New York University.

**Imaging.** Imaging data were collected using a Siemens Allegra 3T head-only scanner equipped with a head coil from Nova Medical (Wakefield, MA). T2*-weighted, BOLD functional images were collected with a standard EPI sequence (TR=2 s, TE=30 ms, 35 axial slices, 3x3x3 mm, 64x64 matrix in a 192 mm field-of-view), and high-resolution, T1-weighted anatomical images were collected using an MPRAGE sequence (TR=2.5 s, TE=3.93 ms, TI=900 ms, flip angle=8°, 144 sagittal slices, 1x1x1 mm, 256x256 matrix in a 256 mm field-of-view). Subjects’ heads were stabilized with foam padding, and stimuli were back-projected through a mirror attached to the head coil. Presentation of stimuli was controlled by a computer running in-house software, and responses were collected using a specially-constructed button box.

**Task.** On each trial, subjects chose between a smaller amount of money to be paid immediately and a larger amount to be paid at a later time (see Figure 1). The smaller immediate amount was $20 on all trials, and subjects were told this reference option at the beginning of the session. Only the variable delayed option was presented on the screen during each trial. This option was constructed using one of six delays (varying from 6 hours to 180 days) and one of six amounts (varying from $20.25 to $110). Thus subjects saw a total of 36 unique choices within each experimental session. Each of these choices was presented four times, for a total of 144 trials per session. Delays were the same for every subject (but changed slightly across sessions to prevent subjects from encountering exactly the same choices in each session); amounts were chosen for each subject individually according to their behavior in previous sessions (and thus also varied across session) to ensure that an approximately equal number of immediate and delayed options
would be chosen. Subjects indicated their choices by releasing a single button. For half of each session, subjects released the button to select the fixed immediate reward, and for half of the session subjects released the button to select the variable delayed reward.

Each subject participated in 3 behavioral sessions outside the scanner and 1-2 scanning sessions. Each behavioral session lasted about an hour, and each scanning session lasted about two hours. Subjects completed all sessions over 1-6 months, with consecutive sessions separated by at least 3 days.

*Payment Mechanism.* Since there is evidence that people’s decisions involving real gains may differ from their decisions involving hypothetical gains, subjects’ choices in the experiment had actual monetary consequences. At the end of each session (except for the very first behavioral session, which subjects were told explicitly involved only hypothetical choices), subjects rolled dice to randomly select four trials from the 144 that they had just completed, and were paid according to their choice on those four selected trials (in addition to a flat $10/hour payment for participating in behavioral sessions or $15/hour payment for participating in scanning sessions). To reduce any uncertainty the subjects may have had about payments they had selected in the future or concerns they may have had about difficulties, or transaction costs associated with receiving future payments, all payments were made using commercially available pre-paid debit cards. These debit cards could be used to make purchases or withdraw money in the same way as any national credit card. Subjects were issued a card after their first visit to the laboratory, and monetary payments were loaded onto the card at the time specified by the subjects’ actual choices. Subjects were also notified by email when these payments were loaded. Using this method, future payments were immediately available at the time of delivery,
and required no more effort from the subject than any other purchase or monetary transaction. This mechanism also allowed us to monitor subjects’ consumption of the monetary rewards. Part of the rationale for having subjects participate in multiple sessions was so they became familiar with and confident in this payment mechanism. By the time of the first scanning session, all subjects had received at least one delayed payment from a previous session. After this session, eight of ten subjects rated their confidence in receiving future payments on a nine-point scale as a nine (the highest), while the other two subjects rated their confidence as an eight.

Data Analysis. Functional data from the scanner were co-registered with each subject’s high-resolution anatomical scan, adjusted for staggered slice acquisition, corrected for any head movement, high-pass filtered to remove low frequency drift in the BOLD signal, and normalized into Talaraich space. For group-level random effects analysis, data were also spatially smoothed with a kernel of 8 mm. Data were first analyzed with multiple linear regression within the framework of the general linear model (GLM). Our basic model included twelve covariates that fit the mean activity, across all trials, for each of the first twelve timepoints in a trial, and twelve that fit the deviations from the mean at each timepoint that were correlated with the subjective value of the delayed reward across trials. Thus the fMRI signal in trial $i$ at timepoint $j$ was modeled as:

$$BOLD_{ij} = \beta_{1,j} \left( \frac{A_i}{(1+kD_i)} - SV_{mean} \right) + \beta_{2,j} + \beta_3 + \epsilon [2];$$

where $A$ is the amount of the delayed reward, $D$ is the imposed delay, $k$ is the subject-specific discount rate estimated behaviorally, and $SV_{mean}$ is the mean subjective value.
\[
\left(\sum A_i/(1+kD_i)\right)/\text{number of trials}.\]

The overlays in Figures 3 and 4 plot \(t\)-values for the contrast testing the significance of the subjective value correlation for timepoints 4-6 (\(\beta_{1,4-6}\)). The fit of this model was also used to scale the y-axis of the neurometric functions in Figures 3 and 5, by calculating the predicted fMRI signal for discount fractions of zero and one. The other models reported in Figure 4 replaced the subjective value term (the term multiplied by \(\beta_{1,j}\) in [2]) with either the mean-centered amount of the larger-later reward, the mean-center inverse of the imposed delay to the larger-later reward, or a categorical variable for the subject’s choice.

To quantitatively evaluate the extent of the psychometric-neurometric match, anatomical regions-of-interest were defined in individual subjects in medial prefrontal cortex, posterior cingulate cortex and ventral striatum. The medial prefrontal ROI included all cortex along the midline anterior to the genu of the corpus callosum, the posterior cingulate ROI included the posterior third of the cingulate gyrus, and the ventral striatal ROI included the ventral portions of the caudate and putamen. Voxels were then selected within each ROI according to their functional responsiveness. For Figure S2, this selection was based on a correlation (\(p<.05\), uncorrected) with subjective value at timepoints 4-6, while for Figure 5 this selection was based on exhibiting greater activity during timepoints 4-6 for either (1) the largest amount compared to the smallest amount of the delayed reward across all delays or (2) the shortest delay compared to the longest delay to the delayed reward across all amounts. Activity was then averaged across all selected voxels within an ROI and the sum of activity at timepoints 4-6 for each trial was calculated. Then, to estimate the neurometric discount rate, the resulting data were fit with a reduced, nonlinear form of the model above, using an iterative algorithm that minimized least squared error:
\[ \text{BOLD}_i = \beta_1((A_i/(1+\beta_k D_i)) - \text{SV}_{\text{mean}}) + \beta_2 + \varepsilon [3]. \]
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of reward preference involves dissociable responses in human ventral midbrain and


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Supplementary Information has been provided.

Acknowledgements. We thank A. Bisin, A. Caplin, and D. Heeger for their comments on an earlier version of this paper. This work was supported by grants from the National Institutes of Health (to J.K. and P.G.), the McDonell Foundation (to P.G.), and the Seaver Foundation.

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Figure Legends

Figure 1. **Intertemporal choice task.** On each trial, subjects chose between an immediate and a delayed reward. The sequence of events within a trial is shown. The immediate reward was the same ($20) on every trial and was never presented visually during the session. A red dot signaled the beginning of a trial, after which the delayed reward was presented for 2 s and then replaced again by the red dot. Subjects then had 6 s to consider their choice. Throughout the trial, subjects were required to hold down a button, and they indicated their decision by continuing to hold or by releasing the button when the dot turned green. For half of the session, subjects released the button to indicate a choice of the delayed reward; for the other half of the session, a button release indicated a choice of the immediate reward. Trials during which subjects released the button before the green light appeared were abandoned and removed from the analysis. The inter-trial interval was 2 s for behavioral sessions and 12 s for scanning sessions.

Figure 2. **Subject-specific discount functions.** (a) Choice data from one subject (JH) during a single session. Points are color-coded according to the delay of the delayed reward, and denote the fraction of times the subject chose the delayed reward over an immediate reward of $20 as a function of the objective value of the delayed reward. The smooth curves are logistic functions fit to these data (similar results were obtained using linear interpolation between the amounts where subjects’ choices switched). Points and curves from different delays are slightly offset so that all the data is visible. (b) Indifference points, estimated in (a), re-plotted as a function of the delay of the delayed reward. These indifference amounts increase as the delay to the delayed reward increases, and this relationship is well fit by a line with a fixed intercept of $20. Delays
are color-coded as in (a). (c) Indifference points from (b), divided into $20 to reveal this subject’s discount function. The subjective value of a delayed reward, expressed as a fraction of its objective value, declines with increasing delay, and this relationship is well fit by a hyperbolic function with one free parameter. Delays are color-coded as in (a). (d) Discount functions for each of our ten subjects, reconstructed from the behavioral data for a single scanning session. Both indifference points and fits are shown for six subjects, and are color-coded by subject. The fit in black is from the subject shown in Figure 2(a), while the fits in gray are from the three subjects shown in Figure 3(a-c). We observed significant heterogeneity in discount functions across subjects.

**Figure 3. Single subject analyses showing areas correlated with subjective value.** Data from three subjects (HM, RA, and CH) are shown. (a-c) Discount functions for these three subjects, as measured behaviorally during a scanning session. These subjects ranged from one of our more patient subjects (HM) to our most impulsive subject (CH). (d-f) Correlation maps between subjective value and neural activity for each subject. Even though these subjects differ markedly in how subjective value changes with delay, the same areas are correlated with subjective value as measured in each subject. The sagittal overlay shows areas of correlation in medial prefrontal cortex and posterior cingulate cortex in each subject, and the coronal overlay shows areas of correlation in the ventral striatum for each subject. The correlations are calculated for a window 6-10 s into the trial (timepoints 4-6), which roughly corresponds to a hemodynamic response to the presentation of the delayed reward. These maps are thresholded at p<.01 (uncorrected), and the color scale ranges from this value to p<.05 (FDR-corrected). Data are shown in radiological convention, with the right hemisphere shown on the left. (g-i) Data from the areas of correlation
in (d-f), replotted to show that this analysis identifies a different pattern of neural activity in each subject. Data are averaged over all voxels in the three correlated areas, and re-plotted as trial averages. Trial averages are color-coded by the delay of the delayed reward. The window of the correlation analysis is shown in gray. The largest standard error is shown on the right in black. For each subject, activity in the window declines as the delay increases, but this decline is steeper for the more impulsive subjects. (j-k) Data from (g-i), averaged over the 6-10s window and re-plotted as a function of delay.

Figure 4. Group analysis showing areas correlated with subjective value. (a) Results from a random-effects group analysis are shown. Areas where neural activity was correlated with subjective value during the 6-10s window are shown as an overlay on the mean anatomical image from our subjects. Areas of correlation can be seen in the medial prefrontal and posterior cingulate cortex (sagittal and axial images) and in the ventral striatum (coronal image). (b) Ventral striatum, medial prefrontal cortex and posterior cingulate cortex are better correlated with subjective value than with the amount of the delayed reward, the inverse delay of the delayed reward, or the choice of the subject. Areas correlated with subjective value from a random-effects group analysis are shown in yellow, areas correlated with the amount of the delayed reward are shown in red, areas correlated with the inverse delay of the delayed reward are shown in purple, and areas correlated with the choice of the subject (delayed > immediate) are shown in green.
Figure 5. Region-of-interest analysis demonstrating a psychometric-neurometric match. 

(a) Regions of interest in the ventral striatum, medial prefrontal cortex and posterior cingulate cortex are shown for one subject (HM, same subject shown in Figure 3(a),(d),(g),and (j)). Voxels were selected within these three anatomically-defined regions which showed either (1) greater activity (p < .05, uncorrected) for trials involving the largest objectively valued delayed reward compared to trials involving the smallest objectively valued delayed reward or (2) greater activity (p < .05, uncorrected) for trials involving the shortest delay to the delayed reward compared to those involving the longest delay. (b-d) A psychometric-neurometric comparison is shown for each ROI for this subject. Points in black are the mean BOLD activity and standard error, summed over the 6-10 s window, plotted as a function of the delay of the delayed reward. The solid black line represents average fitted activity at each delay, where the discount parameter k is allowed to vary. The dotted black lines represent the average fitted activity at each delay for only those trials involving the smallest ($20.25) or largest ($42) objective reward value. The solid red line represents the average fitted activity at each delay where the discount parameter k is fixed at 0.0042, which is the k parameter measured behaviorally for this subject. In the ventral striatum, the discount parameter k estimated from the neural data is 0.0051, which is a close match to behavioral estimate for this subject. In the medial prefrontal cortex, the discount parameter k estimated from the neural data is 0.0012, which is less steep than the behavioral estimate for this subject. In posterior cingulate cortex, the discount parameter k estimated from the neural data is 0.0164, which steeper than the behavioral estimate for this subject. (e-g) For each of the three regions-of-interest, the discount parameter k estimated from the neural data for each of the ten subjects is plotted as a function of that subject’s behaviorally estimated k. The gray point represents the data shown in (b-d). Note the log scale, which is necessitated by the
non-normal distribution of k values. In black is the best fitted line through these data. In red is a line with a slope of 1 and an intercept of 0 (representing a perfect match between the neural and behavioral estimates).
Supplementary Materials

**Supplementary Table 1.** Location of significant correlations with subjective value in the group random-effects analysis.

<table>
<thead>
<tr>
<th>Anatomical Description</th>
<th>Center-of-Gravity (Talaraich)</th>
<th>Size (mm$^3$)</th>
<th>Peak Location (Talaraich)</th>
<th>Peak z-score</th>
</tr>
</thead>
<tbody>
<tr>
<td>Medial Prefrontal/ Rostral Anterior Cingulate* (BA 32/24)</td>
<td>-1, 37, 18</td>
<td>2837</td>
<td>-3, 38, 13</td>
<td>3.90</td>
</tr>
<tr>
<td>Posterior Cingulate* (BA 31/23)</td>
<td>-5, -39, 36</td>
<td>1435</td>
<td>-3, -43, 37</td>
<td>3.92</td>
</tr>
<tr>
<td>Superior Temporal Sulcus/ TPO Junction (BA 39/19)</td>
<td>-55, -62, 15</td>
<td>1512</td>
<td>-48, -67, 13</td>
<td>3.52</td>
</tr>
<tr>
<td>Ventral Striatum</td>
<td>-12, 5, 0</td>
<td>239</td>
<td>-12, 5, 1</td>
<td>3.40</td>
</tr>
<tr>
<td>Dorsal Insula, extending into Pulvinar</td>
<td>-27, -22, 17</td>
<td>202</td>
<td>-21, -25, 13</td>
<td>3.43</td>
</tr>
<tr>
<td>Middle Temporal Gyrus (BA 21/22)</td>
<td>63, -41, -2</td>
<td>201</td>
<td>69, -40, 1</td>
<td>3.06</td>
</tr>
</tbody>
</table>

All clusters >150 mm$^3$ at a significance threshold of p < .005 are reported. Regions marked with an asterisk are also >150 mm$^3$ at a significance threshold of p < .001. The significance test was a $t$-test on the subjective value regressors for timepoints 4-6 in a trial (a window 6-10 s after the start of the trial).
Supplementary Figure Legends

Figure S1. Plotted is the $R^2$ of the best fitting one parameter hyperbolic discount function versus the $R^2$ of the best fitting one parameter exponential discount function. Each point represents the fit from a single subject’s data from a single behavioral or scanning session. Both functions account for the data well, since the majority of points have an $R^2$ above .9 for both functions. However, the majority of points lie above the main diagonal indicating that the hyperbolic function better accounts for the observed data in most cases.

Figure S2. (a-c) For each of the three regions-of-interest, the discount parameter $k$ estimated from the neural data for each of the ten subjects is plotted as a function of that subject’s behaviorally estimated $k$. Regions-of-interest were defined in ventral striatum, medial prefrontal cortex, and posterior cingulate cortex in individual subjects, and voxels were selected based on a correlation with subjective value ($p < .05$, uncorrected). Note the log scale, which is necessitated by the non-normal distribution of $k$ values. In black is the best fitted line through these data, while in red is a line with a slope of 1 and an intercept of 0 (representing a match between the neural and behavioral estimates).
Figure S2

(a) Ventral Striatum

(b) Medial Prefrontal

(c) Posterior Cingulate

Logarithmic plots showing the relationship between Neural k and Behavioral k for different brain regions:

- **Ventral Striatum**
  - Equation: \( \log(\text{neur}) = 1.03 \log(\text{beh}) - 0.36; R^2 = 0.75 \)
  - \( \log(\text{neur}) = \log(\text{beh}); R^2 = 0.66 \)

- **Medial Prefrontal**
  - Equation: \( \log(\text{neur}) = 1.12 \log(\text{beh}) + 0.37; R^2 = 0.66 \)

- **Posterior Cingulate**
  - Equation: \( \log(\text{neur}) = 1.20 \log(\text{beh}) + 0.73; R^2 = 0.63 \)
  - \( \log(\text{neur}) = \log(\text{beh}); R^2 = 0.60 \)