# Episodic Future Thinking Reduces Reward Delay Discounting through an Enhancement of Prefrontal-Mediotemporal Interactions

Jan Peters[1],* and Christian Büchel[1]
[1]NeuroimageNord, Department of Systems Neuroscience, University Medical Center Hamburg-Eppendorf, Hamburg 20246, Germany
*Correspondence: j.peters@uke.uni-hamburg.de
DOI 10.1016/j.neuron.2010.03.026

## SUMMARY

Humans discount the value of future rewards over time. Here we show using functional magnetic resonance imaging (fMRI) and neural coupling analyses that episodic future thinking reduces the rate of delay discounting through a modulation of neural decision-making and episodic future thinking networks. In addition to a standard control condition, real subject-specific episodic event cues were presented during a delay discounting task. Spontaneous episodic imagery during cue processing predicted how much subjects changed their preferences toward more future-minded choice behavior. Neural valuation signals in the anterior cingulate cortex and functional coupling of this region with hippocampus and amygdala predicted the degree to which future thinking modulated individual preference functions. A second experiment replicated the behavioral effects and ruled out alternative explanations such as date-based processing and temporal focus. The present data reveal a mechanism through which neural decision-making and prospection networks can interact to generate future-minded choice behavior.

## INTRODUCTION

The consequences of choices are often delayed in time, and in many cases it pays off to wait. While agents normally prefer larger over smaller rewards, this situation changes when rewards are associated with costs, such as delays, uncertainties, or effort requirements. Agents integrate such costs into a value function in an individual manner. In the hyperbolic model of delay discounting (also referred to as intertemporal choice), for example, a subject-specific discount parameter accurately describes how individuals discount delayed rewards in value (Green and Myerson, 2004; Mazur, 1987). Although the degree of delay discounting varies considerably between individuals, humans in general have a particularly pronounced ability to delay gratification, and many of our choices only pay off after months or even years. It has been speculated that the capacity for episodic future thought (also referred to as mental time travel or prospective thinking) (Bar, 2009; Schacter et al., 2007; Szpunar et al., 2007) may underlie the human ability to make choices with high long-term benefits (Boyer, 2008), yielding higher evolutionary fitness of our species.

At the neural level, a number of models have been proposed for intertemporal decision-making in humans. In the so-called β-δ model (McClure et al., 2004, 2007), a limbic system (β) is thought to place special weight on immediate rewards, whereas a more cognitive, prefrontal-cortex-based system (δ) is more involved in patient choices. In an alternative model, the values of both immediate and delayed rewards are thought to be represented in a unitary system encompassing medial prefrontal cortex (mPFC), posterior cingulate cortex (PCC), and ventral striatum (VS) (Kable and Glimcher, 2007; Kable and Glimcher, 2010; Peters and Büchel, 2009). Finally, in the self-control model, values are assumed to be represented in structures such as the ventromedial prefrontal cortex (vmPFC) but are subject to top-down modulation by prefrontal control regions such as the lateral PFC (Figner et al., 2010; Hare et al., 2009). Both the β-δ model and the self-control model predict that reduced impulsivity in intertemporal choice, induced for example by episodic future thought, would involve prefrontal cortex regions implicated in cognitive control, such as the lateral PFC or the anterior cingulate cortex (ACC).

Lesion studies, on the other hand, also implicated medial temporal lobe regions in decision-making and delay discounting. In rodents, damage to the basolateral amygdala (BLA) increases delay discounting (Winstanley et al., 2004), effort discounting (Floresco and Ghods-Sharifi, 2007; Ghods-Sharifi et al., 2009), and probability discounting (Ghods-Sharifi et al., 2009). Interactions between the ACC and the BLA in particular have been proposed to regulate behavior in order to allow organisms to overcome a variety of different decision costs, including delays (Floresco and Ghods-Sharifi, 2007). In line with these findings, impairments in decision-making are also observed in humans with damage to the ACC or amygdala (Bechara et al., 1994, 1999; Manes et al., 2002; Naccache et al., 2005).

Along similar lines, hippocampal damage affects decision-making. Disadvantageous choice behavior has recently been documented in patients suffering from amnesia due to hippocampal lesions (Gupta et al., 2009), and rats with hippocampal damage show increased delay discounting (Cheung and Cardinal, 2005; Mariano et al., 2009; Rawlins et al., 1985). These observations are of particular interest given that hippocampal
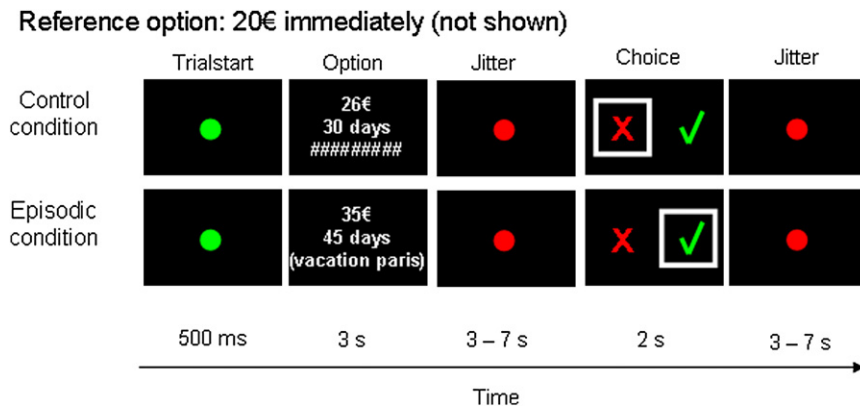
**Figure 1. Behavioral Task**

During fMRI, subjects made repeated choices between a fixed immediate reward of 20€ and larger but delayed amounts. In the control condition, amounts were paired with a waiting time only, whereas in the episodic condition, amounts were paired with a waiting time and a subject-specific verbal episodic tag indicating to the subjects which event they had planned at the respective day of reward delivery. Events were real and collected in a separate testing session prior to the day of scanning.

damage impairs the ability to imagine novel experiences (Hassabis et al., 2007). Based on this and a range of other studies, it has recently been proposed that hippocampus and parahippocampal cortex play a crucial role in the formation of vivid event representations, regardless of whether they lie in the past, present, or future (Schacter and Addis, 2009). The hippocampus may thus contribute to decision-making through its role in self-projection into the future (Bar, 2009; Schacter et al., 2007), allowing an organism to evaluate future payoffs through mental simulation (Johnson and Redish, 2007; Johnson et al., 2007). Future thinking may thus affect intertemporal choice through hippocampal involvement.

Here we used model-based fMRI, analyses of functional coupling, and extensive behavioral procedures to investigate how episodic future thinking affects delay discounting. In Experiment 1, subjects performed a classical delay discounting task (Kable and Glimcher, 2007; Peters and Büchel, 2009) that involved a series of choices between smaller immediate and larger delayed rewards, while brain activity was measured using fMRI. Critically, we introduced a novel episodic condition that involved the presentation of episodic cue words (*tags*) obtained during an extensive prescan interview, referring to real, subject-specific future events planned for the respective day of reward delivery. This design allowed us to assess individual discount rates separately for the two experimental conditions, allowing us to investigate neural mechanisms mediating changes in delay discounting associated with episodic thinking. In a second behavioral study, we replicated the behavioral effects of Experiment 1 and addressed a number of alternative explanations for the observed effects of episodic tags on discount rates.

## RESULTS

### Experiment 1: Prescan Interview

On day 1, healthy young volunteers (n = 30, mean age = 25, 15 male) completed a computer-based delay discounting procedure to estimate their individual discount rate (Peters and Büchel, 2009). This discount rate was used solely for the purpose of constructing subject-specific trials for the fMRI session (see Experimental Procedures). Furthermore, participants compiled a list of events that they had planned in the next 7 months (e.g., vacations, weddings, parties, courses, and so forth) and

rated them on scales from 1 to 6 with respect to personal relevance, arousal, and valence. For each participant, seven subject-specific events were selected such that the spacing between events increased with increasing delay to the episode, and that events were roughly matched based on personal relevance, arousal, and valence. Multiple regression analysis of these ratings across the different delays showed no linear effects (relevance: p = 0.867, arousal: p = 0.120, valence: p = 0.977, see Figure S1 available online). For each subject, a separate set of seven delays was computed that was later used as delays in the control condition. Median and range for the delays used in each condition are listed in Table S1 (available online). For each event, a label was selected that would serve as a verbal tag for the fMRI session.

### Experiment 1: fMRI
#### Behavioral Results

On day 2, volunteers performed two sessions of a delay discounting procedure while fMRI was measured using a 3T Siemens Scanner with a 32-channel head-coil. In each session, subjects made a total of 118 choices between 20€ available immediately and larger but delayed amounts. Subjects were told that one of their choices would be randomly selected and paid out following scanning, with the respective delay. Critically, in half the trials, an additional subject-specific episodic tag (see above, e.g., "vacation paris" or "birthday john") was displayed based on the prescan interview (see Figure 1) indicating which event they had planned on the particular day (episodic condition), whereas in the remaining trials, no episodic tag was presented (control condition). Amount and waiting time were thus displayed in both conditions, but only the episodic condition involved the presentation of an additional subject-specific event tag. Importantly, nonoverlapping sets of delays were used in the two conditions. Following scanning, subjects rated for each episodic tag how often it evoked episodic associations during scanning (frequency of associations: 1, never; to 6, always) and how vivid these associations were (vividness of associations: 1, not vivid at all; to 6, highly vivid; see Figure S1). Additionally, written reports were obtained (see Supplemental Information). Multiple regression revealed no significant linear effects of delay on postscan ratings (frequency: p = 0.224, vividness: p = 0.770). We averaged the postscan ratings across events
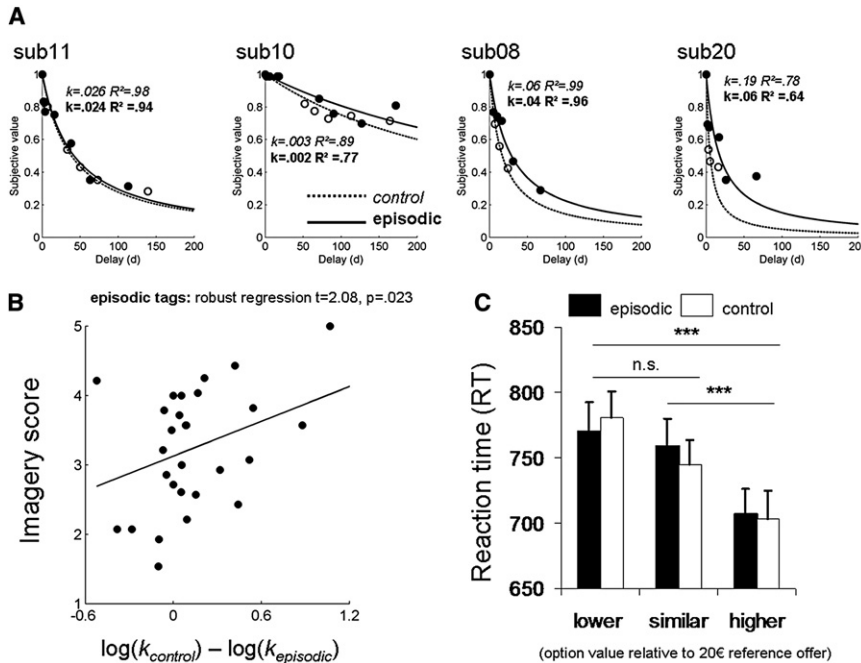
**Figure 2. Behavioral Data from Experiment 1**

Shown are experimentally derived discount functions from the fMRI session for four exemplary participants (A), correlation with imagery scores (B), and reaction times (RTs) (C). (A) Hyperbolic functions were fit to the indifference points separately for the control (dashed lines) and episodic (solid lines, filled circles) conditions, and the best-fitting k-parameters (discount rates) and $R^2$ values are shown for each subject. The log-transformed difference between discount rates was taken as a measure of the effect of the episodic tags on choice preferences. (B) Robust regression revealed an association between log-differences in discount rates and imagery scores obtained from postscan ratings (see text). (C) RTs were significantly modulated by option value (main effect value p < 0.001) with faster responses in trials with a value of the delayed reward higher than the 20€ reference amount. Note that although seven delays were used for each condition, some data points are missing, e.g., only five delay indifference points for the episodic condition are plotted for sub20. This indicates that, for the two longest delays, this subject never chose the delayed reward. ***p < 0.005. Error bars = SEM.

and the frequency/vividness dimensions, yielding an "imagery score" for each subject.

Individual participants' choice data from the fMRI session were then analyzed by fitting hyperbolic discount functions to subject-specific indifference points to obtain discount rates (k-parameters), separately for the episodic and control conditions (see Experimental Procedures). Subjective preferences were well-characterized by hyperbolic functions (median $R^2$ episodic condition = 0.81, control condition = 0.85). Discount functions of four exemplary subjects are shown in Figure 2A. For both conditions, considerable variability in the discount rate was observed (median [range] of discount rates: control condition = 0.014 [0.003–0.19], episodic condition = 0.013 [0.002–0.18]). To account for the skewed distribution of discount rates, all further analyses were conducted on the log-transformed k-parameters. Across subjects, log-transformed discount rates were significantly lower in the episodic condition compared with the control condition ($t_{(29)}$ = 2.27, p = 0.016), indicating that participants' choice behavior was less impulsive in the episodic condition. The difference in log-discount rates between conditions is henceforth referred to as the episodic tag effect. Fitting hyperbolic functions to the median indifference points across subjects also showed reduced discounting in the episodic condition (discount rate control condition = 0.0099, episodic condition = 0.0077). The size of the tag effect was not related to the discount rate in the control condition (p = 0.56).

We next hypothesized that the tag effect would be positively correlated with postscan ratings of episodic thought (imagery scores, see above). Robust regression revealed an increase in the size of the tag effect with increasing imagery scores (t = 2.08, p = 0.023, see Figure 2B), suggesting that the effect of the tags on preferences was stronger the more vividly subjects imagined the episodes. Examples of written postscan reports

are provided in the Supplemental Results for participants from the entire range of imagination ratings. We also correlated the tag effect with standard neuropsychological measures, the Sensation Seeking Scale (SSS) V (Beauducel et al., 2003; Zuckerman, 1996) and the Behavioral Inhibition Scale/Behavioral Approach Scale (BIS/BAS) (Carver and White, 1994). The tag effect was positively correlated with the experience-seeking subscale of the SSS (p = 0.026) and inversely correlated with the reward-responsiveness subscale of the BIS/BAS scales (p < 0.005).

Repeated-measures ANOVA of reaction times (RTs) as a function of option value (lower, similar, or higher relative to the reference option; see Experimental Procedures and Figure 2C) did not show a main effect of condition (p = 0.712) or a condition × value interaction (p = 0.220), but revealed a main effect of value ($F_{(1.8, 53.9)}$ = 16.740, p < 0.001). Post hoc comparisons revealed faster RTs for higher-valued options relative to similarly (p = 0.002) or lower valued options (p < 0.001) but no difference between lower and similarly valued options (p = 0.081).

### FMRI Data

FMRI data were modeled using the general linear model (GLM) as implemented in SPM5. Subjective value of each decision option was calculated by multiplying the objective amount of each delayed reward with the discount fraction estimated behaviorally based on the choices during scanning, and included as a parametric regressor in the GLM. Note that discount rates were estimated separately for the control and episodic conditions (see above and Figure 2), and we thus used condition-specific k-parameters for calculation of the subjective value regressor. Additional parametric regressors for inverse delay-to-reward and absolute reward magnitude, orthogonalized with respect to subjective value, were included in the GLM.
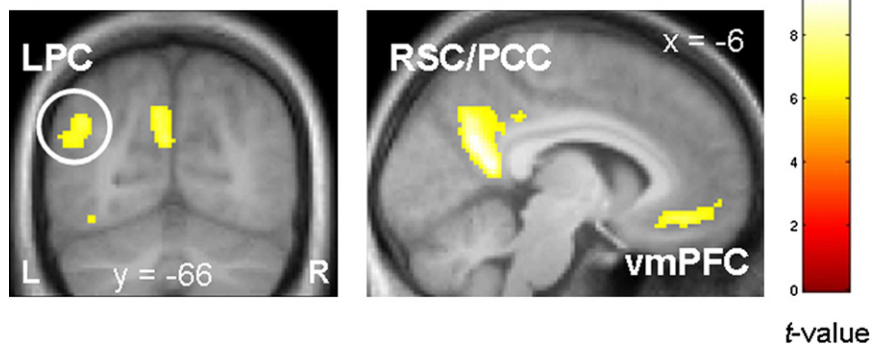
Episodic > control condition: categorical analysis



**Figure 3. Categorical Effect of Episodic Tags on Brain Activity**
Greater activity in lateral parietal cortex (left) and posterior cingulate/retrosplenial and ventromedial prefrontal cortex (right) was observed in the episodic condition compared with the control condition. p < 0.05, FWE-corrected for whole-brain volume.

### Episodic Tags Activate the Future Thinking Network

We first analyzed differences in the condition regressors without parametric modulation. Compared to those of the control condition, BOLD responses to the presentation of the delayed reward in the episodic condition yielded highly significant activations (corrected for whole-brain volume) in an extensive network of brain regions previously implicated in episodic future thinking (Addis et al., 2007; Schacter et al., 2007; Szpunar et al., 2007) (see Figure 3 and Table S2), including retrosplenial cortex (RSC)/ PCC (peak MNI coordinates: −6, −54, 14, peak z value = 6.26), left lateral parietal cortex (LPC, −44, −66, 32, z value = 5.35), and vmPFC (−8, 34, −12, z value = 5.50).

### Distributed Neural Coding of Subjective Value

We then replicated previous findings (Kable and Glimcher, 2007; Kable and Glimcher, 2010; Peters and Büchel, 2009) using a conjunction analysis (Nichols et al., 2005) searching for regions showing a positive correlation between the height of the BOLD response and subjective value in the control and episodic conditions in a parametric analysis (Figure 4A and Table S3). Note that this is a conservative analysis that requires that a given voxel exceed the statistical threshold in both contrasts separately. This analysis revealed clusters in the lateral orbitofrontal cortex (OFC, −36, 50, −10, z value = 4.50) and central OFC (−18, 12, −14, z value = 4.05), bilateral VS (right: 10, 8, 0, z value = 4.22; left: −10, 8, −6, z value = 3.51), mPFC (6, 26, 16, z value = 3.72), and PCC (−2, −28, 24, z value = 4.09), representing subjective (discounted) value in both conditions.

We next analyzed the neural tag effect, i.e., regions in which the subjective value correlation was greater for the episodic condition as compared with the control condition (Figure 4B and Table S4). This analysis revealed clusters in the left LPC (−66, −42, 32, z value = 4.96,), ACC (−2, 16, 36, z value = 4.76), left dorsolateral prefrontal cortex (DLPFC, −38, 36, 36, z value = 4.81), and right amygdala (24, 2, −24, z value = 3.75). Finally, we performed a triple-conjunction analysis, testing for regions that were correlated with subjective value in both conditions, but in which the value correlation increased in the episodic condition. Only left LPC showed this pattern (−66, −42, 30, z value = 3.55, see Figure 4C and Table S5), the same region that we previously identified as delay-specific in valuation (Peters and Büchel, 2009). There were no regions in which the subjective value correlation was greater in the control condition when compared with the episodic condition at p < 0.001 uncorrected.

### ACC Valuation Signals and Functional Connectivity Predict Interindividual Differences in Discount Function Shifts

We next correlated differences in the neural tag effect with interindividual differences in the size of the behavioral tag effect. To this end, we performed a simple regression analysis in SPM5 on the single-subject contrast images of the neural tag effect (i.e., subjective value correlation episodic > control) using the behavioral tag effect [log($k_{control}$) − log($k_{episodic}$)] as an explanatory variable. This analysis revealed clusters in the bilateral ACC (right: 18, 34, 18, z value = 3.95, p = 0.021 corrected, left: −20, 34, 20, z value = 3.52, Figure 5, see Table S6 for a complete list). Coronal sections (Figure 5C) clearly show that both ACC clusters are located in gray matter of the cingulate sulcus.

Because ACC-limbic interactions have previously been implicated in the control of choice behavior (Floresco and Ghods-Sharifi, 2007; Roiser et al., 2009), we next analyzed functional coupling with the right ACC from the above regression contrast (coordinates 18, 34, 18, see Figure 6A) using a psychophysiological interaction analysis (PPI) (Friston et al., 1997). Note that this analysis was conducted on a separate first-level GLM in which control and episodic trials were modeled as 10 s miniblocks (see Experimental Procedures for details). We first identified regions in which coupling with the ACC changed in the episodic condition compared with the control condition (see Table S7) and then performed a simple regression analysis on these coupling parameters using the behavioral tag effect as an explanatory variable. The tag effect was associated with increased coupling between ACC and hippocampus (−32, −18, −16, z value = 3.18, p = 0.031 corrected, Figure 6B) and ACC and left amygdala (−26, −4, −26, z value = 2.95, p = 0.051 corrected, Figure 6B, see Table S8 for a complete list of activations). The same regression analysis in a second PPI with the seed voxel placed in the contralateral ACC region from the same regression contrast (−20, 34, 22, see above) yielded qualitatively similar, though subthreshold, results in these same structures (hippocampus: −28, −32, −6, z value = 1.96, amygdala: −28, −6, −16, z value = 1.97).

### Experiment 2

We conducted an additional behavioral experiment to address a number of alternative explanations for the observed effects of tags on choice behavior. First, it could be argued that episodic
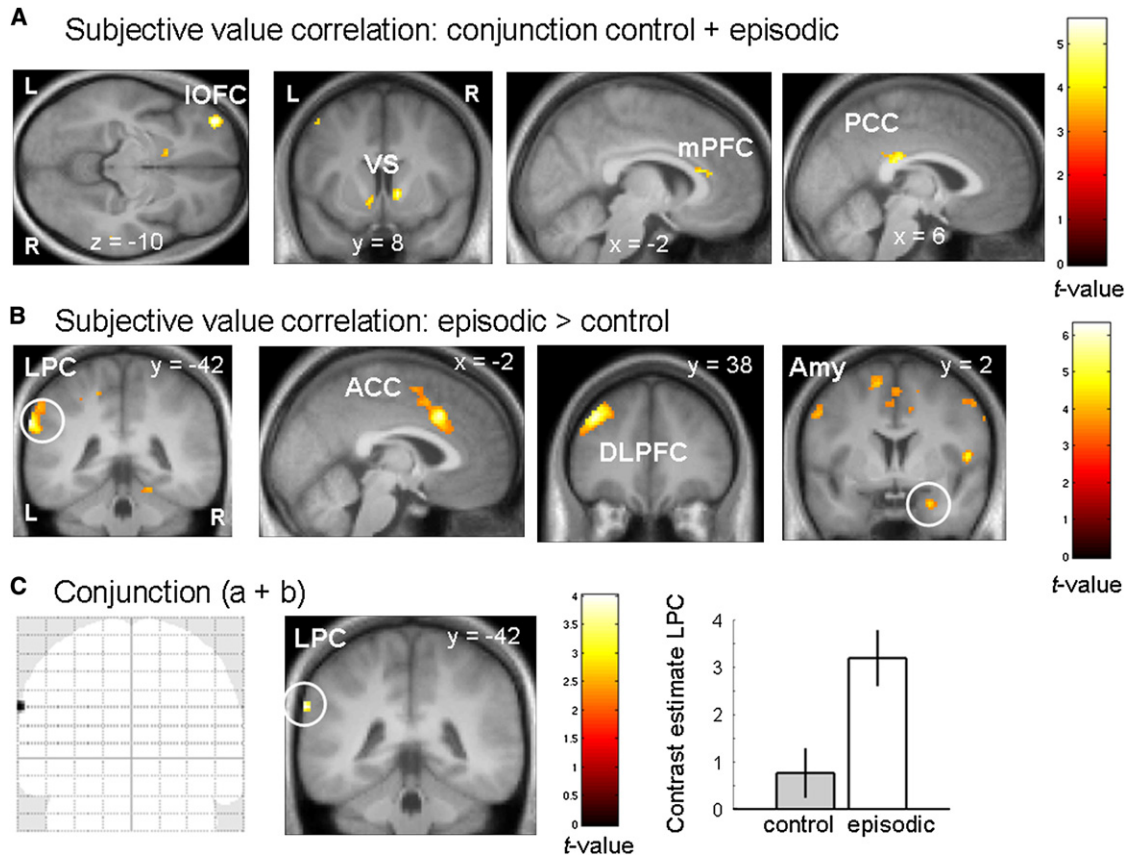
**Figure 4. Neural Representation of Subjective Value (Parametric Analysis)**

(A) Regions in which the correlation with subjective value (parametric analysis) was significant in both the control and the episodic conditions (conjunction analysis) included central and lateral orbitofrontal cortex (OFC), bilateral ventral striatum (VS), medial prefrontal cortex (mPFC), and posterior cingulate cortex (PCC), replicating previous studies (Kable and Glimcher, 2007; Peters and Büchel, 2009).

(B) Regions in which the subjective value correlation was greater for the episodic compared with the control condition included lateral parietal cortex (LPC), anterior cingulate cortex (ACC), dorsolateral prefrontal cortex (DLPFC), and the right amygdala (Amy).

(C) A conjunction analysis revealed that only LPC activity was positively correlated with subjective value in both conditions, but showed a greater regression slope in the episodic condition. No regions showed a better correlation with subjective value in the control condition. Error bars = SEM.

All peaks are significant at p < 0.001, uncorrected; (A) and (B) are thresholded at p < 0.001 uncorrected and (C) is thresholded at p < 0.005, uncorrected for display purposes.

tags increase subjective certainty that a reward would be forthcoming. In Experiment 2, we therefore collected postscan ratings of reward confidence. Second, it could be argued that events, always being associated with a particular date, may have shifted temporal focus from delay-based to more date-based processing. This would represent a potential confound, because date-associated rewards are discounted less than delay-associated rewards (Read et al., 2005). We therefore now collected postscan ratings of temporal focus (date-based versus delay-based). Finally, Experiment 1 left open the question of whether the tag effect depends on the temporal specificity of the episodic cues. We therefore introduced an additional experimental condition that involved the presentation of subject-specific *temporally unspecific* future event cues. These tags (henceforth referred to as unspecific tags) were obtained by asking subjects to imagine events that could realistically happen to them in the next couple of months, but that were not directly tied to a particular point in time (see Experimental Procedures).

### Episodic Imagery, Not Temporal Specificity, Reward Confidence, or Temporal Focus, Predicts the Size of the Tag Effect

In total, data from 16 participants (9 female) are included. Analysis of pretest ratings confirmed that temporally unspecific and specific tags were matched in terms of personal relevance, arousal, valence, and preexisting associations (all p > 0.15). Choice preferences were again well described by hyperbolic functions (median $R^2$ control = 0.84, unspecific = 0.81, specific = 0.80). We replicated the parametric tag effect (i.e., increasing effect of tags on discount rates with increasing posttest imagery scores) in this independent sample for both temporally specific (p = 0.047, Figure 7A) and temporally unspecific (p = 0.022, Figure 7A) tags, showing that the effect depends on future thinking, rather than being specifically tied to the temporal specificity of the event cues. Following testing, subjects rated how certain they were that a particular reward would actually be forthcoming. Overall, confidence in the payment procedure was high
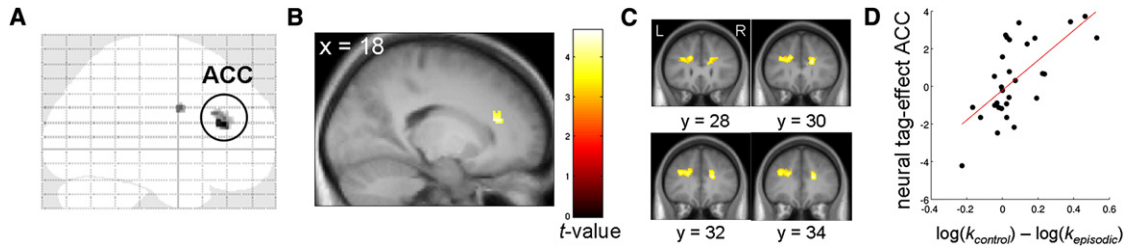
**Figure 5. Correlation between the Neural and Behavioral Tag Effect**
(A) Glass brain and (B and C) anatomical projection of the correlation between the neural tag effect (subjective value correlation episodic > control) and the behavioral tag effect (log difference between discount rates) in the bilateral ACC (p = 0.021, FWE-corrected across an anatomical mask of bilateral ACC). (C) Coronal sections of the same contrast at a liberal threshold of p < 0.01 show that both left and right ACC clusters encompass gray matter of the cingulate gyrus. (D) Scatter-plot depicting the linear relationship between the neural and the behavioral tag effect in the right ACC. (A) and (B) are thresholded at p < 0.001 with 10 contiguous voxels, whereas (C) is thresholded at p < 0.01 with 10 contiguous voxels.

(Figure 7B), and neither unspecific nor specific tags altered these subjective certainty estimates (one-way ANOVA: $F_{(2,45)} = 0.113$, p = 0.894). Subjects also rated their temporal focus as either delay-based or date-based (see Experimental Procedures), i.e., whether they based their decisions on the delay-to-reward that was actually displayed, or whether they attempted to convert delays into the corresponding dates and then made their choices based on these dates. There was no overall significant effect of condition on temporal focus (one-way ANOVA: $F_{(2,45)} = 1.485$, p = 0.237, Figure 7C), but a direct comparison between the control and the temporally specific condition showed a significant difference ($t_{(15)} = 3.18$, p = 0.006). We therefore correlated the differences in temporal focus ratings between conditions (control: unspecific and control: specific) with the respective tag effects (Figure 7D). There were no correlations (unspecific: p = 0.71, specific: p = 0.94), suggesting that the observed differences in discounting cannot be attributed to differences in temporal focus.

### High-Imagery, but Not Low-Imagery, Subjects Adjust Their Discount Function in an Episodic Context
For a final analysis, we pooled the samples of Experiments 1 and 2 (n = 46 subjects in total), using only the temporally specific tag data from Experiment 2. We performed a median split into low- and high-imagery participants according to posttest imagery scores (low-imagery subjects: n = 23 [15/8 Exp1/Exp2], imagery range = 1.5–3.4, high-imagery subjects: n = 23 [15/8 Exp1/Exp2], imagery range = 3.5–5). The tag effect was significantly greater than 0 in the high-imagery group ($t_{(22)} = 2.6$, p = 0.0085, see Figure 7D), where subjects reduced their discount rate by on

average 16% in the presence of episodic tags. In the low-imagery group, on the other hand, the tag effect was not different from zero ($t_{(22)} = 0.573$, p = 0.286), yielding a significant group difference ($t_{(44)} = 2.40$, p = 0.011).

## DISCUSSION

We investigated the interactions between episodic future thought and intertemporal decision-making using behavioral testing and fMRI. Experiment 1 shows that reward delay discounting is modulated by episodic future event cues, and the extent of this modulation is predicted by the degree of spontaneous episodic imagery during decision-making, an effect that we replicated in Experiment 2 (episodic tag effect). The neuroimaging data (Experiment 1) highlight two mechanisms that support this effect: (1) valuation signals in the lateral ACC and (2) neural coupling between ACC and hippocampus/amygdala, both predicting the size of the tag effect.

The size of the tag effect was directly related to posttest imagery scores, strongly suggesting that future thinking significantly contributed to this effect. Pooling subjects across both experiments revealed that high-imagery subjects reduced their discount rate by on average 16% in the episodic condition, whereas low-imagery subjects did not. Experiment 2 addressed a number of alternative accounts for this effect. First, reward confidence was comparable for all conditions, arguing against the possibility that the tags may have somehow altered subjective certainty that a reward would be forthcoming. Second, differences in temporal focus between conditions (date-based
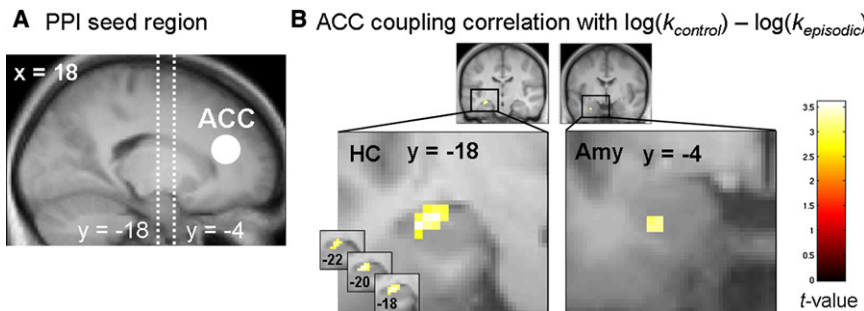


**Figure 6. Results of the Psychophysiological Interaction Analysis**
(A) The seed for the psychophysiological interaction (PPI) analysis was placed in the right ACC (18, 34, 18).
(B) The tag effect was associated with increased ACC-hippocampal coupling (p = 0.031, corrected across bilateral hippocampus) and ACC-amygdala coupling (p = 0.051, corrected across bilateral amygdala). Maps are thresholded at p < 0.005, uncorrected for display purposes and projected onto the mean structural scan of all participants; HC, hippocampus; Amy, Amygdala; rACC, right anterior cingulate cortex.
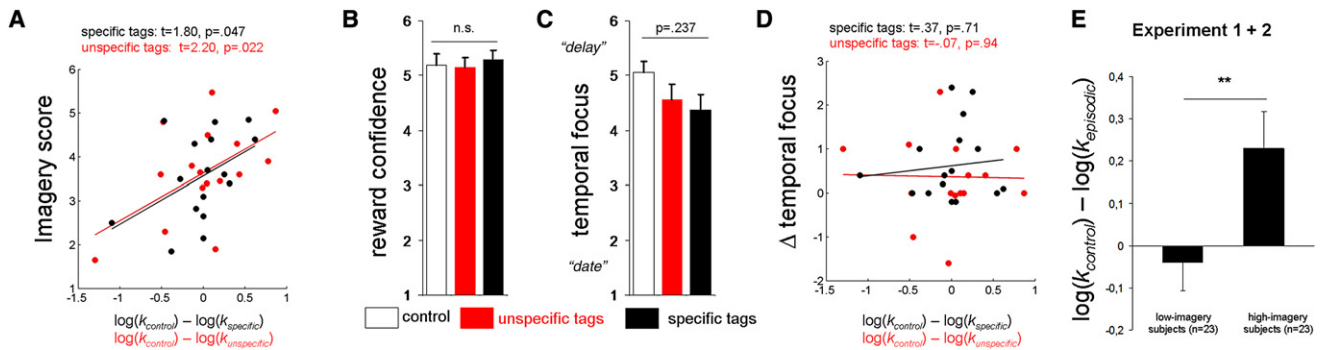
**Figure 7. Behavioral Data from Experiment 2**

(A) Log-differences in discount rates were positively correlated with postscan imagery scores, replicating Experiment 1. This effect was observed both for temporally unspecific future events (red, p = 0.022) and temporally specific events (black, p = 0.047). One-way ANOVA across conditions revealed no differences in postscan ratings of reward confidence (B) and temporal focus (C, delay-based versus date-based; see Results section). Furthermore, differences in temporal focus between control/unspecific and control/specific conditions were not associated with the respective log-differences in discount rates (D), suggesting that differences in temporal focus are unlikely to underlie the observed differences in discount rates. Median-split analysis (E) pooling data from Exp. 1 and Exp. 2 shows that reduced discounting in the episodic condition occurred in high-imagery subjects (n = 23) but not low-imagery subjects (n = 23). **p = 0.01. Error bars = SEM.

versus delay-based) were unrelated to the tag effect, arguing against a date-based processing account. Finally, the temporal specificity of event tags is not a necessary prerequisite for an effect on choice behavior. Like temporally specific tags, temporally unspecific tags exerted a comparable, imagery-dependent influence on choice behavior, supporting the notion that episodic thought, rather than the temporal specificity that is provided by events that are linked to a specific point in time, underlies the observed effects. Nonetheless, similar mechanisms may underlie the decrease in discounting reported for date-based processing relative to that of delay-based processing (Read et al., 2005) and the tag effect. For example, by focusing attention on the reward outcome rather than the delay, date-based processing may result in a more vivid reward anticipation, thereby increasing the subjective value.

We did not obtain postscan imagery ratings of the control condition, and it is conceivable that some degree of future thinking may have occurred in the control condition as well. The observed association of shifts in the value function with imagery scores nonetheless suggests that, over and above a possible role of future thought in influencing the rate of discounting in the control condition, this process significantly modulated the degree to which preferences (and neural activity) changed in the episodic *relative* to the control condition. It should also be noted that discounting can be affected by factors such as utility, one example being the magnitude effect, reflecting the fact that low-magnitude rewards are discounted more steeply than high-magnitude rewards (Green and Myerson, 2004; Green et al., 1997). In the present experiments, temporally specific and unspecific tags affected discount functions, but they may do so by modulating discounting per se (i.e., rewards paired with tags appear closer in time, thereby increasing the subjective value), the utility of future rewards, or even the interaction of discounting and utility. Future studies are necessary to disentangle these different possibilities.

The robustness of the present fMRI data is indicated by two important replications. First, we replicated previous findings

regarding the neural systems coding for subjective value in the context of intertemporal choice (Kable and Glimcher, 2007; Kable and Glimcher, 2010; Peters and Büchel, 2009; Pine et al., 2009). Second, compared with the control condition, the episodic condition was associated with robust activations in an extensive network previously implicated in episodic thinking (Schacter et al., 2007), i.e., LPC, mPFC, and RSC/PCC. Participants were not instructed to use mental imagery, suggesting that the evoked associations occurred spontaneously and, as reflected in the postscan ratings, with considerable between-subject heterogeneity. This is in line with postscan debriefings, where many participants reported that associations were evoked in a spontaneous and automatic manner. Nonetheless, in line with previous findings (Peters et al., 2009), spontaneous associations resulted in a robust recruitment of the same neural systems involved in effortful elaboration (Addis et al., 2008, 2007). Notably, PCC showed both valuation and categorical episodic effects. This region contributes to a range of cognitive phenomena, including memory (Vann et al., 2009), valuation (Peters and Büchel, 2009), and strategy selection (Pearson et al., 2009), making a precise functional characterization of this region difficult.

Turning to the possible neural mechanisms underlying the tag effect, we observed an upregulation of neural value signals in the LPC. This was the only region coding for value in both conditions, but more so in the episodic condition. We have previously found the same LPC region to code for subjective value specifically in the context of delay discounting (as opposed to probability discounting) (Peters and Büchel, 2009). These findings are in line with electrophysiological studies reporting value computations in neurons in the monkey parietal cortex (Dorris and Glimcher, 2004; Platt and Glimcher, 1999). Nonetheless, for a number of reasons we believe that this upregulation of value representations in the LPC is unlikely to underlie the tag effect. It has recently been suggested that lateral (ventral) parietal cortex activity may reflect attention to bottom-up activated memory content (Cabeza et al., 2008) or internal representations in

general (Wagner et al., 2005). Such attentional processes are likely to also occur when tag-related associations are spontaneously evoked in the episodic condition, and the saliency of these representations may be greater for high-value compared with low-value options, thus giving rise to the differences in value regression slopes in the LPC. Such an attentional account of the LPC data is also in line with the observation that these effects were not significantly modulated by interindividual differences in the shift of the discount function, suggesting an all-or-none type effect. These considerations therefore argue against a causal role of the LPC in modulating the tag effect.

Second, regions in which value signals were observed in the episodic, but not the control, condition, included the right amygdala, ACC, and DLPFC. The amygdala involvement may be related to the positive valence of the events (Sharot et al., 2007), although this region is traditionally assumed to be more sensitive to negative affect (Phan et al., 2004). DLPFC and ACC support various forms of decision-making (Rushworth and Behrens, 2008; Tanaka et al., 2004) including intertemporal choice (Figner et al., 2010; Kim et al., 2008; McClure et al., 2004, 2007). Given the role of frontal regions in cognitive control (Miller and Cohen, 2001), one could speculate that such cognitive operations are additionally recruited during valuation in the episodic condition, an interpretation that may be compatible with both the β-δ model and the self-control model. However, some caution is warranted because the present effects in the DLPFC and ACC mostly reflect differences in parametric value effects between conditions, whereas the "δ-areas" from the β-δ model (McClure et al., 2004, 2007) and the self-control areas in lateral PFC (Figner et al., 2010; Hare et al., 2009) have been identified using categorical fMRI analyses or behavioral data from transcranial magnetic stimulation studies. Our findings do show, however, that the neural representation of subjective value is not necessarily confined to mPFC, PCC, and VS, as reported previously (Kable and Glimcher, 2007; Peters and Büchel, 2009), but can extend to lateral PFC (Camus et al., 2009; Kim et al., 2008) and ACC in some decision contexts.

Finally, our analyses of individual differences speak directly to the neural mechanisms mediating the observed shifts in the delay discount function. Value signals in bilateral ACC predicted differences in discount rates between conditions. This is in line with data implicating the ACC in reward-based decision-making, including adaptive decision-making in which action values change dynamically (Rushworth and Behrens, 2008; Walton et al., 2007), choice in settings that require cognitive control over strong innate behavioral tendencies (De Martino et al., 2006; Roiser et al., 2009), and decisions involving cost-benefit computations (Floresco and Ghods-Sharifi, 2007). Also, ACC activity when people think about their futures self-correlated with a behavioral measure of delay discounting (Ersner-Hershfield et al., 2009). Our data thus suggest that the ACC supports the flexible adaptation of the value function to changes in decision context (such as the presence or absence of different episodic settings), with greater ACC involvement accompanying greater adjustments in preference functions.

Greater shifts in the discount function were also associated with increased ACC-hippocampal/amygdala neural coupling, mirroring the finding of increased ACC-amygdala coupling

when subjects choose counter to the framing of a decision option (Roiser et al., 2009). Based on analysis of relatively high resolution functional images, we suggest that the activation is located mainly in the BLA. This supports the observation of BLA involvement (Ghods-Sharifi et al., 2009; Winstanley et al., 2004) and joint ACC-BLA involvement (Floresco and Ghods-Sharifi, 2007) in the incorporation of decision costs into choice behavior. Reciprocal connections between the BLA and mPFC (Carmichael and Price, 1995; McDonald, 1991; McDonald et al., 1996) are likely to mediate these functional interactions.

In addition, we also observed increased functional coupling between ACC and hippocampus with increasing shifts in the discount function. Hippocampal neurons may modulate medial prefrontal information processing through unidirectional projections (Carmichael and Price, 1995; Thierry et al., 2000), which in some cases jointly target the amygdala and mPFC (Ishikawa and Nakamura, 2006). These functional prefrontal-hippocampal interactions are of particular interest in light of a number of recent findings. Rodents with hippocampal lesions show increased impulsive choice in delay discounting tasks (Cheung and Cardinal, 2005; Mariano et al., 2009; Rawlins et al., 1985). Furthermore, it has been argued that the hippocampus may support decision-making processes through its role in mentally simulating potential future outcomes (Johnson et al., 2007), providing downstream prefrontal regions with a prediction signal regarding episodic aspects of a decision outcome (Johnson and Redish, 2007). Enhanced ACC-hippocampal coupling may therefore reflect the degree to which episodic predictions (Bar, 2009; Schacter et al., 2007) are incorporated into prefrontal decision-making circuits, and thus predict the degree of shift in the discount function. In line with these ideas, prefrontal-hippocampal interactions were recently implicated in supporting the incorporation of conceptual information into decision-making processes (Kumaran et al., 2009).

Psychological accounts of decision-making have been proposed (Weber and Johnson, 2009), and the tag effect accords well with such accounts, because it reflects interactions between prospective cognition and choice. Importantly, our data support such psychological considerations by suggesting a plausible neural mechanism that may mediate such an interaction. In this view, hippocampal episodic predictions (Schacter and Addis, 2009) influence preferences and choice through modulating information processing in prefrontal regions such as the ACC.

To conclude, we describe a behavioral effect in intertemporal decision-making, namely that episodic tags presented during a delay discounting procedure reduce impulsive choice through an induction of episodic imagery. We furthermore show that this effect is not due to an alteration of reward confidence or temporal focus, and occurs for both temporally specific and unspecific event cues. Our fMRI data reveal that incorporating episodic predictions into choice behavior involves prefrontal and mediotemporal regions and their interactions. ACC value signals and functional coupling of the ACC with hippocampus and amygdala closely tracked individual adjustments in discount rates in the presence of episodic tags. Our data thus suggest that the ACC, based on episodic predictions involving the hippocampus, supports the dynamic adjustments of preference functions that enable us to make choices that maximize future payoffs.

## EXPERIMENTAL PROCEDURES

### Experiment 1
#### Participants
In total, data from 30 subjects (mean age = 25.4 years, 15 male) are included in the present report. Subjects provided informed written consent, and the study procedure was approved by the local ethics committee. Six additional subjects participated but were excluded from analysis, two because of excessive head movement during scanning, one because of equipment failure during scanning, and three because their discount functions in the fMRI task were classified as nonsystematic (Johnson and Bickel, 2008), i.e., they either did not discount by at least 10% of the immediate reward (i.e., 2€) even at the longest delay (indicating that no discounting occurred), or at least one indifference point was greater than the preceding indifference point by a value of more than 20% of the immediate reward (indicating inconsistent preferences).

#### Prescan Interview and Behavioral Testing
On a separate day prior to scanning, subjects completed an extensive behavioral testing session including a computer-based delay discounting procedure to estimate the discount rate for a reward of 20€ (Peters and Büchel, 2009), and an extensive prescan interview. In short, indifference amounts were determined and converted into proportions of the fixed reward. Then, a hyperbolic function of the form

$$SV = \frac{1}{1 + kD}$$

(SV, subjective value; D, delay in days; k, discount rate) was fit to these data to obtain discount parameters (k) using Matlab (The MathWorks, Natick, MA). During the interview, participants compiled a list of future events that they had planned, with delays ranging from a few days to around 7 months, and rated these events on six-point scales for arousal, valence, and personal relevance. For each participant, seven events were then selected such that the spacing between delays increased with increasing delay, and that events were roughly matched on valence, arousal, and personal relevance. Only neutral or positive events were selected. For each event, a verbal label was selected (episodic tag) that would later be used as a cue stimulus during fMRI.

#### fMRI Task
The fMRI task was a delay discounting procedure based on a previously used task (Peters and Büchel, 2009). In short, participants completed two sessions of 118 trials each. Each trial consisted of the choice between a fixed, immediate reward of 20€ and larger but delayed amounts. In half of the trials, only amount and waiting time were shown (control condition) whereas in the other half of the trials, a verbal episodic tag (see above) was shown, indicating to the subjects what event they had planned at the respective day of reward delivery. Seven distinct delays were calculated for the control condition, such that no delay appeared in both conditions. Amounts ranged from 20.50 to 80€ and were calculated based on the estimated discount rates from the behavioral pretest.

Participants completed a practice session before scanning that only involved trials from the control condition. Immediately prior to scanning, they were told that, for some delays, they had reported planned events in the prescan interview, whereas for other delays, no events had been collected. Thus, for some delays, verbal tags would be presented in addition to the delay, to remind participants what they had planned at the respective delay. For other delays, no events had been collected in the interview, and thus no tags would be shown. Thus, participants were not instructed to use imagery to envision future events. Participants were also told that one of their choices would be randomly selected following scanning, and that, in the case of the choice of the immediate reward, they would receive 20€ in cash. If the delayed reward was chosen, the amount was transferred to the participants' bank account with the respective delay using timed transfers. In addition, participants received 8€/hr reimbursement for scanning and behavioral testing.

Immediately after scanning, participants rated for each event the vividness (not vivid at all … highly vivid) and the frequency (never … always) of associations spontaneously evoked by the event tags on six-point scales. Also, written reports were obtained in which participants provided details of feelings or thoughts evoked by each of the episodic tags.

### fMRI Data Acquisition
MRI data were acquired on a 3T system (Siemens TIM-TRIO) using a 32-channel head-coil. Seven-hundred volumes, aligned to the line connecting anterior and posterior commissures, were acquired for each session, and the first five volumes were discarded to allow the BOLD signal to stabilize. Each volume comprised 40 slices with a voxel size of 2 × 2 × 2 mm and 1 mm gap (TR = 2.38 s, TE = 25 ms). An additional MPRAGE structural image was acquired for anatomical overlay (voxel size 1 × 1 × 1 mm, 240 slices). Subjects viewed the experiment through a head-coil-mounted mirror.

### fMRI Data Analysis
Data preprocessing and analysis was performed using SPM5 (Wellcome Department of Cognitive Neurology, University College London). Functional images were slice-time corrected to the onset of the middle slice and spatially realigned using a 6-parameter affine transformation and unwarped to account for effects of subject movement. The high-resolution T1 image was then coregistered to the functional images and segmented into gray matter, white matter, and cerebrospinal fluid using the voxel-based morphometry toolbox included in SPM5. Functional images were spatially normalized to MNI space using the normalization parameters obtained from the segmentation procedure, and subsequently smoothed with a Gaussian kernel of 8 mm full-width at half-maximum.

Data analysis was performed using the GLM implemented in SPM5. The presentation of each type of option (control or episodic) was modeled by convolving the event-train of stimulus onsets with the canonical heamodynamic response function (HRF) separately for each session. Error trials and button presses were modeled separately. Subjective value of each decision option was calculated by multiplying the absolute amount of the reward with the empirically derived discount fraction (based on the choices during fMRI and separately for control and episodic trials, i.e., condition-specific k-parameters from the scanning session were used for the calculation of subjective value) and included as a parametric regressor in the GLM. Additional parametric regressors coding for the absolute amount of the reward and inverse delay-to-reward were included in the model and orthogonalized with respect to subjective value (Peters and Büchel, 2009). For each subject, contrast images coding for the condition onset (control/episodic) and for the subjective value regressor were constructed. These contrast images were then entered into a second-level random effects analysis using correction for nonsphericity in the context of the flexible factorial design as implemented in SPM5. The model included a subject factor and the factor trial type (control/episodic).

For the analysis of individual differences, the contrast images from the comparison of subjective value correlations between the episodic and control conditions (value correlation episodic > control) were entered into a simple regression in SPM5 using the behavioral tag effect as an explanatory variable.

The PPI analysis involved in a first step the construction of an addition model at the first level. Control and episodic trials were modeled as miniblocks of 10 s length. From this model, the time courses from the ACC peak voxels identified in the analysis of individual differences (right ACC: 18, 34, 18; left ACC: −20, 34, 22) were extracted and an additional condition regressor coding 1 for episodic trials and −1 for control trials was created. The ACC time course, the condition regressor, and the interaction term (the PPI regressor) were then entered into an additional first level model for each subject. The contrast images of the interaction regressor were analyzed at the second level using a one-sample t test and in a simple regression using the behavioral tag effect as an explanatory variable.

For all analyses, the threshold was set to p < 0.05 corrected for multiple comparisons using the family-wise error rate. For the subjective value conjunction analysis (control + episodic), correction for multiple comparisons was for 10 mm spheres centered at activation peaks derived from independent data, i.e., previous studies (Kable and Glimcher, 2007; Peters and Büchel, 2009). For the LPC activation from the triple conjunction (subjective value correlation control + episodic + [episodic > control]), correction was based on a 4 mm sphere on the delay-specific LPC peak identified previously (Peters and Büchel, 2009). Correction for the hippocampus, amygdala, and ACC were performed using bilateral anatomical masks (Maldjian et al., 2003). For display purposes, all maps are thresholded at p < 0.001, uncorrected, with at least 10 contiguous voxels, unless stated otherwise.

## Experiment 2
### Participants
Data from 16 participants (7 male) are included. Subjects provided informed written consent and the study procedure was approved by the local ethics committee. Three additional subjects participated but were excluded from data analysis: one because she never chose an immediate reward, indicating no discounting occurred; one because of misunderstanding instructions; and one because she showed a tag effect that was more than 4 standard deviations above the group mean.

### Pretest Interview and Behavioral Testing
The same procedures as in Experiment 1 were applied (e.g., pretest interview on day 1, behavioral testing on day 2) with the following additions/exceptions. In addition to collecting real future events, participants were now also asked to compile a list of events that could realistically happen to them in the next couple of months, but that were not tied to a particular date. For both the temporally specific and temporally unspecific condition, five events (rather than seven, as in Experiment 1) were selected. In addition to valence, arousal, and personal relevance, subjects now also rated for each event how many associations (such as people, places, activities, etc.) spontaneously came to mind when thinking of the event.

### Behavioral Procedure
The task and payment procedures were the same as in Experiment 1, with the following exceptions. Subjects now completed three sessions of 75 trials each (yielding a total of 75 trials per condition, i.e., control, temporally specific, and temporally unspecific). Control trials, specific trials, and unspecific trials were randomly interspersed with the constraint that no more than three trials of the same type were presented consecutively. Furthermore, the random jitters between events (see Experiment 1) required for fMRI analysis were removed from the experiment. Specific and unspecific tags were shown with blue and light blue backgrounds to make these different categories of tags visually distinct. In addition to the posttest ratings collected in Experiment 1, subjects now rated for each event and each delay from the control condition (1) their *confidence* in the payment scheme on a scale from 1 to 6 and (2) whether their *temporal focus* was on the displayed delay, or whether they converted the delay into the corresponding date and based their decision on this date. This was also rated on a scale from 1 (always date-based decision) to 6 (always delay-based decision).

## SUPPLEMENTAL INFORMATION

Supplemental Information for this article includes one figure and eight tables and can be found with this article online at doi:10.1016/j.neuron.2010.03.026.

## REFERENCES

Addis, D.R., Wong, A.T., and Schacter, D.L. (2007). Remembering the past and imagining the future: common and distinct neural substrates during event construction and elaboration. Neuropsychologia *45*, 1363–1377.

Addis, D.R., Pan, L., Vu, M.-A., Laiser, N., and Schacter, D.L. (2008). Constructive episodic simulation of the future and the past: Distinct subsystems of a core brain network mediate imagining and remembering. Neuropsychologia *11*, 2222–2238.

Bar, M. (2009). The proactive brain: memory for predictions. Philos. Trans. R. Soc. Lond. B Biol. Sci. *364*, 1235–1243.

Beauducel, A., Strobel, A., and Brocke, B. (2003). Psychometrische Eigenschaften und Normen einer deutschsprachigen Fassung der Sensation Seeking-Scale, Form V. Diagnostica *2*, 61–72.

Bechara, A., Damasio, A.R., Damasio, H., and Anderson, S.W. (1994). Insensitivity to future consequences following damage to human prefrontal cortex. Cognition *50*, 7–15.

Bechara, A., Damasio, H., Damasio, A.R., and Lee, G.P. (1999). Different contributions of the human amygdala and ventromedial prefrontal cortex to decision-making. J. Neurosci. *19*, 5473–5481.

Boyer, P. (2008). Evolutionary economics of mental time travel? Trends Cogn. Sci. *12*, 219–224.

Cabeza, R., Ciaramelli, E., Olson, I.R., and Moscovitch, M. (2008). The parietal cortex and episodic memory: an attentional account. Nat. Rev. Neurosci. *9*, 613–625.

Camus, M., Halelamien, N., Plassmann, H., Shimojo, S., O'Doherty, J., Camerer, C., and Rangel, A. (2009). Repetitive transcranial magnetic stimulation over the right dorsolateral prefrontal cortex decreases valuations during food choices. Eur. J. Neurosci. *30*, 1980–1988.

Carmichael, S.T., and Price, J.L. (1995). Limbic connections of the orbital and medial prefrontal cortex in macaque monkeys. J. Comp. Neurol. *363*, 615–641.

Carver, C.S., and White, T.L. (1994). Behavioral inhibition, behavioral activation, and affective responses to impeding reward and punishment: The BIS/BAS scales. J. Pers. Soc. Psychol. *67*, 319–333.

Cheung, T.H., and Cardinal, R.N. (2005). Hippocampal lesions facilitate instrumental learning with delayed reinforcement but induce impulsive choice in rats. BMC Neurosci. *6*, 36.

De Martino, B., Kumaran, D., Seymour, B., and Dolan, R.J. (2006). Frames, biases, and rational decision-making in the human brain. Science *313*, 684–687.

Dorris, M.C., and Glimcher, P.W. (2004). Activity in posterior parietal cortex is correlated with the relative subjective desirability of action. Neuron *44*, 365–378.

Ersner-Hershfield, H., Wimmer, G.E., and Knutson, B. (2009). Saving for the future self: neural measures of future self-continuity predict temporal discounting. Soc. Cogn. Affect. Neurosci. *4*, 85–92.

Figner, B., Knoch, D., Johnson, E.J., Krosch, A.R., Lisanby, S.H., Fehr, E., and Weber, E.U. (2010). Lateral prefrontal cortex and self-control in intertemporal choice. Nat. Neurosci., in press. Published online March 28, 2010. 10.1038/nn.2516.

Floresco, S.B., and Ghods-Sharifi, S. (2007). Amygdala-prefrontal cortical circuitry regulates effort-based decision making. Cereb. Cortex *17*, 251–260.

Friston, K.J., Buechel, C., Fink, G.R., Morris, J., Rolls, E., and Dolan, R.J. (1997). Psychophysiological and modulatory interactions in neuroimaging. Neuroimage *6*, 218–229.

Ghods-Sharifi, S., St Onge, J.R., and Floresco, S.B. (2009). Fundamental contribution by the basolateral amygdala to different forms of decision making. J. Neurosci. *29*, 5251–5259.

Green, L., and Myerson, J. (2004). A discounting framework for choice with delayed and probabilistic rewards. Psychol. Bull. *130*, 769–792.

Green, L., Myerson, J., and McFadden, E. (1997). Rate of temporal discounting decreases with amount of reward. Mem. Cognit. *25*, 715–723.

Gupta, R., Duff, M.C., Denburg, N.L., Cohen, N.J., Bechara, A., and Tranel, D. (2009). Declarative memory is critical for sustained advantageous complex decision-making. Neuropsychologia *47*, 1686–1693.

Hare, T.A., Camerer, C.F., and Rangel, A. (2009). Self-control in decision-making involves modulation of the vmPFC valuation system. Science *324*, 646–648.

Hassabis, D., Kumaran, D., Vann, S.D., and Maguire, E.A. (2007). Patients with hippocampal amnesia cannot imagine new experiences. Proc. Natl. Acad. Sci. USA *104*, 1726–1731.

Ishikawa, A., and Nakamura, S. (2006). Ventral hippocampal neurons project axons simultaneously to the medial prefrontal cortex and amygdala in the rat. J. Neurophysiol. *96*, 2134–2138.

Johnson, M.W., and Bickel, W.K. (2008). An algorithm for identifying nonsystematic delay-discounting data. Exp. Clin. Psychopharmacol. *16*, 264–274.

Johnson, A., and Redish, A.D. (2007). Neural ensembles in CA3 transiently encode paths forward of the animal at a decision point. J. Neurosci. *27*, 12176–12189.

Johnson, A., van der Meer, M.A., and Redish, A.D. (2007). Integrating hippocampus and striatum in decision-making. Curr. Opin. Neurobiol. *17*, 692–697.

Kable, J.W., and Glimcher, P.W. (2007). The neural correlates of subjective value during intertemporal choice. Nat. Neurosci. *10*, 1625–1633.

Kable, J.W., and Glimcher, P.W. (2010). An "As Soon As Possible" Effect in Human Inter-Temporal Decision Making: Behavioral Evidence and Neural Mechanisms. J. Neurophysiol., in press. Published online February 24, 2010. 10.1152/jn.00177.2009.

Kim, S., Hwang, J., and Lee, D. (2008). Prefrontal coding of temporally discounted values during intertemporal choice. Neuron *59*, 161–172.

Kumaran, D., Summerfield, J.J., Hassabis, D., and Maguire, E.A. (2009). Tracking the emergence of conceptual knowledge during human decision making. Neuron *63*, 889–901.

Maldjian, J.A., Laurienti, P.J., Kraft, R.A., and Burdette, J.H. (2003). An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. Neuroimage *19*, 1233–1239.

Manes, F., Sahakian, B., Clark, L., Rogers, R., Antoun, N., Aitken, M., and Robbins, T. (2002). Decision-making processes following damage to the prefrontal cortex. Brain *125*, 624–639.

Mariano, T.Y., Bannerman, D.M., McHugh, S.B., Preston, T.J., Rudebeck, P.H., Rudebeck, S.R., Rawlins, J.N., Walton, M.E., Rushworth, M.F., Baxter, M.G., and Campbell, T.G. (2009). Impulsive choice in hippocampal but not orbitofrontal cortex-lesioned rats on a nonspatial decision-making maze task. Eur. J. Neurosci. *30*, 472–484.

Mazur, J.E. (1987). An adjusting procedure for studying delayed reinforcement. In Quantitative Analyses of Behavior: Vol. 5. The Effect of Delay and of Intervening Events on Reinforcement Value, M.L. Commons, J.E. Mazur, J.A. Nevin, and H. Rachlin, eds. (Hillsdale, NJ: Erlbaum), pp. 55–73.

McClure, S.M., Laibson, D.I., Loewenstein, G., and Cohen, J.D. (2004). Separate neural systems value immediate and delayed monetary rewards. Science *306*, 503–507.

McClure, S.M., Ericson, K.M., Laibson, D.I., Loewenstein, G., and Cohen, J.D. (2007). Time discounting for primary rewards. J. Neurosci. *27*, 5796–5804.

McDonald, A.J. (1991). Organization of amygdaloid projections to the prefrontal cortex and associated striatum in the rat. Neuroscience *44*, 1–14.

McDonald, A.J., Mascagni, F., and Guo, L. (1996). Projections of the medial and lateral prefrontal cortices to the amygdala: a Phaseolus vulgaris leucoagglutinin study in the rat. Neuroscience *71*, 55–75.

Miller, E.K., and Cohen, J.D. (2001). An integrative theory of prefrontal cortex function. Annu. Rev. Neurosci. *24*, 167–202.

Naccache, L., Dehaene, S., Cohen, L., Habert, M.O., Guichart-Gomez, E., Galanaud, D., and Willer, J.C. (2005). Effortless control: executive attention and conscious feeling of mental effort are dissociable. Neuropsychologia *43*, 1318–1328.

Nichols, T., Brett, M., Andersson, J., Wager, T., and Poline, J.B. (2005). Valid conjunction inference with the minimum statistic. Neuroimage *25*, 653–660.

Pearson, J.M., Hayden, B.Y., Raghavachari, S., and Platt, M.L. (2009). Neurons in posterior cingulate cortex signal exploratory decisions in a dynamic multioption choice task. Curr. Biol. *19*, 1532–1537.

Peters, J., and Büchel, C. (2009). Overlapping and distinct neural systems code for subjective value during intertemporal and risky decision making. J. Neurosci. *29*, 15727–15734.

Peters, J., Daum, I., Gizewski, E., Forsting, M., and Suchan, B. (2009). Associations evoked during memory encoding recruit the context-network. Hippocampus *19*, 141–151.

Phan, K.L., Wager, T.D., Taylor, S.F., and Liberzon, I. (2004). Functional neuroimaging studies of human emotions. CNS Spectr. *9*, 258–266.

Pine, A., Seymour, B., Roiser, J.P., Bossaerts, P., Friston, K.J., Curran, H.V., and Dolan, R.J. (2009). Encoding of marginal utility across time in the human brain. J. Neurosci. *29*, 9575–9581.

Platt, M.L., and Glimcher, P.W. (1999). Neural correlates of decision variables in parietal cortex. Nature *400*, 233–238.

Rawlins, J.N., Feldon, J., and Butt, S. (1985). The effects of delaying reward on choice preference in rats with hippocampal or selective septal lesions. Behav. Brain Res. *15*, 191–203.

Read, D., Frederick, S., Orsel, B., and Rahman, J. (2005). Four Score and Seven Years from Now: The Date/Delay Effect in Temporal Discounting. Manage. Sci. *51*, 1326–1335.

Roiser, J.P., de Martino, B., Tan, G.C., Kumaran, D., Seymour, B., Wood, N.W., and Dolan, R.J. (2009). A genetically mediated bias in decision making driven by failure of amygdala control. J. Neurosci. *29*, 5985–5991.

Rushworth, M.F., and Behrens, T.E. (2008). Choice, uncertainty and value in prefrontal and cingulate cortex. Nat. Neurosci. *11*, 389–397.

Schacter, D.L., and Addis, D.R. (2009). On the nature of medial temporal lobe contributions to the constructive simulation of future events. Philos. Trans. R. Soc. Lond. B Biol. Sci. *364*, 1245–1253.

Schacter, D.L., Addis, D.R., and Buckner, R.L. (2007). Remembering the past to imagine the future: the prospective brain. Nat. Rev. Neurosci. *8*, 657–661.

Sharot, T., Riccardi, A.M., Raio, C.M., and Phelps, E.A. (2007). Neural mechanisms mediating optimism bias. Nature *450*, 102–105.

Szpunar, K.K., Watson, J.M., and McDermott, K.B. (2007). Neural substrates of envisioning the future. Proc. Natl. Acad. Sci. USA *104*, 642–647.

Tanaka, S.C., Doya, K., Okada, G., Ueda, K., Okamoto, Y., and Yamawaki, S. (2004). Prediction of immediate and future rewards differentially recruits cortico-basal ganglia loops. Nat. Neurosci. *7*, 887–893.

Thierry, A.M., Gioanni, Y., Dégénétais, E., and Glowinski, J. (2000). Hippocampo-prefrontal cortex pathway: anatomical and electrophysiological characteristics. Hippocampus *10*, 411–419.

Vann, S.D., Aggleton, J.P., and Maguire, E.A. (2009). What does the retrosplenial cortex do? Nat. Rev. Neurosci. *10*, 792–802.

Wagner, A.D., Shannon, B.J., Kahn, I., and Buckner, R.L. (2005). Parietal lobe contributions to episodic memory retrieval. Trends Cogn. Sci. *9*, 445–453.

Walton, M.E., Croxson, P.L., Behrens, T.E., Kennerley, S.W., and Rushworth, M.F. (2007). Adaptive decision making and value in the anterior cingulate cortex. Neuroimage *36* (*Suppl 2*), T142–T154.

Weber, E.U., and Johnson, E.J. (2009). Mindful judgment and decision making. Annu. Rev. Psychol. *60*, 53–85.

Winstanley, C.A., Theobald, D.E., Cardinal, R.N., and Robbins, T.W. (2004). Contrasting roles of basolateral amygdala and orbitofrontal cortex in impulsive choice. J. Neurosci. *24*, 4718–4722.

Zuckerman, M. (1996). Item revisions in the Sensation Seeking Scale Form V (SSS-V). Pers. Individ. Dif. *20*, 515.