Title:

Neural correlates of episodic memory modulated by temporally delayed rewards

Authors:

Jungsun Yoo[a,b] , Seokyoung Min[b], Seung-Koo Lee[c, d], Sanghoon Han[b]

Institutional Affiliations:

[a] Department of Cognitive Sciences, University of California, Irvine, United States of America

[b] Department of Psychology, Yonsei University, Seoul 03722, Republic of Korea

[c] Department of Radiology, Yonsei University College of Medicine, Seoul 03722, Republic of Korea

[d] Integrated Neurocognitive Functional Imaging Center, Yonsei University, Seoul 03722, Republic of Korea

Corresponding Author:

Sanghoon Han, Ph.D., Department of Psychology

Phone: +82-2-2123-5436; Fax: +82-2-2123-8330

Email: sanghoon.han@yonsei.ac.kr

Abstract

When a stimulus is associated with an external reward, its chance of being consolidated into long-term memory is boosted via dopaminergic facilitation of long-term potentiation in the hippocampus. Given that higher temporal distance (TD) has been found to discount the subjective value of a reward, we hypothesized that memory performance associated with a more immediate reward will result in better memory performance. We tested this hypothesis by measuring both behavioral memory performance and brain activation using functional magnetic resonance imaging (fMRI) during memory encoding and retrieval tasks. Contrary to our hypothesis, both behavioral and fMRI results suggest that the TD of rewards might enhance the chance of the associated stimulus being remembered. The fMRI data demonstrate that the lateral prefrontal cortex, which shows encoding-related activation proportional to the TD, is reactivated when searching for regions that show activation proportional to the TD during retrieval. This is not surprising given that this region is not only activated to discriminate between future vs. immediate rewards, it is also a part of the retrieval-success network. These results provide support for the conclusion that the encoding-retrieval overlap provoked as the rewards are more delayed lead to better memory performance of the items associated with the rewards.

1. Introduction

Episodic long-term memory is crucial to our daily lives given that our behavior and decisions are based on past experience. The core of episodic memory formation in the brain is thought to be the medial temporal lobe (MTL), which comprises the hippocampus (HC) and the surrounding gyri (Eichenbaum et. al, 2007). In addition, various studies suggest that successful memory formation does not solely depend on MTL functions but also relies on other cortical regions such as the prefrontal cortex (PFC), the premotor cortex, or the posterior parietal cortex (PPC; Kim, 2011).

However, not all events benefit from these regions to be transformed into long-term memory. To enhance efficiency in memory storage, salient stimuli – either rewarding or aversive – are better remembered than other neutral items (Stephan B. Hamann, Timothy D. Ely, Scott T. Grafton, & Clinton D. Kilts, 1999). Upon encountering rewarding stimuli, dopamine neurons in the substantia nigra and the ventral tegmental area (VTA), two regions that produce most of the dopamine in the brain, are activated (Schultz, 1998). Dopamine is known to facilitate consolidation of long-term memory via direct projections of the VTA to the HC (Lisman, Grace, & Duzel, 2011). This reward-facilitated memory consolidation is observed 24 hours after the initial learning (Miendlarzewska, Bavelier, & Schwartz, 2016) through late long-term potentiation in the HC (O'Carroll, et. al, 2006; Rossato et. al, 2009). Various studies have confirmed the effect of reward-facilitated episodic-memory encoding in the human brain. One study revealed that stimuli that elicit greater activation in the dopaminergic midbrain areas are more likely to be recollected three weeks later (Wittmann et al., 2005), while another study reported that a high-value reward preceding incidental encoding facilitates memory formation

(Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006). In summary, a high-value stimulus has a higher chance of being consolidated into the long-term memory (for a review, see Shohamy & Adcock, 2010).

The subjective value of a reward has been found to vary according to various contexts such as the amount of effort needed for obtaining the reward, probability associated with the reward, or delay before the reward is delivered. Effort discounting refers to the tendency of choosing a reward option associated with less over more required effort. Activation of the nucleus accumbens was negatively correlated with effort demand (Botvinick, Huffstetler, & McGuire, 2009). Likewise, with a fixed objective value of a reward, its subjective value decreases if the probability of obtaining it decreases (Richards, Zhang, Mitchell, & de Wit, 1999). Temporal discounting of reward refers to the tendency of individuals to devalue the reward if its delivery is delayed (Green & Myerson, 2004), often resulting in choosing smaller sooner over larger later rewards. There have been various attempts to capture this phenomenon into mathematical equations, and a model using hyperbolic function has provided the most parsimonious account so far (Kirby & Marakovic, 1995; Myerson & Green, 1995). A neuroimaging study has corroborated this by finding that the subjective value of delayed rewards derived from the hyperbolic model is represented in the ventral striatum, the mPFC, and the posterior cingulate cortex (Kable & Glimcher, 2007).

Given that a TD of a reward reduces the activation of dopamine neurons as if a reward of a smaller magnitude has been expected (Kobayashi & Schultz, 2008; Schultz, 2010; Enomoto et. al, 2011), one could link this with reward-motivated memory-encoding by questioning whether devalued rewards due to a higher TD act like a small-magnitude reward in memory encoding.

With regard to reward contexts other than TD, a study examined effects of reward uncertainty and magnitude on episodic memory and found that only reward outcome, but not reward uncertainty, affects episodic memory (Mason, Farrell, Howard-Jones, & Ludwig, 2017). However, to our knowledge, no study attempted to test whether temporally discounted rewards differentially affect episodic memory formation. Therefore, in this study, we aim to investigate whether temporal discounting of reward is reflected in reward-motivated episodic memory encoding, and if so, whether it involves differential HC-VTA activity.

In this study, we hypothesize that the more temporally distant a reward is, the less likely the stimulus associated with it will be remembered. To test this, we devised an incidental memory-encoding task in which participants encode scene images preceded by a reward cue indicating when the reward will be delivered should the given trial be correct. We assume that the effect of reward modulation by TD will not be seen pre-consolidation but after consolidation, since dopaminergic facilitation of episodic memory is observed after 24 hours (Miendlarzewska, Bavelier, & Schwartz, 2016). To validate this assumption, we divide the retrieval phase into two phases – pre-consolidation (referred to as 'recent retrieval' or 15 minutes after encoding) and post-consolidation (referred to as 'remote retrieval' or one week after encoding) – and acquire functional magnetic resonance imaging (fMRI) images from both retrieval phases to directly test whether the effect of temporally-discounted reward depends on dopamine-facilitated consolidation.

2. Materials and Methods

2.1. Participants and Materials

N = 26 volunteers participated in the study (12 females). Two subjects were excluded from the study due to failure to participate on the second day of the experiment. Two additional participants were excluded since they had at least one condition without a usable regressor for General linear modeling (GLM) analyses of fMRI data. The volunteers' age ranged from 19 to 31, and their mean age was 25. Before study begin, all participants were screened if they matched the inclusion criteria of having no history of psychological or neurological disorder, not being pregnant, having no claustrophobia or tinnitus, and being right-handed. Only volunteers who met all the criteria were enrolled. All participants gave their informed written consent according to a document approved by the Institutional Review Board of Yonsei University. We acquired 22 complete fMRI datasets (244 trials of encoding, 404 trials of retrieval), and two participants' data was partially lost due to malfunction of MRI scanner (1st participant: loss of 41 trials during first retrieval phase; 2nd participant: loss of 114 trials during first retrieval phase, and this participant's data was not used for any analyses).

The experiment and data collection were performed via Cogent 2000 (Wellcome Trust Centre for Neuroimaging) based on MATLAB (The MathWorks; Natick, MA). For scene stimuli, 405 scene stimuli were sampled from a preexisting image database (Konkle, Brady, Alvarez, & Oliva, 2010) or from online royalty-free images. All images were adjusted to a size of 92.1 mm x 92.1 mm and a resolution of 72 pixels. The order of visual stimuli presentation during the encoding and retrieval phase as well as the locations where the binary response options appear (left / right) were randomized. When the participants were placed inside the MRI scanner, visual stimuli were presented to them via MR-compatible goggles and their responses were recorded using an MR-compatible button-box.

2.2. Experimental Paradigm

We devised a novel experiment which crosses reward with TD during memory encoding. The experiment consisted of three main sections, which were a scene-encoding task, a surprise memory-retrieval task, and an intertemporal decision-making task. Subjects performed these tasks while they were scanned for their brain activity inside an MRI scanner. The experiment took place for two days. The first day encompassed encoding and half of the retrieval task. The second day, one week later, comprised the remaining half of the retrieval and the intertemporal choice task (Figure 1). In the encoding task, participants classified whether a given scene was indoors or outdoors and were rewarded if they made the correct classification. The novel part of this classification task is that each trial is preceded by a cue indicating when the reward will be delivered should the following classification be correct, and there were four possible TDs: 0 days (same day), 1 day, 7 days, and 28 days. The reward magnitude was uniform across all trials, resulting in 5,000 Korean Won (KRW) when summed. For retrieval, scenes presented during the encoding task intermixed with new scenes (foils) were shown to the participants who decided whether they had seen the scene in the encoding task (old/new) and how confident they were about the decision (sure/guess). Finally, to estimate participants' discount rate, the intertemporal choice task described in Kable and Glimcher, 2007 was conducted, except that the reward was hypothetical in our study. This deviation can be ignored since no difference has been observed between real and hypothetical rewards in temporal discounting tasks (Johnson & Bickel, 2002).

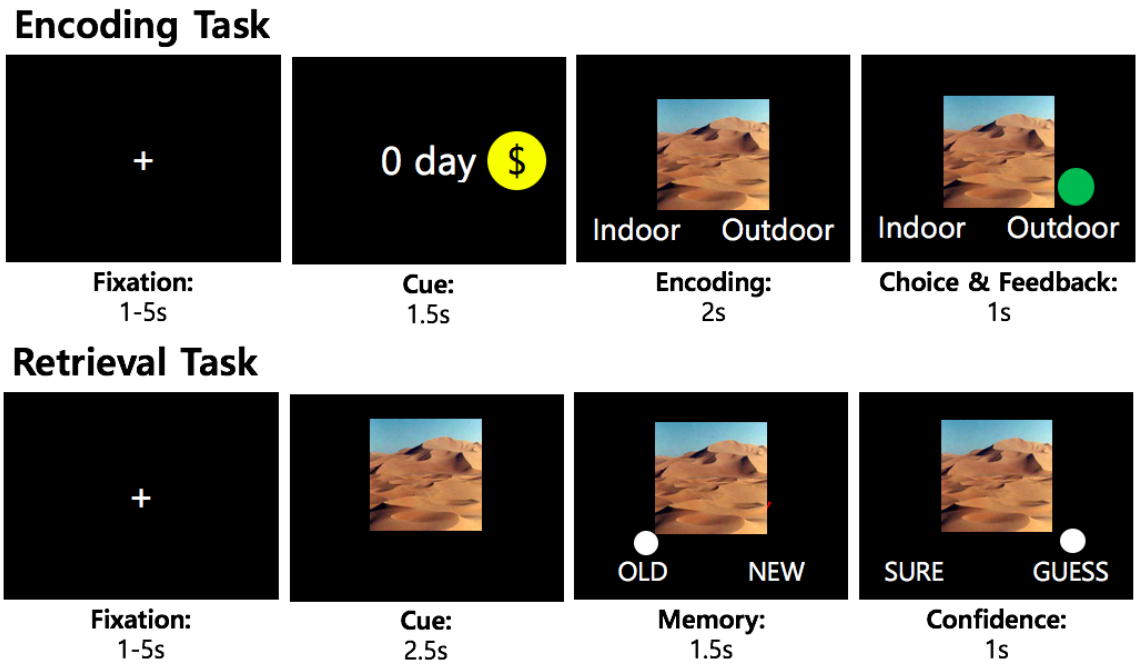

Figure 1 Experimental paradigm. Each trial in encoding and retrieval task was preceded with a jittered fixation. In the encoding task, correct response was followed by a green dot while incorrect response resulted in a red dot.

2.3. Experimental Procedure

Upon arrival, participants were first asked to fill out the consent form and behavioral avoidance / inhibition scales for a measure of reward-sensitivity (Carver and White, 1994). Then they were instructed about the scene-classification task, including the possibility of receiving an additional reward of up to 5,000 KRW depending on their classification accuracy and four possible time points when the reward will be delivered to them. Since the retrieval following encoding was intended to be a surprise memory test, participants were only informed that they will perform a simple cognitive task after the encoding phase. Then they were put inside the MRI scanner and a six-minute pre-encoding resting run was performed. After pre-encoding resting, participants performed six runs of encoding (scene-classification) task, with 44 items per each

run, resulting in 264 scenes in total. Each condition (reward delivery after 0/1/7/28 day(s)) was comprised of 66 items. Then the post-encoding resting phase followed. After resting, participants were informed that the aforementioned 'cognitive task' is actually a recognition task and they performed the first half of the retrieval task inside the scanner, consisting of 202 items divided into five runs. After leaving the scanner, the participants were paid for the reward they earned during the encoding task.

Participants returned a week later and resumed the experiment by performing the intertemporal decision-making task three times. They also answered the Zimbardo Time Perspective Inventory (ZTPI) and an abbreviated 9-item form of Raven Standard Progressive Matrices (RSPM) (Bilker et al., 2012; Raven, 1941) as a measure of their future orientation and intelligence, respectively. However, data collected from ZTPI and RSPM were not used for this study. Then the participants were positioned in the MRI scanner and first performed the identical intertemporal decision-making task which they performed outside the scanner. Afterward, the remaining half of the retrieval task took place, also consisting of 202 items distributed into five blocks. Finally, the structural images of participants (T1- and T2-weighted images) were acquired. The experiment terminated as the subjects were paid the rest of their participation reimbursement and provided their signature for receipt. Note that the bonus was bank-transferred according to each TD, so when returning to the experiment on the second day the participants had already received bonus for 0-days, 1-day and 7-days condition.

2.4. Behavioral Data Analyses

Participants' task-specific performance during the encoding task was assessed by

analyzing the response time (RT) and accuracy during scene classification. This analysis ensured that performance during the encoding task per se does not lead to differential memory performance according to conditions in the retrieval task. For retrieval tasks, participant's memory performance and RT were assessed. First, participants' memory performance for each condition was analyzed by calculating the corrected recognition (CR), which is a model-free memory measure calculating hit minus false alarm rate ('old' responses to targets minus 'old' responses to foils). Based on the previous finding that the reward-motivated subsequent memory effect (SME) is reflected in high-confidence responses (Adcock et al., 2006), we additionally calculated high-confidence hits corrected for high-confidence false alarm rate. The CRs of participants were submitted to 2x4 repeated-measures analyses of variance (ANOVA). Second, participants' RT was assessed for retrieval tasks to ensure that the results of the retrieval tasks are not explainable via RT.

Each participant's discount rate was estimated based on the results of the delay-discounting decision-making task. A logistic function was fit to choices within each delay (*D*) to determine the indifference point, which refers to the amount of money which yields 50% probability of choosing either option. The indifference point for each delay was used to calculate the discounted value (DV):

$$\mathrm{DV} = \frac{\text{magnitude of immediate reward (\$10)}}{\text{indifference point}}$$

Then, the DVs as a function of delays were fitted by a hyperbolic function (Rodriguez and Logue, 1988), where

$$\mathrm{DV} = \frac{1}{1 + k * D}$$

The estimated free parameter *k* was used as a measure for each individual's impulsivity, where higher *k* leads to steeper hyperbolic curve or higher impulsivity. The purpose of deriving each participant's *k* was to estimate the subjective value of delayed rewards in the encoding session tailored to each participant. This was done by multiplying objective numerical value for each trial (5,000 KRW/264 trials = 18.9 KRW) by the respective DV of each delay of each participant (18.9 KRW * DV). The obtained subjective value pertaining to each delay was entered as a parametric modulator for GLM of functional images acquired during retrieval runs.

2.5. Neuroimaging Data Acquisition and Analyses

2.5.1. MRI data acquisition

The MRI data for this study was acquired with a Phillips 3T MRI scanner using a 32-channel head coil. All functional images were T2*-weighted echo-planar images with repetition time of 0.8 s, voxel size of 2.4 x 2.4 x 2.4 mm, multiband factor of 6, and 60 slices in an ascending order, aligned to the anterior commissure – posterior commissure axis. The first ten images of each run were discarded for magnetic stabilization. A full dataset comprised of 500 volumes each for the pre- and post-encoding resting phase, 2520 (6 runs * 420 volumes per run) volumes for the encoding phase, and 3900 (2 phases * 5 runs * 390 volumes per run) volumes for the retrieval phase. For structural images, a T1-weighted MPRAGE (1 mm isotropic voxels) and a T2-weighted image were acquired. The T2 structural images were not used for any

analyses in this study.

2.5.2. Preprocessing

The acquired functional images were first unwarped using the Topup toolbox of FSL software (FMRIB, Oxford, UK) to correct for possible distortions due to magnetic field inhomogeneity (Andersson, Skare, & Ashburner, 2003). Then the differences in the slice acquisition time for the functional images were corrected. Afterwards, the functional images were realigned to the first image of each run to correct for movement, and a mean functional volume was created to use as a representative for coregistration of functional and structural (T1) images. The coregistered structural image was segmented into grey matter, white matter, and cerebrospinal fluid according to tissue probability maps. The deformation fields acquired from this process were used for normalization of functional images into standard Montreal Neurological Institute (MNI) space, and during normalization the functional images were resampled into 2 mm isotropic voxel size. After normalization, the functional images were spatially smoothed by a Gaussian kernel (8 mm, full-width at half-maximum). All of the steps after Topup correction were performed via the SPM12 toolbox (The Wellcome Department of Cognitive Neurology, University College London, London, UK).

2.5.3. General Linear Modeling of Functional Images

We performed whole-brain analyses of functional images using GLM. For GLM of encoding runs, we applied a boxcar function modeled at the beginning of the reward cue presentation extending to the end of scene encoding, resulting in 3.5 s in total, for our main regressor of interest (Table 1). Regarding GLM for retrieval runs, an impulse function was modeled at the

beginning of the scene stimulus presentation. For regressors of no interest for both encoding and retrieval runs, we included impulse functions modeled to participants' response of no interest (encoding runs: scene classification response; retrieval runs: sure/guess response), missed trials, first-order temporal derivatives for each impulse function, session constants and six motion regressors for every GLM. The rationale for employing a boxcar function for only encoding runs is to assume the cue and encoding phase as a single process.

For the group-level analyses of encoding runs, beta coefficients for 16 kinds of regressors of interest, which are the product of 4 (TD: 0, 1, 7, 28 days) x 2 (subsequently remembered/forgotten) x 2 (retrieved 15 minutes/7 days later) conditions, were forwarded to a group analyses where we performed analysis of variance (ANOVA). We tested eight comparisons: (1) main effect of subsequent memory (remembered vs. forgotten) within items retrieved recently, (2) main effect of subsequent memory within items retrieved remotely, (3) main effect of value (0 days > 1 day > 7 days > 28 days), (4) main effect of TD (28 days > 7 days > 1 day > 0 days), (5) 4 x 2 interaction of the subjective value of delayed reward (0, 1, 7, 28 days) and subsequent memory (remembered vs. forgotten) within recent retrieval, (6) 4 x 2 interaction of the subjective value of delayed reward (0 > 1 > 7 > 28 days) and subsequent memory (remembered vs. forgotten) within remote retrieval (7) 4 x 2 interaction of TD of reward (28 > 7 > 1 > 0 days) and subsequent memory (remembered vs. forgotten) within recent retrieval, and (8) 4 x 2 interaction of TD of reward (28 > 7 > 1 > 0 days) and subsequent memory (remembered vs. forgotten) within remote retrieval.

For GLM analysis of fMRI data for retrieval runs, we employed four kinds of regressors of interest: old stimuli which were correctly classified as old (i.e., HIT), old stimuli which were

incorrectly classified as new (i.e., MISS), correct rejection of new stimuli, and junk regressors which were comprised of new stimuli incorrectly classified as old (false alarms) and no responses. For each 'old' regressors (HIT and MISS conditions), two parametric modulators were added according to the delayed reward it was associated during the encoding run: subjective value and objective TD. For subjective value, aforementioned parametric modulators derived by multiplying each trial's object reward value by each delay's discounted ratio of each participant (18.9 KRW * DV of each delay) were entered. On the other hand, the parametric modulators for the objective delay are 10^{-5}, 1, 7, and 28 for 0 days, 1 day, 7 days, and 28 days, respectively. Since more than one parametric modulator was entered for one onset, the 'order effect' of entering multiple parametric modulators specific to SPM arises (see Mumford, Poline, & Poldrack, 2015 for more details). Therefore, we performed two GLMs for each parametric regressor of interest by switching the order of parametric regressors entered to acquire statistics for each modulator, respectively (i.e., 1st GLM: subjective value as the first modulator, objective distance as the second modulator; 2nd GLM: vice versa). Finally, the statistical parametric map for parametrically modulated HIT of each participant acquired from 1st level analysis entered 2nd level analyses which performed t-tests against 0. We assumed that the significant voxels would reflect parametric neural activation according to each condition (subjective value or objective delay) during memory retrieval.

In addition to GLM, we performed small-volume correction (SVC) based on a priori regions of interest (ROI) using Harvard-Oxford atlas (Center for Morphometric Analysis). For encoding runs, we selected regions likely to be involved in reward-facilitated memory consolidation such as the HC (Lisman & Grace, 2005) or scene-related memory processing such as the

parahippocampal cortex (Staresina, Duncan, & Davachi, 2011). We checked whether the striatum and the orbitofrontal cortex (OFC), regions known to be involved in value processing of monetary reward (Adcock et. al, 2006), are involved in representing the main effect of subjective value. Furthermore, for retrieval runs, we selected previously defined regions of the 'retrieval success network' such as frontoparietal control regions and the caudate as ROIs for HIT vs. correct rejection contrast (Kim, 2013).

The multiple comparisons issue upon reporting significant voxels from GLM was dealt with by applying the 3dClustSim function in AFNI (National Institute of Mental Health, Bethesda), in which we entered the median smoothness values of each participant's residual maps and the grey matter mask as input. As a result, the function yielded a set of cluster thresholds that correspond to the alpha value of $p < 0.05$ in a one-tailed test and 18-connected cluster connectivity (edges and faces touch; NN = 2), following the default setting of SPM (Pauli et al., 2016). Entering residual maps from 22 subjects resulted in 102 contiguous voxels upon *p*-threshold of 0.001 or 2896 contiguous voxels under $p < 0.05$. The results of the following analyses follow the latter criterion for reaching the alpha value of $p < 0.05$.

Table 1 Summary of models used for fMRI analyses. Abbreviations are like the following. PM = parametric modulation, Day0/1/7/28 = reward delivered after 0/1/7/28 days, Ret0 = retrieved 15 minutes later, Ret7 = retrieved 1 week later, R/F = subsequently remembered/forgotten.

Model name	**Method**	**Regressors of interest**	**Contrasts**	**Contrast vectors**
Encoding	Factorial design (ANOVA)	1) Day0_R_Ret0 2) Day1_R_Ret0 3) Day7_R_Ret0 4) Day28_R_Ret0	(1) Main effect of subsequent memory for recent retrieval (2) Main effect of subsequent memory for remote retrieval	(1) [1 1 1 1 -1 -1 -1 -1 0 0 0 0 0 0 0 0] (2) [0 0 0 0 0 0 0 0 1 1 1 1 -1 -1 -1 -1] (3) [3 1 -1 -3 3 1 -1 -3 3 1 -1 -3 3 1 -1 -3] (4) [-3 -1 1 3 -3 -1 1 3 -3 -1 1 3 -3 -1 1 3]

		5) Day0_F_Ret0 6) Day1_F_Ret0 7) Day7_F_Ret0 8) Day28_F_Ret0 9) Day0_R_Ret7 10) Day1_R_Ret7 11) Day7_R_Ret7 12)Day28_R_Ret7 13) Day0_F_Ret7 14) Day1_F_Ret7 15) Day7_F_Ret7 16) Day28_F_Ret7	(3) Main effect of value (4) Main effect of TD (5) Interaction of subjective value of delayed reward and subsequent memory within recent retrieval (6) Interaction of subjective value of delayed reward and subsequent memory within remote retrieval (7) Interaction of TD of reward and subsequent memory within recent retrieval (8) Interaction of TD of reward and subsequent memory within remote retrieval	(5) [3 1 -1 -3 -3 -1 1 3 0 0 0 0 0 0 0 0] (6) [0 0 0 0 0 0 0 0 3 1 -1 -3 -3 -1 1 3] (7) [-3 -1 1 3 3 1 -1 -3 0 0 0 0 0 0 0 0] (8) [0 0 0 0 0 0 0 0 -3 -1 1 3 3 1 -1 -3]
Recent retrieval: PM of value	Parametric modulation (t-test against 0)	1) HIT_main 2) HIT_pm_value 3) HIT_pm_TD 4) MISS_main 5)MISS_pm_value 6) MISS_pm_TD 7)Correct rejection 8) Junk	Parametric effect of value on HIT	[0 1 0 0 0 0 0 0]
Recent retrieval: PM of TD	Parametric modulation (t-test against 0)	1) HIT_main 2) HIT_pm_TD 3) HIT_pm_value 4) MISS_main 5) MISS_pm_TD 6)MISS_pm_value 7)Correct rejection 8) Junk	Parametric effect of TD on HIT	[0 1 0 0 0 0 0 0]
Remote	Parametric	1) HIT_main	Parametric effect of value on	[0 1 0 0 0 0 0 0]

retrieval: PM of value	modulation (t-test against 0)	2) HIT_pm_value 3) HIT_pm_TD 4) MISS_main 5)MISS_pm_value 6) MISS_pm_TD 7)Correct rejection 8) Junk	HIT	
Remote retrieval: PM of TD	Parametric modulation (t-test against 0)	1) HIT_main 2) HIT_pm_TD 3) HIT_pm_value 4) MISS_main 5) MISS_pm_TD 6)MISS_pm_value 7)Correct rejection 8) Junk	Parametric effect of TD on HIT	[0 1 0 0 0 0 0 0]

2.5.4. Psychophysiological Interaction

The previous findings that the interaction between the HC and the neocortex during memory formation predicts successful encoding (van Kesteren, Fernandez, Norris, & Hermans, 2010) and a recent study which found bidirectional informational flow between the neocortex and the HC during memory encoding and retrieval (Griffiths et al., 2019) led us to test the possibility of temporal-cue processing regions relaying their information to the HC during successful encoding. To do so, we performed a psychophysiological interaction (PPI) analysis on remotely retrieved trials, with the HC as a seed region. To acquire the variables needed for PPI, we performed an additional GLM on the encoding runs and the regressors of interest were ‘trials remembered

upon remote retrieval modulated by TD (R-pmod)' and 'trials forgotten upon remote retrieval modulated by TD (F-pmod)'. We used R-pmod labeled as 1 and F-pmod labeled as -1 for the psychological variable, and eigenvariate time series of HC pertaining to R-pmod and F-pmod as a physiological variable. The interaction term was obtained by first deconvolving the physiological variable with the hemodynamic response function (HRF) to acquire the assumed neural response, then multiplying the neural response by psychological variables (R-pmod as 1 and F-pmod as -1), and convolving it with the HRF. These three variables (psychological variable, physiological variable and the interaction term) of interest and variables of no interest such as motion regressors and block effects were put into the GLM. The beta values pertaining to the interaction term in the GLM were entered into a group analysis.

3. Results

3.1. Behavioral Results

First, we ensured that the task-related performance during the encoding task was independent of possible differences in memory performance among conditions by performing one-way ANOVA on RT and classification accuracy. First, RT among conditions did not show significant differences (mean ± standard deviation (SD); 0 days: 424.87 ± 30.22 ms, 1 day: 427.35 ± 33.67 ms, 7 days: 427.57 ± 31.95 ms, 28 days: 429.9 ± 27.61 ms). Second, the mean classification accuracy for each condition showed a ceiling effect (0 days: 93.46 ± 5.75%, 1 day: 92.63 ± 5.84%, 7 days: 92.01 ± 5.27%, 28 day: 93.25 ± 6.12%) as well as no significant differences among conditions. Therefore, in further analyses, we claim that the task-related performance of each condition during the encoding session does not account for possible

differences in memory performance of each condition.

Participants' CR was assessed by subtracting hit rate (the number of hits divided by total possible hits in the given condition) by false-alarm rate (the number of false alarms divided by total possible false alarms, identical across all conditions), regardless of the confidence rating for each decision (Figure 2). First, participants' CR was subjected to a 2 x 4 ANOVA (recent vs. remote retrieval x 4 different delays of reward). Only the main effect of retrieval time point turned out to be significant ($F_{(1,21)} = 122.4$, $p < 0.001$). Posthoc analysis of retrieval revealed that CR was significantly higher for items that were retrieved 15 minutes later in contrast to items retrieved one week later ($t_{(22)} = 8.64$, $p < 0.001$), as expected. Although the main-effect of reward-delay conditions turned out to be insignificant in ANOVA using both sure and guess decisions as well as ANOVA using only sure decisions, an exploratory t-test using only sure decisions revealed that while no difference between conditions was observed within recent retrieval, 7-days and 28-days delay showed higher CR than the 1-day delay condition ($t_{(22)} = 2.6$, $p = 0.02$; $t_{(22)} = 2.6$, $p = 0.02$). Also, performing a paired t-test after binning 0 days and 1 day's sure HITs as 'sooner' and 7 days and 28 days as 'later' conditions showed that 'later' conditions' CR is marginally higher than the 'sooner' condition CR ($t_{(22)} = 2.06$, $p = 0.05$).

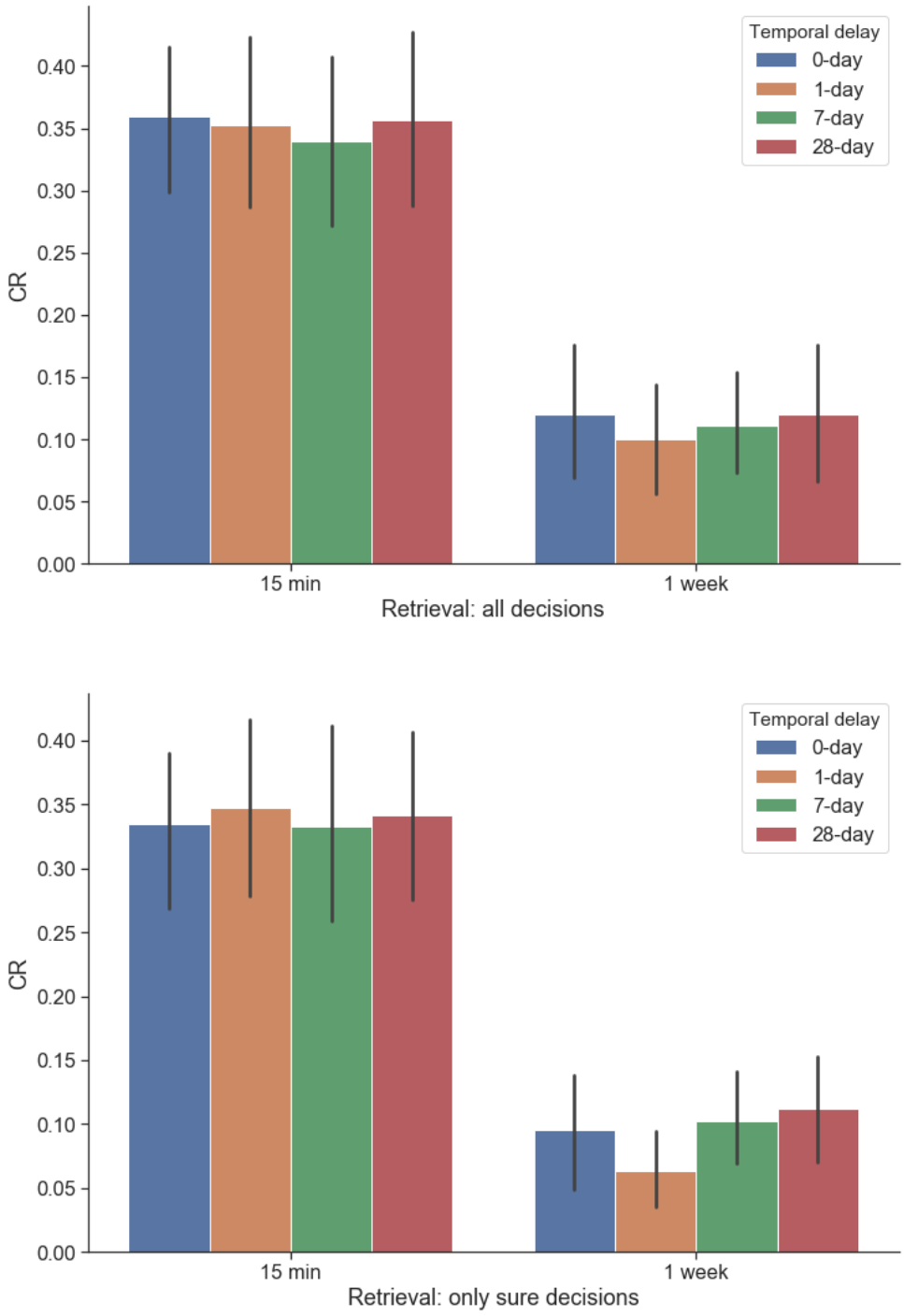

Figure 2 Corrected recognition (CR). Error bars indicate standard deviation, 15 min = retrieval right after encoding, 1 week = retrieval 1 week after encoding, (above) CR using both sure and guessed responses (bottom) CR using only sure responses

Participants' discount rate (k) ranged from 0.0002 to 0.1112 (mean ± standard deviation (SD); 0.0209 ± 0.0309). When assuming subjective value for 0-day as 18.9 KRW, the subjective value for other days were all significantly lower than 0-day (1 day = 18.53 ± 0.53 KRW, $t(21) = 3.28$, $p = 0.004$; 7-days = 16.92 ± 2.41 KRW, $t(21) = 3.86$, $p = 0.001$; 28-days = 14.06 ± 4.38 KRW, $t(21) = 5.19$, $p < 0.001$).

3.2. Neuroimaging Data

3.2.1. Replication of previous literature

We performed a set of analyses to check whether results from previous studies can be replicated and to strengthen the results from the main analyses. In encoding runs, SVC yielded activation for the parahippocampal cortex pertaining to subsequently remembered vs. forgotten items retrieved one week later (MNI coordinates x, y, z = -34, -6, -22; $p_{SVC} = 0.003$; $k = 25$; $z = 2.75$), and activation of the striatum (-24, -10, 8; $p_{SVC} = 0.009$; $k = 20$; $z = 2.37$) and the OFC (32, 30, -22; $p_{SVC} = 0.012$; $k = 42$; $z = 2.27$) when checking for regions showing a main effect of subjective value. For the first retrieval session, the caudate (8, 8, -4; $p_{SVC} < 0.001$; $k = 27$; $z = 3.79$) was activated for retrieval success upon SVC. The same contrast applied to the second retrieval session which yielded whole-brain level activation in a cluster comprising the right inferior parietal lobule, precuneus, posterior cingulate, and a cluster of regions in the frontal lobe (Table 2). All these regions have been reported to be activated upon direct HIT vs. correct rejection contrasts (Kim, 2013). SVC in addition to whole-brain analysis returned activation in the bilateral caudate (left: -12, 8, 8; $p_{SVC} < 0.001$; $k = 165$; $z = 3.64$; right: 12, 6, 10; $p_{SVC} = 0.001$; $k = 201$; $z = 3$).

Table 2 Replication: activation peaks for HIT vs. Correct rejection within remote retrieval runs Abbreviation: BA = Brodmann area number

Contrast	Cluster	Voxels	BA	Hemisphere	Region name	z Stat	X	Y	Z
HITvsCR	1	4339	7	Right	Precuneus	3.93	14	-76	50
			31	Right	Posterior Cingulate	3.00	22	-58	22
			7	Left	Precuneus	2.94	-18	-72	44
			40	Right	Inferior Parietal Lobule	2.56	52	-40	50
			19	Right	Middle Occipital Gyrus	2.48	40	-88	20
			7	Right	Superior Parietal Lobule	2.24	32	-60	54
			19	Right	Cuneus	2.23	30	-92	28
	2	3197	10	Left	Inferior Frontal Gyrus	3.73	-48	42	-2
			8	Right	Middle Frontal Gyrus	3.60	44	38	44
			9	Right	Superior Frontal Gyrus	3.59	46	48	38
			46	Left	Middle Frontal Gyrus	2.98	-44	54	8
			10	Left	Superior Frontal Gyrus	2.65	-24	60	-8

3.2.2. Main Analyses

Among eight contrasts within encoding runs, only three contrasts yielded significant activations at the whole-brain level: (1) main effect of TD, (2) interaction of TD of reward (28 > 7 > 1 > 0 days) and subsequent memory (remembered vs. forgotten) within remote retrieval, and (3) interaction of TD of reward and subsequent memory within recent retrieval (Table 1). First, a cluster of regions encompassing the precentral gyrus, postcentral gyrus, superior temporal gyrus, insula, middle temporal gyrus, superior temporal gyrus, inferior frontal gyrus, cingulate gyrus, and the medial frontal gyrus showed activation in correlation with the TD of the reward,

regardless of other conditions (Figure 3). Second, a cluster including the precentral gyrus, cerebellum, middle temporal gyrus, cingulate gyrus, caudate, anterior cingulate, inferior temporal gyrus, inferior occipital gyrus, precuneus, paracentral lobule, and the fusiform gyrus was activated upon searching for regions showing an SME proportionate to TD for items retrieved recently (Figure 4). Third, a cluster encompassing the frontal lobe, insula, and the precentral gyrus, and a cluster comprised of the temporal gyrus, frontal lobe, and the inferior parietal lobule showed an SME proportionate to the more distant TD for items retrieved remotely (Figure 5).

Table 3 Whole-brain activation of regions during encoding phase. Abbreviations: BA = Brodmann area number, MAIN = main effect, IE = interaction effect.

Contrast	Cluster	Voxels	BA	Hemisphere	Region name	z Stat	X	Y	Z
1. MAIN: TD	1	3831	43	Right	Postcentral Gyrus	3.80	58	-18	18
			38	Right	Superior Temporal Gyrus	3.76	48	2	-12
			13	Right	Insula	3.5	46	-36	24
			6	Right	Precentral Gyrus	3.01	52	-8	56
			21	Right	Middle Temporal Gyrus	2.27	60	8	-14
	2	3752	22	Left	Superior Temporal Gyrus	3.68	-38	-54	18
			7	Left	Precuneus	2.72	-8	-54	46
			7	Right	Precuneus	2.38	2	-54	62
			39	Left	Middle Temporal Gyrus	2.23	-42	-70	24
	3	5144	40	Left	Postcentral Gyrus	3.38	-60	-24	16
			6	Left	Precentral Gyrus	3.1	-50	-2	12
			13	Left	Insula	2.97	-36	4	8
			47	Left	Inferior Frontal Gyrus	2.9	-26	12	-20
			31	Left	Cingulate Gyrus	2.8	-18	-28	42

			6	Left	Medial Frontal Gyrus	2.69	-12	-10	52
2. IE: SME proportionate to TD when retrieved recently	1	22436	6	Right	Precentral Gyrus	3.84	32	0	38
			*	Right	Cerebellum	3.83	44	-58	-26
			21	Right	Middle Temporal Gyrus	3.71	48	-46	4
			24	Left	Cingulate Gyrus	3.70	-14	-4	42
			*	Left	Caudate	3.51	-20	26	2
			8	Left	Middle Frontal Gyrus	3.47	-32	34	40
			19	Right	Inferior Temporal Gyrus	3.43	44	-60	-6
			19	Left	Inferior Occipital Gyrus	3.39	-46	-80	-6
			24	Left	Anterior Cingulate	3.32	-8	24	12
			7	Right	Precuneus	3.28	12	-50	52
			*	Left	Cerebellum	3.25	-34	-62	-10
			5	Right	Paracentral Lobule	3.22	22	-44	48
			37	Right	Fusiform Gyrus	3.16	42	-40	-8
3. IE: SME proportionate to TD when retrieved remotely	1	4434	47	Left	Middle Frontal Gyrus	4.52	-42	32	0
			13	Left	Insula	3.73	-44	2	12
			8	Left	Superior Frontal Gyrus	3.59	-28	26	50
			9	Left	Precentral Gyrus	3.32	-34	14	36
			47	Left	Inferior Frontal Gyrus	3.22	-24	24	-6
			32	Left	Anterior Cingulate	3.15	-8	34	24
			6	Right	Superior Frontal Gyrus	2.47	6	22	58
	2	3387	22	Right	Superior Temporal Gyrus	3.49	68	-40	12
			47	Right	Inferior Frontal Gyrus	3.45	46	36	-10
			22	Right	Middle Temporal Gyrus	3.39	52	-36	0
			11	Right	Middle Frontal Gyrus	3.12	40	46	-10
			13	Right	Insula	2.46	38	20	0
			40	Right	Inferior Parietal Lobule	2.36	52	-38	28

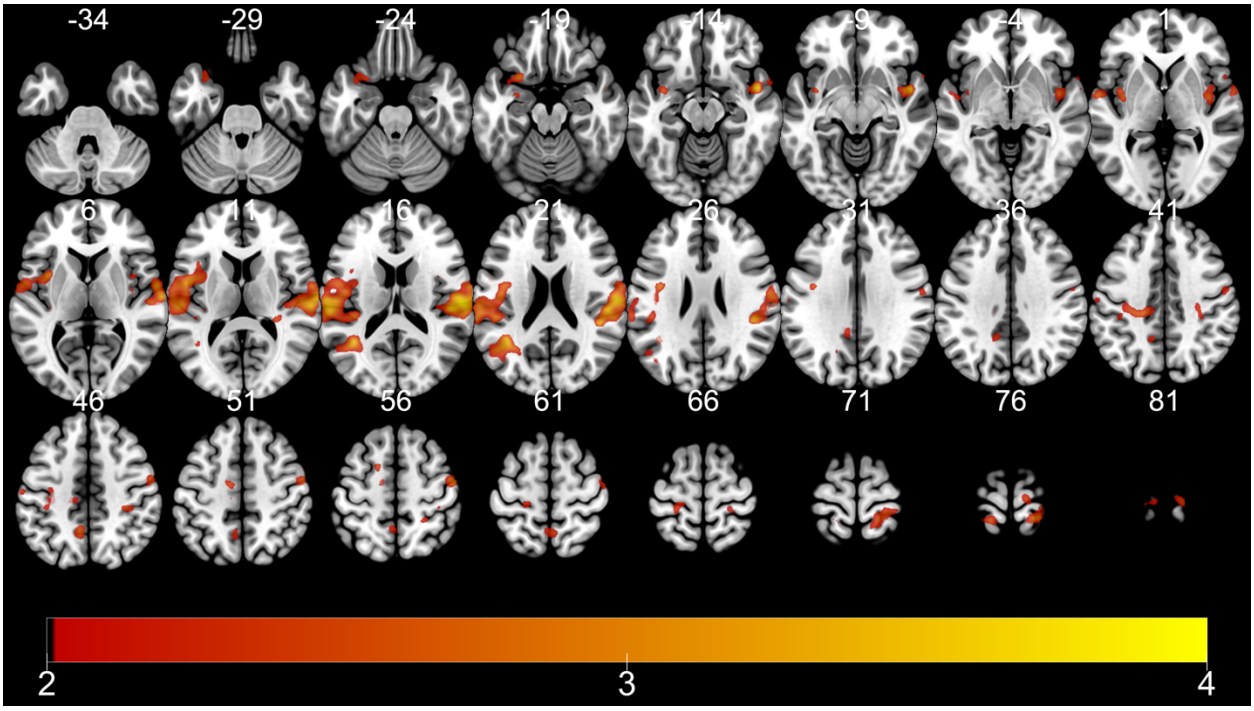

Figure 3 fMRI results (encoding): (1) Main effect of TD. Color bar indicates t-statistics

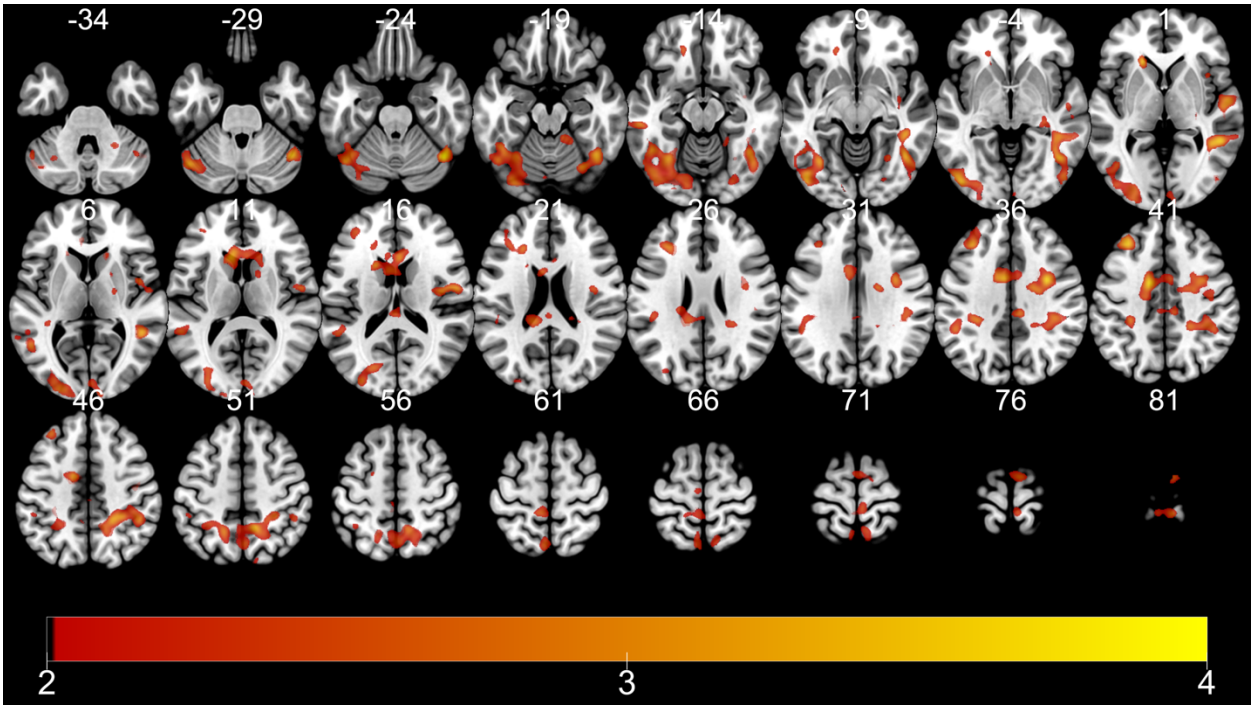

Figure 4 fMRI Results (Encoding). IE: SME proportionate to TD when retrieved recently. Color bar indicates t-statistics.

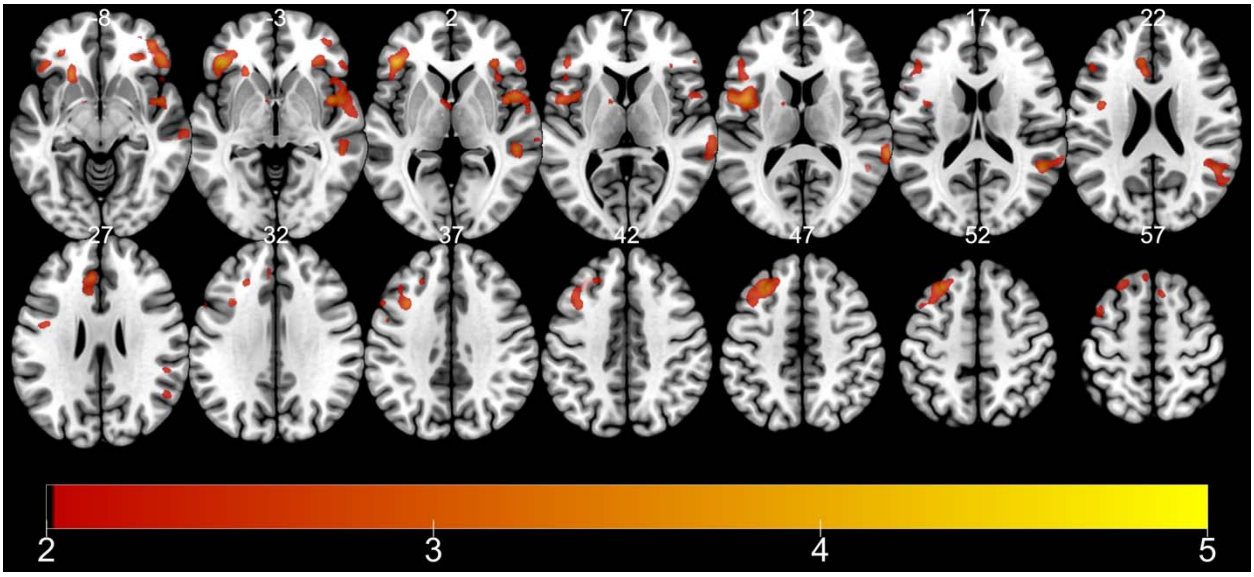

Figure 5 fMRI Results (Encoding). IE: SME proportionate to TD when retrieved remotely. Color bar indicates t-statistics.

Next, for analyses of retrieval runs, we examined areas showing proportionate activation to formerly associated value or TD of the retrieved stimuli. Significant whole-brain level activation was only found for TD during remote retrieval: a range of areas encompassing the bilateral superior frontal gyrus, middle frontal gyrus (MFG), and the medial frontal gyrus (Table 4).

Table 4 Activation peaks for regions showing proportionate SME for TD for items retrieved 1 week later. Abbreviation: BA = Brodmann area number

Cluster	Voxels	BA	Hemisphere	Region name	z Stat	X	Y	Z
1	3732	8	Left	Superior frontal gyrus	4.04	-44	26	52
		8	Right	Superior frontal gyrus	3.57	46	22	54
		6	Left	Middle frontal gyrus	3.12	-34	12	42
		6	Left	Medial frontal gyrus	2.57	-4	44	36

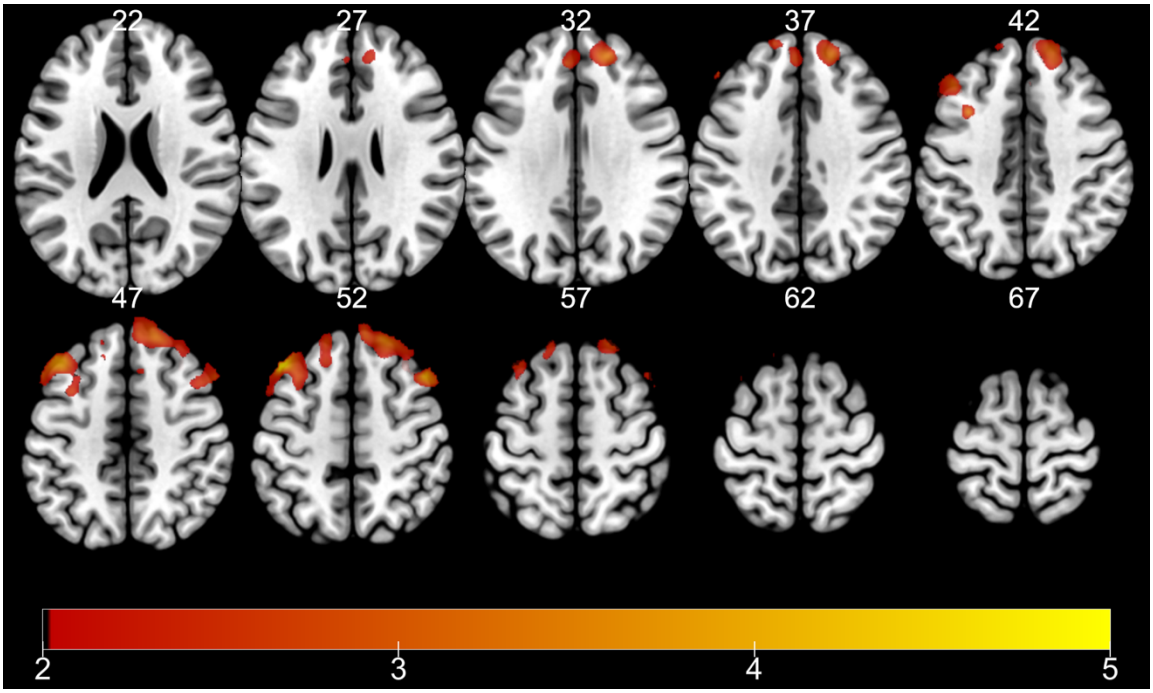

Figure 6 fMRI results: HITs showing commensurate activation with TD during remote retrieval. Color bar indicates t-statistics.

Since it was unexpected that the PFC represents the TD of reward associated with the stimuli during both encoding and remote retrieval, we performed a conjunction analysis to further clarify which regions are activated for both encoding and retrieval. Upon the threshold of $p < 0.001$ with at least ten contiguous voxels for conjunction, the MFG, insula, superior frontal gyrus, precentral gyrus, superior temporal gyrus, cerebellum, inferior frontal gyrus, and the medial frontal gyrus were activated (Table 5 & Figure 7). We performed a posthoc analysis to examine the SME of the MFG, the peak showing the greatest activation among regions identified by the conjunction analysis. The SME was defined as beta values of 'remembered' subtracted by 'forgotten' in each condition (TD). Pairwise t-tests revealed that activation related to the SME for reward without delay (0 days) was significantly lower than activation at 1 day ($t_{(22)} = 2.234$, $p = 0.037$), 7 days ($t_{(22)} = 3.306$, $p = 0.003$), and 28 days ($t_{(22)} = 4.75$, $p < 0.001$). Furthermore, there was a trend that activation at 1 day is smaller than at 7 days ($t_{(22)} = 1.77$, $p = 0.09$) and 28 days ($t_{(22)} = 2.48$, $p = 0.082$). Therefore, the observed interaction of the SME between conditions was mainly driven by the significantly lower SME of the 0-days condition than by the other conditions.

Table 5 Activation peaks for regions showing proportionate activation for TD during both encoding and remote retrieval (*p*<.001). Abbreviation: BA = Brodmann area number

Voxels	BA	Hemisphere	Region name	z Stat	X	Y	Z
88	47	Left	Middle Frontal Gyrus	4.52	-42	32	0
57	13	Left	Insula	3.73	-44	2	12
34	8	Left	Superior Frontal Gyrus	3.59	-28	26	50
36	9	Right	Precentral Gyrus	3.54	36	14	38
14	22	Right	Superior Temporal Gyrus	3.49	68	-40	12
12	*	Right	Cerebellum	3.49	12	-28	-6
17	47	Right	Inferior Frontal Gyrus	3.45	46	36	-10

44	22	Right	Superior Temporal Gyrus	3.43	50	6	0
13	10	Left	Medial Frontal Gyrus	3.38	-14	52	0
27	9	Right	Medial Frontal Gyrus	3.33	16	44	20

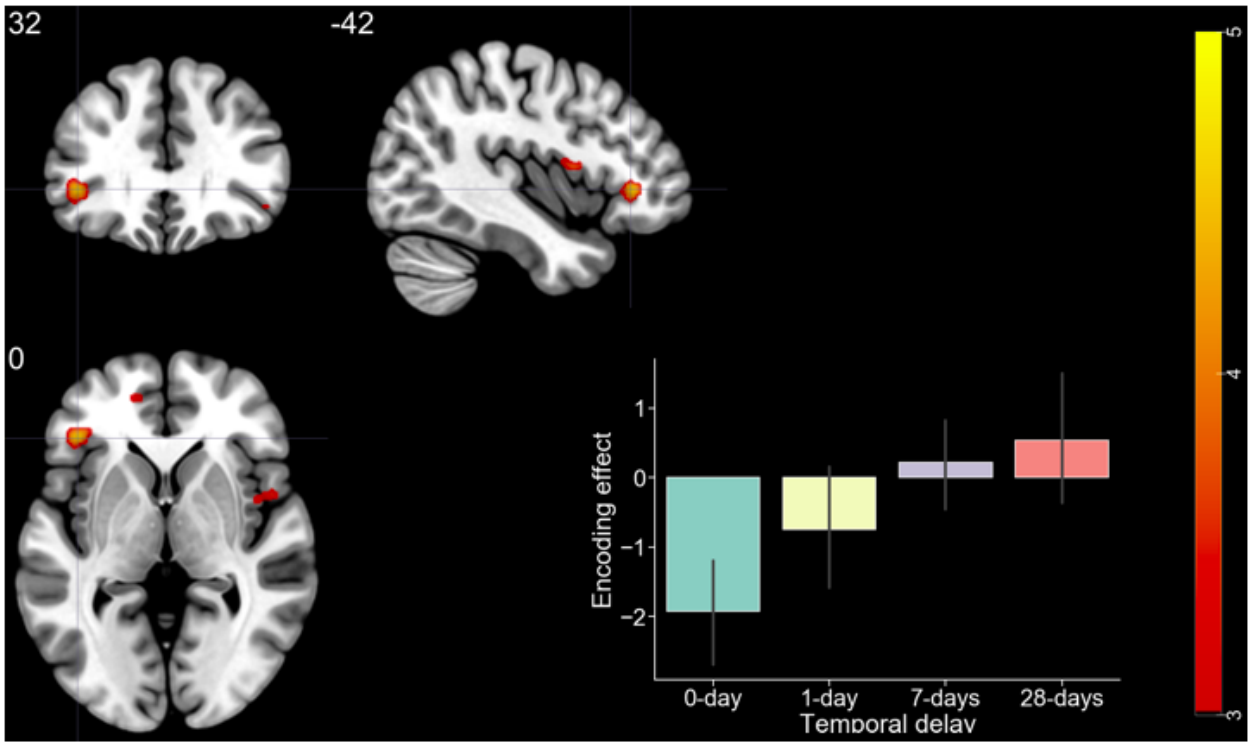

Figure 7 fMRI results: encoding-retrieval overlap Color bar indicates t-statistics, bar plot indicates SME (beta values of Remembered subtracted by Forgotten) of medial frontal gyrus (-42, 32, 0). Error bar indicates standard deviation.

These observations lead to two intermediate conclusions: (1) the greater the distance of the reward associated with a stimulus, the higher the activation of the MFG both during encoding and remote retrieval, and (2) this role of MFG becomes significant once consolidation takes place, given that this pattern of MFG does not emerge when items are retrieved before consolidation.

3.2.3. Psychophysiological Interaction

The HC seed used for the eigenvariate time series extraction was a 6 mm sphere around peak coordinate -22, -20, -20 obtained from R-pmod vs. F-pmod contrast in the whole-brain GLM. According to PPI results, regions including MFG and bilateral IPL showed functional connectivity with the HC (Table 6 & Figure 8).

Table 6 Activation peaks of PPI results. Abbreviation: BA = Brodmann area number

Voxels	BA	Hemisphere	Region name	z Stat	X	Y	Z
8373	6	Left	Middle Frontal Gyrus	4.01	-26	-12	44
	40	Left	Inferior Parietal Lobule	3.25	-64	-38	40
	31	Left	Cingulate Gyrus	3.21	-18	-40	40
	29	Right	Posterior Cingulate	3.15	12	-42	12
	46	Left	Inferior Frontal Gyrus	3.01	-50	36	8
	43	Left	Postcentral Gyrus	2.84	-54	-8	14
	13	Left	Insula	2.82	-32	22	14
	2	Left	Postcentral Gyrus	2.79	-68	-24	30
	5	Left	Paracentral Lobule	2.78	-16	-30	46
	7	Right	Precuneus	2.74	24	-60	52
	6	Left	Precentral Gyrus	2.69	-68	0	16
	6	Left	Medial Frontal Gyrus	2.66	-14	-22	54
4954	*	Right	Caudate	3.84	26	-34	8
	37	Right	Fusiform Gyrus	3.35	36	-42	-10
	2	Right	Postcentral Gyrus	3.25	60	-22	56
	40	Right	Inferior Parietal Lobule	2.59	68	-30	32
	40	Right	Inferior Parietal Lobule	2.52	48	-28	30
	13	Right	Insula	2.41	42	-20	20

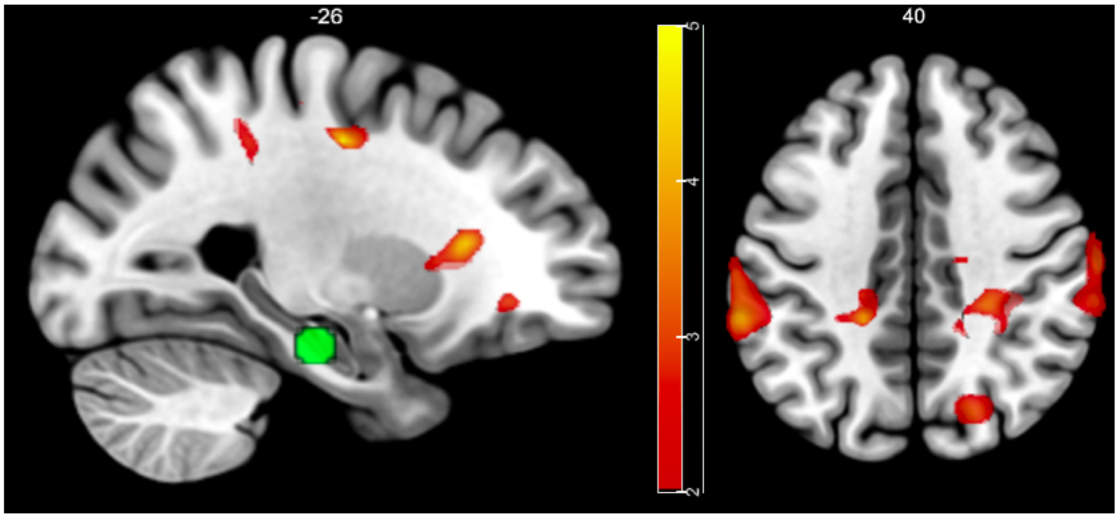

Figure 8 fMRI results: PPI. Color bar indicates t-statistics. (Left) The seed region, the HC (-22, -20, -20), is represented as a green sphere.

4. Discussion

Reward-motivated memory encoding and temporal discounting of a delayed reward are two well-studied fields in cognitive neuroscience. But to our knowledge, no previous study has directly linked these domains. This study is the first to examine whether rewards delivered at different TD lead to differential memory effects. We found that temporally distant rewards might lead to better memory performance, which is in contrast to previous studies. We showed that a) when considering only confident retrieval (sure decisions), behavioral measure of memory performance (CR) showed a trend that the more reward is delayed, the higher is the chance of memory consolidation, b) in the encoding session, while the subjective value of the reward did not yield activation proportional to an SME as expected, TD did, and c) some of these regions were again observed during the second retrieval session when HIT activation was parametrically modulated by TD associated with the stimuli.

Our result seems to be in conflict with the preexisting literature on reward-motivated memory encoding and temporal discounting. While previous studies showed that a) reward is devalued as its delivery is delayed (Green & Myerson, 2004) and b) reward magnitude is positively correlated with the SME (Adcock et al., 2006), our result suggests that a delayed reward acts as if it is more valued (when we put the emphasis on b) or — although reward is temporally discounted — a reward associated with TD might somehow involve a different mechanism than dopaminergic reward-modulation (when we put the emphasis on a). Since we have collected data from a delay-discounting decision-making task and found that participants showed temporal discounting behavior as reported in previous studies, it seems more plausible to assume the latter hypothesis that reward in a temporal context cannot be solely interpreted in light of previous reward-motivated memory literature. Thus, we seek a novel hypothesis to explain this unprecedented SME driven by temporally distant rewards.

To do so, we start by discussing the main effect of TD of reward during encoding that perceiving temporally distant reward engages lateral prefrontal and parietal activation (4th contrast of Encoding GLM; see Table 1). In fact, distant reward cues leading to lateral PFC or parietal activation are not unfamiliar. Lateral prefrontal activation has been reported after choosing delayed reward vs. immediate reward in intertemporal decision-making tasks (Diekhof & Gruber, 2010; McClure, 2004). However, linking these studies with the current results requires caution because intertemporal decision-making tasks typically involve situations in which participants are presented with larger-delayed and smaller-immediate rewards, thereby provoking self-control to inhibit impulsivity when participants choose the former over the latter, especially when taking into account that frontoparietal regions are representative members of the

control network (Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010). If lateral prefrontal activity reported in these studies is solely the product of executive control rather than TD, it would not support our results since our study does not require choosing between delayed and immediate rewards.

However, a study which examined the prediction of future rewards outside the intertemporal decision-making paradigm also reported that in the long vs. short delay contrast, the ventrolateral PFC (vlPFC), insula, dorsolateral PFC (dlPFC), dorsal premotor cortex, and the inferior parietal cortex are activated (Tanaka et al., 2004). In addition, a study that examined single-neuron activity of rats revealed neurons in the OFC / ventromedial PFC (vmPFC) which fire more strongly for delayed than for immediate rewards (Roesch, Taylor, & Schoenbaum, 2006). Frontoparietal regions have been reported to be activated for processing time and future perception in general and it has been previously reported that elaborating a future event activates the inferior frontal gyrus and the supramarginal gyrus (Weiler, Suchan, & Daum, 2010). Additionally, studies on macaques have found activations in the dlPFC and the inferior parietal cortex (Onoe et al., 2001) and the posterior parietal cortex (Leon & Shadlen, 2003) during time perception tasks. These comprehensive studies weaken the possibility that frontoparietal activation associated with choosing a distant reward in intertemporal decision-making tasks solely reflects self-control. Instead, they may indicate that frontoparietal regions also process some portion of temporal information upon perceiving a delayed reward.

Interestingly, in our study, some of these regions such as the PFC or the inferior parietal lobule (IPL) go further from merely representing the TD of reward (4th contrast of Encoding GLM) to showing an SME commensurate with the TD during memory encoding (8th contrast of

Encoding GLM). This is supported by the PPI result that PFC and parietal regions are likely to be transferring their temporal information to the HC during encoding, though causality is not defined in our study. This is consistent with a previous study reporting that the PFC and the IPL are also members of the retrieval success network (Kim, 2013) as the PFC and the IPL are activated upon successful retrievals in contrast to correct rejections in memory retrieval tasks. While it appears to be counterintuitive to find the answer to the 'encoding' results from the 'retrieval' phase, the principle of transfer-appropriate processing supports this hypothesis (Morris, Bransford, & Franks, 1977; Ritchey, Wing, LaBar, & Cabeza, 2013). It assumes that memory will be enhanced if memory retrieval reactivates similar regions as those that were engaged during cognitive operations of encoding. Cortical reinstatement, which refers to the reactivation of the original neural trace of a stimulus during retrieval (Danker & Anderson, 2010), might be an example, since the degree of cortical reinstatement has been found to correlate with memory recall performance (Kuhl & Chun, 2014; Kuhl, Rissman, Chun, & Wagner, 2011). It has also been found that perception-retrieval overlap of the perirhinal cortex and the parahippocampal cortex predicts success recall for object- and scene-stimuli, respectively (Schultz et al., 2019). Given this background, it is not surprising that brain regions that respond to TD during encoding, which are also key regions contributing to retrieval success, enhance memory for items associated with distant reward by the coincidental encoding-retrieval overlap.

However, even if we assume that the SME of delayed reward is proportionate to the TD due to encoding-retrieval overlap of retrieval success (or 'temporal-distance') regions, it is conditional because this phenomenon is only observed when memory is retrieved one week but not 15 minutes later. This is an important argument because we are trying to provide an

alternative account to the dopaminergic account, but the differential effect of reward on memory observed pre- and post-consolidation is what would be expected by the dopamine account. To resolve this, we focus on the fact that the remote retrieval took place one week after encoding in our study. Consolidation continues even after 24 hours, reorganizing the initially constructed engram of memory at a system (network) level (Dudai, 1996). One of the accounts regarding system consolidation of memory proposes that while initially formed memory is rich in episodic details, supported by the HC, it eventually becomes abstract and semantic over time, thereby becoming less dependent on the HC (Nadel, Winocur, Ryan, & Moscovitch, 2007). Indeed, an fMRI study over three months has shown that while recently formed memory relies more on hippocampal representations, systems consolidation shifts the site of memory from the HC to neocortical areas such as the mPFC over time (Takashima et al., 2006). In light of this, our results can be explained by the following: memory performance for recent retrieval is not different among conditions because while recently formed episodic details depend on hippocampal activation, the four temporal conditions did not show differences in HC activation. However, as the HC contributes less to the network, regions which initially represented cognitive information become the site of memory upon encountering the stimulus. In our study, the regions initially coding cognitive information (i.e., TD) such as the PFC showed differential activation for temporal conditions during encoding, and as a function of TD. This initial difference stood out more as memory becomes more dependent on traces in the PFC. This may be one of the reasons that stimuli associated with a more distant reward, triggering stronger activations in the neocortex, became more likely to be remembered as retrieval becomes less dependent on the HC.

This study is the first to examine how the TD of rewards modulates episodic memory and

the dynamics of memory retrieval with time. This study is important because it suggested that temporally varied rewards may not act like rewards which vary in magnitude in the brain. However, this study has limitations because the behavioral effects are statistically weak. Furthermore, the results from this study could also be analyzed by pattern analyses such as multivariate pattern analyses so that representations among temporal conditions for encoding and retrieval can be directly compared.

5. References

Adcock, R. A., Thangavel, A., Whitfield-Gabrieli, S., Knutson, B., & Gabrieli, J. D. E. (2006). Reward-Motivated Learning: Mesolimbic Activation Precedes Memory Formation. *Neuron*, *50*(3), 507–517. https://doi.org/10.1016/j.neuron.2006.03.036

Andersson, J. L. R., Skare, S., & Ashburner, J. (2003). How to correct susceptibility distortions in spin-echo echo-planar images: application to diffusion tensor imaging. *NeuroImage*, *20*(2), 870–888. https://doi.org/10.1016/S1053-8119(03)00336-7

Ballard, K., & Knutson, B. (2009). Dissociable neural representations of future reward magnitude and delay during temporal discounting. *NeuroImage*, *45*(1), 143–150. https://doi.org/10.1016/j.neuroimage.2008.11.004

Bilker, W. B., Hansen, J. A., Brensinger, C. M., Richard, J., Gur, R. E., & Gur, R. C. (2012). Development of Abbreviated Nine-Item Forms of the Raven's Standard Progressive Matrices Test. *Assessment*, *19*(3), 354–369. https://doi.org/10.1177/1073191112446655

Botvinick, M. M., Huffstetler, S., & McGuire, J. T. (2009). Effort discounting in human nucleus accumbens. *Cognitive, Affective, & Behavioral Neuroscience*, *9*(1), 16–27. https://doi.org/10.3758/CABN.9.1.16

Carver, C. S., & White, T. L. (1994). Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: the BIS/BAS scales. *Journal of personality and social psychology*, *67*(2), 319.

Danker, J. F., & Anderson, J. R. (2010). The ghosts of brain states past: Remembering reactivates the brain regions engaged during encoding. *Psychological Bulletin*, *136*(1), 87–102. https://doi.org/10.1037/a0017937

Diekhof, E. K., & Gruber, O. (2010). When Desire Collides with Reason: Functional Interactions between Anteroventral Prefrontal Cortex and Nucleus Accumbens Underlie the Human Ability to Resist Impulsive Desires. *Journal of Neuroscience*, *30*(4), 1488–1493. https://doi.org/10.1523/JNEUROSCI.4690-09.2010

Dudai, Y. (1996). Consolidation: Fragility on the Road to the Engram. *Neuron*, *17*(3), 367–370. https://doi.org/10.1016/S0896-6273(00)80168-3

Eichenbaum, H., Yonelinas, A. P., & Ranganath, C. (2007). The medial temporal lobe and recognition memory. *Annu. Rev. Neurosci.*, *30*, 123-152.

Enomoto, K., Matsumoto, N., Nakai, S., Satoh, T., Sato, T. K., Ueda, Y., ... & Kimura, M. (2011). Dopamine neurons learn to encode the long-term value of multiple future rewards. *Proceedings of the National Academy of Sciences*, *108*(37), 15462-15467.

Green, L., & Myerson, J. (2004). A Discounting Framework for Choice With Delayed and Probabilistic Rewards. *Psychological Bulletin*, *130*(5), 769–792. https://doi.org/10.1037/0033-2909.130.5.769

Griffiths, B. J., Parish, G., Roux, F., Michelmann, S., van der Plas, M., Kolibius, L. D., ... & Gollwitzer, S. (2019). Directional coupling of slow and fast hippocampal gamma with neocortical alpha/beta oscillations in human episodic memory. *Proceedings of the National Academy of Sciences*, 201914180.

Gruber, M. J., Gelman, B. D., & Ranganath, C. (2014). States of Curiosity Modulate Hippocampus-Dependent Learning via the Dopaminergic Circuit. *Neuron*, *84*(2), 486–496. https://doi.org/10.1016/j.neuron.2014.08.060

Gruber, M. J., Ritchey, M., Wang, S.-F., Doss, M. K., & Ranganath, C. (2016). Post-learning

Hippocampal Dynamics Promote Preferential Retention of Rewarding Events. *Neuron*, *89*(5), 1110–1120. https://doi.org/10.1016/j.neuron.2016.01.017

Hamann, J. M., Dayan, E., Hummel, F. C., & Cohen, L. G. (2014). Baseline frontostriatal-limbic connectivity predicts reward-based memory formation: Reward Networks Predict Memory Formation. *Human Brain Mapping*, *35*(12), 5921–5931. https://doi.org/10.1002/hbm.22594

Johnson, M. W., & Bickel, W. K. (2002). Within-subject comparison of real and hypothetical money rewards in delay discounting. *Journal of the experimental analysis of behavior*, *77*(2), 129-146.

Kable, J. W., & Glimcher, P. W. (2007). The neural correlates of subjective value during intertemporal choice. *Nature Neuroscience*, *10*(12), 1625–1633. https://doi.org/10.1038/nn2007

Kim, H. (2011). Neural activity that predicts subsequent memory and forgetting: A meta-analysis of 74 fMRI studies. *NeuroImage*, *54*(3), 2446–2461. https://doi.org/10.1016/j.neuroimage.2010.09.045

Kim, H. (2013). Differential neural activity in the recognition of old versus new events: An Activation Likelihood Estimation Meta-Analysis. *Human Brain Mapping*, *34*(4), 814–836. https://doi.org/10.1002/hbm.21474

Kirby, K. N., & Marakovic, N. N. (1995). Modelling myopic decisions: Evidence for hyperbolic delay-discounting within subjects and amounts. Organisational Behavior and Human Decision Processes, 64, 22–30.

Kobayashi, S., & Schultz, W. (2008). Influence of Reward Delays on Responses of Dopamine

Neurons. *Journal of Neuroscience*, *28*(31), 7837–7846. https://doi.org/10.1523/JNEUROSCI.1600-08.2008

Konkle, T., Brady, T. F., Alvarez, G. A., & Oliva, A. (2010). Scene Memory Is More Detailed Than You Think: The Role of Categories in Visual Long-Term Memory. *Psychological Science*, *21*(11), 1551–1556. https://doi.org/10.1177/0956797610385359

Kuhl, B. A., & Chun, M. M. (2014). Successful Remembering Elicits Event-Specific Activity Patterns in Lateral Parietal Cortex. *Journal of Neuroscience*, *34*(23), 8051–8060. https://doi.org/10.1523/JNEUROSCI.4328-13.2014

Kuhl, B. A., Rissman, J., Chun, M. M., & Wagner, A. D. (2011). Fidelity of neural reactivation reveals competition between memories. *Proceedings of the National Academy of Sciences*, *108*(14), 5903–5908. https://doi.org/10.1073/pnas.1016939108

Leon, M. I., & Shadlen, M. N. (2003). Representation of Time by Neurons in the Posterior Parietal Cortex of the Macaque. *Neuron*, *38*(2), 317–327. https://doi.org/10.1016/S0896-6273(03)00185-5

Levy, D. J., & Glimcher, P. W. (2011). Comparing Apples and Oranges: Using Reward-Specific and Reward-General Subjective Value Representation in the Brain. *Journal of Neuroscience*, *31*(41), 14693–14707. https://doi.org/10.1523/JNEUROSCI.2218-11.2011

Li, N., Ma, N., Liu, Y., He, X.-S., Sun, D.-L., Fu, X.-M., … Zhang, D.-R. (2013). Resting-State Functional Connectivity Predicts Impulsivity in Economic Decision-Making. *Journal of Neuroscience*, *33*(11), 4886–4895. https://doi.org/10.1523/JNEUROSCI.1342-12.2013

Lisman, J. E., & Grace, A. A. (2005). The Hippocampal-VTA Loop: Controlling the Entry of Information into Long-Term Memory. *Neuron*, *46*(5), 703–713.

https://doi.org/10.1016/j.neuron.2005.05.002

Lisman, J., Grace, A. A., & Duzel, E. (2011). A neoHebbian framework for episodic memory; role of dopamine-dependent late LTP. *Trends in Neurosciences*, *34*(10), 536–547. https://doi.org/10.1016/j.tins.2011.07.006

Ludwig, V. U., Nüsser, C., Goschke, T., Wittfoth-Schardt, D., Wiers, C. E., Erk, S., … Walter, H. (2015). Delay discounting without decision-making: medial prefrontal cortex and amygdala activations reflect immediacy processing and correlate with impulsivity and anxious-depressive traits. *Frontiers in Behavioral Neuroscience*, *9*. https://doi.org/10.3389/fnbeh.2015.00280

Mason, A., Farrell, S., Howard-Jones, P., & Ludwig, C. J. H. (2017). The role of reward and reward uncertainty in episodic memory. *Journal of Memory and Language*, *96*, 62–77. https://doi.org/10.1016/j.jml.2017.05.003

McClure, S. M. (2004). Separate Neural Systems Value Immediate and Delayed Monetary Rewards. *Science*, *306*(5695), 503–507. https://doi.org/10.1126/science.1100907

Miendlarzewska, E. A., Bavelier, D., & Schwartz, S. (2016). Influence of reward motivation on human declarative memory. *Neuroscience & Biobehavioral Reviews*, *61*, 156–176. https://doi.org/10.1016/j.neubiorev.2015.11.015

Morris, C. D., Bransford, J. D., & Franks, J. J. (1977). Levels of processing versus transfer appropriate processing. *Journal of Verbal Learning and Verbal Behavior*, *16*(5), 519–533. https://doi.org/10.1016/S0022-5371(77)80016-9

Mumford, J. A., Poline, J.-B., & Poldrack, R. A. (2015). Orthogonalization of Regressors in fMRI Models. *PLOS ONE*, *10*(4), e0126255.

https://doi.org/10.1371/journal.pone.0126255

Myerson, J., & Green, L. (1995). Discounting of delayed rewards: Models of individual choice. Journal of Experimental Analysis of Behavior, 64, 263–276.

Nadel, L., Winocur, G., Ryan, L., & Moscovitch, M. (2007). Systems consolidation and hippocampus: Two views. *Debates in Neuroscience*, *1*(2–4), 55–66. https://doi.org/10.1007/s11559-007-9003-9

O'Carroll, C. M., Martin, S. J., Sandin, J., Frenguelli, B., & Morris, R. G. M. (2006). Dopaminergic modulation of the persistence of one-trial hippocampus-dependent memory. *Learning & Memory*, *13*(6), 760–769. https://doi.org/10.1101/lm.321006

Onoe, H., Komori, M., Onoe, K., Takechi, H., Tsukada, H., & Watanabe, Y. (2001). Cortical Networks Recruited for Time Perception: A Monkey Positron Emission Tomography (PET) Study. *NeuroImage*, *13*(1), 37–45. https://doi.org/10.1006/nimg.2000.0670

Pauli, R., Bowring, A., Reynolds, R., Chen, G., Nichols, T. E., & Maumet, C. (2016). Exploring fMRI Results Space: 31 Variants of an fMRI Analysis in AFNI, FSL, and SPM. *Frontiers in Neuroinformatics*, *10*. https://doi.org/10.3389/fninf.2016.00024

Peters, J., & Büchel, C. (2010). Episodic Future Thinking Reduces Reward Delay Discounting through an Enhancement of Prefrontal-Mediotemporal Interactions. *Neuron*, *66*(1), 138–148. https://doi.org/10.1016/j.neuron.2010.03.026

Peters, J., & Büchel, C. (2010). Neural representations of subjective reward value. *Behavioural Brain Research*, *213*(2), 135–141. https://doi.org/10.1016/j.bbr.2010.04.031

Raven, J. C. (1941). STANDARDIZATION OF PROGRESSIVE MATRICES, 1938. *British Journal of Medical Psychology*, *19*(1), 137–150. https://doi.org/10.1111/j.2044-

8341.1941.tb00316.x

Richards, J. B., Zhang, L., Mitchell, S. H., & de Wit, H. (1999). Delay or probability discounting in a model of impulsive behavior: effect of alcohol. *Journal of the Experimental Analysis of Behavior*, *71*(2), 121–143. https://doi.org/10.1901/jeab.1999.71-121

Ritchey, M., Wing, E. A., LaBar, K. S., & Cabeza, R. (2013). Neural Similarity Between Encoding and Retrieval is Related to Memory Via Hippocampal Interactions. *Cerebral Cortex*, *23*(12), 2818–2828. https://doi.org/10.1093/cercor/bhs258

Rodriguez, M. L., & Logue, A. W. (1988). Adjusting delay to reinforcement: comparing choice in pigeons and humans. *Journal of Experimental Psychology: Animal Behavior Processes*, *14*(1), 105.

Roesch, M. R., Taylor, A. R., & Schoenbaum, G. (2006). Encoding of time-discounted rewards in orbitofrontal cortex is independent of value representation. *Neuron*, *51*(4), 509-520.

Rossato, J. I., Bevilaqua, L. R. M., Izquierdo, I., Medina, J. H., & Cammarota, M. (2009). Dopamine Controls Persistence of Long-Term Memory Storage. *Science*, *325*(5943), 1017–1020. https://doi.org/10.1126/science.1172545

Schmaal, L., Goudriaan, A. E., van der Meer, J., van den Brink, W., & Veltman, D. J. (2012). The association between cingulate cortex glutamate concentration and delay discounting is mediated by resting state functional connectivity. *Brain and Behavior*, *2*(5), 553–562. https://doi.org/10.1002/brb3.74

Schultz, W. (1998). Predictive reward signal of dopamine neurons. *Journal of neurophysiology*, *80*(1), 1-27.

Schultz, W. (2010). Dopamine signals for reward value and risk: basic and recent data. *Behavioral and Brain Functions*, *6*(1), 24. https://doi.org/10.1186/1744-9081-6-24

Schultz, H., Tibon, R., LaRocque, K. F., Gagnon, S. A., Wagner, A. D., & Staresina, B. P. (2019). Content Tuning in the Medial Temporal Lobe Cortex: Voxels that Perceive, Retrieve. *Eneuro*, *6*(5), ENEURO.0291-19.2019. https://doi.org/10.1523/ENEURO.0291-19.2019

Seaman, K. L., Brooks, N., Karrer, T. M., Castrellon, J. J., Perkins, S. F., Dang, L. C., … Samanez-Larkin, G. R. (2018). Subjective value representations during effort, probability and time discounting across adulthood. *Social Cognitive and Affective Neuroscience*, *13*(5), 449–459. https://doi.org/10.1093/scan/nsy021

Shohamy, D., & Adcock, R. A. (2010). Dopamine and adaptive memory. *Trends in Cognitive Sciences*, *14*(10), 464–472. https://doi.org/10.1016/j.tics.2010.08.002

Spreng, R. N., Stevens, W. D., Chamberlain, J. P., Gilmore, A. W., & Schacter, D. L. (2010). Default network activity, coupled with the frontoparietal control network, supports goal-directed cognition. *NeuroImage*, *53*(1), 303–317. https://doi.org/10.1016/j.neuroimage.2010.06.016

Staresina, B. P., Duncan, K. D., & Davachi, L. (2011). Perirhinal and Parahippocampal Cortices Differentially Contribute to Later Recollection of Object- and Scene-Related Event Details. *Journal of Neuroscience*, *31*(24), 8739–8747. https://doi.org/10.1523/JNEUROSCI.4978-10.2011

Stephan B. Hamann, Timothy D. Ely, Scott T. Grafton, & Clinton D. Kilts. (1999). Amygdala

activity related to enhanced memory for pleasant and aversive stimuli. *Nature Neuroscience*, *2*(3).

Takashima, A., Petersson, K. M., Rutters, F., Tendolkar, I., Jensen, O., Zwarts, M. J., … Fernandez, G. (2006). Declarative memory consolidation in humans: A prospective functional magnetic resonance imaging study. *Proceedings of the National Academy of Sciences*, *103*(3), 756–761. https://doi.org/10.1073/pnas.0507774103

Tanaka, S. C., Doya, K., Okada, G., Ueda, K., Okamoto, Y., & Yamawaki, S. (2004). Prediction of immediate and future rewards differentially recruits cortico-basal ganglia loops. *Nature Neuroscience*, *7*(8), 887–893. https://doi.org/10.1038/nn1279

Uncapher, M. R., & Wagner, A. D. (2009). Posterior parietal cortex and episodic encoding: Insights from fMRI subsequent memory effects and dual-attention theory. *Neurobiology of Learning and Memory*, *91*(2), 139–154. https://doi.org/10.1016/j.nlm.2008.10.011

van den Bos, W., Rodriguez, C. A., Schweitzer, J. B., & McClure, S. M. (2014). Connectivity Strength of Dissociable Striatal Tracts Predict Individual Differences in Temporal Discounting. *Journal of Neuroscience*, *34*(31), 10298–10310. https://doi.org/10.1523/JNEUROSCI.4105-13.2014

van Kesteren, M. T., Fernández, G., Norris, D. G., & Hermans, E. J. (2010). Persistent schema-dependent hippocampal-neocortical connectivity during memory encoding and postencoding rest in humans. *Proceedings of the National Academy of Sciences*, *107*(16), 7550-7555.

Weiler, J. A., Suchan, B., & Daum, I. (2010). When the future becomes the past: Differences in

brain activation patterns for episodic memory and episodic future thinking. *Behavioural Brain Research*, *212*(2), 196–203. https://doi.org/10.1016/j.bbr.2010.04.013

Wittmann, B. C., Schott, B. H., Guderian, S., Frey, J. U., Heinze, H.-J., & Düzel, E. (2005). Reward-Related fMRI Activation of Dopaminergic Midbrain Is Associated with Enhanced Hippocampus- Dependent Long-Term Memory Formation. *Neuron*, *45*(3), 459–467. https://doi.org/10.1016/j.neuron.2005.01.010