

Goal-Dependent Hippocampal Representations Facilitate Self-Control

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Hippocampal activity linking past experiences and simulations of the future with current goals can play an important role in decision-making. The representation of information within the hippocampus may be especially critical in situations where one needs to overcome past rewarding experiences and exert self-control. Self-control success or failure may depend on how information is represented in the hippocampus and how effectively the representation process can be modified to achieve a specific goal. We test this hypothesis using representational similarity analyses of human (female/male) neuroimaging data during a dietary self-control task in which individuals must overcome taste temptations to choose healthy foods. We find that self-control is indeed associated with the way individuals represent taste information (valence) in the hippocampus and how taste representations there adapt to align with different goals/contexts. Importantly, individuals who were able to shift their hippocampal representations to a larger degree to align with the current motivation were better able to exert self-control when facing a dietary challenge. These results suggest an alternative or complementary neurobiological pathway leading to self-control success and indicate the need to update the classical view of self-control to continue to advance our understanding of its behavioral and neural underpinnings.

Key words: brain imaging; decision making; memory; multivariate RSA; self-control

Significance Statement

The paper provides a new perspective on what leads to successful self-control at the behavioral and neurobiological levels. Our data suggest that self-control is enhanced when individuals adjust hippocampal processing to align with current goals.

Introduction

The capability to adjust our thoughts and behavior to overcome temptations and pursue a higher-order goal is central to human success and well-being. Despite its importance and a long history of inquiry, the underlying mechanisms leading to successful self-control are still only partially understood. Longstanding theories of the neurobiology of self-control have primarily focused on regulatory functions supported by the PFC and antagonistic interactions between the PFC and subcortical brain regions associated with reward, such as the amygdala and striatum (Hare et al., 2009; Cohen and Lieberman, 2010; Buhle et al., 2014; Maier et al., 2015; Tang et al., 2015; Cohen and Casey, 2017; Shenav, 2017; Sun and Kober, 2020). However, self-control challenges

often require individuals to assess past experiences (rewarding or aversive) and use this information to simulate/map out the effects of current actions. Therefore, another potentially important, yet thus far overlooked, component in self-control success is hippocampal processing.

Given its well-established importance for memory, a role for the hippocampus in self-control would be consistent with the growing body of work on memory sampling theories (Wang et al., 2015; Bornstein and Norman, 2017; Bornstein et al., 2017) and empirical data from human and other animal models on the relationship between hippocampus-mediated memory and decision-making (Johnson and Redish, 2007; Lebreton et al., 2013; Wimmer et al., 2014; Gluth et al., 2015; Palombo et al., 2015; Shadlen and Shohamy, 2016; Fellows, 2018; Bakkour et al., 2019; Pelletier and Fellows, 2019; Biderman et al., 2020; Botvinik-Nezer et al., 2021). Memory sampling theories postulate that, given computational and resource limitations, a decision maker often cannot retrieve all the (potentially hundreds or thousands) past experiences with a given item when making each new consumption choice. Instead, they need to rely on a representative subsample of such experiences that can be selected randomly or in a context-dependent way. Consequently, one key to self-control success can be to adapt the sources of past information that inform the choice so that they align with the context

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of the current goal. To test this hypothesis at the neurobiological level, we focused on the hippocampus because it is theorized to be a prominent source of information and simulations of future outcomes for goal-directed decisions (Schacter et al., 2007; Biderman et al., 2020) and is the region most closely associated with episodic memory retrieval and sampling in past research (Squire et al., 1992; Dudai, 2002; Edelson et al., 2011, 2014; Bornstein and Norman, 2017; Bornstein et al., 2017). We predicted that representations of stimuli and their component attributes in the hippocampus should adjust to current goals, and that self-control success will depend on the extent to which brain representations of attribute-level information align with the current goal. In this work, we examined food choices and focused primarily on taste valance (for brevity in the following sections referred to as taste) representations because they can be associated with concrete episodic experiences that could be the source of mnemonic sampling. For example, the fresh tomatoes at the farmers market last Saturday were extraordinarily tasty or the chocolate cake at a friend's birthday party was too dry and crumbly. Importantly, activity in the hippocampus is multifaceted and does not necessarily need to reflect mnemonic processing *per se* (see Discussion).

We tested our hypothesis using human neuroimaging and behavioral data acquired during a series of food evaluation and consumption choice tasks. The participants in this study were self-reported dieters who evaluated the same 50 food items in the context of three separate goals while undergoing fMRI (Fig. 1). The separate goals were as follows: (1) rate taste, (2) rate health, or (3) decide to consume. To examine the multifaceted, goal-directed representational patterns of the food items, we used representational similarity analyses (RSA), a technique well suited to capture such patterns (Dudai, 2002; Nili et al., 2014; Castegnetti et al., 2021; Freund et al., 2021). RSA quantifies the patterns of neural activity in a given region (i.e., the relative activation levels of each voxel in the region) and can then test how well it aligns with a theoretical model. For example, this approach allows us to test whether brain activity patterns distinguish between subjectively more versus less tasty food items, and whether the current goal can influence this distinction. We found that multidimensional hippocampal representations of food items change to align with task goals. Specifically, greater adaptations of hippocampal representations of the palatability of food items during the decide to consume goal were associated with better self-control and healthier food choices.

Materials and Methods

Participants

We used a dataset originally reported by Hare et al. (2009). In total, 52 participants (20 females, mean age = 25.0 years; age range = 19–35 years) completed the experiment. All participants were right-handed, healthy, had normal or corrected-to-normal vision, had no history of illnesses, and were not taking medications that interfere with the performance of fMRI. Participants had no history of eating disorders or food allergies to any of the items used in the experiment. Participants were told that the goal of the experiment was to study food preferences among dieters and gave written consent before participating. The initial study recruited two types of participants: (1) individuals who self-reported being on a diet to lose or maintain weight, and (2) individuals who self-reported no current monitoring of their diet. Self-reported dieters were included in either the self-control or non-self-control groups based on their choices during the experiment. None of the individuals that were not currently monitoring their diets used self-control during the experiment; thus, all of them were assigned to the non-self-control group. All participants reported that they enjoyed eating sweets, chocolate, and

other “junk food,” and ate these types of foods at least once a week, although they might be trying to restrict them from their current diet. In other words, even the self-reported dieters found unhealthy tasty snacks tempting enough that they ate them regularly despite being on a diet. The review board of the California Institute of Technology approved the study. Five participants were excluded because of multiple large head movements or misalignments exceeding 3 mm. Five participants were excluded because the RSA toolbox (Nili et al., 2014) quality assurance measures indicated that the default correlation metric was not appropriate for their data because of “small relative SDs.” As a conservative measure, we opted to simply exclude these participants from the analyses rather than exploring different distance matrix options, leaving us with 42 participants.

Stimuli and task

We briefly summarize the relevant details of the task here; additional details can be found in Hare et al. (2009). Participants rated and made decisions on 50 different food items, including junk foods (e.g., chips or candy bars) as well as healthy snacks (e.g., apples or broccoli). Critically, these ratings and decisions were made while undergoing fMRI scanning (as opposed to outside the scanner as is often done in other studies). This experimental design feature allows us to compare hippocampal representations of food items across the different task phases. Participants were instructed not to eat for 3 h before the experiment, which is known to increase the value that is placed on food. The task had three parts, all of them done in the scanner. Participants first rated all 50 food items for both their taste and healthiness in two separate blocks (a taste rating block and a health-rating block). The order of the rating blocks was counterbalanced across participants, and the food items were presented in random order. Ratings were made using a 5 point scale that was shown on the screen below each item. The health rating scale was as follows: Very Unhealthy, Unhealthy, Neutral, Healthy, Very Healthy. The taste rating scale was as follows: Very Bad, Bad, Neutral, Good, Very Good. The mapping of rating labels to button orders was counterbalanced across participants. Before the taste rating block, participants were instructed to rate taste as “how tasty you would find the item if eating it right now,” and to “rate the taste of each food item without regard for its healthiness.” Before the health-rating block, they were instructed to “rate the healthiness of each food item without regard for its taste.” Participants had a maximum of 4 s to enter their rating and the trial terminated as soon as they did so. Trials were separated by a random intertrial interval with duration distributed uniformly between 4 and 15 s. Following the two rating blocks, one item that was rated as neutral on both health and taste was selected as the reference food for that participant used in the choice task (see below). Examples of such reference items included wheat crackers, Jello, raisins, granola bars, and yogurt. A small number of subjects (8 of 42) did not have an item that was rated neutral in both dimensions. In these cases, an item that was rated neutral on the taste scale and healthy on the health scale was chosen by the authors of the original publication as the reference item. A neutral-healthy item was selected because it would still present a challenge when paired with liked but unhealthy items for a subject who made decisions based on taste information.

The final session of the experiment was a decision phase. At the beginning of this phase, participants were shown a picture of the reference item and told that on each trial they would have to choose between eating the food item shown in that trial and the reference food. Participants had a maximum of 4 s to enter their decision and the trial terminated as soon as they did so. Trials were separated by a random intertrial interval with duration distributed uniformly between 4 and 15 s. Each food item was shown once for a total of 50 decision trials. Participants were required to eat the food that they chose in a randomly selected trial at the end of the experiment. Although this was a binary decision task, participants were asked to express the strength of their preferences using a 5 point scale as follows: Strong No (=choose reference), No (=choose reference item), Neutral, Yes (=choose shown item), Strong Yes (=choose shown item). In the trials in which the participants choose “Neutral” a coin was flipped to determine the decision.

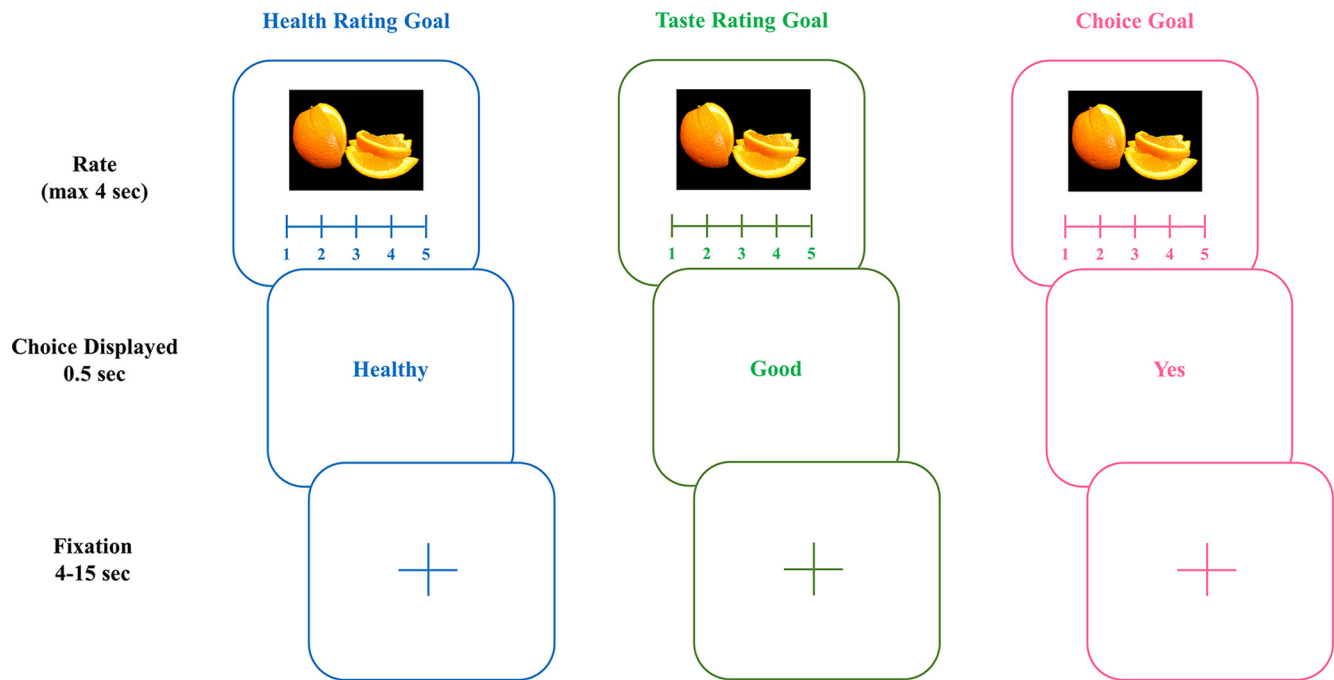


Figure 1. Task structure. Participants evaluated the same 50 food items under three distinct goals. They rated the palatability of each food item independently of its healthiness (goal = evaluate taste). They also rated the healthiness of each food item independently of its palatability (goal = evaluate healthiness) (counterbalanced). Last, they chose whether they would eat the food item currently shown on the screen or a fixed default food item (goal = choose option you want to consume). Ratings and choice were done on a 5 point scale ranging from very low to very high (counterbalanced), and one randomly selected item was actually consumed by participants in the end of the experiment.

Statistical analyses

Statistical tests used were two-sided. Detailed information is provided below.

Self-control success definition. We implemented the same criteria used in the original publication on these data (Hare et al., 2009). These criteria were set so as to have maximal distinction between high and low self-control groups by including only participants with behavior that could be clearly ascribed to either high or low self-control. In order to be classified as a high self-controller, according to the approach, subjects had to meet all of the following three criteria: (1) the subject had to use self-control on >50% of the trials in which self-control was required; (2) in a linear regression model of the decision strength on the health and taste ratings, the coefficient for health had to be greater than the coefficient for taste; and (3) the R^2 of a linear regression of the decision strength on the health ratings had to be greater than the R^2 of a linear regression of the decision strength on the taste ratings.

The combination of these three criteria was imposed to make sure that subjects labeled as high self-controllers were exercising self-control in a majority of the experimental trials and exclude any individual in the gray area between high and low self-control ($N = 12$), resulting in an overall $N = 30$. In order to maintain consistency with previous work (Hare et al., 2009), a neutral decision response was not considered to be a failed self-control event.

To test the robustness of our findings to this categorical definition of self-control success, we also repeated the analysis treating self-control as a continuous rather than categorical measure. For each participant, we calculated the percentage of conflict trials (i.e., trials in which one choice option was healthier but the other was tastier) in which the healthier option was chosen. We define self-control success as choosing a healthier, but less tasty item over a tastier, but less healthy option, and measured the frequency of successful self-control events for each participant (overall $N = 42$). Our findings remained significant using this approach. For these analyses, we used a Bayesian regression with the continuous self-control measure as the dependent variable and the dissimilarity, between representations of palatable and unpalatable foods as the independent measure. In our case, dissimilarity is quantified relative to the absolute difference in taste ratings.

fMRI data acquisition. Functional imaging was conducted using a 3.0 Tesla Siemens Trio MRI scanner to acquire gradient echo T2*-weighted EPI with BOLD contrast. Images were acquired in an oblique orientation of 30° to the anterior commissure–posterior commissure line. Each volume of images had 44 axial slices. A total of 777 volumes were collected over three sessions in an interleaved-ascending manner. The imaging parameters were as follows: TE, 30 ms; FOV, 192 mm; in-plane resolution and slice thickness, 3 mm; TR, 2.75 s.

Image analysis. Statistical Parametric Mapping (SPM 12; Wellcome Trust Center for Neuroimaging, <http://www.fil.ion.ucl.ac.uk/spm>) standard pipeline was used to preprocess the MRI data. Specifically, images were realigned, unwarped, and slice-time corrected (to the middle slice acquisition time). T1-weighted structural images were coregistered with the mean functional image and normalized to the standard T1 template based on the MNI reference brain, using the segment procedure provided by SPM 12. The functional images were then normalized to a standard EPI template using the same transformation.

For each participant, a time series was created indicating the temporal position of each trial convolved with the canonical hemodynamic response using a random-effects GLM. Following the procedure for RSA (outlined in Nili et al., 2014), each event (i.e., each of the 50 food items) was treated as a separate regressor in a model that included regressors for all 150 trials (50 healthiness ratings, 50 taste ratings, and 50 choices). The six movement regressors generated by SPM were also included as covariates of no-interest in the GLM models. All single participant maps were used as the input to a group-level nonparametric analysis using Statistic non-Parametric Mapping (SnPM 13 toolbox, <http://warwick.ac.uk/snmp>).

ROI definition. The hippocampal bilateral ROI was defined anatomically using an automated anatomic labeling atlas (WFU PickAtlas, RRID: SCR_007378) (Lancaster et al., 2000; Maldjian et al., 2003).

RSA. We used the default ROI analysis pipeline (Spearman) detailed in the RSA toolbox (Kriegeskorte et al., 2008; Khaligh-Razavi and Kriegeskorte, 2014; Nili et al., 2014). To compare the correspondence between the theoretical representational dissimilarity matrix (RDM) and the hippocampal neural RDM, we used the default option (Kendall τ_a). Kendall τ_a is the statistic from the nonparametric Kendall rank correlation

test, which is the standard RSA measure for testing the ordinal association or covariance between a given model and a brain activity pattern. Our primary analysis is an ROI approach with the anatomic bilateral hippocampal ROI. For whole-brain results, all ROIs in the basic 71 region WFU PickAtlas atlas were included.

When comparing brain activity to a model reflecting the subjective health and taste ratings for each participant, we used a participant-specific rather than a group average model (Fig. 2A). This was done because the subjective nature of food preferences meant that each participant rated the foods differently and averaging over these values would not be appropriate in this case.

Our main model tests whether representations in the hippocampus ROI corresponded to a theoretical model separating events according to tastiness ratings (on a scale of 1–5; see Materials and Methods). To this end, the hippocampal brain activity RDM was compared with a model RDM created from each individual's food ratings and reflecting the similarity between each pair of items via the absolute distance between participants' ratings of the two items (for example, if one item was rated 3 and the other 2, the value in the model RDM will be 1; see example in Fig. 2A). Thus, the y axis in Figure 3 represents the degree to which hippocampal brain activity distinguishes between different tasting items. The models were constructed separately per condition (e.g., taste, health, or choice blocks) with a focus on within-block comparisons (or contrasts of within block comparisons across blocks) to avoid potential issues related to temporal autocorrelation that can make activity patterns seem more different across blocks regardless of the item-specific representations (Cai et al., 2019).

Bayesian analysis of dissimilarity measures by group and condition. Posterior inferences about the differences between groups (high vs low self-controllers) and conditions (rate taste, rate healthiness, decide) were drawn from 100,000 samples estimated using the default robust priors in the BEST package (Kruschke, 2013; Kruschke and Meredith, 2020) in R (R Core Team, 2020) based on an Markov-Chain Monte Carlo sampling process implemented in JAGS (Plummer, 2003). A Bayesian regression approach using R (R Core Team, 2020) in combination with the Markov-Chain Monte Carlo sampling process (burn-in = 4000, sample = 1000, thinning = 5) implemented in JAGS (Plummer, 2003) was used to test linear associations between dissimilarity values and continuous levels of self-control. The imaging data for these analyses are based on the ROI approach described in Materials and Methods.

Leave-one out cross-validation classifier. To quantify whether the degree to which individuals change their neural representations when transitioning between goals predicts self-control successes, we used a leave-one out cross-validation approach (Friedman et al., 2001). This procedure first calculates the mean shift in tastiness representations between the taste rating and choice tasks using the data from $n-1$ participants (training group). Subsequently, the shift in representations for the independent participant that was not included in the $n-1$ analysis is compared with this value and the participant is assigned to one of two categories. If the left-out individual's shift in representation is larger than the average training group value, she is predicted to be a high self-controller, and vice versa if the change is smaller than the average group value. An n -fold replication of this procedure produces n predicted (i.e., 1 for each participant) values that can be compared with the real values of each participant (i.e., are they indeed high or low self-controllers according to their behavior) to determine average accuracy. This value is then compared with a null distribution created by running the same analysis with shuffled labels 10,000 times to test whether it is significantly different from chance. The imaging data for this analysis are based on the ROI approach described in Materials and Methods. A classification approach with continuous self-control definitions yielded similar results. Specifically, we used a leave-one out classification approach where after excluding the target participant, a regression model is used to estimate the relationship between the shift in hippocampal brain representations (independent) and self-control (dependent) for all remaining participants. The predicted self-control value for the left-out-participant is then obtained simply by entering their real hippocampal brain representations shift in the regression equation with the β values obtained without their data. Finally, we correlated the predicted and actual self-control values (Spearman $\rho = 0.46$ $p = 0.01$).

Data availability statement

Data and code will be publicly available at the Open Science Framework at https://osf.io/baxpf/?view_only=e0e306d96d27440180eebf9ca8e96569.

Results

We hypothesized that the strength of taste representations in the hippocampus would be associated with dietary self-control success. We defined a self-control success as choosing a healthier, but less tasty item over a tastier, but less healthy option, and classified individuals as successful or unsuccessful in using self-control based on previously established criteria (Hare et al., 2009) (for robustness checks related to the definition of self-control, see Self-control success definition). Our primary focus is on taste representations, but we report findings on representations of healthfulness in the final part of Results.

Hippocampal taste representations at the time of choice are associated with successful self-control

When observing the full pattern of taste representations across the different experimental conditions (Fig. 3A), a striking pattern emerges. Better self-controllers show a larger distinction in hippocampal representations between high and low taste items when self-control is not needed (i.e., during the health and taste rating conditions); but when self-control is implemented (i.e., during the choice condition), the pattern flips, and they show less of a distinction (difference in taste representation for high vs low self-control during choice; mean = 0.22, 95% highest density interval: 0.04:0.4, posterior probability = 99.1%, effect size = 0.997; interaction effect of goal (taste vs choice and health vs choice, respectively) $\times$ group (low/high self-control): mean standardized difference = 0.35, 95% highest density intervals: 0.09:0.61, posterior probability low > high self-controllers = 99.5%, effect size = 1.12; mean standardized difference = 0.36, 95% highest density intervals: 0.12:0.6, posterior probability posterior probability low > high self-controllers = 99.7%, effect size = 1.15). For exploratory whole-brain results, see Table 1.

To test the robustness and generalizability of the goal/context-dependent hippocampal representations of taste, we constructed a simple out-of-sample classifier. The classifier uses the degree of dissimilarity in the hippocampal representations of food items between taste rating levels (Very Bad, Bad, Neutral, Good, Very Good) in the decision versus taste rating tasks to predict the self-control level for each individual using a leave-one-out approach (see Materials and Methods). The change in hippocampal representations as a function of taste rating significantly predicted whether an individual would have high versus low self-control success (accuracy = 0.8, probability results are greater than chance = 0.9999; Fig. 3B).

Although our primary focus in this work was on examining the relationship between hippocampal representations and self-control, we ran an additional exploratory whole-brain analysis testing for other brain regions in which changes in the representational similarity as a function of taste ratings between the taste rating and choice phases differed between individuals with high and low self-control success (Table 2). In addition to the hippocampus, we found the largest effects in the NAc and subthalamic nucleus. Activity in these regions has been linked in previous research, in humans and animals, to representations of value and reward as well as impulse control (Galtress and Kirkpatrick, 2010; Lawrence et al., 2012; Rossi et al., 2015). These results from the whole-brain analysis suggest the potential involvement of multiple systems that may operate in parallel or influence each

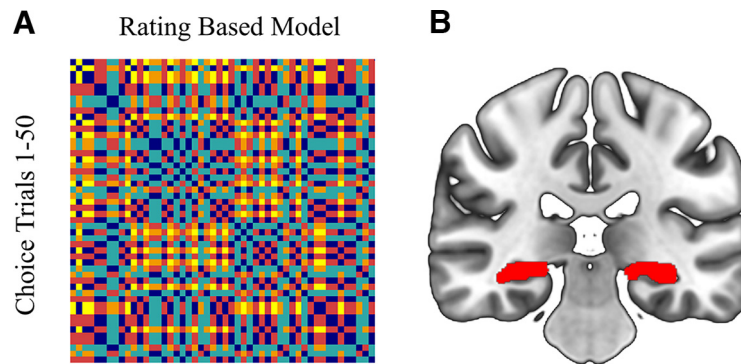


Figure 2. Theoretical RSA models and hippocampal ROI. **A**, An example of a single participant's theoretical model separating ratings in the choice task. Colored squares represent the difference in ratings between each pair of items. Because each participant has different preferences for different food items, each participant's model is unique. **B**, Red represents the hippocampal ROI.

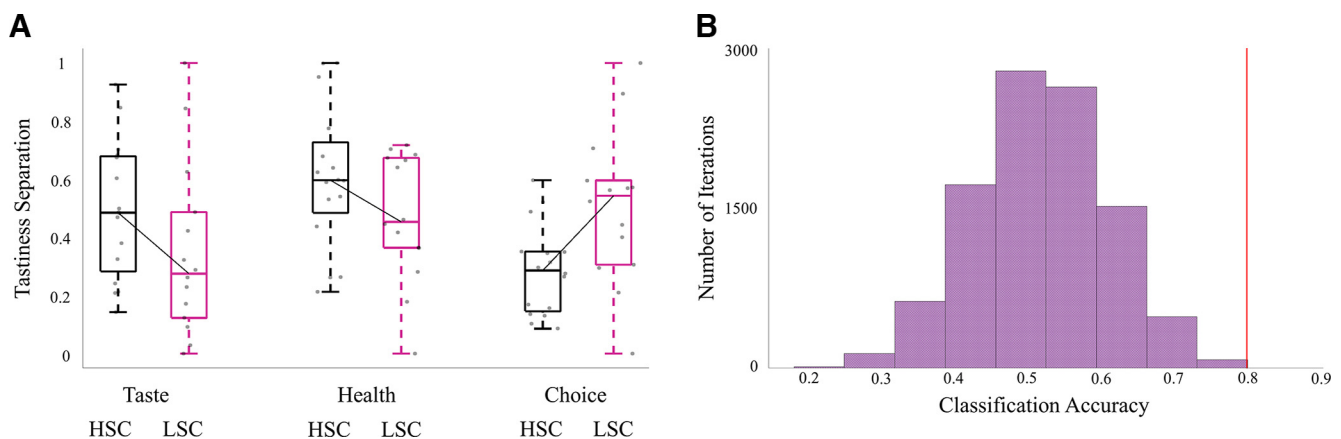


Figure 3. Hippocampal representations of taste differ across task goals and self-control groups. **A**, High self-controllers (HSC) show less dissimilarity between high and low tasting foods, relative to low self-controllers (LSC) but only when self-control is needed (i.e., when making consumption decisions) and not when the same taste information is considered but self-control is not needed (i.e., when rating the tastiness of the foods without making a choice) (mean standardized difference during choice trials = 0.22, 95% highest density intervals: 0.04: 0.4, posterior probability low > high self-controllers = 99.1%, effect size = 0.997; direct comparison of Choice and Taste rating goals: mean standardized difference = 0.35, 95% highest density intervals: 0.09:0.61, posterior probability low > high self-controllers = 99.5%, effect size = 1.12). Data are plotted as boxplots, indicating the median and quartiles with whiskers reaching up to 1.5 times the interquartile range. Each dot represents the raw data for one individual jittered horizontally to increase visibility. The data are normalized to range from 0 to 1. **B**, Purple histogram represents the null distribution obtained via 10,000 repetitions of the classification procedure on the degree of dissimilarity in the hippocampus between food items with different taste levels using randomly shuffled labels (i.e., chance accuracy). Vertical red lines indicate the out-of-sample classification accuracy value (0.8) when using the true labels. Comparing the accuracy with the true and permuted labels reveals that the probability that the classifier performs better than expected by chance is 0.9999.

other to determine self-control success. Future studies are needed to further elucidate the relationships between these different brain regions.

Analysis of health ratings

Our focus in this paper is on the taste rating because both behavioral and imaging data show it has a larger impact on choices in our task. First, when regressing behavioral taste and health ratings versus decision ratings, taste ratings are more influential overall (average coefficient 0.58 and 0.28, respectively; direct comparison of betas, mean standardized difference = 0.29, 95% posterior probability of difference > 0 = 99.8%, effect size = 0.80) (for additional analysis, see also Hare et al., 2009). Second, when examining which hippocampal brain dissimilarity patterns (taste or health) during the choice itself are more associated with self-control scores, we again find taste is more influential (standardized coefficients = −1.84 and 0.76, posterior probability of difference < 0 = 0.9997 and 0.042, respectively; direct comparison of absolute size of taste vs health coefficients; mean difference = 1.071, posterior probability of difference < 0 = 0.966). These results support the hypothesis that, in our task, the

key to self-control is related how you perceive and control the hedonistic outcome (e.g., tastiness). Additionally, we focused on tastiness representations because, under the mnemonic sampling hypothesis, healthiness distinctions would play less of a role in hippocampal representations because they are a more abstract aspect that is not usually directly associated with concrete episodic experiences (O'Reilly, 2010; Binder and Desai, 2011). However, to facilitate future work that may seek to explore the impact of health representations throughout the brain on self-control, we report our whole-brain results for health attributes in Table 3.

Testing for autocorrelation

RSA can be sensitive to autocorrelations in events that occur close together in time (e.g., subsequent ratings or choices). Given that the order of the food items was randomized for each participant in our study, it is unlikely that autocorrelation patterns will emerge. Nevertheless, we computed the autocorrelation across multiple lag times for all conditions (Table 4). We additionally tested for a relationship between the autocorrelation values per subject and their self-control value as well as the differences in brain representation and found no associations.

Table 1. Taste representations during food choices^a

Anatomical atlas area	Coefficient	Posterior probability
Low vs high self-control		
Cerebellum right	0.75	0.990
Superior temporal gyrus left	0.88	0.988
Hippocampal formation right	0.83	0.982
Hippocampal formation left	0.67	0.972
Cerebellum left	0.58	0.963
Postcentral gyrus left	0.67	0.962
Middle temporal gyrus left	0.61	0.955
NAC right	0.71	0.954
Medial occipitotemporal gyrus left	0.64	0.951
Self-control continuous		
Postcentral gyrus left	−0.13	0.987
NAC right	−0.11	0.975
Inferior occipital gyrus right	0.09	0.974
Supramarginal gyrus right	−0.09	0.965
Hippocampal formation right	−0.10	0.958
Medial occipitotemporal gyrus left	−0.10	0.958

^aBrain regions showing differences in taste representations during the choice goal as a function of self-control. Low vs high self-control: regions in which high self-controllers had less dissimilarity between their representations of palatable and unpalatable foods than low self-controllers when making consumption decisions. Self-control continuous: regions in which dissimilarity in taste representations was significantly associated with a continuous measure of self-control (fraction of choices for which self-control was successful). The coefficient values are derived from comparisons of group means and linear regressions in Low vs high self-control and Self-control continuous, respectively.

Table 2. Changes in taste representations between taste ratings and food choices^a

Anatomical atlas area	Coefficient	Posterior probability
Low vs high self-control		
Hippocampal formation right	1.66	0.995
NAC right	1.08	0.968
Subthalamic nucleus right	1.06	0.959
Self-control continuous		
Hippocampal formation right	0.09	0.997
Medial occipitotemporal gyrus left	0.10	0.982
Caudate nucleus left	0.08	0.978
NAC right	0.07	0.973
Inferior occipital gyrus right	−0.07	0.955

^aBrain regions showing condition-dependent changes in Taste representations (high vs low) when self-control is needed, as a function of self-control. Low vs high self-control: regions in which high self-controllers had a larger shift in representations of palatable and unpalatable foods than low self-controllers when self-control is needed (i.e., time of choice) vs when it is not (i.e., time of taste rating). Self-control continuous: regions in which this shift in tastiness representations was significantly associated with a continuous measure of self-control (fraction of choices for which self-control was successful). The coefficient values are derived from comparisons of group means and linear regressions in Low vs high self-control and Self-control continuous, respectively.

Discussion

The way the brain represents choice-relevant information may play a key role in the ability to modify or regulate the decision process. The hippocampus is thought to be a key source of evidence used to construct subjective values and take goal-directed decisions (Johnson and Redish, 2007; Lebreton et al., 2013; Gluth et al., 2015; Ludmer et al., 2015; Palombo et al., 2015; Shadlen and Shohamy, 2016; Bakkour et al., 2019; Biderman et al., 2020). Here, we show that goal-dependent changes in hippocampal representations are associated with the ability to exert self-control during dietary choices.

Our aim was to determine whether goal-dependent changes in the representation of foods' taste in the hippocampus are associated with self-control. Ascertaining the specific sources and purpose of the information represented in the hippocampus (e.g., episodic memories, simulations of expected experiences, and/or cognitive maps) will require additional experiments and data in the future. However, our results, together with

Table 3. Whole-brain results for health attributes^a

Anatomical atlas area	Coefficient	Posterior probability
Low vs high self-control		
Precuneus left	−1.23	0.987
Inferior occipital gyrus right	−1.13	0.976
Self-control continuous		
Precuneus left	0.11	0.999
Superior temporal gyrus left	0.12	0.993

^aBrain regions showing condition-dependent changes in Health representations (high vs low) when self-control is needed, as a function of self-control. Low vs high self-control: regions in which high self-controllers had a larger shift in representations of healthy and unhealthy foods than low self-controllers when self-control is needed (i.e., time of choice) vs when it is not (i.e., time of health rating). Self-control continuous: regions in which this shift in healthiness representations was significantly associated with a continuous measure of self-control (fraction of choices for which self-control was successful). The coefficient values are derived from comparisons of group means and linear regressions in Low vs high self-control and Self-control continuous, respectively.

past literature, suggest that one possible mechanism driving these effects is mnemonic processing, potentially via memory sampling processes.

Memory sampling theories propose that retrieval involves estimation based on repeated sampling of noisy internal representations. These sampling theories can explain mnemonic phenomenon, such as context effects as well as regularities in choice and decision time (Wang et al., 2015; Shadlen and Shohamy, 2016; Bornstein and Norman, 2017; Bornstein et al., 2017) using biologically plausible mechanisms (Schneegans et al., 2020). In this case, to facilitate successful self-control, it may be beneficial to sample from memory the subset of events in which very tasty items (e.g., chocolate cake) were less tasty than average, and the subset of events were less tasty, but healthful items (e.g., cabbage) were unusually appetizing. In other words, these results can support a view that, under a goal to exert self-control, the difference between representations of highly tasty and less tasty items can decrease, or become less distinct, compared with the same contrast when the goal is to evaluate the items' tastiness alone (Fig. 4).

There are multiple plausible mechanisms that might lead to goal-dependent hippocampal representations of palatability. The current goal may determine the accessibility of specific attributes such that, when taste attributes are irrelevant or inconsistent with the goal, they are sampled less often or less precisely. The goal may also influence motivational aspects that could drive the types of past experiences that are retrieved or imagined. For example, if the goal is to eat healthfully, then instances when chocolate cake was dried out and unpleasant or of an unexpectedly tasty broccoli dish may be sampled more often. This shift in the type of information sampled could lead to less distinct representations (Fig. 4). These and other attention-related processes may combine to alter the way individuals recall and/or imagine the taste of foods in different goal contexts, thereby facilitating goal-consistent choices.

Episodic mnemonic processes need not be the only drivers of the differences in hippocampal representations we observed. Hippocampal activity has been robustly associated with map-like representations across various multidimensional axes, such as space, time, context, and semantic distance (O'Keefe and Nadel, 1978; Eichenbaum, 2014; Spiers, 2020). It is possible that the differences between conditions represent differences in the representation of the current position along the multifaceted space of task-relevant dimensions (e.g., tastiness and healthfulness) in terms of their relative behavioral weight. Hippocampal activity could also represent simulations of future outcomes rather than pure memory retrieval processes (Schacter et al., 2007; Biderman et al., 2020). Inferential retrieval of sensory and motivational

Table 4. Autocorrelation across multiple lag times for all conditions^a

Lag	Health rating during Choice	Taste rating during Choice	Choice rating during Choice	Health rating during Health	Taste rating during Health	Choice rating during Health	Health rating during Taste	Taste rating during Taste	Choice rating during Taste
0	1	1	1	1	1	1	1	1	1
1	−0.033	−0.016	−0.027	0.012	0.011	−0.013	−0.017	0.042	−0.043
2	−0.001	−0.001	−0.008	−0.041	−0.024	−0.042	−0.025	−0.026	−0.047
3	−0.048	0.006	−0.004	0.001	0.006	0.024	−0.039	−0.060	−0.070
4	−0.050	−0.002	−0.010	−0.048	−0.066	−0.036	0.030	−0.037	−0.013
5	0.001	0.019	0.035	−0.040	−0.027	−0.039	−0.027	−0.026	−0.043
6	−0.030	−0.005	−0.056	−0.031	0.017	−0.012	−0.031	−0.025	−0.004
7	0.022	−0.052	−0.012	−0.064	−0.003	−0.036	0.006	−0.026	−0.079
8	−0.016	−0.023	−0.005	−0.045	−0.051	−0.019	−0.045	−0.040	−0.025
9	−0.011	0.032	0.026	−0.031	−0.014	0.001	−0.044	0.049	0.037
10	−0.011	−0.051	−0.024	0.029	0.003	−0.007	−0.034	−0.033	−0.009
11	−0.031	0.016	0.022	0.018	−0.035	0.000	0.023	−0.039	−0.007
12	−0.038	−0.047	−0.011	−0.033	0.009	0.018	−0.028	−0.044	−0.011
13	−0.055	−0.028	−0.028	0.012	−0.013	0.003	−0.034	−0.042	−0.019
14	0.010	−0.031	−0.013	0.010	−0.022	−0.012	−0.014	−0.020	−0.014
15	0.004	0.007	−0.020	0.019	−0.011	−0.020	−0.045	−0.009	−0.005
16	−0.006	−0.041	0.017	−0.007	−0.053	−0.011	−0.018	0.004	−0.036
17	−0.003	−0.056	−0.015	−0.013	−0.021	0.019	0.012	−0.010	0.027
18	−0.015	−0.012	−0.035	−0.035	−0.019	−0.014	0.000	0.005	−0.013
19	−0.041	−0.033	−0.031	−0.014	−0.047	−0.044	0.010	−0.030	0.006
20	−0.009	−0.020	−0.018	−0.043	0.022	−0.045	−0.023	−0.015	−0.036

^aAutocorrelation of participant ratings in the different conditions. The table shows the mean autocorrelation between subsequent ratings with different lags averaged across participants. The lag variable represents the size of the shift in the autocorrelation calculation. For example, a lag of 0 means the rating vector is correlated with itself, while a lag of 1 means the rating vector is correlated with the same vector shifted by one position, etc. The table labels define the type of rating (Health, Taste, or Choice) according to the order of presentation in the relevant block (since in each block the item order was randomly determined). For example, Health rating during Choice represents the autocorrelation within health ratings according to the food item presentation order during the choice block.

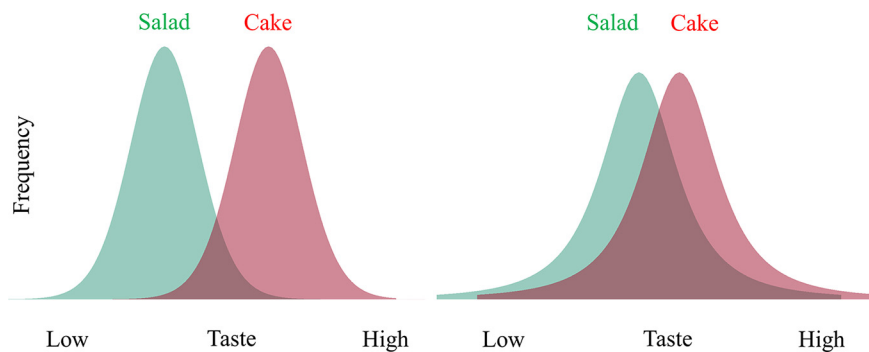


Figure 4. An illustrative example of how the same choice between two options could result in a larger or smaller self-control challenge because of different sampling of taste-related memories. Left, Larger challenge. Right, Smaller challenge. Color distributions represent hypothetically sampled subsets of past experiences for two example food items: one with a high mean value for taste (red, e.g., cake) and one with a low mean value for taste (green, e.g., salad). If an unbiased sample of past consumption experiences is drawn such that the tastier item is clearly distinct from the less tasty item (left), rejecting the tasty item will be more difficult than if the sampling process generates more similar estimates for the two options (right). A larger overlap between the tastier and less tasty items (right) may facilitate self-control and could occur because of (1) biased sampling of past events that favor less positive samples of the highly tasty food and more positive samples of less tasty food, and/or (2) increased noise in the sampling process because fewer samples are drawn or less attention/resources are devoted to taste attributes leading to wider distributions.

features, and the impact of contextual and motivational factors rather than abstract goals could also impact differences in hippocampal representations. Moreover, the current data are correlational and cannot answer questions of causality or the psychological motivations behind the self-control choice. For instance, our data cannot tell us whether high self-controllers are more motivated to discount taste or whether changes in hippocampal representations are a cause or consequence of self-controlled choices. Furthermore, the current results cannot be used to determine whether these processes happen on an intentional conscious level or are driven by habits or other unconscious processes. Finally, it is also possible that hippocampal representations reflect the value of the items themselves to some extent, and that value is changed based on the motivational context (potentially via interactions with striatal or prefrontal regions) (Chen et al., 2018; Bakkour et al., 2019). Regardless of the specific

high-level interpretation, our results clearly show that differences in hippocampal representations are associated with differences in self-control behavior that aligns with the individual's current goal.

Previous work in healthy and clinical populations has demonstrated that successful self-control is associated with PFC activation and/or its connectivity with subcortical areas, such as amygdala, and striatum (Hare et al., 2009; Cohen and Lieberman, 2010; Buhle et al., 2014; Maier et al., 2015; Tang et al., 2015; Cohen and Casey, 2017; Shenhav, 2017; Sun and Kober, 2020; Scholz et al., 2022). Our current findings indicate the need to expand this classical view of control networks to incorporate hippocampal representations as well. In contrast to previous studies, our current work examines multivariate representations, rather than changes in mean activity, and tests how those representations change across contexts. These design and analysis features will be important to consider in future

work. It remains to be seen whether the hippocampal complex interacts with the same prefrontal regions previously linked to self-control or if instead it operates as part of a different subnetwork.

Our results are consistent with choice theories that propose that preferences are not stored in an immutable format, but rather constructed at the time of choice and can be influenced by cognitive and contextual factors (Tversky et al., 1988; Johnson et al., 2007; Weber and Johnson, 2011; Castegnetti et al., 2021). Cognitive reappraisal, or the modification of the way one thinks about a stimulus to change its emotional or other subjective evaluations (Gross, 2002; Sokol-Hessner et al., 2009; Kober et al., 2010; Hutcherson et al., 2012), is a form of goal-dependent evaluation of previous and current experiences. Concurrent as well as previously trained reappraisal of food and drug stimuli reduce craving scores, willingness to pay, and/or consumption of cigarettes and food (Kober et al., 2010; Boswell et al., 2018; Sun and Kober, 2020). Furthermore, greater activity in the hippocampal complex during emotion reappraisal correlates with better dietary self-control (Maier and Hare, 2020). In regulation of craving training (ROC-T) (Boswell et al., 2018), participants view pictures of food items and positively or negatively reappraise their values. Undergoing ROC-T might alter the distribution of experiences with the food items and/or change the accessibility or ease of retrieval for positive versus negative aspects of the foods. Similar to the larger literature on self-control in general, previous neuroimaging studies of reappraising emotional reactions or cigarette craving have focused on univariate interactions between PFC and amygdala or ventral striatum during active reappraisal. However, our results suggest that future studies should test whether ROC-T leads to changes in hippocampal multivariate representations of tempting attributes (e.g., food taste or cigarette pleasure), even when people are no longer explicitly reappraising the stimuli, whether those representations mediate increases in healthful behavior, and how long the altered representations are maintained after training.

Self-control is known to be an important factor in both physical and mental health as well as educational and social achievements (Moffitt et al., 2011; Tang et al., 2015; Krönke et al., 2020). Our results provide new insights into the behavioral and neurobiological processes underlying self-control and indicate that incorporating mechanistic frameworks of memory representations may further advance our understanding of this critical capacity. These insights could lead to new ways to approach treatment of self-control-related disorders or maximize self-control skills in healthy individuals.

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