Neural systems for memory-based value judgment and decision-making

Avinash R. Vaidya[1]

David Badre[1, 2]

[1]Department of Cognitive, Linguistic, and Psychological Sciences, [2]Carney Institute for
Brain Science, Brown University, Providence, RI, 02912

ABBREVIATED TITLE: MEMORY-BASED VALUE JUDGMENT

Address correspondence to:
Avinash R. Vaidya
Brown University
Providence, RI 02912-1978
tel. 401-863-3634, fax 401-863-2255
email avinash_vaidya@brown.edu

Conflicts of interest: The authors declare no competing conflicts of interest.

Acknowledgements: This work was supported by a Multidisciplinary University Research Initiative award from the Office of Naval Research (N00014-16-1-2832), an award from the James S. McDonnell Foundation, and a Ruth L. Kirschstein National Research Service Award to A.V. (NIMH F32 MH116592-01A1). We are grateful to Michael Frank for helpful comments and suggestions on the manuscript, as well as Apoorva Bhandari and Andra Geana for constructive discussion on methods and analysis. Thanks also to Adriane Spiro for help with data collection, and Henry Jones for assistance with behavioral piloting and analysis of normative data.

Abstract

Real life choices often require that we draw inferences about the value of options based on

structured, schematic knowledge about their utility for our current goals. Other times, value

information may be retrieved directly from a specific prior experience with an option. In a

functional magnetic resonance imaging experiment, we investigated the neural systems

involved in retrieving and assessing information from different memory sources to support

value-based choice. Participants completed a task in which items could be conferred positive

or negative value based on schematic associations (i.e. schema value), or learned directly

from experience via deterministic feedback (i.e. experienced value). We found that

ventromedial prefrontal cortex (vmPFC) activity correlated with the influence of both

experience- and schema-based values on participants' decisions. Connectivity between

vmPFC and middle temporal cortex also tracked the inferred value of items based on

schematic associations on the first presentation of ingredients, prior to any feedback. In

contrast, the striatum responded to participants' willingness to bet on ingredients as a

function of the unsigned strength of their memory for those options' values. These results

argue that striatum and vmPFC play distinct roles in memory-based value judgment and

decision-making. Specifically, the vmPFC assesses the value of options based on information

inferred from schematic knowledge and retrieved from prior direct experience, while the

striatum controls a decision to act on options based on memory strength.

Introduction

How can we predict the value of options without prior, explicit experience? For example, when building a table, a hammer has greater value than a ball of yarn. No previous experience using yarn in place of a hammer is needed to make this kind of value judgment. However, this evaluation does depend on knowledge about yarn, hammers and table construction. Structured knowledge about the world that can support this kind of inference is often referred to as a schema (Bartlett, 1932; Ghosh & Gilboa, 2014; Piaget, 1952). Judging the value of options for accomplishing complex goals, like table building, requires inference based on these schematic representations.

Value does not always need to be inferred. In the same example, seeing a certain brand of varnish on display might remind you that your friend had recommended that varnish for your table last week. In this case, value relies on the retrieval of an explicit positive association with the item from a specific time and place. Here, value is a memorized feature of one or a few previous episodes, which may be brought to mind through mechanisms of episodic retrieval.

Relatively little is known about the neural systems involved in retrieving information from different memory sources to support value judgment. Lesion studies have shown that ventromedial prefrontal cortex (vmPFC) and orbitofrontal cortex (OFC) are necessary for decision-making when option values must be inferred from knowledge of task structure, but not when values can be retrieved from directly learned associations (Bradfield, Dezfouli, van Holstein, Chieng, & Balleine, 2015; Izquierdo, Suda, & Murray, 2004; Jones et al., 2012; Reber et al., 2017). It is unclear if these deficits arise because these regions represent task structure (Schuck, Cai, Wilson, & Niv, 2016; Wilson, Takahashi, Schoenbaum, & Niv, 2014), guide

retrieval based on these schemas (Eichenbaum, 2017), or specially utilize structured

knowledge during value judgment.

A parallel line of research has focused on the striatum at the intersection of goal-

directed retrieval and value-based decision-making. Recent work has argued that the

striatum is involved in assessing the value of information stored in memory and using this

information to bias cortical representations of choices with higher value (Shadlen &

Shohamy, 2016). A mutually compatible alternative is that striatum integrates memory

signals into its basic decision making functions, including those related to memory itself

(Han, Huettel, Raposo, Adcock, & Dobbins, 2010; Scimeca & Badre, 2012), though these may

also be separable processes (Elward, Vilberg, & Rugg, 2015).

The function of these regions in value judgment likely further depends on

coordination with several other regions for the retrieval of relevant information. Notably,

overlapping regions within the vmPFC and the striatum are connected with regions

canonically associated with episodic and schematic memory, and adaptive retrieval,

including the hippocampus (HPC), middle temporal cortex (MTC) and anterior ventrolateral

prefrontal cortex (aVLPFC) (Haber & Knutson, 2010; Price, 2007). However, it is not known

how these regions interact to link retrieval to decision-making.

We tested three hypotheses from this prior literature on memory and value-based

decision making using a functional magnetic resonance imaging (fMRI) experiment: (1)

vmPFC is preferentially engaged when value judgments are based on structured knowledge

about the world (i.e. schema memory). (2) Striatum tracks directly experienced (rather than

inferred) values. (3) vmPFC and striatum interact with different memory stores in accord

with their respective roles in constructing values through schema-based inference (vmPFC)

versus direct, explicit experience (striatum).

Our results were inconsistent with these *a priori* hypotheses, but yielded new insights

into the brain systems linking memory with value-based decision-making. Striatum

responded to the effect of the unfamiliarity of options on participants' value judgments, not

the value of the options themselves. On the other hand, vmPFC responded to the influence of

both the experienced and schema-based value information on value judgments. Analysis of

connectivity between these regions and memory stores revealed greater communication

between the striatum and HPC in response to demands on recall of experienced values, while

vmPFC and MTC communication increased in response to inferred schema-based values.

Thus, vmPFC represented retrieved value information from multiple memory sources, and

coordinated with MTC when value was inferred. In contrast, the striatum incorporated basic

memory strength into the decision process, and increased communication with HPC in

response to demand for retrieval of experienced values. These results advance a new

understanding of memory-based value judgements and outline distinct roles for these

regions.

Methods

Behavioral Task and Experimental design

We investigated the neural systems involved in making value judgments based on

different memory sources using a novel experimental task. This task, and all other tasks not

administered through Amazon Mechanical Turk (AMT), were programmed in Psychtoolbox-

3 (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007). In this experiment, participants took the

role of a restaurant chef choosing whether or not to serve ingredients to a customer (Figure

1). Each trial required participants to make a bet based on their belief that the customer

would like or dislike the displayed ingredient. Participants were instructed that if they

served an ingredient that the customer liked, they would receive 50 points, however if they

served an ingredient that the customer did not like, they would lose 25 points. If participants

chose not to serve an ingredient, they would receive 0 points.

Figure 1. Task schematic showing instructions at the start of a block and organization of a single example trial. At the start of the block, participants were informed of the recipes that customer liked and disliked. These recipe names were presented in green and red above the ingredient on all trials. In each trial, participants indicated their decision to feed the displayed ingredient to the current customer, and their confidence in this decision, using a slider. Participants then saw whether or not the customer liked the ingredient, signaled by a box above either response cue, and the points earned or lost in each trial. ITI (inter-trial interval), ISI (inter-stimulus interval).

After the participant made their choice, the customer's preference for a given

ingredient was always signaled by a cue above the correct response during feedback,

regardless of whether the participant chose to feed the customer or not, and all customer

preferences were deterministic. Thus, participants received complete information on each

trial regardless of their response. The feedback provided a source for learning the value of

an individual ingredient. If the participant did not respond in time, no information about the

customer's preferences was given and participants were shown the word 'slow' in place of

feedback about points earned.

In addition to the information about ingredient preferences provided through

feedback, participants were told at the start of a block that the customer liked ingredients

pertaining to one recipe (positive recipe) and disliked another (negative recipe). In this way,

the participant could also infer the value of an ingredient on the basis of schematic

knowledge about what ingredients go with what recipes, without having received feedback.

For example, if the customer liked cake and disliked soup, flour might be positively valued

and onions might be negative by virtue of their association with each recipe.

At the start of each block, participants were told that they were about to feed a new

customer, and were given the names of the recipes that the customer liked and disliked. The

two recipes in each block were randomly selected without replacement from a set of six

recipes. The screen was then left blank for 12 s until the start of the first trial.

Participants were also instructed before the start of the task that each customer liked

and disliked other ingredients that were unrelated to these recipes (i.e. 'independent

ingredients'). The value related to these ingredients could not be anticipated in advance

based on their schematic associations, but rather would have to be acquired through

experience.

Each ingredient was repeated three times throughout a block. For these repeated

ingredients, participants could retrieve a memory of previous feedback to make a decision.

All repetitions were separated by at least one other ingredient so that participants were

never making decisions about the same ingredient for multiple trials successively.

Thus, the experiment had three factors by design: ingredient clustering (recipe or

independent), value (positive or negative) and presentation number (1, 2, 3). For the

purposes of behavioral and fMRI analysis, any missed responses were not considered in the

count of ingredient presentations, as no value information was communicated to the

participant on these trials (e.g. if a participant missed the response deadline on the first

presentation, the second presentation would be considered the first, and the third

presentation would be considered the second in all analyses).

In each trial, participants saw an ingredient and were asked to respond by moving a slider

to either side of a bar to indicate their decision to serve an ingredient and their confidence

in that decision with a single response, similar to Scimeca, Katzman, and Badre (2016).

Moving the slider past the midway point to either side was considered a binary selection of

that side's response, while the distance of the slider from the midway point provided a

continuous index of confidence. The slider would start in a random position on each trial and

participants could then drag it toward the left or the right by holding down a button on a

fiber optic response pad (Current Designs, Philadelphia, PA) using their right index or middle

fingers. The slider would stop moving when it reached an end of the bar, or when

participants let the button go. Participants could not change the slider position after letting

go of the button. The side of bar where participants placed the slider signaled their choice,

and the distance of the from the middle of the bar indicated their confidence.

Before the fMRI experiment, participants completed a practice task in which they

learned to use the slider while verifying various general knowledge statements (e.g., 'Black

bears are omnivores'), and indicate their confidence in their response. Participants received

further practice outside the scanner by completing a short practice block of the restaurant

task where they fed a customer with recipes and ingredients that did not appear in the fMRI

experiment.

Trials were preceded by a jittered inter-trial interval (ITI) drawn from a lognormal

distribution (0.5-6 s). In each trial, participants saw a food ingredient centrally displayed for

up to 2.7 s, during which time they could choose whether or not to feed the ingredient to the

customer ('yes'/'no'). The names of the recipes that each customer liked and disliked

appeared at the top of the screen on each trial, color coded to indicate the customer's

preference.

After a response, there was a jittered inter-stimulus interval (ISI) drawn from a

uniform distribution (0.5-5.5 s). The remaining time from the response window and slider

movement period was also added to this interval. Participants then saw feedback about their

decision for 1 s. A square above the correct answer would light up, and the amount of points

added or subtracted from participants' total would be displayed in this period.

Trial-order, ITI and ISI lengths were drawn from sequences optimized for efficient

estimation of the hemodynamic response across conditions of interest. These sequences

were optimized by generating 5000 random sequences, and using SPM12 to create event-

based design matrices for stimuli and feedback events in each sequence. The average

variance for each regressor explained by all other regressors in the matrix was calculated for

each sequence and multiplied by the total duration of the sequence to approximate design

efficiency. The three sequences with the lowest values in this measure (i.e. least covariance

in regressors with the shortest experiment time) were used for the fMRI experiment and

were randomly ordered for each subject.

Participants

Twenty-six participants were recruited from the Providence, RI area to participate in

the fMRI experiment. Two participants were excluded due to movement greater than our

voxel size on at least one dimension during the functional scan, and one was excluded for

falling asleep during the experiment. Of the remaining 23 participants, four were male, their

mean age was 22.5 years (SD = 4.0), and their mean years of education was 15.5 (SD = 2.3).

All participants were right-handed, had normal or corrected-to-normal vision, and were

screened for the presence of psychiatric or neurological conditions, psychoactive medication

use, and contraindications for MRI. Two participants rejected all ingredients on the first

presentation of the positive independent condition, prohibiting analysis of their behavior or

ROI-level responses in a full 12-condition ANOVA after filtering for correct responses. One

participant did not commit any errors on the second or third presentation of the positive

recipe ingredients, prohibiting analysis of their error trials in this condition.

Two hundred participants from the United States were recruited through Amazon

Mechanical Turk (AMT) to provide normative naming responses for images of food

ingredients. Four of these subjects were rejected for exceptionally low accuracy in this task

(> 50%). The mean age of the remaining participants was 35.4 years (SD = 10.5), and 107 of

them were male.

A second sample of 221 participants were recruited from the United States through

AMT to provide normative data for ingredient-recipe associations. Twenty-nine of these

participants were rejected for failing to follow task instructions (most often by simply

writing the names of the ingredients rather than associated recipes). The remaining

participants had a mean age of 36.0 years (SD = 11.1), and 71 of them were male.

All participants across experimental and norming studies gave informed consent as

approved by the Human Research Protections Office at Brown University, and were

compensated for their participation. Participants in the fMRI experiment also received a

monetary bonus proportional to the points they earned in the main task.

Stimuli

Ingredient stimuli were obtained from the bank of standardized stimuli (BOSS; N =

65) (Brodeur, Dionne-Dostie, Montreuil, & Lepage, 2010; Brodeur, Guerard, & Bouras, 2014),

food-pics database (N = 50) (Blechert, Meule, Busch, & Ohla, 2014), with a small set of

supplemental food images collected by A.V. from Google Images (N = 4). These images were

selected to include basic food ingredients — i.e. items that might be used as parts of a recipe,

rather than completed meals. For example, an image of cheese would be included rather than

an image of a pizza. All images were scaled to the same size and padded with white pixels or

cropped to fit the same area. Ingredients from the BOSS database were excluded if more than

20% of the normative sample either responded that they did not know the name of the

ingredient or did not recognize the ingredient. Ingredients were also rejected if the modal

name for the ingredient given by respondents was incorrect (indicating low recognition

accuracy), and if the H-value (a measure of naming disagreement across participants, similar

to entropy) was above 3.00.

Because similar naming data were not available for ingredients from food-pics or

Google Images, normative naming data were obtained through an AMT experiment.

Participants were shown ingredient images and asked to write the name of the ingredient in

a text box below, or write "I don't know." Responses that included common variants of

ingredient names were considered correct, while overly general names were marked as

incorrect (e.g. 'nuts' for an image of pecans). Ingredients where more than 20% of

participants did not know the name, or gave incorrect answers, were rejected. Naming

agreement was also examined by calculating an H-value for each ingredient; however, this

value did not exceed 3.00 for any ingredient in this set.

Normative recipe associations

Associations between ingredients and recipes were obtained through a norming

experiment conducted on AMT akin to single word generation paradigms used to derive

word associations (Postman & Keppel, 1970). Participants were shown ingredient images

one at a time and were asked to write the name of the first recipe that came to mind using

the ingredient shown on screen. Unique recipe names were then extracted for each

ingredient and two researchers (A.V. and H.J.) manually processed these data. Alternative

names, semantically similar responses and misspellings were all collapsed into single

recipes, and ingredient specific information was removed to facilitate detection of overlap in

ingredient-recipe associations (e.g. responses like 'pumpkin soup' and 'mushroom soup'

were both reclassified as 'soup'). The end result of this process was a matrix with

endorsement counts for 102 ingredients in 1876 recipes. Six ingredients were then dropped

from this set, as they were visually too similar to other ingredients in the experiment, leaving

96 ingredients total.

Of these recipes, many (915) were only named by a single AMT participant for a single

ingredient. As our task design required that each recipe have a large number of associate

ingredients (at least seven recipe ingredients, and some additional ingredients to be used as

independent items), we cycled through different parameters for filtering out recipes. With

each of these filtered lists, ingredients were assigned to hierarchically organized clusters

using the Matlab (Mathworks, Natick, MA) function 'linkage,' which sorted ingredients based

on the mean cosine similarity of their naming frequencies. Through this process we selected

six recipes where the clustering solution provided ingredient cluster sizes that were large

enough for our task design (pasta (N=10), soup (N=13), cake (N=15), pie (N=21), salad

(N=17) and sandwich (N=20)).

Value rating task

At the start of the experimental session, participants completed a short rating task

where they were asked to provide ratings for how much they would hypothetically want to

have each ingredient at the end of the session. Participants provided responses on a seven

point Likert scale from -3 to 3, with labels on -3 reading 'Not at all,' 0 reading 'Indifferent'

and 3 reading 'Very much.' These subjective value ratings were included as a nuisance

variable in each of the parametric GLM analyses. This task also served to visually familiarize

participants with all ingredient images.

Computational modelling of behavior

Computational models of behavior were used to characterize the dynamics

underlying participants' behavior in this task. We developed a simple base model that made

a set of assumptions about behavior in this task that were carried over to all alternative

models. Each alternative model made a modification of this base model, or the best model

from the last step. Alternative models were compared based on their improvement in AIC

scores from the last best fitting model from a previous step. For simplicity, below we present

the final best fitting model that resulted from this process. We also briefly describe

alternative model modifications that did not survive the selection process in the following

section.

Within the best fitting model, the value (*V)* of the ingredient (*i)* on each trial was

calculated as:

$$V_i = \beta_0 + \beta_u(1 - |EV_i|) + \beta_e EV_i + \beta_s SV_i \text{ (Eq. 1)}$$

Where β_e controls the influence of experienced values (*EV*), and β_s controls the influence of

schema values (*SV*) for the current trial ingredient (these two terms were included in the

base model). The parameter β_u is a free temperature parameter that could be positive or

negative and controls the model's tendency to endorse or reject an ingredient based on its

unfamiliarity (the opposite of the absolute value of the experienced value term — described

below; unfamiliarity model). An intercept term, β_0 captures overall, item-independent

biases toward betting or passing (fixed bias). The model's willingness to bet on each trial (i.e.

the model-P(yes)) was then calculated by placing V_i in a simple logistic function.

On each trial where participants responded, the experienced value for each

ingredient was updated according to a simple Rescorla-Wagner learning rule (Rescorla &

Wagner, 1972):

$$EV_i = EV_i + \alpha(outcome - EV_i) \text{ (Eq. 2)}$$

Where the value for *outcome* could be 1 or -1, depending on whether the feedback was

positive or negative. While this rule is more commonly used in the context of reinforcement

learning, it was adopted here as a simple means of operationalizing a graded memory that is

signed and becomes stronger with repetitions of consistent value associations. The

parameter α was a fixed learning rate that was fit for each subject in an alternate version of

the base model where β_e was held at different constant values (1, 2, 5 and 8). The model fit

with a constant value of 5 for β_e had the lowest average negative log-likelihood of constants

tested, and so α values from this fit were used in the base model and all further variations.

This procedure to separately fit α was followed because β_e and α could not be stably

estimated within the same model. Estimating these parameters separately allowed us to

roughly capture individual differences in the encoding of *EV*, while separately estimating the

contribution of *EV* to choice behavior through β_e. Allowing α to vary was also found to reduce

the AIC of the base model over a variant where α was fixed to 1.0.

To reflect forgetting, the values for all ingredients also decayed towards zero with

each trial according to:

$$EV_{t+1} = EV_t - dEV_t \text{ (Eq. 3)}$$

Where *d* is a parameter that controls the rate of this decay (also included in the base model).

Schema values were calculated through a weighted difference of the associative

strength of ingredients with positive and negative recipes. The associative strength of each

ingredient with these recipes was determined through a procedure based on latent semantic

analysis (LSA) (Dumais, 2004; Landauer et al., 1998). The endorsement frequencies for

ingredients across all recipes in the normative AMT data were weighted by their entropy

across recipes and a singular value decomposition (SVD) was carried out on this matrix. This

matrix was then reconstituted with a smaller number of dimensions set by a free parameter

c (dimensions model). This parameter essentially controlled the dimensionality of recipe

space that the model would consider, so that a lower dimensional model would separate

ingredients on only simple features (i.e. savory or sweet), while a higher dimensional model

would include increasingly granular information that separates ingredients along

information about specific recipes (Figure 2). The association of an ingredient with each

recipe was calculated as the mean cosine similarity between that ingredient and all ingredients in each recipe cluster within this reconstituted matrix.

Figure 2. Example ingredient by ingredient cosine similarity matrices from reconstructions of ingredient-recipe associations with increasing dimensions. **a.** Ingredient names and clustering by recipe. **b.** Cosine similarity matrix with two dimensions **c.** with four dimensions, **d.** with 20 dimensions, and **e.** with 58 dimensions.

The recipes in a block could vary in their similarity, making some ingredients plausibly associated with both positive or negative recipes (e.g. pie and cake). To accommodate this possibility, the associative strength of ingredients with the positive and negative schemas to the schema was weighted by an estimate of participants' uncertainty

341   about the recipe associations of each ingredient, calculated as the probability that an

342   ingredient was associated with both recipes (schema similarity model; $P(SR)$):

343
$$P(SR)_i = \frac{1}{1+\exp\left(-\beta_{sim}\left(1-\frac{|PR_i-NR_i|}{RRD}\right)\right)} \text{ (Eq. 4)}$$

344   Where RRD corresponds to the range of recipe association differences (i.e. the difference

345   between the maximum and minimum recipe associative strength for all ingredients and

346   recipes). This probability was then used in calculating weights for the sum and difference of

347   the positive and negative recipe associations, where the weight for the sum of these

348   associations was calculated as

349
$$w_{same} = 2(P(SR)_i - 0.5) \text{ (Eq. 5)}$$

350   And the weight for the difference of these ingredient associations was calculated as

351
$$w_{diff} = 1 - 2|P(SR)_i - 0.5| \text{ (Eq. 6)}$$

352   SV was then calculated as the weighted combination of the difference and sum of each

353   ingredient's associative strength with the positive and negative recipes:

354
$$SV_i = w_{same}(PR_i + NR_i) + w_{diff}(PR_i - NR_i) \text{ (Eq. 7)}$$

The parameter β_{sim} controlled sensitivity to the similarity of ingredients' recipe

associations, and the relative contribution of the difference or sum of positive and recipe

associations to SV. This parameter also controlled the valence of the additive strength of

these associations: positive or negative values for β_{sim} would give the same valence to the

additive strength of recipe associations, respectively. Alternatively, if the β_{sim} parameter was

zero, participants would rely solely on the difference of the ingredient's associative strength

with the positive and negative recipes.

Alternate model parameters

Briefly, the following alternate modifications to the base model were considered, but

did not improve model fitness:

(1) <u>Asymmetric schemas model</u>

This model included separate temperature parameters for positive and negative

schema values, so that the value of an ingredient was:

$$V_i = \beta_e\, EV_i + \beta_{sp} PR_i - \beta_{sn} NR_i \text{ (Eq. 4)}$$

Where β_{sp} and β_{sn} are temperature parameters that control the influence of ingredient

associations with positive and negative recipes, respectively.

(2) <u>Schema discounting model</u>

As participants learned the deterministic values of ingredients from feedback, it

might be useful to use schema information less. This model assumed that when ingredients

were associated with greater memory strength for the experienced values (i.e. the absolute

value of EV), the schema value information would be exponentially discounted. Such a

process might take place if participants traded off in retrieving information from different

memory sources, especially when one is more reliable. For each ingredient, a discount factor

was calculated as:

$$discount = \exp\left(-k|EV_i|\right) \text{ (Eq. 10)}$$

Where k was a free parameter that determined the steepness of this discounting. This

discount factor was then included in the calculation of ingredient values:

$$V_i = \beta_e\, EV_i + discount\, \beta_s\, SV_i \text{ (Eq. 11)}$$

So that the contribution of schema values scaled with this exponential discounting factor.

(3) <u>Dual Process Recollection Model</u>

While the above models assume that experienced values are stored in episodic

memory via a graded process, other models developed in memory judgment tasks suggest

that episodic memory has a graded component (familiarity) and a discrete component

(recollection) (Yonelinas, 1994). To test whether experienced values in this task may also

rely on an additional non-graded recollection process, ingredient values were calculated as:

$$V_i = \beta_e((1 - P_r)EV_i + P_rRV_i) + \beta_sSV_i \text{ (Eq. 12)}$$

Where RV is the recollected value of an ingredient, i.e. the outcome from previous trials that

does not decay or change over time (-1 or 1), and P_r is a fixed probability of recollection that

does not change over trials. Thus, in this model, values learned through feedback contributed

to the decision as the sum of recalled and graded value information, weighted by the

probability of recall.

Model fitting and comparison

Participants' responses consisted of two main features: a binary response indicating

whether or not to feed an ingredient to a customer, and a continuous rating of their

confidence in this binary response. This confidence response could also be transformed into

a continuous measure of participants' belief that a customer would like an ingredient (i.e.

P(yes)) by measuring the position of the slider between the 'yes' and 'no' options rather than

the distance of the slider from the middle, similar to Scimeca et al. (2016). Models were fit to

both participants' continuous and binary choice responses. The overall model likelihood was

calculated as the product of the model likelihood for participants' binary responses, and the

model likelihood of the linear fit between the logit transformed model-P(yes) and

participant-P(yes). The negative log of this likelihood function served as the objective

function to be minimized in the fitting procedure carried out by the Matlab function

'fmincon.'

Computational models were fit to participants' behavior in a step-wise process. At

each step, a simpler preferred model was modified by the addition of new free parameters

and the Akaike Information Criterion (AIC) of the simpler model and modified models were

compared with a one-tailed t-test, as the addition of these new parameters was predicted to

reduce AIC. The model with the best improvement in model fitness across subjects (i.e. the

largest t-statistic in this comparison) was then considered the preferred model in the next

step. Additional parameters that significantly reduced AIC were added to the preferred

model and compared in the next step ($P < 0.05$). The search for the best fitting model was

stopped once additional parameters no longer significantly improved model fitness, or when

the parameters to search across were exhausted.

Each model was fit separately for each subject 20 times with randomized starting

positions. The set of parameters with the lowest negative log-likelihood from each set of fits

was saved and the other parameter fits were discarded. These 20 separate fits helped guard

against the influence of idiosyncratic differences in starting point on the recovered

parameters, and the possibility that the model fitting process would converge on local

minima in the negative log-likelihood function.

Parameter recovery test

To verify that all parameters of the best fitting model could be recovered, we

generated 100 simulated datasets with randomized parameters. The parameter d was

generated from a uniform distribution from 0 to 0.05. Parameters β_e and β_s were generated

from a lognormal distribution with a mean of 5 and standard deviation of 0.5. Parameters

β_0, β_m and β_{sim} were all generated from a standard normal distribution (mean 0, standard

deviation of 1). The c parameter was generated from a uniform distribution ranging from 2

to 58. Given that these parameters were randomly generated and did not share the

covariance of the real parameters fit to participants' behavior, this test could overestimate

their recoverability. Thus, we further verified the recoverability of these parameters by

fitting the model to data simulated using the parameters fit to participants' real behavior.

fMRI data acquisition and preprocessing

Whole-brain imaging was acquired using a Siemens 3T Magnetom Prisma system

with a 64-channel head coil. First, a high resolution T1 weighted MPRAGE image was

acquired for visualization (repetition time (TR), 1900 ms; echo time (TE), 3.02 ms; flip angle,

9°; 160 sagittal slices; 1 x 1 x 1 mm voxels). Functional volumes were acquired using a

gradient-echo echo planar sequence (TR, 2000 ms; TE, 28 ms; flip angle 90°; 38 interleaved

axial slices tilted approximately 15° from the AC-PC plane; 3 x 3 x 3 mm voxels). Functional

data were acquired over three runs. Each run lasted 16.5 min on average (Mean: 494.8

acquisitions). After the functional runs, a brief in-plane anatomical T1 image was collected,

which was used to define a brain mask that respected the contours of the brain and the space

of the functional runs (TR, 350 ms; TE 2.5 ms; flip angle 70°; 38 axial slices; 1.5 x 1.5 x 3 mm

voxels). Soft padding was used to restrict head motion throughout the experiment. Stimuli

were presented on a 32-inch monitor at the back of the bore of the magnet, and subjects

viewed the screen through a mirror attached to the head coil.

Functional data were preprocessed using SPM12. Quality assurance for the functional

data of each subject was first assessed through visual inspection and TSdiffAna

(https://sourceforge.net/projects/spmtools/)   and   ArtRepair

(http://cibsr.stanford.edu/tools/human-brain-project/artrepair-software.html).   Outlier

volumes (defined by standard deviations from the global average signal) were interpolated

after preprocessing. Slice timing correction was carried out by resampling all slices to match

the first slice. Next, motion during functional runs was corrected by registering volumes to

the mean using rigid-body transformation. In any case where movement across runs was in

excess of the voxel size in any direction (3 mm), realignment was recalculated run-by-run.

Any participants where motion within a run was larger than a voxel were excluded from

further analysis (N = 2). Functional volumes were then normalized to Montreal Neurological

Institute (MNI) stereotaxic space using 4th order B-spline interpolation, and resampled to 2

x 2 x 2 mm voxels using trilinear interpolation. Finally, volumes were spatially smoothed

using an 8 mm full-width half-maximum isotropic Gaussian kernel. The in-plane anatomical

T1 image for each subject was normalized to MNI space and used to create a brain mask for

functional   analysis   using   the   Brain   Extraction   Tool   in   FSL

(https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/).

fMRI data analysis

Functional data were analyzed under the assumptions of the GLM using SPM12. All

regressors and parametric modulators were convolved with the SPM canonical

hemodynamic response function (HRF). Subject motion (six translational and rotational

components) were also included as nuisance regressors. Beta coefficients for single subject

effects were estimated using a fixed-effects model in a first-level analysis. For whole-brain

contrasts, these estimates were then included in a second-level analysis using a one-sample

t-test against 0 at each voxel. Whole brain t-statistic maps were thresholded at a cluster

defining threshold of $P < 0.001$ uncorrected, and then evaluated for statistical significance at

the cluster corrected FWE threshold of $P < 0.05$ to control for multiple comparisons. The

cluster extent for this threshold varied by test and is reported with each analysis.

fMRI general linear models

Three different general linear models (GLMs) were fit to fMRI data:

<u>(1) Condition-based GLM</u>

The condition-based GLM included separate regressors at the response and feedback

phases for the following factors: clustering (recipe, independent), value (positive, negative),

presentation number (1, 2, 3) and accuracy (correct, error). The duration of the boxcar for

the response regressors was set to the median of subjects' combined reaction time and slider

movement durations. Trial-by-trial deviation from this median duration was included as an

additional nuisance regressor. This GLM also included a nuisance regressor for the time the

stimulus display was on screen (i.e. the response window, ISI and feedback).

<u>(2) Finite impulse response GLM</u>

For ROI-based analyses on contrasts of task conditions, a separate finite impulse

response (FIR) GLM was fit to each participant. This model had the identical conditions as

the condition-based GLM described immediately above, but used an FIR model with eight

time points (16 s window) as a basis function for the hemodynamic response function. This

allowed us to measure activity within these ROIs without making assumptions about the

shape of the hemodynamic response function.

<u>(3) Model-based value components GLM</u>

Finally, we tested for correlates of model-based value terms and their interaction

with participants' value ratings (i.e. participant-P(yes)) using a parametric GLM. This model

had three boxcar regressors: a response regressor with onsets at stimulus presentation and

durations lasting to the point participants finished moving the slider, a feedback regressor

with onsets and durations lasting the presentation of feedback, and a nuisance regressor for

the stimulus display. There were eight parametric modulators on the response regressor:

participant-P(yes), participant confidence, experienced value, schema value, unfamiliarity,

interactions between participant-P(yes) and experienced value, schema value and

unfamiliarity, as well as subjective value ratings for ingredients. These interactions served

as a filter to focus on neural activity that responded to the influence of these model-based

terms on participants' value judgments. The feedback regressor also had two parametric

modulators: reward prediction errors (RPE; calculated as the difference between

participant-P(yes) and outcomes) and surprise (calculated as the absolute value of RPEs).

Parametric modulators were not orthogonalized in this model.

Region of interest analyses

Regions of interest (ROIs) were defined for testing region-specific hypotheses using

unbiased criteria. These ROIs were either defined using masks from the automated

anatomical labelling atlas (AAL), or using 10 mm spheres around peak coordinates from

independent studies. These spheres were then masked to only include voxels that were more

than 50% likely to be gray matter in SPM's tissue probability map. The coordinates and

references for these ROIs are listed in Table 1.

In ROI analyses contrasting conditions, the time course of activity within each ROI

was estimated using the MarsBar Toolbox (Brett, Anton, Valabregue, & Poline, 2002) from

the FIR GLM. For each ROI, the peak activity was found across conditions and subjects, and

the mean activity ± 1 bin around this time point was extracted and tested using RM-ANOVAs.

In ROI analyses of parametric GLM models, the mean beta weights within ROI voxels were

extracted instead.

Table 1. Description of ROIs

Region of interest	Definition	Center of mass (MNI)
vmPFC	Positive>Negative effects of subjective value (Bartra, McGuire, & Kable, 2013), masked using AAL definition of vmPFC from same reference	-1, 44, -7
mPFC	10 mm sphere around peak activation in a preference construction task (Barron, Dolan, & Behrens, 2013)	-6, 53, 13
HPC	Left and right hippocampal AAL masks (Tzourio-Mazoyer et al., 2002)	
Striatum	Left and right putamen and caudate AAL masks	
aVLPFC	10 mm sphere around peak activation in semantic retrieval task (Badre, Poldrack, Pare-Blagoev, Insler, & Wagner, 2005a)	-54, 27, -9
MTC	10 mm sphere around peak activation in semantic classification task (Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997)	-52, -55, 2

524
Generalized psychophysical interaction analysis

Generalized psychophysical interaction (gPPI) analyses were carried out using the

CONN toolbox in conjunction with SPM12 (Whitfield-Gabrieli & Nieto-Castanon, 2012). The

same ROIs described in Table 1 were used as seeds for focused ROI-ROI connectivity

analyses and exploratory whole-brain analyses. Task-related activity was regressed out

using the condition-based GLM described above, including six regressors for translational

and rotational motion and trial-by-trial deviations from the median of reaction time and

slider movement durations, as well as additional nuisance regressors including five principal

components for both cerebrospinal fluid voxels and white matter, and a regressor for linear

trends in the signal. The residuals of this model were then high-pass filtered at 0.008 Hz and

used in the analysis of functional connectivity.

gPPI analyses involved a two-step process. In a first-level analysis, connectivity

between *a priori* pairs of ROIs was measured as the bivariate correlation between the mean

residuals of voxel activities. In a second level analysis, correlation coefficients for each ROI-

ROI in each subject were Fisher transformed and subjected to a one-sample *t*-test against

zero. Exploratory seed-to-voxel whole brain connectivity analyses were similarly carried out

by calculating the bivariate correlation of mean residual activity within an ROI and all other

voxels in each subject. These correlations were then Fisher-transformed and compared to

zero with one-sample t-tests. As with above fMRI analyses, all whole-brain effects were first

peak thresholded at $P < 0.001$ and further thresholded at FWE cluster corrected threshold of

$P < 0.05$ to control for multiple comparisons. Cluster thresholds are reported separately for

each analysis.

Results

Behavioral data

To test if participants took advantage of schematic knowledge to make decisions, we

first examined whether participants choices reflected customers' recipe preferences on the

first presentation of ingredients before seeing any external feedback (Figure 3a). On these

trials, participants accepted ingredients associated with the positive value recipe more often

than ingredients associated with the negative value recipe and more often than positive

value independent ingredients. This was evident in a significant three-way interaction

between value, clustering and presentation number on participants' choices (RM-ANOVA: F

$_{2, 44}$ = 27.20, P < 0.0001, η_p^2 = 0.55), and direct contrasts between the ingredient types

(Bonferroni corrected t-tests: $t(22) \geq 7.79$, P's < 0.0001, d's ≥ 1.62).

In contrast, there was no significant difference between acceptance rates for positive

and negatively valued independent ingredients on the first presentation. This was as

expected, as the ingredients in this condition did not have inferable value based on an

association with a positive or negative recipe. The interaction between value and clustering

on participants' choices was confirmed with a separate RM-ANOVA on the first presentation

only (F $_{1, 22}$ = 61.31, P < 0.0001, η_p^2 = 0.73). Participants accepted ingredients associated with

the negative value recipe numerically less often than negative independent ingredients, but

this difference was not significant after correction for multiple comparisons. Overall, the

choice results indicate that participants successfully inferred value information from recipe

associations, though these effects were stronger for the positively valued recipe.

There was clear evidence that participants learned ingredient values from feedback.

Participants made choices consistent with the values of ingredients more often in the second

and third presentations than in the first in all conditions, demonstrating retention of

feedback from previous trials (Bonferroni corrected t-tests: t's(22) ≥ 4.54, P's < 0.01, d's ≥

0.95). Similarly, participants' rate of value consistent choices increased significantly from the

second presentation to the third in all conditions, except for independent positive

ingredients (Bonferroni corrected t-tests: t's(22) ≥ 4.69, P's < 0.01, d's ≥ 0.98).

Notably, participants also tended to reject both positive and negative independent

ingredients in the first presentation significantly more often than chance (One sample t-

tests: t's(22) ≥ 8.69, P's < 0.0001, d's ≥ 1.81). Thus, participants strategically avoided

endorsing independent ingredients before learning their values through feedback.

Figure 3. Behavioral data. Choices, reaction times (RT) and confidence ratings for positive (pos) and negative (neg) ingredients in the recipe and independent conditions across presentations. **a.** Frequency of 'yes' choices, **b.** Confidence ratings for correct responses. **c**. Reaction times for correct responses in recipe and independent conditions, for positive (pos) and negative (neg) ingredients. **d.** Confidence ratings for errors and correct responses in recipe and independent conditions, collapsing across value. Second and third presentations are also collapsed. **e.** Reaction times for correct and error responses in the same conditions as **d**. Boxes represent 25th, 50th and 75th quantiles of the data. Whiskers are approximately ±2.7 SD.

To test how participants' belief in their choices changed during the task, we next

examined how reported confidence changed on correct responses (Figure 3b). Confidence

increased with repeated presentations, and was also greater overall for recipe and positive

value ingredients (RM-ANOVA: F's $\geq$ 27.88, $P \leq$ 0.0001, $\eta_p^2 \geq 0.58$).   Confidence for

acceptance of positive recipe ingredients was significantly higher than positive independent

ingredients on the first presentation (Bonferroni corrected t-test: $t(20)$ = 4.57, P < 0.01, d =

0.99) and third presentation (Bonferroni corrected t-test: $t(20)$ = 4.96, P < 0.01, d = 1.08).

However, there was no comparable difference in confidence for rejections of negative recipe

and independent ingredients, resulting in a significant interaction between clustering and

value (RM-ANOVA: F $_{1, 20}$ = 9.28, P = 0.006, $\eta_p^2 = 0.32$),

Confidence also increased significantly from the first presentation to the second and

third presentations in all conditions (Bonferroni corrected t-tests: t's(20) $\geq$ 4.57, P's $\leq$ 0.01,

d's $\geq$ 1.29), and from the second to the third presentation in all conditions, except for negative

recipe ingredients (Bonferroni corrected t-tests: t's(20) $\geq$ 3.98, P's $\leq$ 0.05, d's $\geq$ 0.87), leading

to a modest interaction of value and presentation number (F $_{2, 40}$ = 3.34, P = 0.04, $\eta_p^2 = 0.14$).

Similar to reported confidence, participants' reaction times were also strongly

influenced by experience with ingredients with stronger decrements in subsequent

presentations of positive recipe ingredients (Figure 3c). There was a significant interactions

between value with presentation number (F $_{2, 40}$ = 8.50, P = 0.0008, $\eta_p^2 = 0.30$), with larger

drops in reaction times for positive ingredients, consistent with better recall. There was also

an interaction between value and clustering (RM-ANOVA: F $_{1, 20}$ = 4.66, P = 0.04, $\eta_p^2 = 0.19$),

owing to comparatively bigger effect of value on recipe ingredients compared to

independent ingredients. Responses in the first presentation did not significantly differ by

cluster condition or value.

In anticipation of analyzing the effects of memory retrieval failures on brain activity,

we also tested if were associated with lower confidence and longer reaction times, as would

be expected for retrieval failures. We collapsed across value levels and the second and third

presentations to have enough error trials per participant for this analysis. Confidence ratings

were influenced by significant interactions between accuracy and clustering (Figure 3d; RM-

ANOVA: $F_{1, 21}$ = 15.43, P = 0.0007, η_p^2 = 0.42), and accuracy and presentation number ($F_{1, 21}$

= 43.69, P < 0.0001, η_p^2 = 0.67). On the first presentation, participants were significantly

more confident on correct responses for recipe ingredients than independent ingredients

(Bonferroni corrected t-tests: $t(21)$ = 3.77, P < 0.05, d = 0.80), and error responses on recipe

ingredients (Bonferroni corrected t-tests: $t(21)$ = 5.60, P < 0.01, d = 1.19). There was no

comparable significant difference in confidence for correct and error responses for

independent ingredients in the first presentation. We confirmed that the effects of accuracy

differed between clustering conditions on this first presentation by separately testing this

interaction (RM-ANOVA: $F_{1, 21}$ = 14.34, P = 0.001, η_p^2 = 0.40). Thus, confidence on the first

presentation appeared to selectively depend on retrieval of relevant recipe associations.

Confidence was also higher on accurate responses compared to errors on the second and

third presentations of both recipe and independent ingredients (Bonferroni corrected t-

tests: $t's(21)$ ≥ 6.64, P's < 0.0001, d = 1.42).

Reaction times were influenced by an interaction of accuracy and presentation

number (Figure 3e; RM-ANOVA: $F_{1, 21}$ = 49.84, P < 0.0001, η_p^2 = 0.70), but there was only a

trend toward an interaction between accuracy and clustering ($F_{1, 21}$ = 3.81, P = 0.06, η_p^2 =

0.15), and no three-way interaction. Participants were significantly faster on correct

responses than errors on the second and third presentations of both recipe and independent

ingredients (Bonferroni corrected t-tests: t's(21) ≥ 5.03, P's < 0.01, d ≥ 1.07). This pattern is

consistent with longer reaction times on errors reflecting retrieval failures (Ratcliff, 1978).

In contrast, there were no significant differences in reaction times for correct and error

responses in the first presentation for either clustering condition.

In summary, behavioral results established that participants were able to infer the

value of ingredients based on their recipe association and used these inferred values to make

choices. Participants also showed a generally risk averse attitude on this first presentation

by tending to reject independent ingredients. On subsequent presentations of an ingredient,

participants accurately retrieved explicit memory of deterministic feedback to make faster,

more confident decisions. This was the case across both recipe and independent items.

However, participants continued to benefit from recipe associations in these later

presentations, with generally faster reaction times and greater confidence for correct

responses in this condition compared to independent ingredients. Finally, participants

tended to asymmetrically utilize knowledge about the positive recipe more than the negative

recipe throughout all trials.

Main effects of task conditions in whole-brain analyses

We hypothesized that vmPFC and striatum would respond to schema-based and

experienced values of ingredients respectively, and interact with different memory systems

in retrieving and constructing these values. Thus, we predicted that vmPFC activity would

be modulated by schema values more than directly experienced values, and the opposite

would be true of the striatum. We also predicted that a network of regions, including the

striatum, HPC and middle temporal cortex would be engaged by successful retrieval (Spaniol et al., 2009), while aVLPFC would be engaged by retrieval difficulty (Badre, Poldrack, Pare-Blagoev, Insler, & Wagner, 2005b). We first tested how ingredient clustering, value, presentation number and accuracy affected activity using simple contrasts from our condition-based GLM at a whole-brain level (Table 2). These analyses were filtered to focus on correct responses, excluding trials where participants may have made errors due to failure to appropriately recall information relevant to ingredient values, except where trials with different response accuracy were directly contrasted.

Figure 4. Whole brain contrasts projected onto inflated cortical surfaces and coronal slices for main effects of **a**. ingredient-recipe clustering, **b**. ingredient value, **c**. presentation number and **d**. response accuracy. All images are thresholded at $P < 0.05$, FWE cluster corrected. All main effects, except for accuracy, are filtered to only include correct responses. Cluster extent threshold for each contrast is given by value of k.

Recipe ingredients elicited greater activity than independent ingredients in medial

OFC (Figure 4a), but not elsewhere. Ingredients associated with positive value elicited

greater activity in OFC and medial PFC, as well as the ventral striatum (Figure 4b). Compared

with later ingredient presentations, the first encounter with an ingredient was associated

with widespread activity in lateral PFC, including left VLPFC, inclusive of the aVLPFC, and

the caudate nucleus (Figure 4c). Activity in left MTC, bilateral HPC and putamen was higher

in correct responses compared to errors across all presentations (Figure 4d).

Table 2. fMRI activations for main effects of task conditions shown in Figure 4

Region (AAL2)	MNI Coordinates			Number of voxels	Peak *t*-value
	x	y	z		
Recipe > Independent, correct (k = 148)					
Left superior frontal gyrus, medial orbital	-10	44	-12	240	4.31
Positive > Negative Value, correct (k = 157)					
Right anterior cingulate	12	40	8	4134	7.60
Left superior frontal gyrus, medial	-10	54	14		7.54
Right superior frontal gyrus, medial orbital	4	34	-14		5.84
Right posterior orbital gyrus	24	26	-14	282	5.78
Right caudate nucleus	6	12	-4	172	4.66
Presentation 1 > 2 > 3 (k = 173)					
Left inferior frontal gyrus, opercularis	-42	4	28	8816	12.39
Left supplementary motor area	-6	22	46		11.67
Left inferior frontal gyrus, triangularis	-46	24	16		11.30
Left inferior temporal gyrus	-48	-52	-16	4672	11.83
Left fusiform gyrus	-22	-86	-12		8.76
Left fusiform gyrus	-36	-70	-12		8.59
Right fusiform gyrus	36	-58	-12	3287	10.21
Right inferior occipital gyrus	34	-88	-6		8.51
Right fusiform gyrus	36	-28	-28		6.24
Right middle frontal gyrus	50	32	22	578	8.27
Left middle occipital gyrus	-24	-68	36		7.59
Left superior parietal gyrus	-30	-62	66		4.14
Right inferior frontal gyrus, orbital	32	30	-10	621	6.91

Left thalamus	-8	-8	4	370	5.36
Correct > error (k = 210)					
Right pallidum	26	-6	-6	4394	8.87
Right superior temporal gyrus	56	-26	4	4394	6.39
Right middle temporal gyrus	62	-2	-18	4394	6.13
Right paracentral lobule	10	-26	68	1065	5.29
Left precentral lobule	-22	-22	60	1065	4.61
Left middle temporal gyrus	-46	2	-28	6667	8.37
Left hippocampus	-24	-10	-22	6667	7.70
Left putamen	-30	-2	2	6667	7.68
Right superior occipital gyrus	24	-90	30	1195	7.21
Left cuneus	-8	-94	22	1195	5.31
Left anterior cingulate	-2	28	-8	241	4.54
Right superior frontal gyrus, medial	6	50	0	241	3.79

All reported clusters were significant at the $P < 0.05$, FWE-corrected threshold at the cluster level after peak thresholding at $P < 0.001$. The critical cluster extent threshold for each contrast is given by the value of k.

Region of interest analyses

To follow-up the whole-brain voxel-wise contrasts, we tested for more specific task-dependent changes in activity within a set of *a priori* regions of interest (ROIs) defined in Table 1 using a finite impulse response (FIR) model of the hemodynamic response. We were primarily interested in how the clustering status of ingredients influenced value-related activity across ingredient repetitions on correct responses. Here we focused on vmPFC and the striatum, since we had *a priori* expectations that these regions would differentially process value related to episodic and schematic memory. As the medial frontal wall is functionally heterogeneous (Braga & Buckner, 2017; Roy, Shohamy, & Wager, 2012), we included two ROIs from this region, one that was defined by a meta-analysis of studies of expected-value (Bartra et al., 2013), and a more dorsal ROI (mPFC) that responded to shared associations between components of a recipe schema in another experiment (Barron et al.,

2013). This dorsal mPFC ROI responded to ingredient value, but not any other task

manipulations.

vmPFC was more active for positive than negative expected value, evident in a main

effect of value (Figure 5a; RM-ANOVA: F $_{1, 20}$ = 9.13, P = 0.007, η_p^2 = 0.31), consistent with the

whole-brain analysis. Activity in this region was greater for positive compared to negative

recipe ingredients in the third presentation (Bonferroni corrected t-test: t(20) = 4.90, P <

0.01, d = 1.07), but there was no comparable value difference for independent ingredients

(Bonferroni corrected t-test: t(20) = 1.13, P > 0.05, d = 0.25). There was no significant

difference between vmPFC activity in response to positive and negative recipe ingredients

on the first presentation, leading to a three-way interaction between value, presentation

number and clustering (F $_{1, 20}$ = 5.06, P = 0.01, η_p^2 = 0.20). This null result of value on the first

presentation was not merely due to the ROI selection; an exploratory whole-brain contrast

of positive and negative recipe conditions on the first presentation in the condition-based

GLM was similarly null. vmPFC activity was also generally higher in later presentations,

reflected in a marginal main effect of presentation number (F $_{2, 20}$ = 3.29, P = 0.05, η_p^2 = 0.14),

but there was no significant main effect of clustering (F $_{1, 20}$ = 1.42, P = 0.2, η_p^2 = 0.06).

Within the striatum ROI, there was greater activation for positive than negative value,

evident in a strong main effect of value (Figure 5b; F $_{1, 20}$ = 9.17, P = 0.007, η_p^2 = 0.31),

consistent with the observation from the whole brain voxel-wise analysis. However, there

were no other significant main effects or interactions.

We hypothesized that value judgments in this task would rely on different neural

systems supporting different types of memory. In particular, we predicted that retrieval of

values associated with independent ingredients learned through feedback would place

greater demands on the HPC, while the MTC would be involved more in trials where

semantic memory about recipes was needed to infer ingredient values and aVLPFC would be

engaged by greater retrieval demands on the first presentation. To test these predictions, we

evaluated the effects of clustering status, presentation number and accuracy in ROI-based

analyses of the HPC, MTC and aVLPFC. We collapsed across value conditions and combined

presentations two and three into a single level to have enough error trials for this analysis.

HPC activity was greater on accurate trials, confirming the whole-brain results

(Figure 5c; RM-ANOVA: $F_{1,21} = 13.14$, $P = 0.002$, $\eta_p^2 = 0.38$). HPC activity was also generally

lower on later presentations ($F_{1,21} = 6.54$, $P = 0.02$, $\eta_p^2 = 0.24$). The effect of accuracy on HPC

activity was modulated marginally by clustering ($F_{1,21} = 4.65$, $P = 0.04$, $\eta_p^2 = 0.18$).

Surprisingly, we found greater HPC activity on correct trials than error trials for recipe

ingredients, collapsing across presentations (Bonferroni corrected t-test: $t(21) = 3.47$, P <

0.01, $d = 0.74$), but no such accuracy effect for independent ingredients. There was no main

effect of clustering, or three-way interaction of clustering, accuracy and presentation.

MTC activity responded to an interaction of clustering and presentation number

(Figure 5d; $F_{1,21} = 5.60$, $P = 0.03$, $\eta_p^2 = 0.21$). Posthoc tests collapsed across accuracy revealed

a significantly greater reduction in MTC activity for independent ingredients in the second

and third presentations compared to the first presentation (Bonferroni corrected t-test:

$t(21) = 2.87$, P < 0.05, $d = 0.61$), but no significant difference for recipe ingredients. While

MTC seemed to be engaged on the first presentation in all conditions, this reduced in

subsequent presentations for independent ingredients, consistent with less reliance on

semantic knowledge in this condition.

Figure 5. Region-of-interest analyses showing percent signal change in **a.** ventromedial prefrontal cortex (vmPFC) and **b.** the bilateral striatum across conditions for correct responses. **c.** Percent signal change in the hippocampus (HPC) for correct and erroneous responses, collapsed across value conditions. Second and third presentations are collapsed. **d.** Middle temporal cortex (MTC) and **e.** anterior ventrolateral prefrontal cortex (aVLPFC), same conditions as **c.**

aVLPFC activity was larger on the first presentation compared to the second and

third, consistent with the whole-brain analysis, revealed in a main effect of presentation

number (Figure 5e; F $_{1, 21}$ = 10.76, P = 0.004, η_p^2 = 0.34). The response of aVLPFC did not

change with accuracy or clustering status, or with any interaction between task variables.

In summary, ROI-based analyses confirmed whole-brain contrasts demonstrating

that the vmPFC and striatum carried information about ingredient values. Unlike the

striatum, value-related activity in vmPFC was greater for recipe ingredients compared to

independent ingredients in later presentations, but not in the first presentation where the

demand for inferring ingredient values from recipe associations was the greatest. In line with

our predictions, the MTC responded to differential demands on semantic memory, though

this was only true in later presentations. aVLPFC activity reduced in subsequent

presentations overall, in line with engagement by increased retrieval demands. While the

HPC responded differentially to retrieval success and failures in later presentations, this

effect was surprisingly greater for recipe ingredients than independent ingredients, possibly

due to the stronger encoding of these recipe ingredients, evident in participants' behavior

on these trials.

Computational model comparison

We had hypothesized that vmPFC would be preferentially engaged by schema-based

values, while the striatum would be involved in evaluating the contents of episodically

encoded value information. While value-related differences in vmPFC activity grew larger in

later presentations of recipe ingredients compared to independent ingredients, this change

in activity could not be easily differentiated from value information learned from feedback.

Importantly, this condition-based analysis also ignores the continuous nature of associations

between independent ingredients and recipes. For example, strawberries are considered

part of the 'cake' cluster, but also have some association with 'pie.' Further, filtering trials by

accuracy based on participant responses and task-defined values ignores that responses to

independent ingredients on the first presentation are made without any useful experienced

or schematic value information, and ignores systematic biases or strategies participants may

use in making choices that are not explicitly captured by our experimental design (e.g. a bias

against endorsing independent ingredients on their first presentation).

To better separate these components of expected value for testing our first two

hypotheses regarding the neural systems supporting valuation of information from different

memory sources, we developed a computational model of behavior to estimate the

contribution of information learned directly from experience and inferred from schematic

associations to participants' choices in each trial. We then used these values in a model-based

parametric GLM to determine the correlates of this information during value judgment.

Our computational model of behavior made a few basic assumptions about learning

in this task that are described in more detail in the Materials and Methods section. Briefly,

each ingredient had an 'experienced value' (*EV*), which depended on feedback and decayed

over time, and a 'schema value' (*SV*), which was derived from the differences in associative

strength between an ingredient and the positive and negative recipes. The associative

strength of an ingredient with each recipe was based on a latent semantic analysis of

normative ingredient-recipe associations (Dumais, 2004; Landauer et al., 1998). Each of

these value terms were weighted by a temperature parameter that determined their

contribution to the model's output, a continuous estimate of the probability that it would

endorse an ingredient, which we will refer to as model-P(yes).

Starting with these assumptions, we followed a step-wise process of adding

parameters to a model with these features and comparing the AIC of the new model against

the best simpler model. This allowed us to test if the new model better explained

participants' behavior while penalizing for the addition of a new parameter. Figure 6 shows

the AIC scores for these alternative models against the base model. Please see the methods

section for a fuller accounting of the parameters in the best fitting model and alternative

models in this figure.

The final best fitting model allowed for a more sophisticated parameterization of SV

where the number of dimensions in the latent semantic analysis of recipe-ingredient

associations was allowed to vary. This parameter essentially controlled the depth of recipe

information considered in computing *SV* (from simple distinctions like savory-sweet to more

fine-grained information about particular recipes; Figure 2). The model also allowed

participants' perception of the similarity of an ingredient's associations with positive and

negative recipes to act as a weight on the respective contributions of the difference and sum

of these associations in the calculation of *SV*. This enabled the model to determine whether

ingredients, like the strawberry example above, would be attributed positive, negative, or

null value if it had a strong association with both the positive and negative recipes (e.g. cake

and pie).

Unfamiliarity with an ingredient was also allowed to influence decisions about betting

or passing in the best fitting model. Unfamiliarity was operationalized as the opposite of the

unsigned experienced value of items. In other words, unfamiliarity was highest when

ingredients were seen on the first presentation, or when ingredients had not been seen for

many trials and memory for their experienced value had decayed. This parameter thus

effectively accounted for variance in participants' willingness to bet on ingredients when

information about their experienced values was weaker. Lastly, an additional free parameter

acted as an intercept term in the decision function, which effectively acted as a fixed bias on

the model's tendency to bet on ingredients.

Figure 6. Difference in model Akaike Information Criteria (AIC) compared against base model. Model parameters were added in a step-wise process where the parameters that best improved on the previous best fitting model were added to the next step (indicated in the legend). See Materials and Methods section for a more complete description of these models. *, $P < 0.05$, one-tail t-test indicating significant improvement on previous best fitting model. ***, best model within a step and significant improvement.

Computational model validation

To ensure that our computational model was capturing participants' decisions and

understand how it was accomplishing this, we carried out a series of analyses to validate its

parameters and behavior. We first examined if there were general tendencies for the two

bias and schema similarity temperature parameters towards positive or negative values by

conducting two-tailed, one-sample t-tests against zero (Table 3). While the unfamiliarity bias

parameter was significantly lower than zero ($t(22) = 3.91$, $P = 0.0008$, $d = 0.81$), the opposite

was true of the fixed bias parameter ($t(22) = 3.18$, $P = 0.004$, $d = 0.66$). The schema similarity

temperature parameter was not significantly different from zero ($t(22) = 0.90$, $P = 0.4$, $d =$

0.19). Thus, the unfamiliarity temperature parameter captured participants' aversion to

betting on ingredients on their first presentation or when memory for these ingredients was

weak, while the fixed bias parameter exerted a uniform inverse tendency across all trials,

moving the model towards endorsing ingredients in opposition to the unfamiliarity

parameter.

Table 3. Mean parameter values and Pearson correlations between parameters in the
best-fitting behavioral model

	Mean (SD)	Decay	EV temp.	SV temp.	Schema similarity temp.	UF temp.	Fixed bias
Decay	**0.02 (0.01)**	-					
EV temp.	**5.05 (0.32)**	0.35	-				
SV temp.	**2.07 (1.42)**	0.05	0.02	-			
Schema similarity temp.	**0.33 (1.75)**	-0.27	-0.01	0.25	-		
UF temp.	**-0.81 (0.99)**	0.09	0.31	0.31	0.06	-	
Fixed bias	**0.55 (0.83)**	0.15	-0.17	-0.45*	-0.47*	-0.85***	-
Recipe dimensions (log-space)	**2.56 (1.04)**	-0.04	0.07	0.60**	0.21	-0.04	-0.11

816　Experienced value (EV), schema value (SV), unfamiliarity (UF), *P < 0.05, **P < 0.01, ***P <
817　0.001
818
We also examined the covariance between parameters recovered from fitting this

model to participants' behavioral data to test their independence (Table 3). The fixed bias

parameter was negatively correlated with *SV* temperature, the schema similarity

temperature, and the memory bias parameter. There was also a positive correlation between

the recipe dimensions and *SV* temperature parameters, likely due to the cosine similarities

between ingredients growing smaller on average with higher recipe dimensions (Figure 2).

To confirm that all of these parameters could be uniquely recovered in our model

fitting procedure, we generated 100 simulated participants with randomly assigned

parameters using the best fitting model. We reliably and accurately recovered all parameters

in these data, with high correlations between simulated and recovered parameters (Pearson

r's(98) ≥ 0.99, P's < 0.0001). However, as these data were simulated from randomly

generated parameters, they did not share the covariance structure of the parameter

estimates fit to participants' behavior described above. To assure that we could recover

these parameters with the same covariance, we fit the model to simulated data generated

using parameter estimates from the model fit to participants' behavior. For all seven

parameters, there was a perfect correlation between the parameter estimates from

participants' behavior and the simulated data (Pearson r's(21) = 1.00, P's < 0.0001).

Finally, we generated simulated behavior from the model using participants'

recovered parameters to test that the model recapitulated key features of participants'

behavior across task conditions. To directly compare the model and participants' behavior,

we focused on participants' continuous estimate of whether or not they should endorse an

ingredient, based on position of the slider between the 'yes' and 'no' ends of the bar (i.e.

participant-P(yes)). We compared these ratings to the model-P(yes) measure, and

transformed model-P(yes) to confidence based on the distance from the point of maximum

uncertainty (i.e. 0.5). Participant-P(yes) ratings followed a similar pattern to their averaged

binary choices, including key features on the first presentation like higher P(yes) for positive

recipe ingredients compared to negative recipe, and positive independent, ingredients, and

a bias against endorsing independent ingredients (data not shown)

We analyzed model-P(yes) and confidence ratings in the same way as participants'

responses. Like with participants' choices, there was a strong three-way interaction between

value, clustering and presentation number (Figure 7a; RM-ANOVA: $F_{2, 44} = 53.82$, $P < 0.0001$,

$\eta_p^2 = 0.71$). The model used recipe information to make decisions on the first presentation,

with higher model-P(yes) ratings for positive recipe ingredients over negative recipe

ingredients, and over independent positive ingredients (Bonferroni corrected t-tests: t's(22)

≥ 7.38, P's < 0.0001, d's ≥ 1.54). There was also no significant difference in model-P(yes) for

positive and negative independent ingredients on this first presentation. Unlike real

participants, the model gave significantly lower ratings to negative recipe ingredients than

negative independent ingredients on the first presentation (Bonferroni corrected t-test:

$t(22) = 6.64$, P < 0.0001, $d = 1.38$), suggesting that it used information about the negative

recipe more than participants did. In subsequent presentations, the model also followed the

values of options learned through feedback, hewing closer to ingredient values in

presentation two and three compared to one (Bonferroni corrected t-tests: t's(22) ≥ 9.23, P's

< 0.0001, $d \geq 1.93$), and presentation three compared to two (Bonferroni corrected t-tests:

t's(22) ≥ 5.72, P's < 0.01, $d \geq 1.19$).

Similarly, we examined whether the model's predicted confidence followed the same

pattern as participants' responses across task conditions on trials where participants

responded correctly (Figure 7b). Model confidence rose predictably with presentation

number (RM-ANOVA: $F_{2, 40} = 150.65$, $P < 0.0001$, $\eta_p^2 = 0.88$), and was higher overall for recipe

ingredients than independent ingredients ($F_{1, 20} = 46.18$, $P < 0.0001$, $\eta_p^2 = 0.70$), however

there was only a trend toward a main effect of value ($F_{1, 20} = 3.45$, $P = 0.08$, $\eta_p^2 = 0.15$). Model

confidence was also notably higher for both positive and negative recipe ingredients

compared to independent ingredients on the first presentation (Bonferroni corrected t-tests:

t's(20) ≥ 4.02, P's < 0.05, d's ≥ 0.88), rather than just positive recipe ingredients.

Figure 7. Model behavior across task conditions. **a.** Model-P(yes), a continuous indicator of the model's estimate of the value of these options. **B.** Model confidence on correct responses only.

In summary, our model captured core aspects of participants' behavior in this task,

including utilization of recipe-based values and a bias against endorsing independent

ingredients on the first presentation. The model was also able to recreate the basic pattern

of participants' reported confidence rising with repeated presentations, with benefits for

positive value and recipe associations. However, the model gave greater weight to the

negative value recipe than participants and underestimated the effects of value on

confidence. While an alternative model with asymmetric weights for positive and negative

recipes improved model fitness, this addition did not survive our model selection process

(Figure 6), possibly due to variance between participants in the extent of this asymmetry.

Model-based fMRI

We had hypothesized that vmPFC would be engaged more by values inferred from

schematic associations than directly experienced values, which we hypothesized would be

tracked by activity in the striatum. Our computational model showed that ingredient values

could be captured by a combination of experienced value, schema value and unfamiliarity,

and allowed us to leverage these terms in testing these hypotheses by examining their

correlates in brain activity.

To focus on brain activity that responded to the influence of these model-based value

terms on participants' value judgments, we included interactions between these three terms

and participant-P(yes) in our GLM. These interactions selectively captured activity that

responded to the conjunction (or agreement) between the participants' responses with

experienced and schema values (e.g. when schema value was high and participant-P(yes)

were high, or when both were low). The interaction of unfamiliarity with value ratings

similarly let us capture where activity increased in response to higher participant-P(yes)

when unfamiliarity was high, or lower participant-P(yes) when unfamiliarity was low. In

doing so, we could focus on activity where behavior and model predictions were in

agreement. In contrast, the main effects of these model-based terms only captured the extent

to which correlates of this information were present in the brain, independent of

participants' response. This analysis may seem circular, as we are looking for correlates of

an interaction between these model-based terms with the behavior to which these terms

were fit. However, the fMRI correlates that are the dependent measure in this analysis were

not part of the model fitting, breaking any potential circularity in our results. This GLM also

included parametric modulators for participants' confidence ratings and participants'

subjective value ratings (provided separately in a different task) on the response regressor

as nuisance terms.

Whole-brain cluster corrected analyses found no significant main effects of

participant-P(yes), experienced or schema-based value, or participants' subjective value

ratings. There were significant correlates for the main effect of unfamiliarity, with increased

activity in lateral PFC, visual cortex and several other regions, similar to the main effect of

presentation number in the condition-based contrast above. There were also significant

main effects for response confidence in the superior frontal gyrus and visual cortex (Table

4).

Figure 8. Whole brain t-statistic maps for interactions of model-based terms with participant-P(yes). **a.**. Interaction of participant-P(yes) and schema value (SV), **b.** Interaction of participant-P(yes) and experienced value (EV), **c**. Interaction of participant-P(yes) and unfamiliarity. All images are thresholded at *P* < 0.05, FWE cluster corrected, except for those shown in **c**. Cluster extent threshold for each map is given by value of k.

The interaction of schema value and participant-P(yes) was associated with activity

in the pregenual ACC and medial OFC, as well as the right VLPFC and bilateral supramarginal

gyri (Figure 8a). The interaction of experienced value and participant P(yes) was also

associated with activity in medial OFC and a large area of the medial superior frontal gyrus

and left angular gyrus (Figure 8b). There were no clusters that passed the whole-brain FWE

cluster-corrected threshold for the interaction of unfamiliarity and participant-P(yes).

However, given the challenge of detecting cluster corrected effects in deep brain structures,

we applied a small volume correction using the striatum ROI. This analysis found that two

clusters in the bilateral caudate nucleus responded to the interaction of unfamiliarity with

participant-P(yes) (Figure 8c; FWE-corrected *P*'s ≤ 0.03, MNI: 18, 20, -4; -8, 22, 0). Whole

brain peak activations for this GLM are described in Table 4.

Table 4. fMRI activations for model-based values GLM, including those from Figure 8

Region (AAL2)	MNI Coordinates			Number of voxels	Peak *t*-value
	x	y	z		
Unfamiliarity (k = 164)					
Left fusiform gyrus	-36	-44	-20	5360	11.10
Left inferior occipital gyrus	-28	-84	-10		8.81
Left parahippocampal gyrus	-28	-26	-24		7.25
Right fusiform gyrus	36	-56	-12	4216	11.08
Right lingual gyrus	24	-88	-6		9.38
Right fusiform gyrus	32	-38	-22		7.73
Left inferior frontal gyrus, orbitalis	-40	30	-12	3795	10.97
Left inferior frontal gyrus, opercularis	-40	4	28		9.16
Left inferior frontal gyrus, triangularis	-42	24	14		8.56
Left supplementary motor area	-8	24	48	2195	9.29
Left superior frontal gyrus, medial	-8	52	44		7.15
Left superior frontal gyrus, medial	-6	50	24		5.37
Right anterior orbital gyrus	38	40	-18	196	7.37
Left middle occipital gyrus	-24	-66	36	625	6.79
Left gyrus rectus	-4	48	-18	465	6.61
Right gyrus rectus	2	28	-20		3.94

Confidence (k = 177)					
Left superior frontal gyrus, medial	-6	50	46	302	6.00
Left cuneus	-6	-96	20	1136	5.03
Schema value x participant-P(yes) (k = 175)					
Right Rolandic operculum	52	-24	20	581	6.83
Right supramarginal gyrus	64	-28	38	581	4.27
Right superior temporal gyrus	68	-12	8	581	4.15
Right hippocampus	38	-18	-22	266	6.69
Right inferior temporal gyrus	54	-12	-36	266	3.79
Right inferior frontal gyrus, triangularis	54	34	10	383	6.48
Left paracentral lobule	-16	-12	66	176	6.42
Right middle temporal gyrus	66	-52	-2	616	6.06
Left superior temporal gyrus	-64	-30	20	483	5.88
Left postcentral gyrus	-40	-36	64	593	5.69
Left postcentral gyrus	-20	-36	74	593	5.22
Left paracentral lobule	-6	-18	68	593	3.60
Right gyrus rectus	8	44	-22	330	5.37
Right anterior cingulate	4	38	-2	330	4.42
Left lingual gyrus	-8	-68	-4	196	4.75
Right postcentral gyrus	30	-40	64	282	4.72
Left superior temporal gyrus	-60	2	-12	212	4.42
Right lingual gyrus	8	-60	4	221	4.39
Right calcarine fissure	16	-78	10	221	3.84
Experienced value x participant-P(yes) (k = 194)					
Left superior frontal gyrus, medial	-4	60	12	1439	6.92
Right superior frontal gyrus, medial	14	52	18	1439	5.08
Left gyrus rectus	-8	38	-16	1439	4.88
Left middle occipital gyrus	-34	-86	36	477	4.57
Left superior frontal gyrus	-20	32	36	201	5.01

All reported clusters were significant at the $P < 0.05$, FWE-corrected threshold at the

cluster level after peak thresholding at $P < 0.001$. The critical cluster extent threshold for

each contrast is given by the value of k.

We next specifically compared how activity related to participant-P(yes) in vmPFC

and striatum, the two regions we identified *a priori* as being associated with valuation, was

modulated by experienced value, schema value and unfamiliarity. We extracted the mean

beta coefficients for the interaction between participant-P(yes) and these three terms in the

vmPFC and striatum ROIs. The interaction of participant-P(yes) with experienced and

schema value was significant in vmPFC (one-tailed, one sample t-tests against zero: t's(22) ≥

2.99, P ≤ 0.003, d's ≥ 0.62), but not the striatum (t(22) ≤ 1.25, P ≥ 0.1, d's ≤ 0.26), whereas

the interaction of participant-P(yes) with unfamiliarity was significant in the striatum (t(22)

= 2.65, P = 0.007, d = 0.55), but not vmPFC (t(22) = 1.30, P = 0.1, d = 0.27). Thus, vmPFC

responded to greater agreement between both experienced and schema values with

participant-P(yes), while striatum activity increased in response to participant-P(yes) when

unfamiliarity was high.

To examine whether ROIs differed in their response to these value-related terms, we

then tested an ROI (striatum, vmPFC) by modulator (interactions of participant-P(yes) with

experienced value, schema value and unfamiliarity) interaction on these average beta

coefficients (Figure 9). This interaction was highly significant ($F_{2,44}$ = 12.01, P < 0.0001, η_p^2 =

0.35), as was a main effect of ROI ($F_{1,22}$ = 14.09, P < 0.01, η_p^2 = 0.39), but not modulator ($F_{2,44}$

= 0.25, P = 0.8, η_p^2 = 0.01). To determine the source of this interaction, we compared the

difference of the betas in the vmPFC and striatum for each modulator (i.e. the effect of each

interaction between ROIs). This difference was significantly greater for the interaction of

participant-P(yes) with experienced value compared to both schema value and unfamiliarity

(Bonferroni corrected t-tests t's(22) ≥ 3.75, P's < 0.01, d ≥ 0.78), but there was no comparable

significant difference between schema value and unfamiliarity.

To summarize, vmPFC activity reflected the influence of experienced and schema

values on participants' value judgments, and preferentially reflected the influence of

explicitly experienced values on participants' value judgments compared to the striatum.

Striatal activity reflected the effect of unfamiliarity on participants' value judgments, but not

value information stored directly in memory or inferred from schematic associations.

Figure 9. Boxplots showing mean beta coefficients from voxels in ventromedial prefrontal cortex (vmPFC) and striatum ROIs for interactions of participant-P(yes) with experienced value (EV), schema value (SV) and unfamiliarity (UF). *** $P < 0.001$, ** $P < 0.01$, one-tailed one-sample t-test against zero.

Generalized psychophysical interactions

We hypothesized that differential demand on memory systems during decision-

making would also lead to distinct patterns of functional connectivity, reflecting the

contributions of different memory stores to the assessment of options. vmPFC has reciprocal

connections with regions of middle temporal cortex (MTC) and anterior ventrolateral

prefrontal cortex (aVLPFC) (Price, 2007; Saleem, Kondo, & Price, 2008). Both vmPFC and

striatum also receive input from the hippocampus (HPC). We were principally interested in

whether vmPFC and MTC connectivity increased with greater demands on schema-based

decision-making, and whether striatum and HPC connectivity increased during the

assessment of directly experienced values. To address this hypothesis, we carried out

generalized psychophysical interaction (gPPI) analyses that contrasted how connectivity

between pairs of ROIs listed in Table 1 changed between task conditions, as well as more

exploratory seed-to-voxel whole-brain gPPI analyses focused on vmPFC, MTC, HPC and

striatum.

We first examined whether connectivity with vmPFC and MTC was modulated by

demands on schematic knowledge about ingredients and their value on correct responses in

the first presentation. Within an MTC seed, there was increased connectivity with vmPFC on

the first presentation of positive recipe ingredients compared to negative recipe ingredients

(Bonferroni corrected t-test: $t(21) = 4.00$, $P < 0.01$, $d = 0.85$), but not any other ROI ($P \geq 0.2$,

Bonferroni corrected). Similarly, using vmPFC as a seed ROI revealed increased connectivity

with the MTC ROI in the same contrast (Bonferroni corrected t-test: $t(21) = 3.68$, $P < 0.05$, d

$= 0.78$), but not any other ROI. An exploratory whole-brain seed-to-voxel analysis on this

contrast with the MTC ROI as a seed found that this region had significantly greater

connectivity with a cluster on the medial frontal wall overlapping with our vmPFC ROI

(Figure 10a, MNI: -2, 46, -12), and a second cluster in lateral occipital cortex (MNI: -52, -68,

12). The same whole-brain ROI-to-voxel contrast with the vmPFC ROI as a seed did not reveal

any significant clusters at an FWE cluster-corrected threshold.

These data provide evidence that vmPFC and MTC connectivity changed depending

on the value of recipe ingredients on the first presentation. To examine whether this effect

might depend on successful retrieval of relevant schema-value information, we tested the

interaction of value and accuracy on the first presentation of recipe ingredients. This

interaction was significant when either vmPFC and MTC was used as a seed (Bonferroni

corrected t-tests: t's$(20) \geq 2.95$, $P < 0.05$, $d \geq 0.64$), but not between these seeds and any

other ROIs. There was no main effect of accuracy on connectivity between ROIs on these

trials. We further examined whether this value related increase in vmPFC-MTC connectivity

was higher on the first presentation than subsequent presentations by testing the interaction

of presentation number and value for recipe ingredients, but this interaction did not reach

significance after correction for multiple comparisons in either seed.

Thus, vmPFC-MTC connectivity increased in response to retrieval of positive values

inferred from schematic knowledge on this first presentation, and though this increase was

greater on correct trials compared to errors, there were no main effects of clustering

condition or accuracy. These null effects could partially stem from participants attempting

to retrieve schematic associations on the first presentation in all conditions, consistent with

greater MTC activity in these presentations compared to repetitions in the independent

condition.

We also tested whether connectivity between MTC and vmPFC and any other ROIs

depended on clustering status by contrasting the recipe and independent conditions on the

first presentation, collapsing across value. There was no significant change in connectivity

between MTC, vmPFC and any other ROIs in this contrast. Exploratory seed-to-voxel

analyses for both of these contrasts were similarly null.

Next, we investigated if connectivity between with the HPC and striatum and other

ROIs depended on the value of options in the second and third presentations. Contrasting

positive and negative independent ingredients in these trials, we did not find any significant

increase in connectivity between HPC and striatum with each other or any other region in

ROI-to-ROI, or seed-to-voxel analyses. We further examined if connectivity with these ROIs

was higher for positive than negative ingredients in the independent condition relative to

the recipe condition by testing the interaction of value and clustering. This analysis was

similarly null for both seeds.

Figure 10. Whole brain t-statistic maps for seed-to-voxel generalized psychophysical interaction analyses. **a.** Voxels with increased connectivity with the middle temporal cortex (MTC) seed on the first presentation of positive recipe trials compared to negative recipe trials. **b.** Voxels with greater connectivity with the hippocampus (HPC) seed on the second and third presentation of independent trials compared to recipe trials. **c.** Voxels with increased connectivity with HPC on correct compared to error trials on the second and third presentations of independent ingredients. Voxels passing the $P < 0.05$ FWE cluster corrected threshold are shown in all panels except for top row of **c.** Cluster extent threshold is given by k.

1016

We also tested if HPC and striatum connectivity depended on demands for retrieving

previously experienced feedback associated with particular ingredient instance. Collapsing

across value conditions, we contrasted independent and recipe ingredients on the second

and third presentations where ingredient values could be retrieved from episodic memory,

with the expectation that demand on episodic memory would be greater in the independent

condition. There was no significant difference in connectivity between the striatum or HPC

with any other ROIs in this contrast. However, a seed-to-voxel whole-brain analysis with the

HPC seed showed significantly greater connectivity with a cluster in the right putamen and

insula (Figure 10b; MNI: 26, 10, 0). The reverse seed-to-voxel analysis with the striatum ROI

as a seed did not reveal significant clusters within a small-volume corrected HPC ROI.

To test if this increase in HPC and hippocampus connectivity was related to retrieval

success we also contrasted correct and error responses on the second and third presentation

of independent ingredients. Using the HPC as a seed in a seed-to-voxel analysis, we found

increased connectivity with this ROI and the right putamen (MNI: 28, 2, 4) after small volume

correction within the striatum ROI. An exploratory whole-brain analysis also found that HPC

significantly increased connectivity with clusters in bilateral anterior rostrolateral PFC and

right insula (Figure 10c). However, there were no significant differences in connectivity

between these conditions in ROI-to-ROI contrasts with either HPC or striatum as seeds. The

reverse ROI-to-voxel analysis with the striatum ROI as a seed did not reveal significant

increase in connectivity in a small-volume corrected HPC ROI. All peaks from seed-to-voxel

analyses are reported in Table 5.

1038

1039

1040

1041

1042 **Table 5. Whole brain seed-to-voxel connectivity effects from Figure 10**

Region (AAL2)	MNI Coordinates			Number of voxels	Peak *t*-value
	x	y	z		
Recipe Positive > Recipe negative, presentation 1, correct — MTC seed (k = 96)					
Left superior frontal gyrus, medial orbital	-2	46	-12	351	6.42
Left middle temporal gyrus	-52	-68	12	112	5.30
Correct > Error, independent presentations 2 and 3, correct — HPC seed (k = 83)					
Left middle frontal gyrus	-40	52	20	253	6.14
Left superior frontal gyrus, dorsolateral	-18	54	-4	253	5.66
Right insula	36	18	0	100	5.76
Right superior frontal gyrus, dorsolateral	30	54	14	122	5.76

1043 All reported clusters were significant at the *P* < 0.05, FWE-corrected threshold at the
1044 cluster level after peak thresholding at *P* < 0.001. The critical cluster extent threshold for
1045 each contrast is given by the value of k.
1046
In summary, we found that vmPFC-MTC connectivity depended on recipe value

associations on the first presentation where this information was key to guiding choice.

Meanwhile, HPC increased connectivity with the right putamen in response to greater

demand on episodic memory compared to trials where schema memory could still be used,

and trials where value information was not successfully retrieved.

Discussion

Here we investigated the neural circuitry involved in value judgments based on

distinct memory sources. Functional neuroimaging results implicated the vmPFC in

representing both experienced and inferred values, while striatal activity correlated with the

influence of unsigned memory strength on value judgment. Thus, these regions play separate

roles in memory-based value judgment and decision-making.

Participants were able to infer the value of ingredients based on schematic knowledge

without feedback, and continued showing a benefit from recipe information in subsequent

presentations. Our computational model captured this behavior using normative

information about ingredient-recipe associations. Notably, freely fitting the number of

dimensions used in reconstructing these recipe-ingredient associations substantially

improved the fit of the model, implying that participants varied in the depth of semantic

knowledge they employed in this task. The positive recipe also had a greater influence on

behavior compared to the negative recipe, indicating that participants prioritized searching

associations with this recipe first — possibly because they adopted a default response to

pass on ingredients where they could not retrieve positive value information.

Memory strength, expressed as unfamiliarity, also had a substantial impact on

participants' willingness to endorse ingredients. Participants demonstrated a general

tendency against betting on independent ingredients on the first presentation. Given that

there was an equal proportion of positive and negative value ingredients, and a 2:1 ratio of

points gained to lost on a bet, this behavior reflects a deviation from a rational maximization

of expected value, akin to loss aversion (Kahneman & Tversky, 1979). Whereas uncertainty

is often operationalized as descriptive or experienced probabilities of outcomes in

behavioral economics, here it depended on the strength of participants' memory of

outcomes. These results are also consistent with work showing a bias toward remembered

items in preference-based choice (Gluth, Sommer, Rieskamp, & Buchel, 2015). In real terms,

people appear to apply a meta-cognitive strategy where the strength of evidence from

memory affects option value, regardless of its content. We would thus predict that a strong

memory for a weakly positive or negative value would be more likely to drive a response

than a weak memory for a strongly positive or negative value.

Our results indicate that vmPFC represents values based on multiple memory

sources. These findings add to past work demonstrating that the value function represented

in vmPFC can flexibly bend to accommodate attentional priority toward different option

attributes (Hare, Malmaud, & Rangel, 2011; Hunt, Dolan, & Behrens, 2014; Leong, Radulescu,

Daniel, DeWoskin, & Niv, 2017; Rudorf & Hare, 2014).

We had predicted that vmPFC would be engaged more by schema-based value

inference that retrieval of a specific experience. This prediction was based on lesion evidence

demonstrating that vmPFC is not necessary for value judgment *per se* (Reber et al., 2017;

Vaidya & Fellows, 2015; Yu, Dana, & Kable, 2018), but is needed for incorporating higher-

order information into value judgments (Vaidya, Sefranek, & Fellows, 2017; Xia, Stolle,

Gidengil, & Fellows, 2015). Other work has shown that inactivation or damage to vmPFC or

OFC does not affect decision-making or value judgment in situations where values can be

retrieved from prior direct experience, but does so when this information must be inferred

from structured knowledge about a task (Bradfield et al., 2015; Izquierdo et al., 2004; Jones

et al., 2012; Rudebeck, Saunders, Prescott, Chau, & Murray, 2013).

There may be a few factors contributing to this discrepancy. While experienced

values were learned over many repeated exposures in these lesion experiments, here they

were learned from just one or two trials. Recent work has shown that spaced, brief training

over a period of days in a reinforcement learning task increases fMRI value signals in vmPFC

compared to an equivalent number of trials within a single session (Wimmer, Li,

Gorgolewski, & Poldrack, 2018), implying that this region is engaged more when value

judgments rely on episodic memory rather than massed experience. Although our results

suggest the involvement of vmPFC in representing both directly experienced and schema-

based values, this information may be robustly represented by other regions that do not

depend on vmPFC to influence behavior. Studying the effects of vmPFC damage in this task

could help assess when this region is critical for memory-based value judgment.

Our hypotheses are not fully committed to the precise format of experienced values

in this task. Our design required that participants store information about feedback paired

with ingredients in a small number of trials as a specific experience separated by other trials

over a long interval. We assumed that participants would mostly rely on episodic memory

for robust retention of such information. However, we cannot rule out the possibility that

value information would also be stored in other ways (e.g. in working memory, or through

conditioned stimulus-response mappings). Nonetheless, this possibility does not change our

ability to contrast inference of values from a memory schema and reliance on direct

experience more generally.

Notably, our results indicate that interactions between vmPFC and MTC support

inference of values from semantic knowledge. Other work has shown that utilization of

semantic meaning in value judgments increases interactions between vmPFC and regions of

left middle and superior temporal cortex (Lim, O'Doherty, & Rangel, 2013). Here, vmPFC-

MTC connectivity depended on the value of schematic associations. This result could reflect

the accumulation of value information through the interaction between these regions, or the

differential weight given to positive and negative recipes, as there was behavioral evidence

that participants prioritized positive recipe associations. In either case, these data provide

evidence that engagement between vmPFC and semantic memory stores is involved in

inferential value judgments based on real-world structured knowledge in absence of explicit

experience values.

This experiment explicitly crossed two features commonly associated with the

vmPFC, but rarely compared within the same task: value coding and schema-based memory

and inference (Chan, Niv, & Norman, 2016; Delgado et al., 2016; Ghosh, Moscovitch, Melo

Colella, & Gilboa, 2014). Our data are consistent both proposed roles for this region: with

schema-related knowledge playing a role in value construction in vmPFC, and with this

region responding to utilization of schema-related knowledge more generally. Recent rodent

electrophysiological data also indicate that value and schematic task representations co-

exist in separable codes within OFC (Zhou et al., 2019), suggesting these functions may co-

exist within the same regions.

The role of striatum in memory tasks has been the focus of recent research, with

several hypotheses being considered (Elward et al., 2015; King, Chastelaine, Elward, Wang,

& Rugg, 2018; Schwarze, Bingel, Badre, & Sommer, 2013; Scimeca & Badre, 2012). Here,

activity in the striatum integrated the influence of memory strength on participants'

decisions to bet or pass on ingredients, as its activity correlated with the interaction of

participant-P(yes) and unfamiliarity. Relatedly, recent work from our group has observed

that the striatum tracked prediction errors for retrieval success during a recognition

memory task (Scimeca et al., 2016), analogous to its role in action selection and

reinforcement-learning (Garrison, Erdeniz, & Done, 2013; Haber & Knutson, 2010;

Pessiglione, Seymour, Flandin, Dolan, & Frith, 2006). These prediction errors were

correlated with changes in the criterion by which evidence from memory was evaluated.

Unlike conventional reinforcement learning settings, the striatum was sensitive to

prediction errors that derived from memory strength rather than the value of a response.

We expand on those findings here, demonstrating that the striatum responds to the influence

of memory strength on participants' willingness to make a bet in a value-based decision-

making task, independent of memory valence. Together, these results imply a role for the

striatum in a cognitive decision about when to act based on memory strength, equivalent to

its role in controlling a tendency to bet in risky decision-making (Knutson, Wimmer, Kuhnen,

& Winkielman, 2008; Nachev et al., 2015; Zalocusky et al., 2016), or in gating working

memory (Chatham & Badre, 2015).

Notably, the striatum responded to the strength of memory for experienced values

rather than the values of options themselves. The striatum responds to successful memory

retrieval (Spaniol et al., 2009), though the functional significance of this activation is debated.

Some work has argued that these signals reflect a value signal that depends on the

congruence of the memory task with participants' goals (Han et al., 2010), while others have

suggested that striatal reward and retrieval signals are distinct (Elward et al., 2015). Here

we found evidence that unsigned memory strength modulates striatal value signals, but the

signed experienced value of options did not. These data indicate that value and retrieval

signals in the striatum may follow a common dimension that corresponds to the utility of

retrieved information given task demands — biasing cortical representations of associated

actions based on the strength of information recovered from retrieval.

We also observed that connectivity between HPC and the striatum increased in the

second and third presentations of independent ingredients compared to recipe ingredients,

and on correct choices for independent ingredients compared to error trials. This result

implies that HPC-striatal communication is involved in successful retrieval of experienced

ingredient-value associations. While this result depended on the choice of seed ROI, this

apparent selectivity might owe to our striatal ROI averaging over functionally distinct

subregions.

In conclusion, we demonstrated the involvement of the striatum and vmPFC in

distinct processes within memory-based decision-making. Our data provide fresh insights

into the dynamics of this circuitry, with a view into the intersection of decision-making and

memory that is the seat of much real-world choice behavior. These results have implications

for understanding the origins of decision-making impairments in neurodegenerative

diseases such as Alzheimer's disease and frontotemporal dementia (Salmon & Bondi, 2009),

as well as Parkinson's disease (Edelstyn, Shepherd, Mayes, Sherman, & Ellis, 2010). New

insights into the interaction of these circuits may have relevance for clinical interventions or

treatments.

1184

References

Badre, D., Poldrack, R. A., Pare-Blagoev, E. J., Insler, R. Z., & Wagner, A. D. (2005a). Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. *Neuron, 47*(6), 907-918. doi:10.1016/j.neuron.2005.07.023

Badre, D., Poldrack, R. A., Pare-Blagoev, E. J., Insler, R. Z., & Wagner, A. D. (2005b). Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. *Neuron, 47*(6), 907-918. doi:10.1016/j.neuron.2005.07.023

Barron, H. C., Dolan, R. J., & Behrens, T. E. (2013). Online evaluation of novel choices by simultaneous representation of multiple memories. *Nat Neurosci, 16*(10), 1492-1498. doi:10.1038/nn.3515

Bartlett, F. C. (1932). *Remembering: A Study in Experimental and Social Psychology*: Cambridge University Press.

Bartra, O., McGuire, J. T., & Kable, J. W. (2013). The valuation system: a coordinate-based meta-analysis of BOLD fMRI experiments examining neural correlates of subjective value. *Neuroimage, 76*, 412-427. doi:10.1016/j.neuroimage.2013.02.063

Blechert, J., Meule, A., Busch, N. A., & Ohla, K. (2014). Food-pics: an image database for experimental research on eating and appetite. *Front Psychol, 5*, 617. doi:10.3389/fpsyg.2014.00617

Bradfield, L. A., Dezfouli, A., van Holstein, M., Chieng, B., & Balleine, B. W. (2015). Medial Orbitofrontal Cortex Mediates Outcome Retrieval in Partially Observable Task Situations. *Neuron, 88*(6), 1268-1280. doi:10.1016/j.neuron.2015.10.044

Braga, R. M., & Buckner, R. L. (2017). Parallel Interdigitated Distributed Networks within the Individual Estimated by Intrinsic Functional Connectivity. *Neuron, 95*(2), 457-471 e455. doi:10.1016/j.neuron.2017.06.038

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision, 10*(4), 433-436. doi:Doi 10.1163/156856897x00357

Brett, M., Anton, J., Valabregue, R., & Poline, J. (2002). *Region of interest analysis using an SPM toolbox*. Paper presented at the 8th International Conference on Functional Mapping of the Human Brain, Sendai, Japan.

Brodeur, M. B., Dionne-Dostie, E., Montreuil, T., & Lepage, M. (2010). The Bank of Standardized Stimuli (BOSS), a new set of 480 normative photos of objects to be used as visual stimuli in cognitive research. *PLoS One, 5*(5), e10773. doi:10.1371/journal.pone.0010773

Brodeur, M. B., Guerard, K., & Bouras, M. (2014). Bank of Standardized Stimuli (BOSS) phase II: 930 new normative photos. *PLoS One, 9*(9), e106953. doi:10.1371/journal.pone.0106953

Chan, S. C. Y., Niv, Y., & Norman, K. A. (2016). A Probability Distribution over Latent Causes, in the Orbitofrontal Cortex. *Journal of Neuroscience, 36*(30), 7817-7828. doi:10.1523/JNEUROSCI.0659-16.2016

Chatham, C. H., & Badre, D. (2015). Multiple gates on working memory. *Curr Opin Behav Sci, 1*, 23-31. doi:10.1016/j.cobeha.2014.08.001

Delgado, M. R., Beer, J. S., Fellows, L. K., Huettel, S. A., Platt, M. L., Quirk, G. J., & Schiller, D.
(2016). Viewpoints: Dialogues on the functional role of the ventromedial prefrontal
cortex. *Nat Neurosci, 19*(12), 1545-1552. doi:10.1038/nn.4438
Dumais, S. T. (2004). Latent semantic analysis. *Annual Review of Information Science and*
Technology, 38, 189-230.
Edelstyn, N. M., Shepherd, T. A., Mayes, A. R., Sherman, S. M., & Ellis, S. J. (2010). Effect of
disease severity and dopaminergic medication on recollection and familiarity in
patients with idiopathic nondementing Parkinson's. *Neuropsychologia, 48*(5), 1367-
1375. doi:10.1016/j.neuropsychologia.2009.12.039
Eichenbaum, H. (2017). Memory: Organization and Control. *Annu Rev Psychol, 68*, 19-45.
doi:10.1146/annurev-psych-010416-044131
Elward, R. L., Vilberg, K. L., & Rugg, M. D. (2015). Motivated Memories: Effects of Reward
and Recollection in the Core Recollection Network and Beyond. *Cereb Cortex, 25*(9),
3159-3166. doi:10.1093/cercor/bhu109
Garrison, J., Erdeniz, B., & Done, J. (2013). Prediction error in reinforcement learning: a
meta-analysis of neuroimaging studies. *Neurosci Biobehav Rev, 37*(7), 1297-1310.
doi:10.1016/j.neubiorev.2013.03.023
Ghosh, V. E., & Gilboa, A. (2014). What is a memory schema? A historical perspective on
current neuroscience literature. *Neuropsychologia, 53*, 104-114.
doi:10.1016/j.neuropsychologia.2013.11.010
Ghosh, V. E., Moscovitch, M., Melo Colella, B., & Gilboa, A. (2014). Schema representation in
patients with ventromedial PFC lesions. *J Neurosci, 34*(36), 12057-12070.
doi:10.1523/JNEUROSCI.0740-14.2014
Gluth, S., Sommer, T., Rieskamp, J., & Buchel, C. (2015). Effective Connectivity between
Hippocampus and Ventromedial Prefrontal Cortex Controls Preferential Choices
from Memory. *Neuron, 86*(4), 1078-1090. doi:10.1016/j.neuron.2015.04.023
Haber, S. N., & Knutson, B. (2010). The reward circuit: linking primate anatomy and human
imaging. *Neuropsychopharmacology, 35*(1), 4-26. doi:10.1038/npp.2009.129
Han, S., Huettel, S. A., Raposo, A., Adcock, R. A., & Dobbins, I. G. (2010). Functional
Significance of Striatal Responses during Episodic Decisions: Recovery or Goal
Attainment? *Journal of Neuroscience, 30*(13), 4767-4775.
doi:10.1523/Jneurosci.3077-09.2010
Hare, T. A., Malmaud, J., & Rangel, A. (2011). Focusing attention on the health aspects of
foods changes value signals in vmPFC and improves dietary choice. *J Neurosci,*
31(30), 11077-11087. doi:10.1523/JNEUROSCI.6383-10.2011
Hunt, L. T., Dolan, R. J., & Behrens, T. E. (2014). Hierarchical competitions subserving multi-
attribute choice. *Nat Neurosci, 17*(11), 1613-1622. doi:10.1038/nn.3836
Izquierdo, A., Suda, R. K., & Murray, E. A. (2004). Bilateral orbital prefrontal cortex lesions
in rhesus monkeys disrupt choices guided by both reward value and reward
contingency. *J Neurosci, 24*(34), 7540-7548. doi:10.1523/JNEUROSCI.1921-04.2004
Jones, J. L., Esber, G. R., McDannald, M. A., Gruber, A. J., Hernandez, A., Mirenzi, A., &
Schoenbaum, G. (2012). Orbitofrontal Cortex Supports Behavior and Learning Using
Inferred But Not Cached Values. *Science, 338*(6109), 953-956. doi:Doi
10.1126/Science.1227489
Kahneman, D., & Tversky, A. (1979). Prospect Theory - Analysis of Decision under Risk.
Econometrica, 47(2), 263-291. doi:Doi 10.2307/1914185

King, D. R., Chastelaine, M., Elward, R. L., Wang, T. H., & Rugg, M. D. (2018). Dissociation
between the neural correlates of recollection and familiarity in the striatum and
hippocampus: Across-study convergence. *Behav Brain Res, 354*, 1-7.
doi:10.1016/j.bbr.2017.07.031
Kleiner, M., Brainard, D., & Pelli, D. (2007). What's new in Psychtoolbox-3? *Perception, 36*,
14-14.
Knutson, B., Wimmer, G. E., Kuhnen, C. M., & Winkielman, P. (2008). Nucleus accumbens
activation mediates the influence of reward cues on financial risk taking.
Neuroreport, 19(5), 509-513. doi:10.1097/WNR.0b013e3282f85c01
Landauer, T. K., Foltz, P. W., & Laham, D. (1998). An introduction to latent semantic
analysis. *Discourse Processes, 25*(2-3), 259-284. doi:Doi
10.1080/01638539809545028
Leong, Y. C., Radulescu, A., Daniel, R., DeWoskin, V., & Niv, Y. (2017). Dynamic Interaction
between Reinforcement Learning and Attention in Multidimensional Environments.
Neuron, 93(2), 451-463. doi:10.1016/j.neuron.2016.12.040
Lim, S. L., O'Doherty, J. P., & Rangel, A. (2013). Stimulus value signals in ventromedial PFC
reflect the integration of attribute value signals computed in fusiform gyrus and
posterior superior temporal gyrus. *J Neurosci, 33*(20), 8729-8741.
doi:10.1523/JNEUROSCI.4809-12.2013
Nachev, P., Lopez-Sosa, F., Gonzalez-Rosa, J. J., Galarza, A., Avecillas, J., Pineda-Pardo, J. A., . . .
Strange, B. (2015). Dynamic risk control by human nucleus accumbens. *Brain, 138*,
3496-3502. doi:10.1093/brain/awv285
Pessiglione, M., Seymour, B., Flandin, G., Dolan, R. J., & Frith, C. D. (2006). Dopamine-
dependent prediction errors underpin reward-seeking behaviour in humans.
Nature, 442(7106), 1042-1045. doi:10.1038/nature05051
Piaget, J. (1952). *The Origins of Intelligence in Children* (Vol. 8). International Universities
Press.
Postman, L., & Keppel, G. (1970). *Norms of Word Asociation*. New York, New York: Academic
Press.
Price, J. L. (2007). Definition of the orbital cortex in relation to specific connections with
limbic and visceral structures and other cortical regions. *Ann N Y Acad Sci, 1121*, 54-
71. doi:annals.1401.008 [pii]
10.1196/annals.1401.008
Ratcliff, R. (1978). Theory of Memory Retrieval. *Psychological Review, 85*(2), 59-108.
doi:Doi 10.1037//0033-295x.85.2.59
Reber, J., Feinstein, J. S., O'Doherty, J. P., Liljeholm, M., Adolphs, R., & Tranel, D. (2017).
Selective impairment of goal-directed decision-making following lesions to the
human ventromedial prefrontal cortex. *Brain, 140*(6), 1743-1756.
doi:10.1093/brain/awx105
Rescorla, R. A., & Wagner, A. R. (1972). A theory of Pavlovian conditioning: Variations in the
effective- ness of reinforcement and non-reinforcement. In A. H. Black & W. F.
Prokasy (Eds.), *Classical conditioning. II. Current research and theory* (pp. 64-99).
New York: Appleton-Century-Crofts.
Roy, M., Shohamy, D., & Wager, T. D. (2012). Ventromedial prefrontal-subcortical systems
and the generation of affective meaning. *Trends Cogn Sci, 16*(3), 147-156.
doi:10.1016/j.tics.2012.01.005

Rudebeck, P. H., Saunders, R. C., Prescott, A. T., Chau, L. S., & Murray, E. A. (2013). Prefrontal
mechanisms of behavioral flexibility, emotion regulation and value updating. *Nat*
Neurosci, 16(8), 1140-1145. doi:10.1038/nn.3440
Rudorf, S., & Hare, T. A. (2014). Interactions between Dorsolateral and Ventromedial
Prefrontal Cortex Underlie Context-Dependent Stimulus Valuation in Goal-Directed
Choice. *Journal of Neuroscience, 34*(48), 15988-15996.
doi:10.1523/JNEUROSCI.3192-14.2014
Saleem, K. S., Kondo, H., & Price, J. L. (2008). Complementary circuits connecting the orbital
and medial prefrontal networks with the temporal, insular, and opercular cortex in
the macaque monkey. *J Comp Neurol, 506*(4), 659-693. doi:10.1002/cne.21577
Salmon, D. P., & Bondi, M. W. (2009). Neuropsychological assessment of dementia. *Annu Rev*
Psychol, 60, 257-282. doi:10.1146/annurev.psych.57.102904.190024
Schuck, N. W., Cai, M. B., Wilson, R. C., & Niv, Y. (2016). Human Orbitofrontal Cortex
Represents a Cognitive Map of State Space. *Neuron, 91*(6), 1402-1412.
doi:10.1016/j.neuron.2016.08.019
Schwarze, U., Bingel, U., Badre, D., & Sommer, T. (2013). Ventral striatal activity correlates
with memory confidence for old- and new-responses in a difficult recognition test.
PLoS One, 8(3), e54324. doi:10.1371/journal.pone.0054324
Scimeca, J. M., & Badre, D. (2012). Striatal contributions to declarative memory retrieval.
Neuron, 75(3), 380-392. doi:10.1016/j.neuron.2012.07.014
Scimeca, J. M., Katzman, P. L., & Badre, D. (2016). Striatal prediction errors support dynamic
control of declarative memory decisions. *Nat Commun, 7*, 13061.
doi:10.1038/ncomms13061
Shadlen, M. N., & Shohamy, D. (2016). Decision Making and Sequential Sampling from
Memory. *Neuron, 90*(5), 927-939. doi:10.1016/j.neuron.2016.04.036
Spaniol, J., Davidson, P. S., Kim, A. S., Han, H., Moscovitch, M., & Grady, C. L. (2009). Event-
related fMRI studies of episodic encoding and retrieval: meta-analyses using
activation likelihood estimation. *Neuropsychologia, 47*(8-9), 1765-1779.
doi:10.1016/j.neuropsychologia.2009.02.028
Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left
inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proc*
Natl Acad Sci U S A, 94(26), 14792-14797.
Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., . . .
Joliot, M. (2002). Automated anatomical labeling of activations in SPM using a
macroscopic anatomical parcellation of the MNI MRI single-subject brain.
Neuroimage, 15(1), 273-289. doi:10.1006/nimg.2001.0978
Vaidya, A. R., & Fellows, L. K. (2015). Testing necessary regional frontal contributions to
value assessment and fixation-based updating. *Nat Commun, 6*, 10120.
doi:10.1038/ncomms10120
Vaidya, A. R., Sefranek, M., & Fellows, L. K. (2017). Ventromedial Frontal Lobe Damage
Alters how Specific Attributes are Weighed in Subjective Valuation. *Cereb Cortex*, 1-
11. doi:10.1093/cercor/bhx246
Whitfield-Gabrieli, S., & Nieto-Castanon, A. (2012). Conn: a functional connectivity toolbox
for correlated and anticorrelated brain networks. *Brain Connect, 2*(3), 125-141.
doi:10.1089/brain.2012.0073

Wilson, R. C., Takahashi, Y. K., Schoenbaum, G., & Niv, Y. (2014). Orbitofrontal cortex as a
cognitive map of task space. *Neuron, 81*(2), 267-279.
doi:10.1016/j.neuron.2013.11.005
Wimmer, G. E., Li, J. M. K., Gorgolewski, K. J., & Poldrack, R. A. (2018). Reward Learning over
Weeks Versus Minutes Increases the Neural Representation of Value in the Human
Brain. *Journal of Neuroscience, 38*(35), 7649-7666. doi:10.1523/Jneurosci.0075-
18.2018
Xia, C., Stolle, D., Gidengil, E., & Fellows, L. K. (2015). Lateral orbitofrontal cortex links social
impressions to political choices. *J Neurosci, 35*(22), 8507-8514.
doi:10.1523/JNEUROSCI.0526-15.2015
Yonelinas, A. P. (1994). Receiver-Operating Characteristics in Recognition Memory -
Evidence for a Dual-Process Model. *Journal of Experimental Psychology-Learning*
Memory and Cognition, 20(6), 1341-1354. doi:Doi 10.1037/0278-7393.20.6.1341
Yu, L. Q., Dana, J., & Kable, J. W. (2018). Individuals with ventromedial frontal damage have
more unstable but still fundamentally transitive preferences. *bioRxiv, 384024*.
doi:10.1101/384024
Zalocusky, K. A., Ramakrishnan, C., Lerner, T. N., Davidson, T. J., Knutson, B., & Deisseroth, K.
(2016). Nucleus accumbens D2R cells signal prior outcomes and control risky
decision-making. *Nature, 531*(7596), 642-646. doi:10.1038/nature17400
Zhou, J., Gardner, M. P. H., Stalnaker, T. A., Ramus, S. J., Wikenheiser, A. M., Niv, Y., &
Schoenbaum, G. (2019). Rat Orbitofrontal Ensemble Activity Contains Multiplexed
but Dissociable Representations of Value and Task Structure in an Odor Sequence
Task. *Curr Biol, 29*(6), 897-907 e893. doi:10.1016/j.cub.2019.01.048
1388
1389