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

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ABBREVIATED TITLE: MEMORY-BASED VALUE JUDGMENT

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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 (fMRI) 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 preferentially tracks experienced values,

in keeping with its role in both episodic memory and valuation. (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).

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. This asymmetry in the points

rewarded versus lost for betting trials was chosen to offset the overall loss aversion of

participants. In this task, loss aversion is expressed as a tendency to avoid endorsing

ingredients on the first presentation, as revealed in behavioral piloting.

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. Participants

were instructed that these recipes were general and could encompass many potential

variants (e.g. the recipe 'tacos' might include both beef and fish tacos). The names of these

recipes were displayed at the top of the screen in each trial, with the positive recipe shown

in green and the negative recipe in red text.

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 within each block. For these repeated

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

All repeated presentations 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. Before completing this practice block, all participants had to provide a detailed

verbal description of the task instructions, including the payoff structure, to the

experimenter. The experimenter verbally filled in any gaps in the participants' explanation

of the task before allowing participants to proceed into the practice phase.

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'). Stimulus presentations duration did not depend on response time. 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 completed three blocks of this task in

the scanner, each a separate fMRI run. Each block consisted of 84 trials total, with seven trials

for each value-clustering-presentation condition in each block (21 trials per condition total).

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, and used to test if participants' personal

preferences influenced their decisions in the task in model-based 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 model modifications were assessed and compared using a

cross-validation procedure, described in detail below. For simplicity, 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 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

improve the fitness 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, Foltz, & Laham, 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). Notably, allowing this

parameter to vary did not dramatically influence the overall choice behavior of the model in

simulations, but did change the shape of schema values so that increased dimensionality

increased the discretization within this term. 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. The schema value for

each ingredient was then calculated as the difference in the associative strength for the

positive and negative recipe.

In subsequent presentations, the model discounted schema values with an

exponential function based on memory strength for experienced values (i.e. the absolute

value of EV):

$$discount = \exp\left(-k|EV_i|\right) \text{ (Eq. 4)}$$

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:

$$V_i = \beta_e\, EV_i + discount\, \beta_s\, SV_i \text{ (Eq. 5)}$$

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

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:

$$V_i = \beta_e\, EV_i + \beta_{sp}PR_i - \beta_{sn}NR_i \text{ (Eq. 6)}$$

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

associations with positive and negative recipes, respectively.

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

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, we tested a model where the associative strength of

ingredients with the positive and negative schemas to the schema was weighted by an

estimate of participants' uncertainty about the recipe associations of each ingredient,

calculated as the probability that an ingredient was associated with both recipes (schema

similarity model; $P(SR)$):

$$P(SR)_i = \frac{1}{1+\exp\left(-\beta_{sim}\left(1-\frac{|PR_i-NR_i|}{RRD}\right)\right)} \text{ (Eq. 7)}$$

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

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

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

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

associations was calculated as

$$w_{same} = 2(\,P(SR)_i - 0.5)\;(\text{Eq. 8})$$

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

$$w_{diff} = 1 - 2\,|P(SR)_i - 0.5|\;(\text{Eq. 9})$$

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

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

$$SV_i = w_{same}\,(PR_i + NR_i) + w_{diff}\,(PR_i - NR_i)\;(\text{Eq. 10})$$

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.

<u>(3) Dual process recollection model</u>
386   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:

$$V_i = \beta_e((1 - P_r)EV_i + P_r RV_i) + \beta_s SV_i\;(\text{Eq. 11})$$

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.

(4) Schema spreading model

Rather than treat experienced and schema-based values separately, it is possible that

participants may have used schematic knowledge to try and facilitate feedback-based

learning. To test this hypothesis, we created a model where values learned through feedback

were broadcast to other ingredients, weighted by their similarity in recipe space. Upon

feedback, the experienced value for ingredient *i* was used to update a schema spread value

term (SSV) for all other ingredients (*j*) according to:

$$SSV_j = SSV_j + \left(1 - cos\big(Ingredient_i, Ingredient_j\big)\right)\alpha(outcome - SSV_j) \text{ (Eq. 12)}$$

Where α is the same learning rate used for updating experienced values and *cos* refers to

the cosine distance between ingredients in the normative ingredient-recipe association

matrix produced through LSA.

This SSV term was included in calculating the value of each ingredient *i* in each trial,

weighted by an additional free temperature parameter.

(5) Participant subjective value

We also tested an alternate model that included participants' own subjective value

ratings for ingredients in the computation of ingredient values weighted by an additional

free temperature parameter. This model tested whether participants' choices would be

better accounted for by taking into account their personal preferences.

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.

Models were compared with a cross-validation procedure. For each participant, we

generated 100 independent training and test datasets where a set of 16 ingredients (19% of

the total ingredients) were randomly held out of the data used for fitting model parameters

and treated as deadline failures (as to maintain the same number of trials in the experiment).

We chose to randomly subsample ingredients rather than blocks or trials because of the

structure of the task: participants encounter a new customer, and thus a new set of recipe

schemas in each block, while trials are not independent from each other, as each ingredient

is repeated three times and the value must be retained from one trial to the next.

To test model fitness, we estimated the mean difference in the negative log-likelihood

of each model relative to the base model for the held out 16 ingredients, averaged across all

100 test datasets and summed across participants. At each step in the model comparison

process, the model that resulted in the largest reduction in the negative log-likelihood for the

test data set was considered the preferred model. Additional parameters reduced the

negative log-likelihood were added to the preferred model and compared in the next step,

while any parameters that did not improve model fitness were discarded in future steps. The

search for the best fitting model was stopped once additional parameters no longer

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:

(1) Condition-based GLM

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 as a means of controlling for the influence of RT on a trial-to-

trial basis independent of the effects of condition. This GLM also included a nuisance

regressor for the time the stimulus display was on screen (i.e. the response window, ISI and

feedback).

(2) Finite impulse response GLM

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 contrast activity between conditions within different ROIs without

assumptions about the shape of the hemodynamic response function made for simplification

in whole-brain and model-based analyses.

(3) Model-based value components GLM

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. We examined the covariance structure of these

modulators to assess their independence. The mean R^2 for all pairs of parametric modulators

was 0.08, while the maximum R^2 was 0.56 for the correlation between experienced value and

participant-P(yes). This stronger correlation was not surprising given that experienced

value was a major determinant of participants' P(yes) ratings. 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. Specifically, we chose ROIs within a network previously identified by our

lab and others as forming a network involved in the storage and retrieval of semantic and

episodically encoded information (MTC, aVLPFC, HPC; (Badre, Poldrack, Pare-Blagoev,

Insler, & Wagner, 2005a; Barredo, Verstynen, & Badre, 2016; Thompson-Schill, D'Esposito,

Aguirre, & Farah, 1997)), and in forming estimates of subjective and expected value (vmPFC,

mPFC, striatum; (Barron, Dolan, & Behrens, 2013; Bartra, McGuire, & Kable, 2013)). 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 for using the grand-average of this

timecourse across conditions and subjects (with equal weight for each conditions), 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.

Generalized psychophysical interaction analysis

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

CONN toolbox in conjunction with SPM12 (McLaren, Ries, Xu, & Johnson, 2012; 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.

Following this denoising process, gPPI analyses involved a two-step process. The

regressors from the condition-based GLM, the timecourse of each ROI and the interaction of

this timecourse with the condition-based regressors were included in a multiple linear

regression model. Task-related changes in the relationship between activity in pairs of

regions was estimated using the bivariate correlation between these interactions.

Correlation coefficients for each subject were Fisher transformed and contrasted between

conditions. In a second level analysis, these differences were 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 this interaction term between an ROI

and each target voxel. These correlations were then Fisher-transformed and the difference

between transformed correlations in task conditions was 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, $P < 0.0001$, $\eta_p^2 = 0.55$), 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, $P < 0.0001$, $\eta_p^2 = 0.73$). 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 positive 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$(22) \geq 4.54$, P's < 0.01, d's $\geq$

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$(22) \geq 4.69$, 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$(22) \geq 8.69$, P's < 0.0001, d's ≥ 1.81). Thus, participants strategically avoided

endorsing independent ingredients before learning their values through feedback.

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 ≥ 27.88, $P ≤ 0.0001$, $\eta_p^2 ≥ 0.58$). 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: $t's(20) ≥ 4.57$, P's ≤ 0.01,

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

recipe ingredients (Bonferroni corrected t-tests: $t's(20) ≥ 3.98$, P's ≤ 0.05, $d's ≥ 0.87$), 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 interaction

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

reductions 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 errors 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: $F_{1, 21} = 15.43$, $P = 0.0007$, $\eta_p^2 = 0.42$), and accuracy and presentation number

($F_{1, 21} = 43.69$, $P < 0.0001$, $\eta_p^2 = 0.67$). 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: $F_{1, 21} = 14.34$, $P = 0.001$, $\eta_p^2 = 0.40$). 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: $t's(21) \geq 6.64$, P's < 0.0001, $d = 1.42$).

Reaction times were influenced by an interaction of accuracy and presentation

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

trend toward an interaction between accuracy and clustering ($F_{1, 21} = 3.81$, $P = 0.06$, $\eta_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.

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).

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 and was

independent and non-overlapping with the vmPFC ROI (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: $F_{1, 20} = 9.13$, $P = 0.007$, $\eta_p^2 = 0.31$), 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 ($F_{1, 20} = 5.06$, $P = 0.01$, $\eta_p^2 = 0.20$). 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 ($F_{2, 20} = 3.29$, $P = 0.05$, $\eta_p^2 = 0.14$),

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

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

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

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, η_p^2 = 0.38). HPC activity was also generally

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

activity was modulated marginally by clustering ($F_{1, 21}$ = 4.65, P = 0.04, η_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, η_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.

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

third, consistent with the whole-brain analysis (Figure 5e; Presentation Main Effect: $F_{1, 21}$ =

10.76, $P = 0.004$, $\eta_p^2 = 0.34$). 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 diminished with presentation

overall, perhaps in line with greater retrieval demands early on. 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 using cross-validation to compare the new

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

explained participants' behavior on trials that were held out from the dataset used to fit

parameter values. Figure 6 shows the difference in the negative log likelihoods 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 discounted the

influence of SV based on the memory strength of the ingredients' experienced value, with

schema values contributing less to ingredient values when these experienced values were

stronger.

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.

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 ($t(22) = 4.13$, $P = 0.0004$, $d = 0.86$), the opposite

was true of the fixed bias parameter ($t(22) = 4.69$, $P = 0.0001$, $d = 0.98$).

It is possible that this unfamiliarity term simply captures a bias to pass on the first

presentation of ingredients rather than an effect of unfamiliarity more generally — i.e. the

additional effect of the passage of time and repeated presentations. To examine if there was

an effect of unfamiliarity on participants' willingness to endorse an ingredient in later trials,

we used a logistic regression in each participant to test if there was a relationship between

the model-based unfamiliarity term on betting decisions on the second and third

presentations. A one-sample t-test revealed that these logistic regression coefficients were

significantly lower than zero across participants, indicating a persistent negative influence

for unfamiliarity on participants' decisions in later presentations ($t(22) = 3.62$, $P = 0.001$, d

= 0.75). Thus, this unfamiliarity term captures additional variance in decision behavior that

beyond an aversion to betting on the first presentation of an ingredient.

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 had a strong negative correlation with the unfamiliarity bias parameter,

indicating that this fixed bias in effect acted to counter the aversion to betting related to

unfamiliarity. Despite this strong relationship, both parameters resulted in large

improvements in model fitness when included together (Figure 6), indicating that they were

complimentary.

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) ≥ 0.82, 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 near perfect correlation between the parameter estimates from

participants' behavior and the simulated data (Pearson r's(21) ≥ 0.99, 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: $F_{2,44} = 73.09$, $P < 0.0001$,

$\eta_p^2 = 0.77$). 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)

≥ 9.12, P's < 0.0001, d's ≥ 1.90). 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:

$t(22) = 9.52$, P < 0.0001, $d = 1.99$), suggesting that it used information about the negative

recipe more than participants did. Model-P(yes) on the first presentation of independent

ingredients trended negatively, but was not significantly lower than chance ($t(22) = 1.65$, P

= 0.1, $d = 0.34$), indicating a modest difference from participant behavior. 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) ≥ 8.19, P's < 0.0001, d ≥ 1.71), and presentation three

compared to two (Bonferroni corrected t-tests: t's(22) ≥ 6.03, P's < 0.01, d ≥ 1.26).

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: $F_{2, 40}$ = 165.64, P < 0.0001, η_p^2 = 0.89), and was higher overall for recipe

ingredients than independent ingredients ($F_{1, 20}$ = 46.48, P < 0.0001, η_p^2 = 0.70), however

there was no main effect of value ($F_{1, 20}$ = 1.96, P = 0.2, η_p^2 = 0.09). 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) ≥ 4.50, P's < 0.01,

d's ≥ 0.98), rather than just positive recipe ingredients.

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

task, including utilization of recipe-based values. 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.

The model also underestimated the effects of unfamiliarity on P(yes) on the first

presentation of independent ingredients, though was trending in the same direction as

participants.

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).

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

in the left and right middle temporal gyrus, 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 a cluster in the

bilateral caudate nucleus responded to the interaction of unfamiliarity with participant-

P(yes) (Figure 8c; FWE-corrected $P < 0.05$, MNI: 18, 20, -4). Whole brain peak activations for

this GLM are described in Table 4.

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: $t(22)$ =

2.38, $P \leq 0.01$, d's ≥ 0.50). There was also a significant effect for the interaction of schema

value with participant-P(yes) in the striatum ($t(22) = 2.05$, $P = 0.03$, $d = 0.43$), but not for

the interaction of participant-P(yes) with experienced value. Further, the interaction of

participant-P(yes) with unfamiliarity was significant in the striatum ($t(22) = 2.30$, $P = 0.02$,

$d = 0.48$), but not vmPFC. 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, as well as the agreement of

schema values with participant-P(yes).

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 ($F_{2,44} = 8.67$, $P = 0.007$, η_p^2 =

0.28), as was a main effect of ROI ($F_{1,22} = 10.59$, $P = 0.004$, $\eta_p^2 = 0.32$), but not modulator (F

$_{2,44} = 0.10$, $P = 09$, $\eta_p^2 = 0.005$). 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$(22) \geq 3.09$, P's < 0.05, $d \geq 0.64$), 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 and

values inferred from a schema, but not value information stored directly in memory.

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 the

schema-based value of ingredients on correct responses in the first presentation – i.e. when

these values are correctly inferred from schematic knowledge and not retrieved from

experience. 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.

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.

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. We had put forward three main hypotheses: (1) vmPFC is

preferentially involved in inferred value judgments based on schematic world knowledge,

(2) striatum is preferentially involved in representing experienced values, (3) vmPFC and

striatum interact with distinct memory networks in line with their respective involvement

in building values from schematic knowledge and experience.

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 and

schema-based values. In contrast, vmPFC responded to the influence of value judgments

based both on direct experience and schema memory. Analysis of connectivity between

these regions and memory stores revealed greater connectivity between the striatum and

HPC in response to demands on recall of experienced values, while vmPFC and MTC

connectivity increased in response to values derived from schema memory. 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 connectivity with HPC in response to

demand for retrieval of experienced values.

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 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. Variance in how participants

engage with these schemas to form value estimates may also be reflected in neural activity,

however we did not have a sufficient sample size to make a strong test of such individual

differences.

Memory strength, expressed as unfamiliarity, had a substantial impact on

participants' willingness to endorse ingredients. Participants demonstrated a general

tendency against betting on independent ingredients on the first presentation and against

betting on ingredients where memory strength was lower on subsequent presentations.

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). While

the proportion of positive to negative value trials was not made explicit to the participants,

and we cannot be sure that participants were aware of this equal weighting, this proportion

was the same in the practice phase and main experiment, so that participants would have

had experience with an equal proportion of positive and negative trials before starting the

main task. 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). However, we cannot be sure if the

values represented here are ultimately referenced to the points earned by the participant, or

reflect a social value based on the experience of the "customer" whom they are ostensibly

feeding according to the cover story for the task.

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

experienced 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 with 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 experienced values of options themselves. The striatum responds to

successful memory retrieval in many tasks (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 (i.e.

unfamiliarity) 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 found that the striatum responded to the interaction of participant-P(yes)

and schema value. While of a smaller effect size, these data imply that the striatum encodes

these inferred values in addition to the effects of unfamiliarity. Indeed, previous work has

found that the striatum responds to prediction errors inferred structured knowledge about

a task (Daw, Gershman, Seymour, Dayan, & Dolan, 2011; Lohrenz, McCabe, Camerer, &

Montague, 2007).

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 information shared in a HPC-striatal circuit 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.

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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
Barredo, J., Verstynen, T. D., & Badre, D. (2016). Organization of cortico-cortical pathways
supporting memory retrieval across subregions of the left ventrolateral prefrontal
cortex. *J Neurophysiol, 116*(3), 920-937. doi:10.1152/jn.00157.2016
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

Daw, N. D., Gershman, S. J., Seymour, B., Dayan, P., & Dolan, R. J. (2011). Model-based influences on humans' choices and striatal prediction errors. *Neuron, 69*(6), 1204-1215. doi:10.1016/j.neuron.2011.02.027

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

Lohrenz, T., McCabe, K., Camerer, C. F., & Montague, P. R. (2007). Neural signature of fictive learning signals in a sequential investment task. *Proc Natl Acad Sci U S A, 104*(22), 9493-9498. doi:10.1073/pnas.0608842104

McLaren, D. G., Ries, M. L., Xu, G., & Johnson, S. C. (2012). A generalized form of context-dependent psychophysiological interactions (gPPI): a comparison to standard approaches. *Neuroimage, 61*(4), 1277-1286. doi:10.1016/j.neuroimage.2012.03.068

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
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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).

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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.

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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.

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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.

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Figure 5. Region-of-interest analyses showing percent signal change in **a.** ventromedial prefrontal cortex (vmPFC) and **b.** the bilateral striatum on correct response trials for positive (pos) and negative (neg) ingredients in the recipe and independent conditions across presentations. **c.** Percent signal change in the hippocampus (HPC) for correct and erroneous responses in the recipe and independent conditions, 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**.

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Figure 6. Difference in negative log-likelihood for held-out data in cross-validation procedure for additional model parameters compared to 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. * Reduction in negative log-likelihood compared to next best fitting model. ***, best model within a step and an improvement in fitness compared to next best model.

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Figure 7. Model behavior for positive (pos) and negative (neg) ingredients in the recipe and independent conditions across presentations. **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.

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.

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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* < 0.01, * *P* < 0.05, one-tailed one-sample t-test against zero.

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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.

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1474   **Table 1.** Description of ROIs

Region of interest	Definition	Center of mass (MNI)
vmPFC	Positive>Negative effects of subjective value (Bartra et al., 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 et al., 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 et al., 2005a)	-54, 27, -9
MTC	10 mm sphere around peak activation in semantic classification task (Thompson-Schill et al., 1997)	-52, -55, 2

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1476 **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

1477 All reported clusters were significant at the $P < 0.05$, FWE-corrected threshold at the
1478 cluster level after peak thresholding at $P < 0.001$. The critical cluster extent threshold for
1479 each contrast is given by the value of k.
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Table 3. Mean parameter values and Pearson correlations between parameters in the best-fitting behavioral model

	Mean (SD)	Decay	EV temp.	SV temp.	UF temp.	Fixed bias	Schema discount (log-space)
Decay	**0.02 (0.01)**	-					
EV temp.	**5.18 (0.31)**	0.28	-				
SV temp.	**2.45 (1.70)**	0.04	0.37	-			
UF temp.	**-0.84 (0.97)**	0.12	0.27	0.21	-		
Fixed bias	**0.69 (0.70)**	0.06	-0.29	-0.29	-0.94***	-	
Schema discount (log-space)	**-2.47 (6.05)**	-0.20	0.28	0.15	-0.03	-0.06	-
Recipe dimensions (log-space)	**1.10 (0.36)**	-0.12	-0.05	0.40	-0.37	0.24	0.36

Experienced value (EV), schema value (SV), unfamiliarity (UF), ***$P < 0.0001$

1485 **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 = 161)					
Left fusiform gyrus	-36	-44	-20	5443	11.02
Left inferior occipital gyrus	-28	-84	-10	5443	9.20
Left middle temporal gyrus	-60	-48	-8	5443	7.03
Right fusiform gyrus	34	-52	-12	3877	9.98
Right lingual gyrus	24	-88	-6	3877	9.50
Right fusiform gyrus	34	-28	-28	3877	7.42
Left inferior frontal gyrus, orbitalis	-40	32	-12	2995	9.54
Left inferior frontal gyrus, opercularis	-40	4	28	2995	9.17
Left inferior frontal gyrus, triangularis	-42	24	14	2995	8.45
Left superior frontal gyrus, dorsolateral	-16	38	50	1843	7.67
Left middle frontal gyrus	-32	18	58	1843	5.32
Left supplementary motor area	-6	12	56	1843	7.15
Left gyrus rectus	-2	48	-18	403	7.08
Left precuneus	-4	-54	18	173	6.80
Left hippocampus	-18	-8	-20	173	6.31
Right gyrus rectus	2	28	-20	173	3.94
Confidence (k = 158)					
Left superior frontal gyrus, medial	-6	50	46	240	5.84
Left superior frontal gyrus, medial	-4	56	22	240	4.01
Left middle temporal gyrus	-58	-12	-16	187	4.25
Left middle temporal gyrus	-64	-30	0	159	4.87
Right Postcentral gyrus	24	-32	64	196	4.58
Schema value x participant-P(yes) (k = 161)					
Right middle temporal gyrus	52	-42	4	559	5.789
Right inferior temporal gyrus	58	-60	-14	559	4.243
Right inferior frontal gyrus	48	36	0	229	5.664
Left superior temporal gyrus	-54	-6	-2	256	5.168
Left middle temporal gyrus	-58	4	-22	256	3.93
Right superior temporal gyrus	66	-10	2	269	5.015
Left cuneus	2	-82	38	301	4.872
Right cuneus	18	-86	26	301	3.882

Left middle temporal gyrus	-66	-50	2	250	4.747
Right supramarginal gyrus	58	-26	20	182	4.682
Left superior temporal gyrus	-64	-30	18	193	4.657
Experienced value x participant-P(yes) (k = 168)					
Left superior frontal gyrus, medial	-4	60	8	1198	6.92
Left gyrus rectus	-8	38	-16	1198	4.95
Right superior frontal gyrus, medial	10	58	28	1198	4.18
Left angular gyrus	-50	-76	24	185	5.21

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.

1490 **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

1491 All reported clusters were significant at the $P < 0.05$, FWE-corrected threshold at the
1492 cluster level after peak thresholding at $P < 0.001$. The critical cluster extent threshold for
1493 each contrast is given by the value of k.
1494