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The orbitofrontal cortex spontaneously encodes food health and contains more distinct representations for foods highest in tastiness

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Abstract

The human orbitofrontal cortex (OFC) has long been associated with food reward processing and is thought to represent modality-independent signals of value. Food tastiness and health are core attributes of many models of food choice and dietary self-control. Here we used functional neuroimaging to examine the neural representation of tastiness and health for a set of 28 food categories selected to be orthogonal with respect to both dimensions. Using representational similarity analysis, in conjunction with linear mixed-effects modeling, we demonstrate that the OFC spontaneously encodes food health, whereas tastiness was associated with greater neural dissimilarity. Subsequent analyses using model dissimilarity matrices that encode overall tastiness magnitude demonstrated that the neural representation of foods grows more distinct with increasing tastiness but not with increasing health. In a separate study, we use lexical analysis of natural language descriptions of food to show that food tastiness is associated with more elaborate descriptions of food. Together these data show not only that the OFC spontaneously encodes the dimensions of health and tastiness when viewing appetitive food cues, but also that the neural and cognitive representations of food categories that are the highest in tastiness are more refined than those lower in tastiness.

Key words: food; reward; orbitofrontal cortex; multivariate pattern analysis; representational similarity analysis

Introduction

The orbitofrontal cortex (OFC) is an important region for representing the reward value of appetitive stimuli such as food and drugs (Jasinska *et al.*, 2014; van der Laan *et al.*, 2011; Wagner, 2017). Activity in this region has been shown to vary as a function

of hunger (Small, 2001; Kringsbach *et al.*, 2003), pleasantness (Simmons *et al.*, 2014), liking and desire (Wagner *et al.*, 2013; Jiang *et al.*, 2015). Moreover, individuals' differences in the degree to which people activate this region when viewing appetitive food images predict both body mass index (BMI; Rapuano *et al.*, 2016) and prospective weight gain (Yokum *et al.*, 2011).

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Non-human animal research suggests that the OFC is a convergence zone for multiple sensory features of foods (Rolls and Baylis, 1994), such as fat (Rolls et al., 1999), umami (Baylis and Rolls, 1991), sweet, salty, bitter, and sour (Rolls et al., 1990). Human neuroscience studies further suggest a role for this region in representing the identity of food rewards. For instance, Howard et al. (2015) found that the OFC was able to discriminate between identity-specific features of food rewards (i.e. sweet vs savory), independent of reward value (i.e. strong or weak odor concentration). Despite these findings, there are relatively few studies that have examined whether the OFC encodes complex food attributes automatically (i.e. in the absence of explicit task instructions to evaluate food along these dimensions). One recent exception is a study that examined how the brain represents the nutritional attributes of foods (e.g. calories, vitamins, fat), using representational similarity analysis (RSA), they found that foods with similar nutrient values were associated with similar patterns of neural activity in the OFC (Suzuki et al., 2017).

When it comes to dietary choice and self-control, researchers have focused on the more high-level motivationally relevant features of appetitive food (e.g. a food's tastiness and health properties). A wealth of experimental work in humans demonstrates that dietary choices are heavily influenced by the dimensions of tastiness (a more immediate sensory feature) and health (a more general feature related to long-term goals). For instance, attitudes toward food tastiness and healthiness have been shown to predict food consumption patterns across a range of studies (Zandstra et al., 2001; Hearty et al., 2007; Pelletier et al., 2013; Aggarwal et al., 2014; Nguyen et al., 2015; Kowalkowska et al., 2018). Furthermore, research has shown that focusing attention on the tastiness vs the healthiness of a food item leads to an increased desire to consume unhealthy foods (Young and Fazio, 2013). Finally, a growing literature on value-based decision-making has highlighted the important role of tastiness and health in guiding dietary choices and dietary self-control (Hare et al., 2009; Hare et al., 2011; Harris et al., 2018). Sullivan, Hutcherson, Harris & Rangel, 2015. Taken together, these studies argue for the fundamental role of tastiness and health in guiding food choice. Understanding how these dimensions are encoded in the brain may be critically important for understanding both the cognitive and neural mechanisms underlying real-world dietary choices as well as dietary self-control failure.

In the current study, we developed a novel food category visual stimulus set that varied orthogonally in the dimensions of tastiness and health in order to investigate the neural representation of these motivationally relevant dimensions of appetitive foods. Specifically, we used RSA in conjunction with linear mixed-effects modeling to test whether the OFC spontaneously encodes the dimensions of tastiness and health when viewing food items and whether these representations might become more distinct the more a food is considered desirable (i.e. increasing tastiness). The results of this analysis are corroborated by a second experiment that examines whether individuals' cognitive representation of food, as assessed through verbal descriptions of foods and analyzed with the linguistic inquiry and word count (LIWC) tool (Pennebaker et al., 2015), also shows evidence of greater distinctiveness with increasing tastiness.

Materials and methods

Participants

Twenty healthy right-handed non-dieting participants with normal or corrected-to-normal visual acuity and no dietary

restrictions or food allergies participated in the functional neuroimaging experiment (12 female; mean age = 21.1; range 18–29). Two participants were excluded from analyses: one due to excessive head motion (i.e. several instances of >2 mm head motion) and another for falling asleep during the imaging task as indicated by a lack of behavioral responses for a portion of the study. The second experiment involving natural language descriptions of food categories consisted of 59 participants (41 female; mean age = 19.6; range 18–30). Three participants were excluded due to a lack of familiarity with one or more of the food categories included in the task. All participants gave informed consent in both sessions in accordance with the guidelines set by the internal review board at The Ohio State University and were compensated for their participation.

Stimuli

Stimuli consisted of a novel set of food images that were designed to vary in health and tastiness. The images used in the present study are a subset of a larger image database under development and were chosen to vary orthogonally and to represent the maximum amount of variance along the dimensions of tastiness and health. Images in this database consisted of high-quality photographs of plated foods taken in a 'tabletop photo studio' (i.e. lightbox) ensuring identical image background and lighting. Each image was captured in RAW format and white balance corrected in Adobe Lightroom to ensure approximately identical image background characteristics. Although other food image databases exist (e.g. Food-pics: Blechert, Meule, Busch and Ohla, 2014; Food4Health: Charbonnier et al., 2016; OLAF: Miccoli et al., 2014), none of these were amenable to the present study due to a combination of: (i) image variability (e.g. food 'scenes' with no consistent background) that could potentially drive the similarity of neural patterns between food categories above and beyond the foods themselves; (ii) insufficient number of exemplars per category to be amenable to a multivariate pattern analysis that, optimally, ought to have multiple trials and exemplars per category to obtain stable estimates of neural activity while minimizing habituation to individual exemplars (e.g. Dimsdale-Zucker and Ranganath, 2018); (iii) consisted largely of European foods that were not readily recognizable by Americans or likely to be considered desirable to an American palate (e.g. french fries with Mayonnaise, egg cake, liver sausage and other meats of dubious provenance).

For inclusion in the following study, a set of 183 unique food images were pre-tested from a larger database of 373 food images. A separate set of 64 participants (female = 48; mean age = 18.9; range 18–35) with no dietary restrictions rated each of the food images using a Likert scale (–5 to +5) on the following dimensions: liking, tastiness and healthiness. From this set of ratings, 28 food categories selected to span the range of tastiness and health values were selected. For each food category, the five exemplars with the lowest distance to the centroid of each cluster in the dimensions of tastiness and health were selected. In other words, exemplars that were most dissimilar from the overall mean tastiness and healthiness of the cluster were excluded from the final stimulus set. Based on these ratings, a final stimulus set consisting of 28 categories of foods (e.g. apple, cake, salad) each with five exemplars for a total of 140 unique food image exemplars (i.e. granny smith apple, chocolate cake, Caesar salad). An example of the images comprising select food categories is shown in Figure 1 and the distribution of tastiness and health scores for each category is shown in Figure 2. A

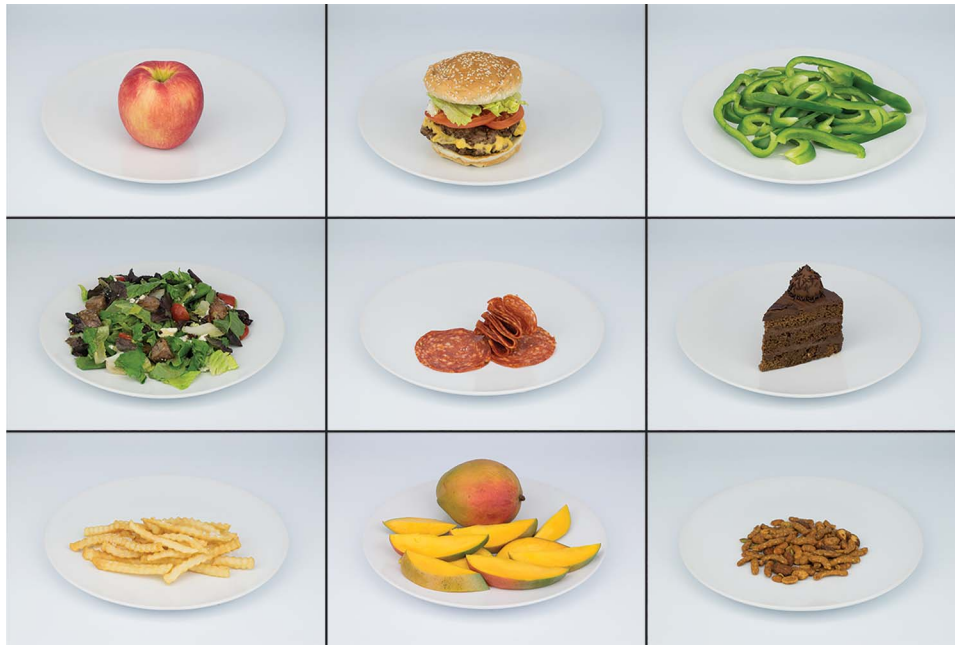


Fig. 1. Example food images. All food images were created in-house and plated on a uniform background. From left to right—Row 1: gala apple, Five Guys burger, green peppers; Row 2: steak salad, pepperoni, double chocolate cake; Row 3: White Castle fries, mango, sesame trail mix.

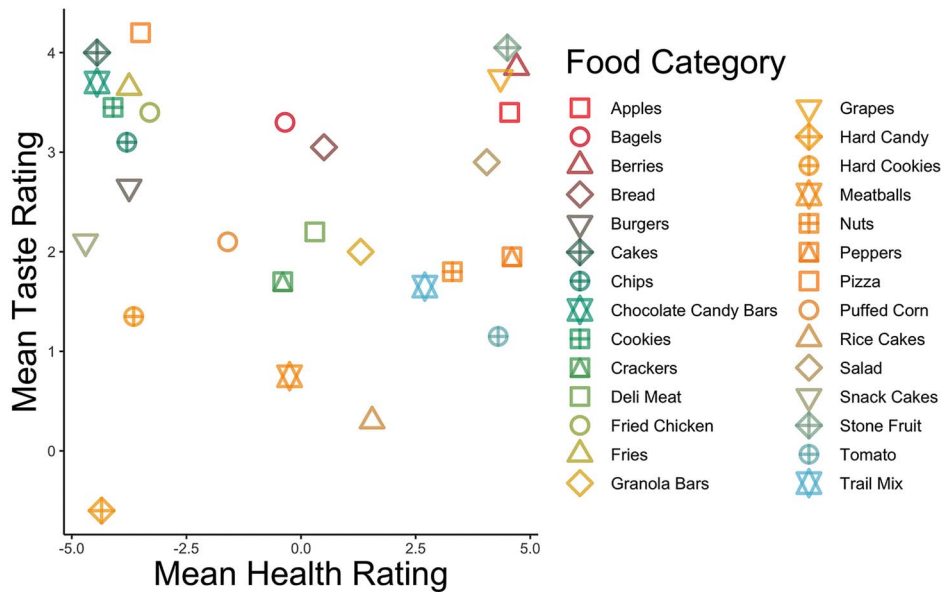


Fig. 2. Distribution of ratings of tastiness and healthiness per category from participants in the functional neuroimaging experiment. Each point represents the average rating across all five food items in the category.

complete list of food exemplars and categories can be found in [Supplementary Table S1](#).

Procedure

Participants were instructed to refrain from eating for at least 2 hours prior to the in-lab session so they would not be satiated during the experiment. Upon arrival to the experiment, they were asked to rate their present hunger, fullness and time since last eaten. This information was not collected for one participant

prior to participation but was collected at the end of the experiment. Following this, participants completed the functional neuroimaging food viewing task, followed by a separate food rating task outside the scanner (both tasks are described below). Upon completion of both study tasks, participants provided additional demographic information, again reported their hunger, fullness and hours since last meal and, finally, they completed both the Revised Restraint Scale (Heatherton et al., 1988) and the Dutch Eating Behavior Questionnaire (van Strien et al., 1986). A summary of these participant characteristics is provided in [Supplementary Table S2](#).

Table 1. Average correlation across participants between food category ratings

Measures	1	2	3	4	5	6
1. Tastiness		0.01	0.90**	0.79**	0.27	0.17
2. Healthiness			0.07	0.03	-0.40	-0.63*
3. Liking				0.83**	0.23	0.13
4. Willingness to consume					0.21	0.11
5. Carbohydrate content						0.39
6. Fat content						

Note: Values reflect the average correlation across all 18 participants between each rating dimension for the 28 food categories. Ratings for each food category took place on a -5 to +5 scale. * $P < 0.05$; ** $P < 0.01$.

Taste/Health food task

Participants completed the food-viewing task while undergoing functional magnetic resonance imaging (fMRI). Stimulus presentation and behavioral responses were recorded using PsychoPy (Peirce, 2007, 2008). On each trial, participants were presented with a food image and responded whether they liked or disliked the food. The task consisted of six imaging runs, each including 140 food image trials and 45 null-event trials consisting of a black fixation cross against a gray background. For each run, every food category and exemplar (i.e. 28 food categories with five exemplars each) was presented. Thus, every exemplar was presented six times, and the neural response for each food category was estimated from 30 trials (i.e. five exemplars presented six times). The order of event presentation was optimized per run using Opseq2 (Dale, 1999), and the order of run presentations was randomized across all participants. Each image was presented for 1800 ms followed by a 200 ms fixation cross.

Food category ratings

After scanning, participants provided additional ratings of each food category. In this task, participants were shown a collage of all five food image exemplars that comprised each of the 28 food categories and asked to rate each category based on how they viewed the category in general, and not to base their rating off any one individual exemplar. Six ratings were collected: (i) 'How much do you like this food?'; (ii) 'If the food was given to you for free, how willing would you be to consume it?'; (iii) 'Is this food healthy?'; (iv) 'Is this food tasty?'; (v) 'How high is this food in fat?' and (vi) 'How high is this food in carbohydrates?'. Participants responded to ratings on a -5 to +5 scale ranging from 'Not at All' to 'Very Much'. Overall, participant ratings for tastiness and health were uncorrelated [average $r(26) = 0.007$]. A summary of the average correlation between all pairs of ratings across all subjects is provided in Table 1.

Image acquisition

Magnetic resonance imaging (MRI) was collected with a Siemens Prisma 3.0 Tesla MRI scanner using a 32-channel phased array coil. Structural images were acquired using a T_1 -weighted [176 sagittal slices, time repetitions (TR): 1900 ms; time echo (TE): 4.44 ms; flip angle: 12°; 1 mm isotropic voxels]. Functional images were acquired using a T_2 -weighted echo-planar sequence (TR: 2000 ms; TE: 28 ms; flip angle: 76°). For each participant, six functional runs of 185 whole-brain volumes were collected (60 axial slices per whole-brain volume; 3 mm thickness; 3 × 3 in-plane resolution; multiband acceleration factor of 3).

Image pre-processing

fMRI data were analyzed using SPM12 in conjunction with a set of in-house tools for pre-processing and analysis (SPM12w, available at <https://github.com/wagner-lab/spm12w>). For each functional run, data were pre-processed to remove sources of noise and artifact. Images were corrected for differences in acquisition time between slices, realigned within and across runs and unwarped to reduce residual movement-related distortions. Data were normalized into a standard stereotaxic space (3 mm isotropic voxels) based on the SPM12 EPI template that conforms to the International Consortium for Brain Mapping 152 brain template space. Normalized images were spatially smoothed with an 8 mm full-width-at-half-maximum Gaussian kernel. Volumes were inspected for scanner- and motion-related artifacts based on the realignment parameters and temporal signal to noise ratio (SNR) profiles for each run.

Region-of-interest selection

For each participant, a general linear model (GLM) containing task effects and covariates of non-interest (a session mean, a linear trend to account for low-frequency drift and six movement parameters) was constructed to investigate food-related brain activity. The GLM was then convolved with a canonical hemodynamic response function. Whole-brain contrast maps of activity for all food over baseline trials were entered into a second level random effects analysis (Supplementary Figure S1 and Supplementary Table S3). Consistent with prior studies by our group and others, viewing food images was associated with increased activity in the left OFC. This analysis was used to select a functionally defined left OFC cluster (88 voxels, $P < 0.05$ family-wise error rate corrected at the cluster level using random field theory and with a cluster-defining threshold of $P = 0.001$) centered at -30,27, -18 ($t(17) = 7.45$, $P < 0.001$ at the voxel level) that was then used as a functional region-of-interest (ROI) to extract patterns of activity for each food category for all subsequent multivariate RSA analyses (Figure 3). Additional ROIs in primary and secondary visual cortex were selected to use in a second control analysis comparing OFC representations to those located in visual areas. Three 6mm spherical ROIs (located in: left Middle Occipital Gyrus, right inferior Occipital Gyrus and the right Fusiform Gyrus) were identified based on the peak location of activity within clusters of activity in the visual cortex and thresholded as described above.

Linear mixed-effects RSA

Multivariate analyses of imaging data were conducted using a combination of the PyMVPA toolbox (Hanke et al., 2009)

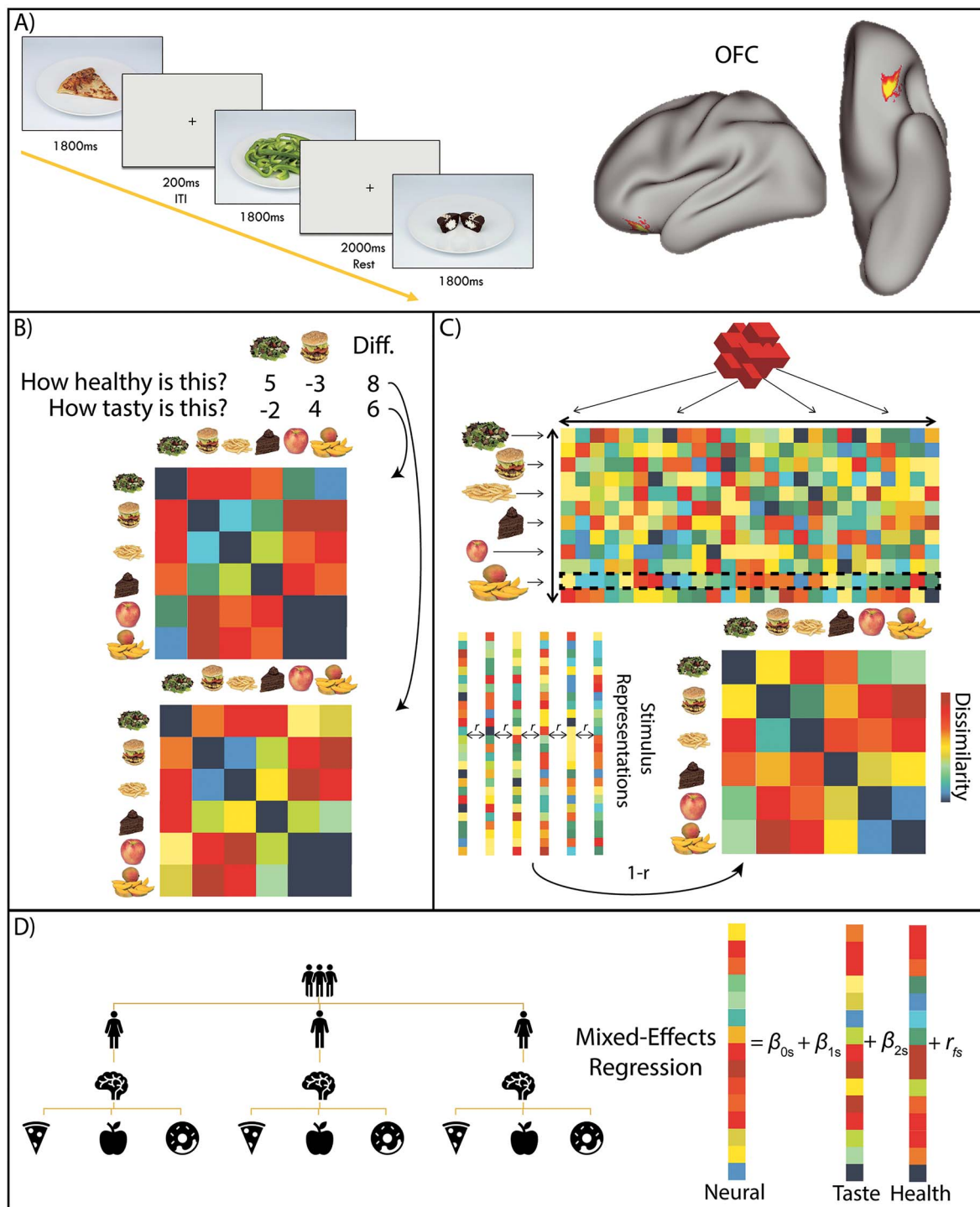


Fig. 3. Schematic depicting the localization of the left OFC cluster and the mixed effects representational similarity analysis. (A) Task consisted of food and rest trials. Univariate analysis of functional imaging data revealed a cluster located in the left OFC ($k=88$, highlighted in red) that responded to food images. This cluster was used for subsequent RSAs. (B) Participants' ratings of food category taste and health were used to generate model dissimilarity matrices. (C) A neural dissimilarity matrix was created from activity patterns in the left OFC based on each of the 28 food categories and using a correlation-based distance metric. (D) A linear mixed-effects model was used to compute the relationship between neural representational dissimilarity and model dissimilarity matrices based on taste and health ratings.

within JupyterLab (Kluyver et al., 2016) with linear mixed-effects modeling implemented in the R statistical language (R Core Team, 2016) using the lme4 package (Bates et al., 2015) and the lmerTest package (Kuznetsova, Brockhoff and Christensen, 2017). Confidence intervals for each fixed-effect parameter were

estimated using the confint function of the lme4 package. RSA was used to investigate whether the multivariate patterns of activity within the OFC encode information related to tastiness and/or health when viewing appetitive food cues. Unlike decoding-based approaches for multivariate pattern analysis,

RSA takes as input the similarity of neural responses between experimental conditions to define a neural representational space (Kriegeskorte, Mur and Bandettini, 2008) that can in turn be characterized via data-driven methods (e.g. dimensionality reduction or clustering approaches) or by comparison to similar representational spaces derived from computational models (e.g. models of visual cortical function) or participant's behavior (e.g. stimulus ratings). Thus, RSA enables one to examine whether the ensemble of neural patterns for a set of conditions is best captured by a hypothesized model of the neural dissimilarity based on, for example in the present case, a participant's own idiosyncratic ratings of tastiness and health. Here, we implemented RSA by taking, for each participant, the pattern of activity corresponding to each of the 28 food categories within the functionally defined left OFC ROI. Neural representational dissimilarity matrices (RDM) were computed by taking the Pearson correlational distance (i.e. one correlation) for each pair of food categories (a 2D projection of these neural dissimilarity matrices using metric multidimensional scaling is available in [Supplementary Figure S2](#)). Model RDMs for tastiness and health were in turn created by computing a single-value distance matrix consisting of the absolute value of the difference between tastiness or health ratings for each food item ($|\text{value } x - \text{value } y|$), yielding a per-dimension representational dissimilarity matrix (DSM) that indexes the dissimilarity between two food categories. Two additional RDMs were constructed that instead indexed the magnitude of tastiness and health for pairs of food categories by taking the sum of these dimensions for each pair. Thus, higher values in these matrices correspond to higher vs lower ratings of tastiness or health for each pair of food categories. To investigate the relationship between neural and behavioral RDMs, RSA was conducted within a linear mixed-effects modeling framework using tastiness and health RDMs as independent predictors of the left OFC neural RDM while accounting for random intercepts for participants. The formula for the linear mixed-effects model is shown below, where s represents the s -th subject and f represents the f -th food category.

$$\text{OFC}_{fs} = \gamma_{00} + \mu_{0s} + \beta_{1s} \text{Tastiness}_{fs} + \beta_{2s} \text{Health}_{fs} + r_{fs}$$

As food categories were, by design, orthogonal with respect to tastiness and health, we were able to efficiently test the ability of these two predictors to explain the neural dissimilarity structure in the left OFC. All models were estimated using restricted maximum likelihood.

V1 model (HMAX) estimation and similarity analysis

To investigate if low-level visual features of the stimuli may have contributed to differences in pattern of activity in the left OFC, a computational model of early visual cortex (i.e. HMAX; Serre, Wolf, Bileschi, Riesenhuber and Poggio, 2007; code adapted from <https://maxlab.neuro.georgetown.edu/hmax.html>) was implemented on our stimulus set. Images were reduced in size to 825×550 to reduce computational load prior to model estimation. Following the approach described by Connolly et al. (2012), the C1 units (corresponding to complex cells in V1 cortex) in the second layer of this model were extracted then flattened (across patch sizes) into a single vector per category by averaging across vectors for all five food exemplars per category. An RDM was constructed by computing the Pearson correlational distance of the average C1 vector for each pair of food categories, yielding a V1 model dissimilarity structure. In order to see if low-level visual features may account for representations of

tastiness and health in the left OFC, the V1 RDM was added as a predictor in each of the linear mixed-effects models described above.

Linguistic analysis of natural language food descriptions for foods high and low in taste and health

A separate sample of 59 participants ranked the 28 food categories used in the functional neuroimaging experiment according to tastiness and, separately, for health. Next participants were presented with the three highest and lowest ranked food categories for tastiness and again for health. If a food category appeared more than once in either of the ranked groupings, that category was omitted, thus participants provided 12 or fewer food category descriptions. Natural language descriptions for each category were typed by participants in answer to the question: 'Imagine you are talking to someone who has never eaten [food category] before, how would you describe it?'. Following this task, participants completed the same food ratings tasks as the participants in the functional neuroimaging experiment with the addition of one question assessing their familiarity with each food category (i.e. 'How familiar are you with this food?').

Verbal responses were analyzed using LIWC (Pennebaker et al., 2015), focusing on words related to eating (i.e. the ingest LIWC subset including, dish, eat, etc.). Other variables we considered were the overall adjective, adverb and total word counts. For this analysis, the average difference score for each measure across the top and bottom three ranked food categories for tastiness and health were computed for each participant and compared using a one-sample t -test against a difference of zero (i.e. no difference between top and bottom ranked food categories).

Results

Linear mixed-effects RSA of tastiness and health

To investigate whether left OFC activation patterns in response to food category presentation represented the dimensions of tastiness or health (or both), we implemented a random linear mixed-effects RSA (Figure 3). The results of this analysis showed that the left OFC simultaneously encoded both the dimensions of tastiness and health [taste: $\beta = -0.0053$, $SE = 0.002$, 95% confidence interval (CI) = $(-0.0093$ to $-0.0013)$, $P = 0.01$; health: $\beta = 0.0044$, $SE = 0.001$, 95% CI = $(0.0017$ – $0.007)$, $P = 0.002$]. As our stimulus set was designed to be orthogonal with respect to the dimensions of tastiness and health and individual participants tended to rate these dimensions orthogonally, this analysis was an efficient test of whether the left OFC encoded tastiness, health or some combination thereof.

Neural representational similarity of tastiness is more distinct with increasing tastiness

Given the direction of the effect for tastiness in left OFC, the results of the previous analysis suggested that the neural representations of food categories may grow more distinct as the similarity in tastiness between food categories increases. This suggests the possibility that categories higher in tastiness may have more distinct neural representations. However, as the tastiness RDM encodes only dissimilarity, we constructed a new model RDM based on the sum of tastiness ratings for each pair of food to more directly test this last possibility. In this way, food category pairs low in tastiness would have lower values

and food categories high in tastiness would have higher values (note that technically this is no longer a dissimilarity matrix; however, we will continue to refer to it as an RDM to be consistent with the previous analyses). In order to provide a comparison to the same metric computed for health, we calculated an RDM for health magnitude and repeated the previous representational similarity regression analysis above using these two new predictors. The results of this analysis revealed a significant relationship between the neural representation of food category in the left OFC and a model RDM that encodes tastiness magnitude [$\beta = 0.0080$, $SE = 0.001$, 95% $CI = (0.0053-0.0107)$, $P < 0.001$] but not for the model RDM encoding health magnitude [$\beta = 0.0004$, $SE = 0.001$, 95% $CI = (-0.0013-0.0021)$, $P = 0.67$].

Finally, an additional analysis was conducted testing the above two models at varying level of smoothness (i.e. 4, 6, and 8 mm Gaussian kernels) demonstrating that the above findings are relatively invariant to moderate levels of smoothing during pre-processing (Supplementary Table S4). Taken together, these findings indicate that left OFC neural patterns associated with food categories become more distinct for food pairs higher in tastiness but not for those higher in health.

Controlling for low-level visual feature similarity

Based on a computational model of complex cells in V1 cortex, we generated a model RDM encoding the dissimilarity between food categories based on the output of this V1 model. Including the V1 model RDM in the above analyses did not impact our results, nor demonstrate evidence that the left OFC encodes visual feature similarity. Specifically, when adding the V1 RDM as an additional predictor to our tastiness and health linear mixed effects (LME) model, the V1 model does not predict left OFC neural dissimilarity [$\beta = 0.0017$, $SE = 0.046$, 95% $CI = (-0.0896$ to $0.0932)$, $P = 0.97$], and both tastiness and health remain significant predictors of left OFC responses [taste: $\beta = -0.0053$, $SE = 0.002$, 95% $CI = (-0.0093$ to $-0.0013)$, $P = 0.01$; health: $\beta = 0.0044$, $SE = 0.001$, 95% $CI = (0.0016-0.0071)$, $P = 0.002$].

Linear mixed-effects RSA of tastiness and health in three clusters of the visual cortex

In order to investigate whether regions other than the left OFC encode the dimensions of tastiness or health, we analyzed three significant clusters from the visual cortex: two in early visual cortex (BA18 and BA19) and one in late visual cortex located in the fusiform gyrus (BA37). An LME regression-based RSA of these regions including tastiness, health and V1 model RDMs as predictors found that none of these visual ROIs encoded the dimensions of tastiness or health (all $P > 0.1$; Supplementary Table S5); however, neural responses in each region was predicted by the V1 model, with the early regions showing the strongest effect (left middle occipital gyrus: $\beta = 1.281$, $P < 0.001$; inferior occipital gyrus: $\beta = 0.2339$, $P < 0.001$) and the fusiform ROI demonstrating a comparatively smaller association with the V1 model ($\beta = 0.0291$, $P = 0.029$).

Linguistic analysis of natural language food descriptions

In a separate experiment, participants provided natural language descriptions for the three highest and lowest ranked food categories based on tastiness and health. For each of the 12 possible food categories (six for tastiness and six for health) participants were tasked with writing, in their own words,

how they would describe the food category to someone who was unfamiliar with it. In addition, participants also rated food categories for general familiarity. Overall, participants indicated being highly familiar with all food categories (mean familiarity = 3.36 on a scale of -5 to +5, $s.d. = 1.65$). Nevertheless, food categories ranked higher in tastiness were rated as being more familiar than those ranked lower in tastiness ($t(55) = 6.40$, $P < 0.001$). No difference in familiarity was found for the higher and lower ranked food categories for the dimension of health ($t(55) = 0.0$, $P = 1.0$).

A lexical analysis using the LIWC tool revealed that food categories ranked higher in tastiness had a greater number of ingestion related words (i.e. LIWC category ingest) than those ranked lower in tastiness ($t(55) = 2.9$, $P = 0.005$). Moreover, the difference score between high and low ranked food categories was greater for tastiness than for health ($t(55) = 4.14$, $P < 0.001$). Similar findings were found for overall word count ($t(55) = 3.37$, $P < 0.001$), number of adverbs ($t(55) = 2.035$, $P = 0.047$) and adjectives ($t(55) = 3.60$, $P = 0.001$). Although the mean difference scores for these other three lexical attributes were always in the direction of greater for tastiness than for health, they were not, however, statistically different from the same measures computed for the health dimension (all $P > 0.08$).

Discussion

Food tastiness and health are fundamental attributes of food choice and important determinants of dietary self-control failure (Hare et al., 2009, 2011; Harris et al., 2018). Animal and human neuroscience research has long highlighted a role of the OFC in representing the reward and motivational value of appetitive stimuli such as food and drugs (Rolls, 2000). In the present study, we employed an RSA in a linear mixed-effects framework to examine whether individuals spontaneously encode tastiness and health features when viewing appetitive food cues. Using a stimulus set designed to be orthogonal with respect to these two dimensions, our results show that the left OFC encodes both the dimensions of tastiness and health, even when participants were not tasked with explicitly evaluating foods along these dimensions. However, with respect to tastiness, the relationship between neural representations in this region and taste was more complex. In a follow-up representational similarity regression analysis, we demonstrate that the neural representation of food in fact grows more distinct with increasing tastiness (e.g. fries and cake vs tomatoes and rice cakes) but not with increasing health indicating that foods high in tastiness might be encoded with more refined neural representations than low taste foods. In addition, these findings were found to obtain even when accounting for low-level visual feature similarity based on a model of V1 cortex. Moreover, among the four regions we tested (the left OFC and three control regions in the visual cortex), these findings were found to be specific to the left OFC. None of the visual regions showed any evidence of encoding food taste or health. Finally, a separate behavioral experiment provided additional evidence supporting this notion by demonstrating that participants' cognitive representations of foods high in tastiness were similarly more elaborate (i.e. used more 'ingestion'-related words) than foods considered to be low in tastiness.

Over 15 years of functional neuroimaging research in humans has shown that activation of the OFC is associated with processing rewards and other motivationally relevant stimuli (e.g. food, drugs, money, social reputation). In the domain of food, the left OFC has been demonstrated to show increased activity when people view appetitive food compared with

non-food items (Kringelbach *et al.*, 2003; van der Laan *et al.*, 2011; Wagner *et al.*, 2013), is associated with the experience of pleasantness during consumption (Kringelbach *et al.*, 2003), and shows decreased activity during satiety (O'Doherty *et al.*, 2000). Activity in this region is also altered during emotional and motivational states that are thought to increase the desire for foods high in tastiness (Stice *et al.*, 2008; Wagner *et al.*, 2013) and is reduced in the presence of health information such as calorie counts (Courtney *et al.*, 2018a). In addition, research has shown that activity in this region in response to food or alcohol cues is associated with prospective weight gain (Yokum *et al.*, 2011) and frequency of drinking (Courtney *et al.*, 2018b). More recently, researchers have turned to the use of multivariate pattern analysis to better understand how patterns of activity in this region might encode different food attributes (Suzuki *et al.*, 2017) or might be altered by the attributes attended to when viewing food cues (Courtney *et al.*, 2018a). For instance, Courtney and colleagues used RSA to show that appetitive food representations in the OFC are altered by calorie information more so in dieters than non-dieters. From this result, they speculate that when presented with calorie information, dieters may switch from a default of attending to tastiness to instead attending to health, whereas non-dieters do this to a lesser extent (Courtney *et al.*, 2018b). Another study that also uses RSA, focused on the nutritive attributes of food and showed that the OFC spontaneously encodes low-level food attributes such as fat content and carbohydrates (Suzuki *et al.*, 2017). The present study expands on this work by focusing directly on the higher-level motivational attributes that have been shown to be important to behavioral models of dietary decision-making and self-control (Hare *et al.*, 2009, 2011; Harris *et al.*, 2018) and further by showing that these are automatically (or at least spontaneously) encoded by the OFC when viewing appetitive food cues.

In a follow-up analysis, we found that the neural representation of food in the left OFC (Study 1) and the descriptions people assign foods (Study 2) become more distinct with increasing tastiness, indicating that individuals have more refined representations for those foods they find the most desirable. There are several theoretical accounts that might help explain this phenomenon. Social psychological research on attitudes has shown that positive attitudes toward a category of objects (e.g. movies, music) lead to increased differentiation of items within that category (i.e. the preference-categorization effect; Smallman and Becker, 2017; Smallman *et al.*, 2014). For instance, craft beer aficionados might split hairs over the aroma and flavor differences between two different local breweries, whereas others who are less exuberant about craft beer may simply lump these into broader categories such as ales and lagers. This argues that the more distinct neural and cognitive representations that we see for food items higher in tastiness are a result of greater differentiation of items for food categories for which we have a positive attitude.

A second, more speculative account, borrows from construal-level theory (Trope and Liberman, 2003) which posits that the complexity of how we think about and categorize objects varies as a function of psychological distance. For example, research in this domain (Liberman *et al.*, 2002) shows that when individuals are more psychologically distant from an event or object, these are categorized in a broader, more general manner focusing less on the fine-grained features of the object and more on its general ones (i.e. 'bagels are a form of bread'). In contrast, when individuals are psychologically close to an event or object they represent these with more fine-grained details, focusing on

the specific sensations or individuating features of the object (i.e. 'Montreal bagels possess a true artisanal purity, with their subtle sweet taste and satisfying initial crunch followed by a softer chewier texture, they stand in stark contrast to the bread donut that is the inferior New York bagel'). From this perspective, tastiness might lead people to adopt a lower-level construal of the object that focuses on its finer-grained features at the expense of more general ones, thus leading to more distinct neural representations compared with food categories that are lower in tastiness.

A third and final account instead considers the amount of knowledge an individual might possess about a given food category. For example, familiar objects tend to also be those objects that individuals possess more knowledge of and, it stands to reason, more differentiated representations for. Recently, Thornton and colleagues used RSA to show that individuals have more distinct neural representations for their own mental states than they do for other individuals. They speculate that this may be a result of the privileged access that individuals have of their own internal states, resulting in markedly greater knowledge for one's own mental states than those of the others (Thornton *et al.*, 2019). In the case of our study, we found that, even though individuals were highly familiar with the food categories we used in this experiment, we nevertheless found that high-tastiness foods were rated to be more familiar than foods lower in tastiness. Thus, the increased distinctiveness of neural and cognitive representations of high-tastiness foods may be a result of individuals having more knowledge of this category and therefore more unique representations (Thornton *et al.*, 2019).

The reward circuitry underlying appetitive food cue reactivity has been shown to be similar across several other appetitive domains, such as tobacco (Wagner *et al.*, 2011), alcohol (Schacht *et al.*, 2013; Courtney *et al.*, 2018b), and drugs (Garavan *et al.*, 2000). Beyond these more primary forms of reward, secondary rewards have also been shown to activate similar neural circuitry. For example, social cues like smiling (Somerville *et al.*, 2011), attractive faces (Cloutier *et al.*, 2008) and recalling pleasant memories (Speer *et al.*, 2014) all activate the OFC, albeit the precise location may differ depending on domain. Given these common neural underpinnings, our approach could be adapted to these different reward domains to investigate whether the neural representations of these rewards share common psychological dimensions (e.g. fried chicken, cigarettes, and drugs of abuse are all low on healthiness). Moreover, if the finding that appetitive items that are higher in liking (i.e. tastiness in our study) have more distinct neural and cognitive representations proves to be true across domains, this may highlight an important neural mechanism that may help explain how individuals come to crave specific appetitive items and how these can turn to obsession in the case of addicted individuals.

Tastiness and health are two fundamental features of foods that guide people's dietary choices and influence their ability and motivation to engage in dietary self-regulation. Although both dimensions form the basis of many decision-making models of dietary choice and self-control (Hare *et al.*, 2009, 2011; Harris *et al.*, 2018), the dimension of tastiness may be particularly important in predicting self-control failure. For instance, when individuals attend to tastiness, their desire for tasty food items increases but the same is not true when they attend to health (Young and Fazio, 2013). In the present study, we show that the left OFC, a region implicated in food reward value representations and associated with a variety of real-world outcomes (i.e. BMI, drinking, etc.), appears to automatically represent the food health and tastiness when viewing food cues. Moreover, our

findings show that the neural and cognitive representation of foods becomes more distinct with increasing tastiness, suggesting that individuals have more elaborate representations of precisely those foods that are most likely to tempt them to engage in unhealthy eating behaviors. Together, these findings suggest that food tastiness and health are primary dimensions of food evaluations and may be computed automatically by individuals when confronting foods in their environment. A remaining question for future work is whether individual differences in motivational state or in self-regulation strategy alter the weight placed on tastiness and health when viewing food cues. Understanding how neural representations within the brain's reward system are altered by these factors may offer novel insights into how self-regulation strategies (e.g. reappraisal, response inhibition) reshape the neural representations to better enable success or to cause individuals to spiral into failure.

Supplementary material

Supplementary data are available at SCAN online.

Author Contributions

A.M.L. and D.D.W. designed the research. A.M.L. gathered all research data; A.M.L. analyzed the data under the supervision of D.D.W. A.M.L. and D.D.W. wrote the manuscript.

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Conflict of interest

None declared.

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