Research Article

Psychological Science
2014, Vol. 25(12) 2168–2176

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DOI: 10.1177/0956797614552081
pss.sagepub.com

Behavioral and Neural Valuation of Foods Is Driven by Implicit Knowledge of Caloric Content

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Abstract

The factors that affect food choices are critical to understanding obesity. In the present study, healthy participants were shown pictures of foods to determine the impact of caloric content on food choice. Brain activity was then measured while participants bid for a chance to purchase and eat one item. True caloric density, but not individual estimates of calorie content, predicted how much participants were willing to pay for each item. Caloric density also correlated with the neural response to food pictures in the ventromedial prefrontal cortex, a brain area that encodes the value of stimuli and predicts immediate consumption. That same region exhibited functional connectivity with an appetitive brain network, and this connectivity was modulated by willingness to pay. Despite the fact that participants were poor at explicitly judging caloric content, their willingness to pay and brain activity both correlated with actual caloric density. This suggests that the reward value of a familiar food is dependent on implicit knowledge of its caloric content.

Keywords

fMRI, value, food, reward, calories, willingness to pay

Received 3/5/14; Revision accepted 8/11/14

Obesity results largely from excess intake of calories, and food choices determine caloric intake. In this study, we set out to explore the impact of explicit versus implicit awareness of energy content on food choices by measuring brain responses to familiar food items as a function of the foods' estimated and true caloric density.

Children and adults prefer calorically dense foods, and consumption of these foods predicts body weight (Drewnowski, 1998). The ubiquity of low-cost, calorie-dense foods has been blamed for the recent rise in the incidence of obesity (Drewnowski & Darmon, 2005), especially in low-income groups in which constraints on food expenditure lead to increased consumption of calorically dense foods (Darmon, Ferguson, & Briend, 2003).

Food choices and consumption are largely governed by the anticipated effects of available foods (Brunstrom, 2007). These effects are likely learned through experience in a Pavlovian manner, with the sensory properties of foods acting as conditioned stimuli predictive of the rewarding effects of the contained nutrients. Similarly, the neural response to food cues, as assessed by functional neuroimaging, reflects the learned incentive value of the foods and predicts consumption (Dagher, 2012).

Here, we sought to determine how awareness of caloric content influenced neural predictors of food choice by combining an auction paradigm with functional MRI (fMRI). Prior to scanning, we asked healthy, lean individuals to rate how many calories they thought were in each of 50 familiar food items (i.e., estimated calories) presented as pictures. We then exposed participants to these food pictures while they underwent fMRI and measured their real-time valuation of each food item using the Becker-DeGroot-Marshak auction, a measure of how much a person is willing to pay for an item (*willingness to pay*; Becker, DeGroot, & Marschak, 1964). We

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then modeled brain activity as a function of willingness to pay, estimated calories, and true caloric density.

Following previous research using the Becker-DeGroot-Marshak auction, we expected to find value-related activity in the ventromedial prefrontal cortex (vmPFC) and, possibly, the nucleus accumbens. Previous work has shown that willingness to pay is reflected in neural activity in the vmPFC (Plassmann, O'Doherty, & Rangel, 2007). Brain activity in the nucleus accumbens in response to food cues has also been shown to predict subsequent consumption (Lawrence, Hinton, Parkinson, & Lawrence, 2012), which suggests that it also reflects aspects of value. A recent meta-analysis identified the vmPFC and nucleus accumbens as encoding subjective value at the time of a decision (Bartra, McGuire, & Kable, 2013). Understanding the attributes of foods that predict value, and the influence of learned attributes of food, may provide information on how food choices are made in an increasingly obesogenic food environment.

Method

We first showed 29 healthy, normal-weight individuals pictures of 50 familiar food items (20 low calorie and 30 high calorie) and asked them to rate, on a continuous scale between 1 and 20, how much they liked each item and the range of calories each item contained. Sample size was determined a priori on the basis of the effect sizes obtained in our previous fMRI study with food stimuli (Malik, McGlone, Bedrossian, & Dagher, 2008). Caloric density (calories/gram) of each food item was determined from the package label for processed foods and from an online calorie counter (http://caloriecount.about.com) for fruits and vegetables. On a separate day, we administered the Becker-DeGroot-Marshak task (Becker et al., 1964; Plassmann et al., 2007) while the same participants underwent fMRI to measure brain activity associated with the valuation of these same food items. Participants were included in the study if they had a body mass index (BMI) between 19.5 and 24.5, reported no history of neurological or psychiatric illness, did not currently use medications or drugs of abuse, and showed no evidence of disordered eating, as assessed by the Dutch Eating Behavior Questionnaire (Van Strien, Frijters, Bergers, and Defares, 1986) and the Three-Factor Eating Questionnaire (Stunkard & Messick, 1985).

On scanning day, participants were given a standard meal (either breakfast or lunch depending on the time of the scan) 3 hr prior to scanning and were not allowed to eat anything else until after the scan. These meals were chosen by a nutritionist to have moderately low glycemic indices and low protein contents to avoid elevating plasma amino acids, which can affect brain function. The breakfast included orange juice (125 ml), cheddar cheese (42 g), whole wheat toast (1 slice), white toast (1 slice), strawberry jam (15 ml), butter (10 ml), 1 cup of coffee or tea with 2% milk (20 ml), and one sachet of white sugar, for a total of 480 calories. The lunch consisted of deli-style chicken or turkey (47 g), whole wheat bread (2 slices), 3% fat yogurt (100 g), high-fiber cookies (30g), and water, for a total of 426 calories. All participants ate the meal in its entirety.

These results are part of a larger study on the effects of the hormone ghrelin on the evaluation of food and nonfood objects. Participants in the study were scanned twice (once after a saline injection and a second time after a ghrelin injection) on different days. For this report on caloric density, results from only the saline injection (placebo) are presented.

Becker-DeGroot-Marshak auction

In the Becker-DeGroot-Marshak auction, participants bid between $0 and $5 in $0.50 increments for each auction item, and they are told that one of the items will be randomly chosen for an auction at the end of the session. During this auction, the computer randomly generates a price between $0 and $5. If the participant's bid is higher than the computer's price, he or she purchases the item at the computer's (lower) price and receives the remainder of the $5 in cash. Otherwise, the participant receives the entire $5 but does not get the item. Participants are told that they will remain in a supervised setting for 30 min after the scan, during which time they will be allowed to consume the chosen item if they won it. The optimum strategy is to bid what one is willing to pay for the item (Becker et al., 1964), a fact that is emphasized to the participants. For further details on instructions, see Plassmann et al. (2007).

Items had a wide distribution of actual price ($0.21–$4.19), and prior pilot testing in a separate group ensured that they were all rated positively on a liking scale and were highly familiar to our target population of local university students. Thirty of the food items were high-calorie sweet or savory junk foods (e.g., chocolate bars and chips), and 20 were low-calorie sweet or savory foods (e.g., fruits and vegetables).

Pearson's correlations were calculated between food bids (willingness to pay) and liking ratings, estimated calories, true caloric density, and true retail value. A mixed effects regression on caloric density, estimated calories, and retail price was also used to determine which variable was contributing the most to willingness to pay using SPSS 19.0 for Mac.

Brain-imaging methods

Neuroimaging was carried out with a 3T Siemens Magnetom Trio MRI scanner. Sessions began with the acquisition of high-resolution (voxel size of 1 mm^3), T1-weighted sagittal images for anatomical localization of the functional data. This was followed by acquisition of functional data, which consisted of six 8-min runs for the measurement of blood-oxygen-level-dependent (BOLD) signals during performance of the cue paradigm described in the following paragraph (repetition time = 2,110 ms, echo time = 30 ms, flip angle = 90°, voxel size = 3.5 mm × 3.5 mm × 3.5 mm, number of slices = 40).

In each of the six runs, photographs of 25 food items and 10 nonfood trinkets (e.g., DVDs, small toys) were presented, for a total of 150 different food and 60 different trinket trials. Each item was presented for 4 s, followed by a bid period. During bidding, participants moved a marker across a scale ranging from $0 to $5 and entered their bid using an MRI-compatible button device. Following the bid, there was an interstimulus interval of 3 to 4 s. Stimuli, presented using E-Prime software (Schneider, Eschman, & Zuccolotto, 2001), were projected onto a screen that could be viewed via a mirror in the MRI scanner. Before and after each run, participants rated their hunger levels on a continuous visual analog scale from "*not at all*" to "*extremely*."

Imaging data were analyzed with Statistical Parametric Mapping (SPM) software (Version 8; Wellcome Department of Imaging Neuroscience, Institute of Neurology, London, England). Preprocessing consisted of correction for slice-acquisition timing and motion, coregistration of the anatomical and functional volumes, and spatial smoothing with an 8-mm full-width at half-maximum Gaussian filter. All data were transformed into Montreal Neurological Institute (MNI) space (Collins, Neelin, Peters, & Evans, 1994) using the ICBM152 template. We then applied a general linear model (GLM), using an autoregressive AR(1) model to account for temporal autocorrelation of fMRI data; this model used the following regressors: food-image presentation, trinket presentation, food bidding period, trinket bidding period, missed bid trial, and missed image presentation. A trial was defined as a missed image presentation and missed bid trial if no bid was entered. All events were modeled using stick functions. Six motion parameters were also included as regressors of no interest.

Next, we generated two separate GLMs with distinct parametric modulators, in order to map the regions where activity correlated with stimulus value. In GLM 1, we used the bid amount entered for each food item. In GLM 2, we used the following parametric modulators in the following order: participants' estimates of caloric content, true caloric density, and retail price. Note that the order for the parametric modulation used in GLM 2 is important, as modulators were successively orthogonalized relative to the first factor that was defined. In this case, caloric density was orthogonalized with respect to estimated calories, and retail price was orthogonalized with respect to estimated calories and caloric density. We set up the parameters in this manner so that all effects would be attributed to estimated calories first. This would ensure that any effect of true calories would not be attributable to an influence of estimated calories.

Because subjective hunger levels measured after each functional run tended to increase, a repeated measures analysis of variance (ANOVA) was used in all analyses of imaging data to control for the effect of time, using run as the repeated measure. We first applied the GLM to each of the six runs for each participant. We then entered each participant's six contrast images from this GLM into a second-level within-subject ANOVA with run as a repeated measure to combine data across participants. For results reported in this article, we used an uncorrected threshold of $p < .001$ ($t = 3.45$) and a minimum cluster size of 10 voxels.

Analysis of functional connectivity in the vmPFC

To investigate brain networks involved in evaluating caloric density of food stimuli, we carried out a psychophysiological interaction (PPI) analysis. We used two GLMs for our PPI analyses: (a) neural response when passively viewing food images and (b) neural response when passively viewing food images as modulated by willingness to pay. The seed region for the connectivity analysis was a sphere of 6 mm centered on the vmPFC peak where activity correlated with caloric density of foods as identified in the preceding analysis. Results for the PPI are presented at a threshold of $p < .001$, uncorrected, with a minimum of 10 contiguous voxels.

Results

Four data sets were excluded for excessive movement during scanning, which left 25 for the final analysis.

Behavioral results

Bid amounts (willingness to pay) correlated with true caloric density ($r = .659$, $p < .001$, two-tailed; Fig. 1a). Retail value also significantly correlated with willingness to pay ($r = .503$, $p < .001$, two-tailed). However, when retail value was controlled for, willingness to pay still correlated with caloric density ($r = .664$, $p < .001$, two-tailed). Willingness to pay did not correlate with liking rating ($p = .78$, two-tailed) or estimated calories ($p = .56$, two-tailed; Fig. 1b). Neither the true total caloric content of the food items nor their caloric density correlated with estimated calories (ps = .91 and .66, two-tailed, respectively; Fig. 1c). Caloric density did not correlate with liking rating ($p = .99$, two-tailed).

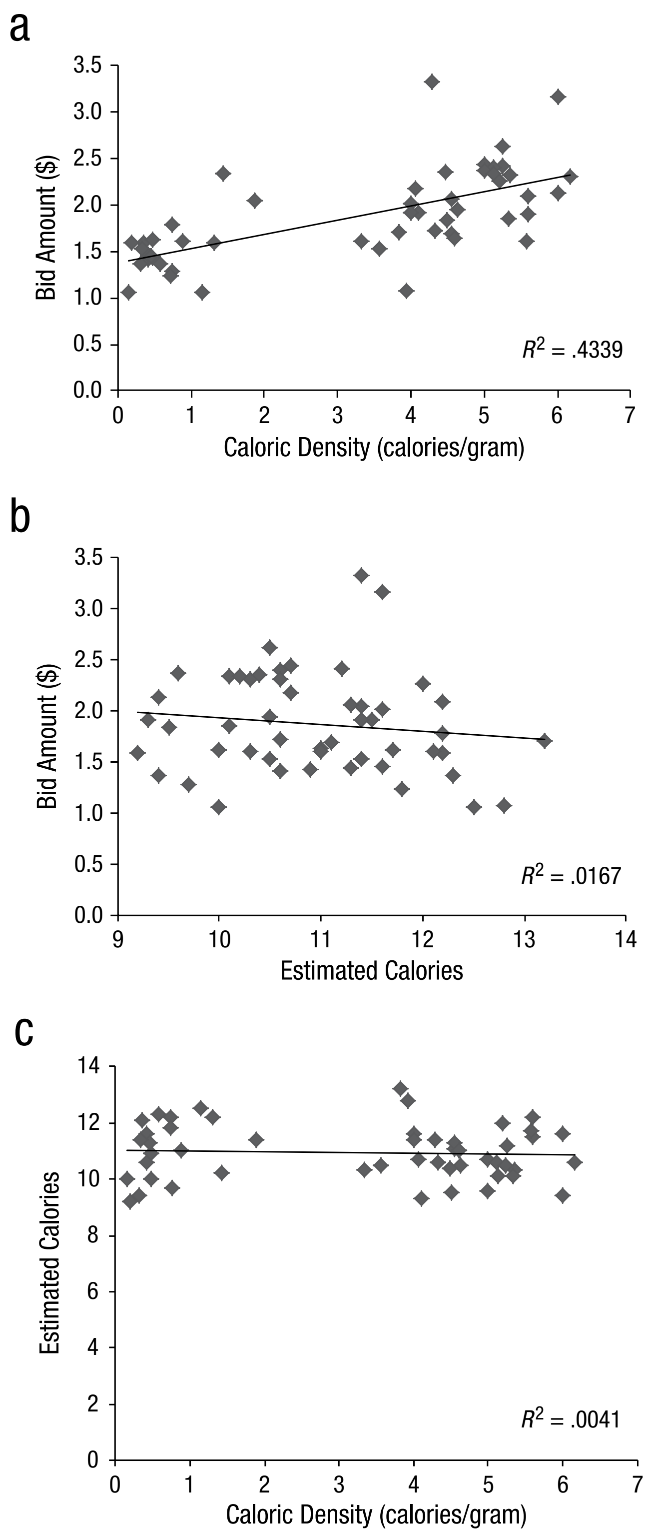

Fig. 1. Behavioral results. The scatter plots (with best-fitting regression lines) show associations between (a) bid amount and caloric density, (b) bid amount and estimated calories, and (c) estimated calories and caloric density. Each data point represents a group average for one food item used in the study.

A mixed effects regression using caloric density and estimated calories as independent variables, willingness to pay as the dependent variable, and retail price as a covariate showed that only caloric density trended toward a significant contribution to willingness to pay (p = .057).

Brain-imaging results

BOLD signals during the viewing of food images significantly correlated with caloric density in the vmPFC at MNI coordinates x = 3, y = 45, and z = −1 (Fig. 2, Table 1), as well as in the anterior cingulate cortex (ACC), striatum, and visual areas. BOLD signals correlated with bid amount (willingness to pay) in a slightly different vmPFC peak, as well as in the nucleus accumbens, ventral tegmental area and substantia nigra, orbitofrontal cortex (OFC), dorsomedial thalamus, anterior insula, ventrolateral prefrontal cortex, ACC, posterior cingulate cortex, posterior parietal cortex, pulvinar, and precuneus (Figs. 2 and 3, Table 2).

BOLD signals did not correlate with estimated calories in any part of the vmPFC. They did, however, correlate with estimated calories in primary and extrastriate visual areas: left lingual gyrus (x = −13, y = −91, z = −7; t = 7.62) and right occipital gyrus (x = 29, y = −90, z = −7; t = 4.58). BOLD signals did not correlate with retail price in any reward-related brain regions, but they did so in the left (x = −23, y = −94, z = −5; t value = 4.26) and right (x = 29, y = −87, z = −5; t = 4.22) occipital lobes.

Functional connectivity of the vmPFC

To better understand the networks involved in evaluating caloric density, we used a PPI analysis to explore connectivity of the vmPFC peak where BOLD signals were correlated with caloric density (x = 3, y = 45, z = −1). During the viewing of food images, the vmPFC was functionally connected to the anterior and mid insula (Fig. 4a; Table 3), which correspond to the primary taste and ingestive cortex. When this same brain activity was modulated by bid amount (i.e., willingness to pay), functional connectivity was found in the amygdala, hippocampus, and ventral striatum (Fig. 4b; Table 4), which means that functional connectivity between vmPFC and these areas was modulated by bid amount.

Discussion

In the present study, the true caloric density of familiar foods predicted neural value signals, whereas the estimated number of calories explicitly reported by participants did not. Caloric density of food items was also significantly correlated with subjective value, as measured

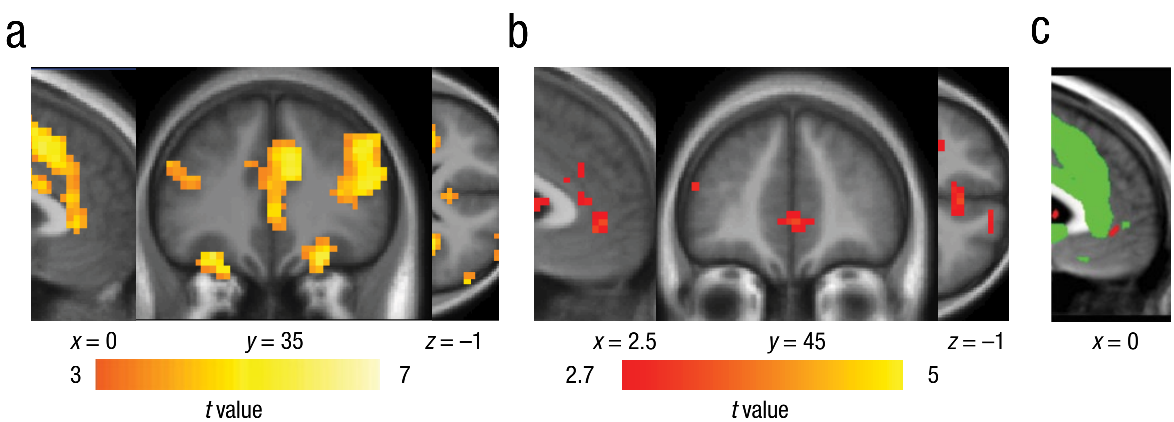

Fig. 2. Brain regions showing a blood-oxygen-level-dependent (BOLD) response to food cues. The images in (a) show regions where BOLD response correlated with food bids, and the images in (b) show regions where BOLD response correlated with caloric density. The image in (c) shows areas where the t values for the correlations between BOLD signal and bid amount (green) and between BOLD signal and caloric density (red) were greater than 3.

by the amount participants bid on those items (an index of willingness to pay; $p < .05$), whereas estimated calories were not. Notably, estimated calories also did not correlate with true caloric density or total calories of the food items. Despite participants being unable to accurately report the caloric content of the food items, their bids reflected the true caloric density of these familiar foods.

Consistent with the behavioral results, the brain response to food cues correlated with caloric density in the key brain region involved in computation of subjective value: the vmPFC. This finding is consistent with previous research showing that normal-weight individuals have greater BOLD responses to high- versus low-calorie food pictures in the vmPFC (Killgore & Yurgelun-Todd, 2006). In contrast, estimated calories did not correlate with brain response to food cues in the vmPFC.

We found that, consistent with prior work, when participants were evaluating the food items, BOLD responses in the vmPFC correlated with willingness to pay (Plassmann et al., 2007). Brain activity also correlated with willingness to pay in other regions previously associated with decision making and value (Tang, Fellows, Small, & Dagher, 2012), including the OFC (Padoa-Schioppa & Assad, 2006; Wallis, 2007), striatum (Schultz, 2005), and ACC (Kennerley, Walton, Behrens, Buckley, & Rushworth, 2006). Other research has shown that damage affecting the vmPFC and OFC disrupts value-maximizing choices of food stimuli, which further supports a role for these regions in value-based decisions (Camille, Griffiths, Vo, Fellows, & Kable, 2011; Henri-Bhargava, Simioni, & Fellows, 2012). Liking ratings, on the other hand, were primarily correlated with activity in the insula (see the Supplemental Material available online), which has been previously associated with processing the sensory properties of food (de Araujo, Geha, & Small, 2012; Scott & Plata-Salaman, 1999). Our findings are also consistent with prior work showing that after a few exposures to fruit-flavored solutions, activity in the insula correlated with liking ratings but not caloric content, whereas activity in the nucleus accumbens correlated with the caloric

Table 1. Brain Regions Where Activation During Viewing of Food Cues Correlated With the Caloric Density of the Foods Depicted

Brain region	Side	MNI coordinates of peak voxel x	y	z	t value
Ventromedial prefrontal cortex	—	3	45	−1	4.01
Anterior cingulate cortex	—	−8	32	13	4.94
Caudate	Left	−15	−18	27	4.71
Fusiform gyrus	Right	30	−35	−22	4.77
Fusiform and lingual gyrus, occipital lobe	Right	38	−88	−12	6.68
Fusiform and lingual gyrus, occipital lobe	Left	−22	−94	−12	12.22

Note: The table presents results only for those brain regions with a minimum cluster size of 10 voxels, $p < .0005$, uncorrected. MNI = Montreal Neurological Institute.

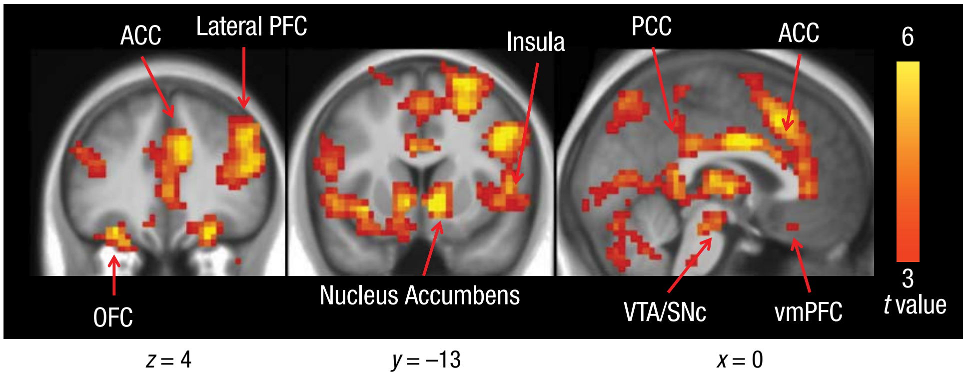

Fig. 3. Blood-oxygen-level-dependent signals in response to the correlation between food cues and bid amount (willingness to pay) in the bilateral orbitofrontal cortex (OFC), lateral prefrontal cortex (PFC), bilateral nucleus accumbens, insula, anterior cingulate cortex (ACC), posterior cingulate cortex (PCC), ventral tegmental area/substantia nigra pars compacta (VTA/SNc), and ventrolateral prefrontal cortex (vmPFC). Montreal Neurological Institute coordinates are shown.

content of the solutions, as indexed by plasma glucose (de Araujo, Lin, Veldhuizen, & Small, 2013).

The vmPFC region in which activation was most strongly related to caloric density was functionally connected during food-item viewing to the middle and anterior insula, a region referred to as the ingestive cortex (Scott & Plata-Salaman, 1999) because it responds to taste information as well as to the sensory and incentive properties of

Table 2. Brain Regions Where Activation During Viewing of Food Cues Correlated With the Amount Participants Bid for the Foods Depicted

		MNI coordinates of peak voxel			
Brain region	Side	*x*	*y*	*z*	*t* value
Ventrolateral prefrontal cortex (BA 10)	Left	–36	42	6	4.32
Ventrolateral prefrontal cortex (BA 10)	Right	44	42	13	6.10
Ventromedial prefrontal cortex	—	3	35	3	4.84
Orbitofrontal cortex	Left	–29	35	–18	5.89
Orbitofrontal cortex	Right	24	32	–22	6.08
Anterior insula	Right	34	21	2	6.24
Anterior insula	Left	–36	21	–1	5.24
Nucleus accumbens	Left	10	14	–5	7.76
Nucleus accumbens	Right	–8	11	–5	5.86
Anterior insula	Left	–32	10	–8	5.81
Anterior insula	Right	52	11	3	5.12
Inferior-middle frontal gyrus	Right	48	10	34	7.11
Postcentral gyrus (BA 6)	Left	–43	0	27	5.15
Middle frontal gyrus (BA 6)	Left	–29	0	58	4.50
Caudal anterior cingulate cortex/posterior cingulate cortex	—	–1	–4	30	7.16
Dorsomedial thalamus	—	2	–15	6	5.53
Ventral tegmental area/substantia nigra compacta	—	–8	–25	–15	5.31
Inferior parietal lobule (BA 40)	Left	–54	–32	44	6.72
Inferior parietal lobule (BA 40)	Right	52	–32	48	5.72
Pulvinar	Right	13	–35	2	7.85
Pulvinar	Left	–12	–39	6	5.91
Precuneus	Left	–15	–63	30	4.21
Precuneus	Right	17	–63	31	6.30
Cerebellum	Right	27	–66	–46	4.66
Cerebellum	Left	–22	–70	–46	6.90
Superior parietal lobule (BA 7)	Right	16	–74	58	6.90

Note: The table presents results only for those brain regions with a minimum cluster size of 10 voxels, $p < .0005$, uncorrected. BA = Brodmann's area, MNI = Montreal Neurological Institute.

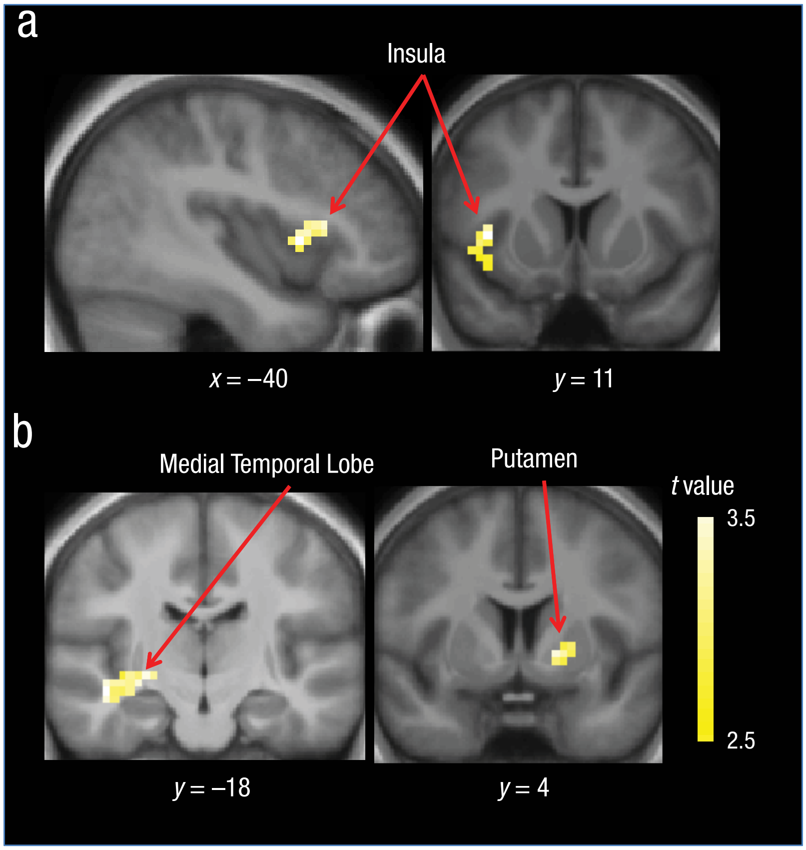

Fig. 4. Brain regions that showed functional connectivity with the ventromedial prefrontal cortex during evaluation of food cues. The images are from a psychophysiological interaction analysis evaluating participants' neural responses (a) when passively viewing food images and (b) when passively viewing food images as modulated by willingness to pay. Montreal Neurological Institute coordinates are shown.

food stimuli (de Araujo et al., 2012). This finding is consistent with the theory that the vmPFC draws on sensory information to establish value, integrating responses from brain regions that represent relevant attributes of the stimuli. Lim, O'Doherty, and Rangel (2013), using a valuation task of faces and money, found functional connectivity of the vmPFC and the fusiform gyrus (a region associated with processing visual features) during evaluation of visual esthetics, and they also uncovered connections to the posterior temporal gyrus (a region associated with semantic meaning) when participants evaluated semantic attributes. A different study found functional connectivity among striatal regions, the vmPFC, and primary auditory cortices when participants were estimating the subjective value of music (Salimpoor et al., 2013).

Table 3. Results of the Psychophysiological Interaction Analyses: Brain Regions Where Activation During Viewing of Food Cues Correlated With Activation in the Ventromedial Prefrontal Cortex Seed Region

		MNI coordinates of peak voxel			
Brain region	Side	*x*	*y*	*z*	*t* value
Anterior insula	Left	−40	11	3	3.66
Mid insula	Left	−40	−24	−1	3.71

Note: The table presents results only for those brain regions with a minimum cluster size of 10 voxels, $p < .001$, uncorrected. MNI = Montreal Neurological Institute.

When we shifted our analysis to the neural correlates of willingness to pay per se (i.e., value), functional connectivity to the vmPFC now involved the amygdala, hippocampus, and ventral striatum, all regions that are part of the mesolimbic pathway, but not the insula. One interpretation of this finding is that the insula is involved in recalling the sensory characteristics of the food item, irrespective of current subjective value, but that the vmPFC and mesolimbic regions are implicated in the computation of current subjective value.

Despite the fact that participants were poor at explicitly judging the caloric content of familiar food items,

Table 4. Results of the Psychophysiological Interaction Analyses: Brain Regions Where Functional Connectivity (Correlation) With the Ventromedial Prefrontal Cortex Seed Region Was Modulated by Willingness to Pay

		MNI coordinates of peak voxel			
Brain region	Side	*x*	*y*	*z*	*t* value
Ventral striatum (putamen)	Right	16	4	–1	3.60
Putamen	Left	–22	0	13	3.24
Caudate	Right	10	0	10	3.66
Precentral gyrus	Left	–26	–14	34	3.83
Medial temporal lobe (hippocampus/amygdala)	Left	–43	–18	–12	3.81
Medial temporal lobe (hippocampus/amygdala)	Left	–26	–18	–4	3.62
Midbrain (ventral tegmental area)	—	–4	–24	–22	3.31

Note: The table presents results only for those brain regions with a minimum cluster size of 10 voxels, $p < .001$, uncorrected. MNI = Montreal Neurological Institute.

caloric density of the foods was a determinant of willingness to pay and brain activity. This suggests that the reward value of a food is dependent on its nutritional constituents, notably on its caloric content, acquired through experience. One study showed that human visual-evoked potentials detected very rapidly after exposure to food images (165 ms) correlated with the caloric content of the foods, which suggests the occurrence of implicit processing of energy density (Toepel, Knebel, Hudry, le Coutre, & Murray, 2009). Previous animal evidence also suggests that fuel oxidation in the brain following food ingestion activates dopamine neurons (Ren et al., 2010). This dopaminergic signal may condition individuals, in a Pavlovian sense, to the caloric content of foods. Indeed, in rodents, conditioning to the caloric content of foods depends on dopamine signaling in the amygdala and ventral striatum (Touzani, Bodnar, & Sclafani, 2010), areas that demonstrated value-dependent functional connectivity with the calorie-sensitive vmPFC peak in our study.

Our finding that perceived calories have no impact on food valuation may appear to conflict with previous work showing that people eat less when they think calories are higher (Provencher, Polivy, & Herman, 2009). However, in that study, participants were explicitly told the "caloric content" of the food items, whereas our study explored the implicit knowledge of true caloric density.

Finally, while caloric density is usually thought to promote satiety, another possibility is that calorically dense foods act as cues to overconsumption. Here, we found that the caloric density of foods was tracked by the vmPFC and striatum, two areas where response to food cues predicts subsequent consumption (Lawrence et al., 2012). The work presented here is a first step in understanding the attribution of value to food by brain circuits that control motivated choice.

Author Contributions

D. W. Tang and A. Dagher designed the study and analyzed the data. D. W. Tang, L. K. Fellows, and A. Dagher contributed to writing the manuscript.

Acknowledgments

We thank Kevin Larcher and Marie Thomas for help with data analysis, Jung Eun (Claire) Han for help gathering the data, and Todd Hare for providing analysis scripts. We especially thank Antonio Rangel for generous guidance and inspiration throughout all phases of this experiment.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

Funding

This work was funded by the Canadian Institutes of Health Research.

Supplemental Material

Additional supporting information can be found at http://pss.sagepub.com/content/by/supplemental-data

References

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.

Becker, G. M., DeGroot, M. H., & Marschak, J. (1964). Measuring utility by a single-response sequential method. *Behavioral Sciences*, *9*, 226–232.

Brunstrom, J. M. (2007). Associative learning and the control of human dietary behavior. *Appetite*, *49*, 268–271.

Camille, N., Griffiths, C. A., Vo, K., Fellows, L. K., & Kable, J. W. (2011). Ventromedial frontal lobe damage disrupts value maximization in humans. *The Journal of Neuroscience*, *31*, 7527–7532.

Collins, D. L., Neelin, P., Peters, T. M., & Evans, A. C. (1994). Automatic 3D intersubject registration of MR volumetric data in standardized Talairach space. *Journal of Computer Assisted Tomography*, *18*, 192–205.

Dagher, A. (2012). Functional brain imaging of appetite. *Trends in Endocrinology & Metabolism*, *23*, 250–260.

Darmon, N., Ferguson, E., & Briend, A. (2003). Do economic constraints encourage the selection of energy dense diets? *Appetite*, *41*, 315–322.

de Araujo, I. E., Geha, P., & Small, D. M. (2012). Orosensory and homeostatic functions of the insular taste cortex. *Chemosensory Perception*, *5*, 64–79.

de Araujo, I. E., Lin, T., Veldhuizen, M. G., & Small, D. M. (2013). Metabolic regulation of brain response to food cues. *Current Biology*, *23*, 878–883.

Drewnowski, A. (1998). Energy density, palatability, and satiety: Implications for weight control. *Nutrition Reviews*, *56*, 347–353.

Drewnowski, A., & Darmon, N. (2005). Food choices and diet costs: An economic analysis. *The Journal of Nutrition*, *135*, 900–904.

Henri-Bhargava, A., Simioni, A., & Fellows, L. K. (2012). Ventromedial frontal lobe damage disrupts the accuracy, but not the speed, of value-based preference judgments. *Neuropsychologia*, *50*, 1536–1542.

Kennerley, S. W., Walton, M. E., Behrens, T. E., Buckley, M. J., & Rushworth, M. F. (2006). Optimal decision making and the anterior cingulate cortex. *Nature Neuroscience*, *9*, 940–947.

Killgore, W. D., & Yurgelun-Todd, D. A. (2006). Affect modulates appetite-related brain activity to images of food. *International Journal of Eating Disorders*, *39*, 357–363.

Lawrence, N. S., Hinton, E. C., Parkinson, J. A., & Lawrence, A. D. (2012). Nucleus accumbens response to food cues predicts subsequent snack consumption in women and increased body mass index in those with reduced self-control. *NeuroImage*, *63*, 415–422.

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. *The Journal of Neuroscience*, *33*, 8729–8741.

Malik, S., McGlone, F., Bedrossian, D., & Dagher, A. (2008). Ghrelin modulates brain activity in areas that control appetitive behavior. *Cell Metabolism*, *7*, 400–409.

Padoa-Schioppa, C., & Assad, J. A. (2006). Neurons in the orbitofrontal cortex encode economic value. *Nature*, *441*, 223–226.

Plassmann, H., O'Doherty, J., & Rangel, A. (2007). Orbitofrontal cortex encodes willingness to pay in everyday economic transactions. *The Journal of Neuroscience*, *27*, 9984–9988. doi:10.1523/jneurosci.2131-07.2007

Provencher, V., Polivy, J., & Herman, C. P. (2009). Perceived healthiness of food: If it's healthy, you can eat more! *Appetite*, *52*, 340–344.

Ren, X., Ferreira, J. G., Zhou, L., Shammah-Lagnado, S. J., Yeckel, C. W., & de Araujo, I. E. (2010). Nutrient selection in the absence of taste receptor signaling. *The Journal of Neuroscience*, *30*, 8012–8023.

Salimpoor, V. N., van den Bosch, I., Kovacevic, N., McIntosh, A. R., Dagher, A., & Zatorre, R. J. (2013). Interactions between the nucleus accumbens and auditory cortices predict music reward value. *Science*, *340*, 216–219.

Schneider, W., Eschman, A., & Zuccolotto, A. (2001). *E-Prime user's guide*. Pittsburgh, PA: Psychology Software Tools.

Schultz, W. (2005). Behavioral theories and the neurophysiology of reward. *Annual Review of Psychology*, *57*, 87–115.

Scott, T. R., & Plata-Salaman, C. R. (1999). Taste in the monkey cortex. *Physiology & Behavior*, *67*, 489–511.

Stunkard, A. J., & Messick, S. (1985). The Three-Factor Eating Questionnaire to measure dietary restraint, disinhibition and hunger. *Journal of Psychosomatic Research*, *29*, 71–83.

Tang, D. W., Fellows, L. K., Small, D. M., & Dagher, A. (2012). Food and drug cues activate similar brain regions: A meta-analysis of functional MRI studies. *Physiology & Behavior*, *106*, 317–324.

Toepel, U., Knebel, J.-F., Hudry, J., le Coutre, J., & Murray, M. M. (2009). The brain tracks the energetic value in food images. *NeuroImage*, *44*, 967–974.

Touzani, K., Bodnar, R. J., & Sclafani, A. (2010). Neuropharmacology of learned flavor preferences. *Pharmacology Biochemistry & Behavior*, *97*, 55–62.

Van Strien, T., Frijters, J. E. R., Bergers, G. P. A., & Defares, P. B. (1986). The Dutch Eating Behavior Questionnaire (DEBQ) for assessment of restrained, emotional and external eating behavior. *International Journal of Eating Disorders*, *5*, 295–315.

Wallis, J. D. (2007). Orbitofrontal cortex and its contribution to decision-making. *Annual Review of Neuroscience*, *30*, 31–56.