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Taste at first (person) sight: Visual perspective modulates brain activity implicitly associated with viewing unhealthy but not healthy foods

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Title: Taste at first (person) sight: Visual perspective modulates brain activity implicitly associated with viewing unhealthy but not healthy foods

Abstract

Every day, people are exposed to images of appetizing foods that can lead to high-calorie intake and contribute to overweight and obesity. Research has documented that manipulating the visual perspective from which eating is viewed helps resist temptation by altering the appraisal of unhealthy foods. However, the neural basis of this effect has not yet been examined using neuroimaging methods. Moreover, it is not known whether the benefits of this strategy can be observed when people, especially overweight, are not explicitly asked to imagine themselves eating. Last, it remains to be investigated if visual perspective could be used to promote healthy foods. The present work manipulated camera angles and tested whether visual perspective modulates activity in brain regions associated with taste and reward processing while participants watch videos featuring a hand grasping (unhealthy or healthy) foods from a plate during functional magnetic resonance imaging (fMRI). The plate was filmed from the perspective of the participant (first-person perspective; 1PP), or from a frontal view as if watching someone else eating (third-person perspective; 3PP). Our findings reveal that merely viewing unhealthy food cues from a 1PP (vs. 3PP) increases activity in brain regions that underlie representations of rewarding (appetitive) experiences (amygdala) and food intake (superior parietal gyrus). Additionally, our results show that ventral striatal activity is positively correlated with body mass index (BMI) during exposure to unhealthy foods from a 1PP (vs. 3PP). These findings suggest that unhealthy foods should be promoted through third-person (video) images to weaken the reward associated with their simulated consumption, especially amongst overweight people. It appears however that, as such, manipulating visual perspective fails to enhance the perception of healthy foods. Their promotion thus requires complementary solutions.

Keywords: Embodied cognition; functional Magnetic Resonance Imaging (fMRI); Taste and reward processing; Visual food cues; Visual perspective.

Introduction

Since 1980, worldwide obesity has at least doubled, totaling today more than 1.9 billion overweight adults, and of these, over 600 million obese (World Health Organization, 2017). We are currently facing an obesity epidemic that takes place in an environment that promotes excessive food intake (Hill & Peters, 1998) and where the exposure to images (or ads) of foods high in fat has dramatically increased ('gastroporn' or 'food porn') (Petit, Cheok, & Oullier, 2016b; Spence, Okajima, Cheok, Petit, & Michel, 2016).

Research showed that merely reading (tempting) food words or perceiving food images can lead people to simulate the experience of eating, including how rewarding it would be to consume food (Barrós-Loscertales et al., 2012; Papies, 2013; Simmons, Martin, & Barsalou, 2005). In this vein, a growing body of literature drawing from neuroimaging studies reports that viewing food pictures enhances brain activity in the ventral pathway of the 'core eating network' that underlies taste and reward processing and can potentially motivate food consumption (Chen, Papies, & Barsalou, 2016; García-García et al., 2013; Huerta, Sarkar, Duong, Laird, & Fox, 2014; Van der Laan, De Ridder, Viergever, & Smeets, 2011).

Along the same line of argument, when compared to healthy (low-calorie) foods, pictures of unhealthy (high-calorie) foods lead to heightened attention and reward responses (Frank et al., 2010; Killgore et al., 2003; Schur et al., 2009; Van der Laan et al., 2011). Unhealthy food is thus more tempting than healthy food (Papies & Barsalou, 2015), and choosing healthy over unhealthy food is a matter of self-regulation (Hare, Camerer, & Rangel, 2009), especially amongst overweight participants living in an obesogenic environment (Petit et al., 2016c).

Furthermore, it appears that body mass index (BMI) tends to be positively correlated with individuals' perceived ability to form vivid mental images of foods (Patel, Aschenbrenner, Shamah, & Small, 2015) and with enhanced neural activity in the ventral reward pathway when people are presented with food pictures (Chen et al., 2016; Rothemund et al., 2007; Stice, Yokum, Bohon, Marti, & Smolen, 2010; Stoeckel et al., 2008). This might help explain why higher-BMI people are more likely to yield to temptation and to engage in appetitive behavior (Giuliani, Mann, Tomiyama, & Berkman, 2014), which reinforces the vicious circle of an obesogenic environment.

Evidence nevertheless suggests that visual perspective could help resist unhealthy food temptation and regulate food intake (Christian, Miles, Kenyeri, Mattscheck, & Macrae, 2016). There are two main types of visual perspective: the first-person perspective (1PP) and the third-person perspective (3PP). In 3PP, individuals experience events through the eyes of

others, as observers, whereas a 1PP encourages them to experience events through their own eyes, as actors (Jones & Nisbett, 1987). Remarkably, first- and third-person perspectives highlight different properties of an imaginary experience (Christian, Parkinson, Macrae, Miles, & Wheatley, 2015; Gallese, 2005; Lorey et al., 2009; Ruby & Decety, 2001). The 3PP imagery represents actions (e.g., eating a peach) on a more abstract level (e.g., getting nutrition) than the 1PP (Libby, Shaeffer, & Eibach, 2009), which is associated with the recollection of concrete details of embodied and situated experiences (Libby & Eibach, 2011). When asked to *imagine* eating unhealthy foods from a 1PP (vs. 3PP), participants report heightened sensory representations of taste, smell and touch. The 3PP (vs. 1PP) is then presented as a strategy to weaken the simulation of the reward associated with the consumption of a tempting unhealthy food item (Christian et al., 2016).

This latter finding suggests that visual perspective could be an appropriate strategy to reduce taste representations and feelings of reward that lead to unhealthy food intake. However, neuroimaging studies are needed to examine the neural basis of this effect (Christian et al. 2016). Moreover, as in most studies manipulating visual perspective, participants were explicitly asked to *imagine* themselves eating from either a 1PP or 3PP (Libby & Eibach, 2011), which is acknowledged as being different from their common experience (Christian et al., 2016). Last, two questions remain open. The first question is whether this strategy could benefit overweight people, a population of key interest in relation to obesity prevention efforts. The second one is whether a 1PP could promote healthy foods. Thus, the aim of the present work is to assess whether visual perspective modulates brain activity underlying taste and reward processing implicitly associated with viewing unhealthy and healthy foods, and which is correlated with BMI.

To investigate this effect at the neural level, participants watched videos featuring a hand grasping unhealthy or healthy food (vs. non-food) items from a plate, while they were completing an implicit task in a functional magnetic resonance imaging (fMRI) study. We manipulated visual perspective by means of camera angles (Jackson, Meltzoff, & Decety, 2006; Libby et al., 2009). The plate was filmed from the perspective of the participant (actor; 1PP) or from a frontal view as if watching someone else eating (observer; 3PP), which should increase activity in motor-related areas (postcentral and superior parietal gyri) contra- and ipsi-lateral to the observed grasping hand (Shmuelof & Zohary, 2005; Vingerhoets, 2014; Vingerhoets et al., 2012)

We selected the anterior insula (AI) / lateral orbitofrontal cortex (lOFC), the amygdala and the ventral striatum (VS) as the main regions of interest (ROIs) identified in the literature to

be responsive to food pictures and whose activity correlates with BMI in the ventral reward pathway of the core eating network (Chen et al., 2016; Huerta et al., 2014; Van der Laan et al., 2011). Together, the AI and the IOFC constitute the primary and the secondary gustatory cortices (Kringelbach, 2005; Small, 2010; Veldhuizen et al., 2011). They are the most concurrent brain regions that are activated in response to viewing food (vs. non-food) images (Huerta et al., 2014; Van der Laan et al., 2011) and support taste representations (O'Doherty, Rolls, Francis, Bowtell, & McGlone, 2001; Simmons et al., 2005). The amygdala is also responsive to visual food (vs. non-food) cues (Davids et al., 2010; Killgore et al., 2003; LaBar, Gitelman, Parrish, et al., 2001; Schienle, Schäfer, Hermann, & Vaitl, 2009; Schur et al., 2009; Van der Laan et al., 2011). In the context of eating, the amygdala is a motivation- and attention-related region that responds to the intensity of gustatory stimuli (Chen et al., 2016; Haber & Knutson, 2009; Small et al., 2003; Zald, 2003). The VS, which receives information from the AI and the amygdala, is a key region for the processing of sensory and motivational information (Haber, 2011). Involved in food reward processing (Chen et al., 2016; Kringelbach, 2005), the VS contributes to expressing the greater value associated with viewing appetizing foods (Beaver et al., 2006; Goldstone et al., 2009; Passamonti et al., 2009; Van der Laan et al., 2011). Furthermore, research finds that activity in the AI/IOFC and the VS correlates with BMI during exposure to pictures of appetizing foods (Rothmund et al., 2007; Stice et al., 2010). Similarly, viewing images of high-calorie foods produces significantly higher activations in the insula, IOFC, amygdala and VS for obese participants (Stoeckel et al., 2008).

In addition to activations in motor-related areas, we thus tested whether activity within the AI/IOFC, the amygdala and the VS would be increased and positively correlated with BMI when viewing unhealthy foods from 1PP (vs. 3PP). We also tested whether these hypotheses would extend to viewing healthy foods. Last, we tested whether the visual perspective could modulate activity in these ROIs when viewing unhealthy foods is compared with viewing healthy foods.

In the context of the current obesity epidemic, this study therefore contributes to research exploring how visual perspective could be a useful tool for policy-makers looking to regulate unhealthy food intake and consumption in everyday life (Christian et al., 2016) and might help develop recommendations about health interventions to promote the attractiveness of healthy foods to overweight participants (Petit et al., 2016a).

Material and Methods

Ethics statement. All participants underwent a mandatory medical screening to check for their compatibility with the MRI environment. They gave their written informed consent prior to participating in the neuroimaging exam. The experimental procedure received the approval of local (Aix-Marseille Université Ethics Committee, France; Department of Psychological and Behavioural Science Ethics Committee, London School of Economics, UK), regional (Comité de Protection des Personnes Sud Méditerranée 1, France) and national ethics and regulatory agencies (Agence Nationale de Sécurité du Médicament et des Produits de Santé (ANSM), France).

Participants and procedure. Twenty-one participants, who were instructed not to eat food for at least 4h prior to the imaging session (Basso et al., 2014; Petit et al., 2016c), took part in the experiment conducted at the Marseille Functional MRI Center (La Timone Hospital, France). They received 50€ compensation for their time. One male participant was excluded from analysis because he completed the fMRI task with his left hand, resulting in a total of 20 native French participants (Female=11; Male=9; $M_{Age}=25.50$, $SD=4.86$; $M_{BMI}=23.81$, $SD=3.06$; right handed; normal or corrected-to-normal vision; with no significant history of medical, psychiatric or neurological illness) (see Supplementary material for further details).

Stimuli selection. We selected 12 healthy (e.g., cherry tomato, white grape, banana) and 12 unhealthy (e.g., pizza, brownie, cookie), sweet and salty food items that match in terms of grasping affordances (Cheng, Meltzoff, & Decety, 2007). We ensured that these stimuli were rated similarly in terms of tastiness but differed with regard to healthiness. We also controlled calories per serving and per plate, so that unhealthy food servings and plates were on average at least three times more caloric than healthy food (see Supplementary material – Table A1 for further details).

Task and fMRI block design. A functional session consisted of one functional run as localizer run and three subsequent experimental runs designed to test our hypotheses.

In the localizer run, participants were instructed to look at 144 static pictures of (non-grasped) unhealthy and healthy food items (or non-food items: stationary objects) taken from a lateral perspective, perpendicular to the 1PP and the 3PP. In the experimental runs, participants watched 216 videos featuring a hand grasping food and non-food items from a plate filmed from the 1PP and 3PP. To keep their attention focused, the participants were instructed to

complete a visual discrimination task. They had to indicate on a button-press response device which geometrical shape was appearing 1,000ms into each trial of 2,000ms length. Shapes were a circle, a rectangle, or a triangle (Figure 1; see also Supplementary material for the description of stimuli preparation). In line with the literature on visual food perception, this task involved implicit processing since participants were not explicitly asked to imagine (or even evaluate) the taste of each food item (Basso et al., 2014; Frank et al., 2010; Simmons et al., 2005) and since no identification of the stimulus as food or non-food was needed (Pohl, Tempelmann, & Noesselt, 2017).

The localizer run included four orthogonal conditions: healthy foods (HF), unhealthy foods (UF), non-food objects (O) and empty plate (EP). Experimental runs included six orthogonal conditions: non-food objects (O1PP), healthy (HF1PP), and unhealthy foods (UF1PP) from a 1PP; non-food objects (O3PP), healthy (HF3PP), and unhealthy foods (UF3PP) from a 3PP (Figure 2). Each condition was composed of six blocks separated by a 2,000ms [1,800 to 2,870ms] jittered inter-block interval (IBI), during which a black screen with a gray fixation cross was presented. Each block included six stimuli from the same condition separated by a 400ms inter-stimulus interval (ISI), during which a black screen with a gray fixation cross was displayed. In each run, each item from each category was presented three times, each time associated with a different geometrical shape (triangle, rectangle or circle). In any given block, the same (food or non-food) item was never presented more than once. All geometric shapes were presented at least once. A given geometric shape was never presented more than three times, and was never consecutively repeated more than once.

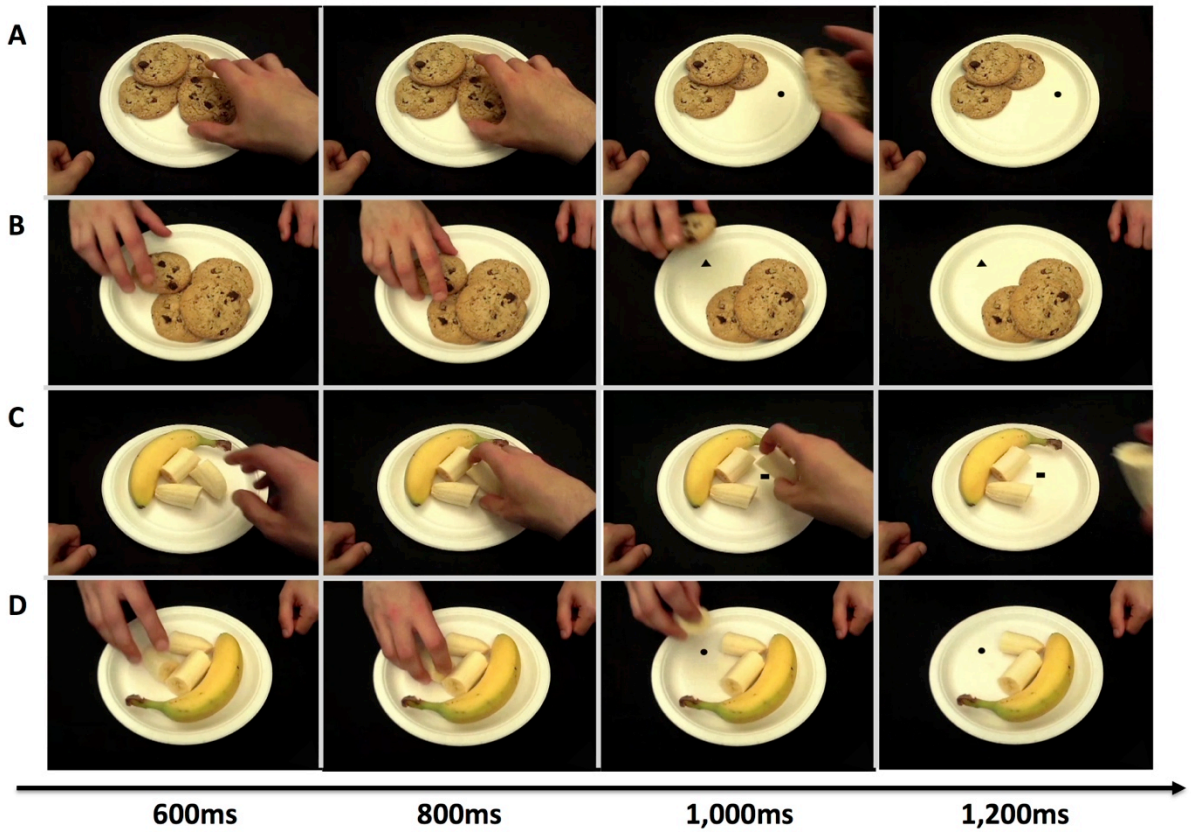


Figure 1. Still frames of representative videos taken at different times and featuring a hand grasping food from a plate from first- (1PP) and third-person perspectives (3PP) in the experimental runs. (A) Unhealthy food item from 1PP. (B) Unhealthy food item from 3PP. (C) Healthy food item from 1PP. (D) Healthy food item from 3PP.

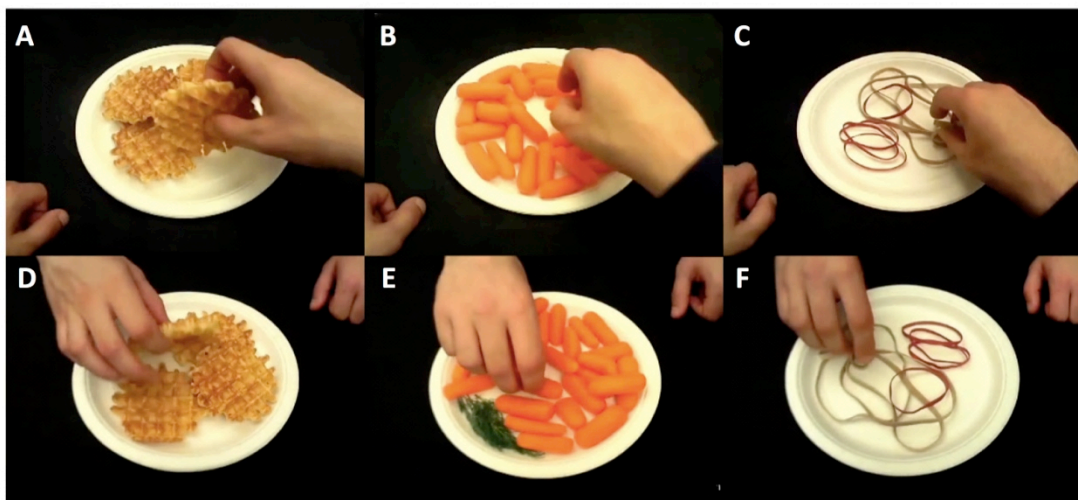


Figure 2. Conditions in the experimental runs. (A) Unhealthy food item from 1PP. (B) Healthy food item from 1PP. (C) Object from 1PP. (D) Unhealthy food item from 3PP. (E) Healthy food item from 3PP. (F) Object from 3PP.

Data acquisition and preprocessing. All imaging data were analyzed on a subject-by-subject basis using the general linear model (GLM) (see Supplementary material). We modeled one regressor per condition, using a 2-second box-car waveform convolved with the canonical hemodynamic response function (HRF). Subject-specific realignment parameters were added as covariates of no interest. To account for inter-subject variability, we conducted a random effects analysis at group level, by including the contrast images obtained during the first level analysis in a second level *t*-test. The BMI was entered as a covariate of interest to perform separate regression analysis.

We created functional and structural ROIs to avoid the risk of invalid statistical inference that can result from circularity (“double-dipping”) inherent in non-independent ROI selection (Kriegeskorte, Simmons, Bellgowan, & Baker, 2009). We first defined Food vs. Objects [F–O] as contrast of interest in the localizer run to identify bilateral clusters of activity as functional ROIs in the AI/IOFC ($p < .001$ uncorrected at voxel level and $p < .05$ FDR corrected at cluster level). Peak coordinates of left and right clusters were both located in the IOFC (orbital part of the inferior frontal gyrus) and extended to the AI, as labelled by the SPM Anatomy Toolbox 2.2c (Eickhoff et al., 2005) (see Table 1). As structural ROI, the bilateral amygdala was taken from the probabilistic cytoarchitectonic map which is available as part of the SPM Anatomy Toolbox (Amunts et al., 2005). Last, a 10mm sphere was placed on the coordinates of the VS ($x=6, y=0, z=-12$) identified in a meta-analysis on the neural correlates of processing visual food cues (Van der Laan et al., 2011).

We also used the Food vs. Objects [F–O] contrast to test whether food items from the present study increased activity in the bilateral amygdala and the VS as suggested in the literature (see Table 1). Due to space limitations, additional analyses involving conditions in the localizer run (Unhealthy food vs. Objects [UF–O], Healthy food vs. Objects [HF–O] and Unhealthy food vs. Healthy food [UF–HF]) are reported in supplementary material (see Supplementary results – Tables A2 and A3).

In the experimental runs, we tested whether viewing (unhealthy and/or healthy) foods yielded significant activity in taste and reward areas when compared with objects ([F–O], [UF–O] and [HF–O]). We then assessed the visual perspective effect (1PP or 3PP) on these responses to

grasping both kinds of food items relative to objects. We defined as contrasts of interest: the main effects of 1PP ([F1PP–O1PP], [UF1PP–O1PP], [UF1PP–O1PP]) and 3PP ([F3PP–O3PP], [UF3PP–O3PP], [UF3PP–O3PP]). We also tested whether viewing food items from the 1PP led to more activation in taste and reward areas than the 3PP ([F1PP–F3PP], [UF1PP–UF3PP], [HF1PP–HF3PP]), contrary to the inverse contrasts ([F3PP–F1PP], [UF3PP–UF1PP], [HF3PP–HF1PP]). Last, we tested whether viewing unhealthy foods increased activity in taste and reward areas when compared with healthy foods [UF–HF] and we assessed the visual perspective effect (1PP or 3PP) on these responses ([UF1PP–HF1PP] and [UF3PP–HF3PP]).

We conducted separate regression analyses to assess the modification of BOLD responses as a function of a participant's BMI.

Images resulting from random effects analyses were inclusively masked by a single ROI mask created in MarsBaR SPM Toolbox (Brett, Anton, Valabregue, & Poline, 2002). Activity in the selected ROIs was considered significant with a $p < .005$ (uncorrected, justified by *a priori* hypotheses), and a spatial extent threshold of at least 5 contiguous voxels (Ho, Kennedy, & Dimitropoulos, 2012). Whole brain activity was considered significant with a $p < .05$ FWE corrected for multiple comparisons at cluster level.

For each participant, mean parameter estimates of activity of each spherical (radius=10mm) area of interest, based around significant peaks, were extracted using MarsBaR, and correlated with BMI in SPSS 22 (SPSS Inc., Chicago, IL). Activations were labeled using the SPM Anatomy Toolbox 2.2c (Eickhoff et al., 2005) or Talairach Daemon names and Automated Anatomical Labeling (AAL) (Tzourio-Mazoyer et al., 2002) implemented in xjview 8.14 toolbox (<http://www.alivelearn.net/xjview>).

Results

Behavioral results

Behavioral results indicated that participants were attentive during the implicit task. They correctly detected the geometrical shapes on more than 95% of the trials in the localizer and experimental runs. Nonparametric ANOVAs (Friedman tests) showed that there was no significant difference in correct responses between the conditions in the localizer run ($N=20$; Chi-square=3.86; $dof=3$; $p=.28$), and in the 3 experimental runs considered together ($N=20$; Chi-square=1.55; $dof=5$; $p=.91$) (see also Supplementary results).

Neuroimaging results

Localizer run

In addition to the clusters of activity in the bilateral AI/IOFC that are identified as functional ROIs, structural ROI analyses revealed increased activation in the bilateral amygdala and the VS while participants were viewing food (vs. objects) pictures [F–O]. On the whole brain level, the Food vs. Objects [F–O] contrast also revealed a robust activation across the limbic system (thalamus, amygdala extending into the parahippocampal gyrus), and motor (precentral gyrus, middle frontal gyrus) and visuomotor areas (around the inferior and superior parietal lobules, and the superior occipital gyrus) (see Table 1).

Peak	# of voxels	Coordinates			T value
		x	y	z	
L Thalamus	592	-24	-27	-3	7.74**
L Amygdala extending into parahippocampal gyrus	122 ^a	-24	-6	-15	6.98**
R OFC (Inferior frontal gyrus, orbital part)	168 ^b	39	24	-15	6.86**
R Insula	–	33	24	0	5.88**
L Inferior parietal gyrus	521	-27	-60	42	6.60**
R Superior occipital gyrus	407	27	-72	33	6.35**
L Precentral gyrus	137	-36	0	63	6.02**
L OFC (Inferior frontal gyrus, orbital part)	75 ^b	-30	24	-9	5.63**
L Insula	–	-27	30	6	4.84**
R Middle frontal gyrus	47	30	-3	54	5.63**
VS	9	0	-6	-15	4.92*
R Amygdala	29	27	0	-18	4.32*

^a Seventy-three voxels of this cluster are located in the left amygdala ROI.

^b Cluster of activity identified as functional ROI (AI/IOFC).

Table 1. Brain regions obtained by a random effect model showing significant activations when viewing foods (vs. objects) [F–O] in the localizer run (x, y and z refer to spatial coordinates in the MNI space; (*) ROI analysis, $p < .005$ uncorrected, cluster size $k > 5$ contiguous voxels; (**) whole brain analysis, $p < .001$ uncorrected at voxel level and $p < .05$ FWE corrected for multiple comparisons at cluster level).

Experimental runs

In the experimental runs, we first tested whether viewing (unhealthy and/or healthy) foods led to significant activity when compared with objects ([F–O], [UF–O] and [HF–O]) (see Table 2). ROI analyses revealed significant amygdalar activity when viewing (unhealthy) foods (vs. objects; [F–O] and [UF–O]) but did not give rise to any significant activation above threshold criteria when viewing healthy foods (vs. objects; [HF–O]). At the whole brain level, activations were located in parieto-occipital areas (see Supplementary results – Neuroimaging results).

Peak	# of voxels	Coordinates			T value
		x	y	z	
F–O					
R Middle occipital gyrus (BA19) extending into cuneus and superior parietal gyrus (BA7)	239	36	-75	24	6.51**
L Amygdala	12	-18	-3	-21	3.87*
UF–O					
R Middle occipital gyrus extending into cuneus, precuneus and superior parietal gyrus	346	33	-69	21	7.31**
L Amygdala	12	-18	0	-21	3.74*
R Amygdala	5	24	-3	-18	3.11*
HF–O					
R Cuneus extending into middle occipital gyrus, precuneus and superior parietal gyrus	101	21	-84	45	5.30**

Table 2. Brain regions obtained by a random effect model showing significant activations when viewing unhealthy and/or healthy foods (vs. objects) ([F–O], [UF–O] and [HF–O]) in the experimental runs (x, y and z refer to spatial coordinates in the MNI space; (*) ROI analysis, $p < .005$ uncorrected, cluster size $k > 5$ contiguous voxels; (**) whole brain analysis, $p < .001$ uncorrected at voxel level and $p < .05$ corrected for multiple comparisons at cluster level).

These contrasts were then broken down by condition to assess the visual perspective effect (1PP or 3PP) on responses to grasping food (vs. objects) (see Table 3).

In 1PP trials, viewing (unhealthy and/or healthy) foods (vs. objects; [F1PP–O1PP], [UF1PP–O1PP] and [HF1PP–O1PP]) did not reveal any significant activity above threshold criteria in the ROIs. However, at the whole brain level, activations were located in parieto-occipital

areas when viewing (unhealthy) foods (vs. objects; see Supplementary results – Neuroimaging results).

In 3PP trials, ROI analyses revealed significant ventral striatal activity when viewing (unhealthy and/or healthy) foods (vs. objects; [F3PP–O3PP], [UF3PP–O3PP] and [HF3PP–O3PP]). When compared with objects, viewing unhealthy foods from 3PP [UF3PP–O3PP] also led to a significant cluster of activations in temporo-parieto-occipital areas at the whole brain level (see Supplementary results – Neuroimaging results).

Peak	# of voxels	Coordinates			T value
		x	y	z	
F1PP–O1PP					
R Cuneus extending into middle occipital gyrus, precuneus (BA7) and superior parietal gyrus	112	24	-81	45	5.28**
UF1PP–O1PP					
R Cuneus (BA19) extending into middle occipital gyrus, precuneus and superior parietal gyrus	178	12	-87	39	5.40**
HF1PP–O1PP					
<i>No suprathreshold voxel.</i>					
F3PP–O3PP					
VS	19	6	-3	-9	4.30*
UF3PP–O3PP					
R Middle temporal gyrus extending into superior occipital gyrus, cuneus, precuneus (BA7) and superior parietal gyrus	238	36	-72	18	7.54**
VS	20	6	-3	-6	4.58*
HF3PP–O3PP					
VS	9	9	-3	-12	3.68*

Table 3. Brain regions obtained by a random effect model showing significant activations when viewing unhealthy and/or healthy foods (vs. objects) from 1PP and 3PP ([F1PP–O1PP], [UF1PP–O1PP], [HF1PP–O1PP], [F3PP–O3PP], [UF3PP–O3PP] and [HF3PP–O3PP]) in the experimental runs (x, y and z refer to spatial coordinates in the MNI space; (*) ROI analysis, $p < .005$ uncorrected, cluster size $k > 5$ contiguous voxels; (**) whole brain analysis, $p < .001$ uncorrected at voxel level and $p < .05$ FWE corrected for multiple comparisons at cluster level).

We also tested whether viewing food items from 1PP led to significant brain activity when compared with viewing food items from 3PP ([F1PP–F3PP], [UF1PP–UF3PP], [HF1PP–HF3PP]) (see Table 4). ROI analyses revealed activity in the bilateral amygdala when viewing unhealthy foods from 1PP (vs. 3PP) [UF1PP–UF3PP] (see Figure 3). Viewing unhealthy and/or healthy foods from 3PP (vs. 1PP) ([F3PP–F1PP], [UF3PP–UF1PP] and [HF3PP–HF1PP]) did not give rise to increased activity in the taste and reward areas. At the whole brain level, activations from these contrasts were located in motor areas (see Supplementary results – Neuroimaging results).

Peak	# of voxels	Coordinates			T value
		x	y	z	
F1PP–F3PP					
L Superior parietal gyrus (BA5) extending into postcentral gyrus	191	-33	-48	63	8.55**
L Superior occipital gyrus	102	-18	-87	30	6.02**
UF1PP–UF3PP					
L Superior parietal gyrus (BA7) extending into superior parietal gyrus and postcentral gyrus	184	-30	-51	63	9.90**
L Superior occipital gyrus	128	-15	-87	30	7.40**
R Amygdala	5	24	-6	-27	3.43*
L Amygdala	5	-30	-6	-24	3.33*
HF1PP–HF3PP					
L Superior parietal gyrus extending into postcentral gyrus	131	-30	-48	66	5.34**
F3PP–F1PP					
R Postcentral gyrus extending into superior parietal gyrus	414	30	-45	60	8.25**
R Superior frontal gyrus extending into precentral gyrus	162	24	-12	60	7.05**
UF3PP–UF1PP					
R Postcentral gyrus (BA5) extending into superior parietal gyrus	258	33	-45	63	7.44**
HF3PP–HF1PP					
R Postcentral gyrus (BA40) extending into superior parietal gyrus (BA7) and postcentral gyrus (BA5)	158	33	-42	57	5.86**

Table 4. Brain regions obtained by a random effect model showing significant activations when viewing unhealthy and/or healthy foods from 1PP (vs. 3PP) ([F1PP–F3PP], [UF1PP–UF3PP] and [HF1PP–HF3PP]) and when viewing unhealthy and/or healthy foods from 3PP

(vs. 1PP) ([F3PP–F1PP], [UF3PP–UF1PP] and [HF3PP–HF1PP]) in the experimental runs (x, y and z refer to spatial coordinates in the MNI space; (*) ROI analysis, $p < .005$ uncorrected, cluster size $k > 5$ contiguous voxels; (**) whole brain analysis, $p < .001$ uncorrected at voxel level and $p < .05$ FWE corrected for multiple comparisons at cluster level).

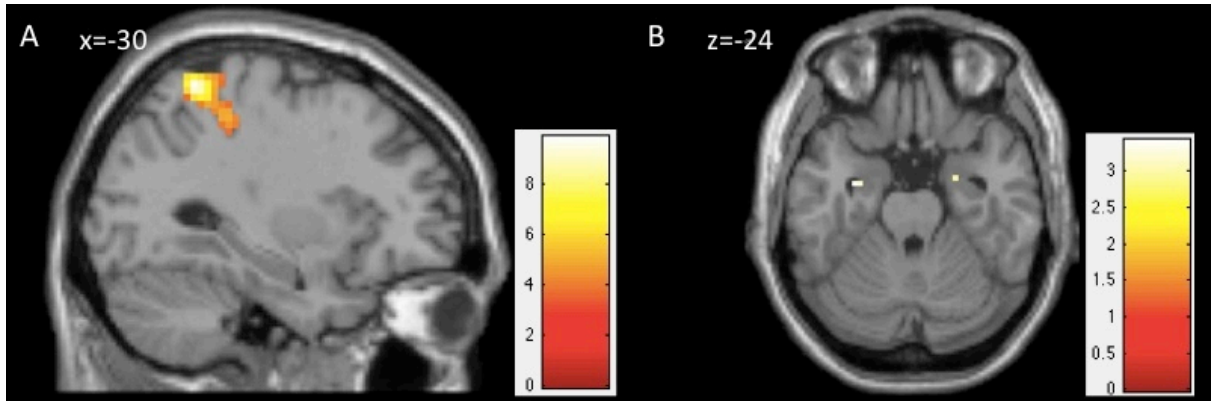


Figure 3. fMRI results. Increased brain activity when viewing unhealthy foods from 1PP (vs. 3PP) [UF1PP–UF3PP] in the experimental runs. (A) Increased activity in the left superior parietal gyrus visualized in sagittal section ($x = -30$; $y = -51$; $z = 63$; $p < .001$ uncorrected at voxel level and $p < .05$ FWE corrected at cluster level). (B) Increased activity in the bilateral amygdala visualized in coronal section (right amygdala, $x = 24$; $y = -6$; $z = -27$; left amygdala, $x = -30$; $y = -6$; $z = -24$; $p < .005$, $k > 5$ voxels, uncorrected).

Last, the Unhealthy food vs. Healthy food [UF–HF] contrast did not reveal any significant activation at the whole brain level. However, ROI analyses yielded significant activity in the right AI/IOFC and right amygdala. Further ROI analyses on this contrast broken down by condition revealed that, when compared to healthy foods, viewing unhealthy foods from 1PP contributed to significant activity in the bilateral amygdala [UF1PP–HF1PP] while viewing unhealthy foods from 3PP contributed to significant activity in the right AI/IOFC [UF3PP–HF3PP] (see Table 5).

Peak	# of voxels	Coordinates			T value
		x	y	z	
UF–HF					
R AI/IOFC	24	42	24	-12	4.50
R Amygdala	7	27	-3	-18	3.77
UF1PP–HF1PP					

R Amygdala	23	30	0	-24	4.17
L Amygdala	5	-30	-6	-21	3.41
UF3PP–HF3PP					
R AI/IOFC	7	42	27	-18	4.04

Table 5. Brain regions obtained by a random effect model showing significant activations when viewing unhealthy (vs. healthy) foods from 1PP and 3PP ([UF–HF], [UF1PP–HF1PP] and [UF3PP–HF3PP]) in the experimental runs (x, y and z refer to spatial coordinates in the MNI space; ROI analysis, $p < .005$ uncorrected, cluster size $k > 5$ contiguous voxels).

Regression analyses

We conducted separate regression analyses to assess whether BMI modulated brain activity in the previous contrasts.

Viewing food (vs. objects) [F–O] led to increased activity positively correlated with BMI in the VS. Activations during exposure to unhealthy foods were also significantly correlated with BMI in the VS and in the right AI/IOFC when compared with objects [UF–O]. The effect sizes from these analyses were all large as per Cohen’s (1988) criteria ($r = .54–.64$), with a mean r of .60 (all $ps < .05$, bilateral). However, healthy food-related activity (vs. objects) [HF–O] did not significantly correlate with BMI (see Table 6).

Peak	# of voxels	Coordinates			T value	Effect size r
		x	y	z		
F–O						
VS	27	0	3	-9	4.01	.64 ^b
UF–O						
R AI/IOFC	11	42	21	-24	4.13	.54 ^a
VS	44	3	3	-12	3.90	.63 ^b
HF–O						
<i>No suprathreshold voxel.</i>						

Table 6. Brain regions obtained by a random effect model showing significant activations positively correlated with BMI when viewing unhealthy and/or healthy foods (vs. objects) ([F–O], [UF–O] and [HF–O]) in the experimental runs (x, y and z refer to spatial coordinates in the MNI space; ROI analysis, $p < .005$ uncorrected, cluster size $k > 5$ contiguous voxels; ^(a) denotes $p < .05$ bilateral, ^(b) denotes $p < .01$ bilateral).

In 1PP trials, whole brain level analyses showed that viewing foods (vs. objects) [F1PP–O1PP] gives rise to a cluster of activations correlated with BMI in the left medial OFC/gyrus rectus (extending into the caudate). ROI analyses revealed additional activity correlated with BMI in the right AI/IOFC, right amygdala and VS. Activations during exposure to unhealthy foods were also significantly correlated with BMI in the right AI/IOFC and VS when compared with objects [UF1PP–O1PP]. The effect sizes from these analyses were all large as per Cohen’s (1988) criteria ($r=.51-.63$), with a mean r of .59 (all $ps<.05$, bilateral) (see Table 7).

Again, healthy food-related activity (vs. objects) [HF1PP–O1PP] did not significantly correlate with BMI in 1PP trials. Similarly, in 3PP trials, (unhealthy and/or healthy) food-related activity did not significantly correlate with BMI ([F3PP–O3PP], [UF3PP–O3PP] and [HF3PP–O3PP]) (see Table 7).

Peak	# of voxels	Coordinates			T value	Effect size r
		x	y	z		
F1PP–O1PP						
L Medial OFC extending into gyrus rectus	339	-9	12	-12	4.54**	.65 ^b
VS	53	12	6	-9	4.35*	.63 ^b
R AI/IOFC	7	42	21	-21	3.20*	.51 ^a
R Amygdala	9	18	-6	-18	3.07*	.52 ^a
UF1PP–O1PP						
VS ROI	56	6	3	-15	4.73*	.62 ^b
R AI/IOFC	23	39	24	-21	4.32*	.59 ^a
HF1PP–O1PP						
<i>No suprathreshold voxel.</i>						
F3PP–O3PP						
<i>No suprathreshold voxel.</i>						
UF3PP–O3PP						
<i>No suprathreshold voxel.</i>						
HF3PP–O3PP						
<i>No suprathreshold voxel.</i>						

Table 7. Brain regions obtained by a random effect model showing significant activations positively correlated with BMI when viewing unhealthy and/or healthy foods (vs. objects) from 1PP and 3PP ([F1PP–O1PP], [UF1PP–O1PP], [HF1PP–O1PP], [F3PP–O3PP], [UF3PP–O3PP] and [HF3PP–O3PP]) in the experimental runs (x, y and z refer to spatial coordinates in the MNI space; (*) ROI analysis, $p<.005$ uncorrected, cluster size $k>5$

contiguous voxels; (**) whole brain analysis, $p < .005$ uncorrected at voxel level and $p < .05$ FWE corrected for multiple comparisons at cluster level; (a) denotes $p < .05$ bilateral, (b) denotes $p < .01$ bilateral).

Further regression analyses revealed that food-related activity correlated with BMI was significantly higher from the 1PP (vs. 3PP) [F1PP–F3PP] in the right amygdala and the VS. Viewing unhealthy foods from 1PP (vs. 3PP) also led to activations correlated with BMI within the VS [UF1PP–UF3PP] (see Figure 4). The effect sizes from these analyses were all large as per Cohen’s (1988) criteria ($r = .49–.54$), with a mean r of .53 (all $ps < .05$, bilateral) (see Table 8). Healthy food-related activity from 1PP (vs. 3PP) [HF1PP–HF3PP] did not significantly correlate with BMI within ROIs.

Peak	# of voxels	Coordinates			T value	Effect size r
		x	y	z		
F1PP–F3PP						
VS	10	15	0	-6	4.15	.55 ^a
R Amygdala	6	30	0	-24	3.54	.54 ^a
UF1PP–UF3PP						
VS	8	12	3	-9	3.22	.49 ^a
HF1PP–HF3PP						
<i>No suprathreshold voxel.</i>						
F3PP–F1PP						
<i>No suprathreshold voxel.</i>						
UF3PP–UF1PP						
<i>No suprathreshold voxel.</i>						
HF3PP–HF1PP						
<i>No suprathreshold voxel.</i>						

Table 8. Brain regions obtained by a random effect model showing significant activations positively correlated with BMI when viewing unhealthy and/or healthy foods from 1PP (vs. 3PP) ([F1PP–F3PP], [UF1PP–UF3PP] and [HF1PP–HF3PP]) and when viewing unhealthy and/or healthy foods from 3PP (vs. 1PP) ([F3PP–F1PP], [UF3PP–UF1PP] and [HF3PP–HF1PP]) in the experimental runs (x, y and z refer to spatial coordinates in the MNI space; ROI analysis, $p < .005$ uncorrected, cluster size $k > 5$ contiguous voxels; (a) denotes $p < .05$ bilateral).

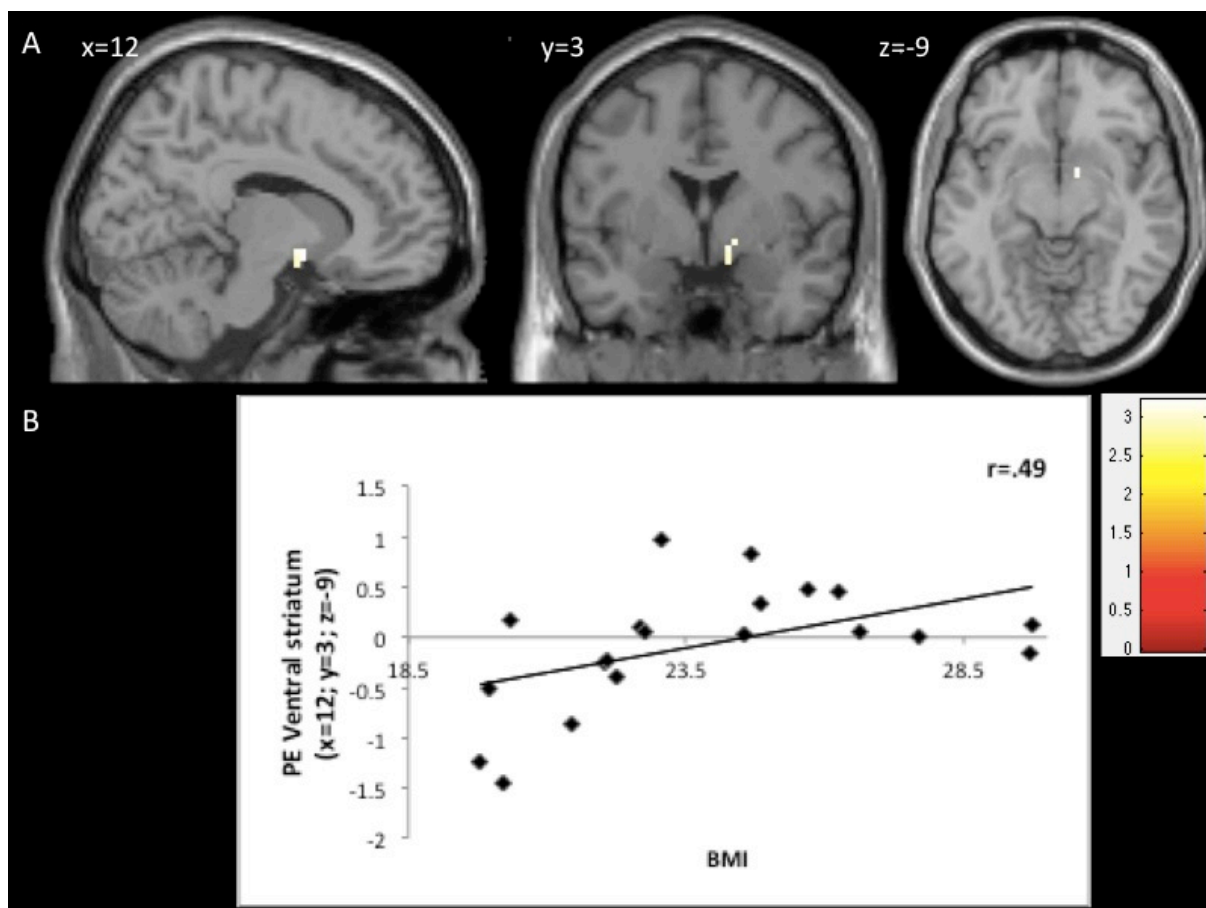


Figure 4. fMRI results. (A) Sagittal, coronal and axial sections of increased brain activity in a spherical (radius=10mm) region of the VS ($x=12$; $y=3$; $z=-9$; $p<.005$ uncorrected, $k>5$ voxels) when viewing unhealthy foods from 1PP (vs. 3PP) [UF1PP–UF3PP] as a function of BMI in the experimental runs with (B) the graph of parameter estimates (PE) from that region.

When compared with healthy foods, exposure to unhealthy foods [UF–HF] revealed activations correlated with BMI in the VS. When this contrast was then broken down by condition, regression analyses revealed that viewing unhealthy (vs. healthy) foods contributed to ventral striatal activity correlated with BMI in 1PP trials [UF1PP–HF1PP] (see Figure 5), but did not lead to any significant activity in 3PP trials [UF3PP–HF3PP] (see Table 9). The effect sizes from these analyses were all large as per Cohen’s (1988) criteria ($r=.47-.48$), with a mean r of .48 (all $ps<.05$, bilateral).

Peak	# of voxels	Coordinates			T value	Effect size r
		x	y	z		
UF–HF						

VS	16	6	6	-18	4.33	.48 ^a
UF1PP–HF1PP						
VS	12	6	3	-18	3.89	.47 ^a
UF3PP–HF3PP						
<i>No suprathreshold voxel.</i>						

Table 9. Brain regions obtained by a random effect model showing significant activations positively correlated with BMI when viewing unhealthy (vs. healthy) foods from 1PP and 3PP ([UF–HF], [UF1PP–HF1PP] and [UF3PP–HF3PP]) in the experimental runs (x, y and z refer to spatial coordinates in the MNI space; ROI analysis, $p < .005$ uncorrected, cluster size $k > 5$ contiguous voxels; (^a) denotes $p < .05$ bilateral).

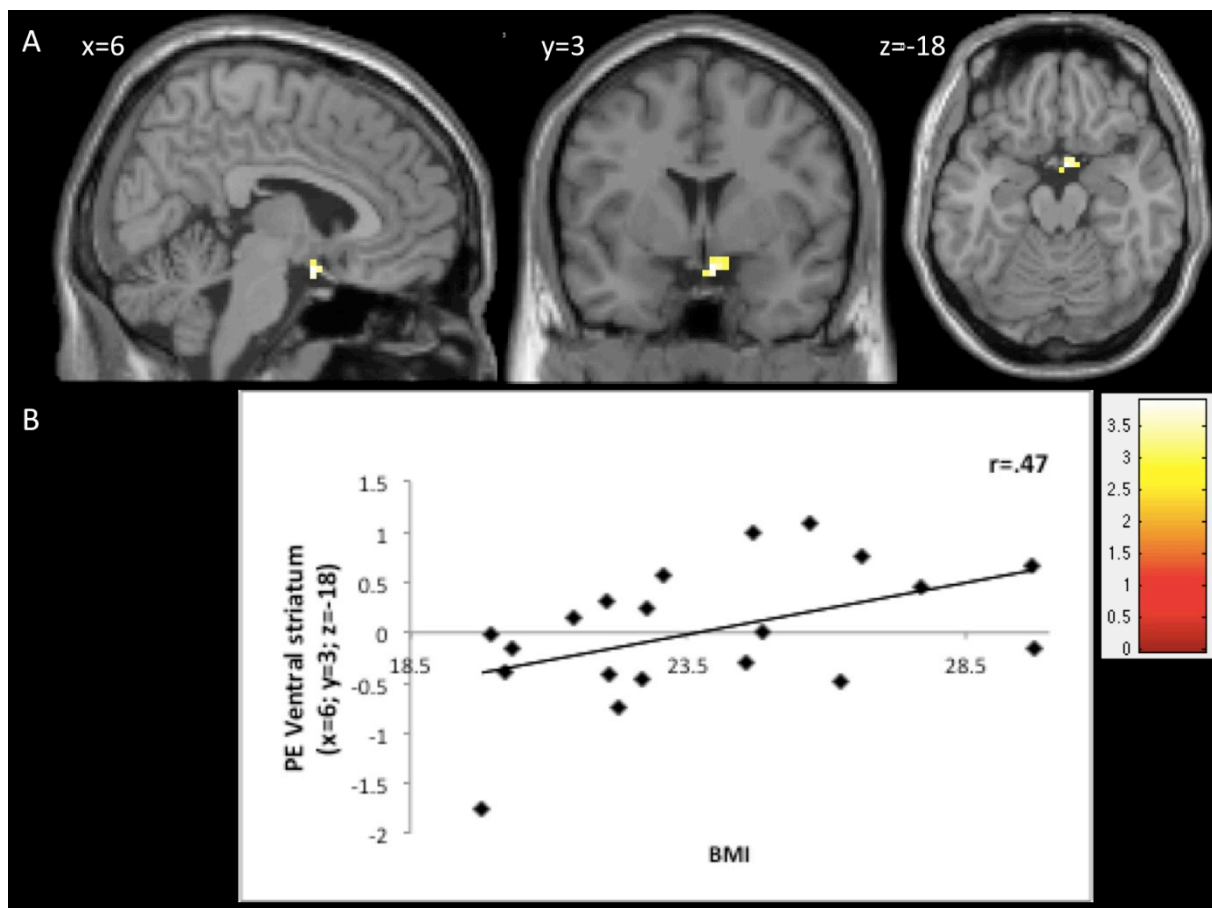


Figure 5. fMRI results. (A) Sagittal, coronal and axial sections of increased brain activity in a spherical (radius=10mm) region of the VS ($x=6$; $y=3$; $z=-18$; $p < .005$ uncorrected, $k > 5$ voxels) when viewing unhealthy (vs. healthy) foods from 1PP [UF1PP–HF1PP] as a function of BMI in the experimental runs with (B) the graph of parameter estimates (PE) from that region.

Discussion

To our knowledge, this is the first neuroimaging study to assess whether visual perspective modulates brain activity within regions involved in taste and reward processing during exposure to food cues. More specifically, we tested whether viewing unhealthy and/or healthy food videos while completing an implicit task increases activity in taste and reward areas (1) from 1PP and 3PP, (2) when 1PP is compared to the 3PP, and (3) that is positively correlated with BMI. Our results mainly suggest that activity in these regions is increased and positively correlated with BMI when viewing unhealthy foods, but not healthy foods, from 1PP. Results from the localizer run as well as activity in motor and visuomotor areas from the experimental runs are further discussed in the supplementary material (see Supplementary results – Discussion).

1) Increased activity in taste and reward areas when viewing videos of unhealthy foods from first- and third-person perspective.

Watching videos featuring a hand grasping unhealthy foods (vs. objects) [UF–O] leads to increased activity in the bilateral amygdala, whose activity is driven by stimulus intensity and saliency (Small et al., 2003; Zald, 2003) and could foster temptation (Papies & Barsalou, 2015). However, we did not observe any activation in taste and reward areas when videos featured healthy foods (vs. objects) [HF–O]. Further analyses reveal increased activity in motor and visuomotor areas when viewing unhealthy foods, but not healthy foods, from 1PP [UF1PP–O1PP] and 3PP [UF3PP–O3PP]. These findings support the idea that unhealthy foods are more likely to attract greater attention than healthy foods (Cornier, Von Kaenel, Bessesen, & Tregellas, 2007; Passamonti et al., 2009; Schur et al., 2009) and to result in approach behaviors (Chen et al., 2016) (see also supplementary material – Supplementary results – Discussion).

Along this line of argument, as expected, when compared with healthy foods, viewing unhealthy foods [UF–HF] gives rise to activations in taste and reward areas (right AI/IOFC and right amygdala). Interestingly, when this contrast is broken down by condition, it appears that the 3PP [UF3PP–HF3PP] contributes to AI/IOFC activity and thus to taste representations associated with viewing unhealthy (vs. healthy) food (O’Doherty et al., 2001; Simmons et al., 2005); while the 1PP [UF1PP–HF1PP] contributes to amygdalar activity and therefore to make it more salient and intense (Chen et al., 2016; Haber & Knutson, 2009;

Small et al., 2003; Zald, 2003). Unexpectedly, we did not observe any ventral striatal activity in the localizer run (see Supplemental results – Table A3) or in the experimental runs (see Table 5) when unhealthy foods are compared with healthy foods. This could be due to the fact that, contrary to most of previous studies included in the referred meta-analysis (Van der Laan et al., 2011), our stimuli were matched on tastiness and valence, and our participants in the current study were native French sharing the intuition that what is healthy is tasty (Raghunathan, Naylor, & Hoyer, 2006; Werle, Trendel, & Ardito, 2013) (see Supplementary methods – Stimuli selection, and Supplementary results – Scales).

It is worth noting that, contrary to our expectations, we observed increased ventral striatal activity when viewing unhealthy and/or healthy foods from 3PP ([F3PP–O3PP], [UF3PP–O3PP], and [HF3PP–O3PP]), but not from 1PP ([F1PP–O1PP], [UF1PP–O1PP], and [HF1PP–O1PP]). More generally, we did not observe increased activity in taste and reward areas, notably in the AI/IOFC, when viewing videos of foods (vs. objects), especially in 1PP trials. A first explanation is that the grasping hand might have contributed to diverting participants' attention away from food items. This may account for decreased activity in the anterior insular cortex (AI/IOFC) whose reward-related responses depend on available attentional resources (Rothkirch, Schmack, Deserno, Darmohray, & Sterzer, 2014). However, this mechanism falls short of explaining the absence of ventral striatal activity. Indeed, it appears that, contrary to the AI, the VS signals the motivational salience of reward cues even when attention is fully engaged elsewhere (Rothkirch et al., 2014).

Further analyses that compare food items from 1PP with objects from 3PP suggest an additional explanation to the lack of ventral striatal activity. They show that viewing unhealthy and/or healthy foods items from 1PP significantly increased activity in taste and reward areas, namely the VS and amygdala, when contrasted with objects viewed from 3PP ([F1PP–O3PP], [UF1PP–O3PP] and [HF1PP–O3PP]; see Supplemental results – Table A4). These results indicate that the control condition, in which the participants were presented with videos featuring stationary objects grasped from a plate, was more “neutral” in 3PP than in 1PP trials, probably because of its unusual nature. This can contribute to explaining why we observed increased ventral striatal activity when viewing foods (vs. objects) from 3PP but not from 1PP¹. Using static pictures of objects instead of videos as a control condition might have

¹ Although the videos were distance controlled, we cannot exclude the possibility that the food actually appeared closer to (some of) the participants when presented from a 3PP because of the subtle difference between the angle in 1PP and 3PP. Moreover, one can consider that there were more obstructions between them and the food items from a 1PP, in

actually increased the magnitude and size of the neural response to visual food cues in the experimental runs (Cheng et al., 2007).

Overall, we acknowledge that the shape identification task and the grasping hand could have diverted participants' attention away from the food items and could have led to a rather unusual control (objects) condition with unexpected effects, namely to attenuate activity in taste and reward areas. We expect that future studies will find even more pronounced results, in a less contrived setting where, for instance, participants are instructed to passively view or to imagine the food items that are depicted from different visual perspectives.

2) Increased activity in taste and reward areas when viewing unhealthy foods, but not healthy foods, from first- versus third-person perspective.

Viewing unhealthy food items from 1PP (vs. 3PP) [UF1PP–UF3PP] increases activity in the bilateral amygdala which is responsive to gustatory stimuli intensity (Chen et al., 2016; Haber & Knutson, 2009; Small et al., 2003; Zald, 2003). It has also been hypothesized to deliver contextual information used for adjusting motivational level (Haber & Knutson, 2009) and to influence behavior by providing a “direct memory link” between a food stimulus and its incentive value (Siep et al., 2009). Amygdalar activations together with activations in motor areas (see also supplementary material – Supplementary results – Discussion) are thus consistent with previous food studies showing that first- (vs. third-) person imagery involves more simulation of direct interaction with the environment (Libby & Eibach, 2011). Such activations also support the assumption that the 1PP (vs. 3PP) can enhance sensorimotor representations of unhealthy foods (Christian et al., 2016).

This finding does not extend to healthy food items [HF1PP–HF3PP], even though analyses in the localizer run showed that viewing pictures of healthy foods (vs. objects) leads to increased activity in the bilateral AI/IOFC and the left amygdala (see Supplementary results – Table A2). At least two explanations can account for this lack of activity in taste and reward areas. First, it might be that healthy foods could be valued because of the abstract health benefits

which a white hand was separating them from the food. However, it is rather unlikely that this could have significantly influenced the VS activity. As suggested in the literature, reducing the size of emotional pictures does not affect the magnitude of the late positive potential (De Cesarei & Codispoti, 2006), an electrophysiological index of emotional perception in humans (Liu, Huang, McGinnis-Deweese, Keil, & Ding, 2012), which in turn is correlated with fMRI-based activation measures in motivational regions, such as the ventral striatum (Ihssen, Sokunbi, Lawrence, Lawrence, & Linden, 2017; Sabatinelli, Keil, Frank, & Lang, 2013). Therefore, this is probably not a subtle change in terms of size perception that could have had significantly attenuated the VS activity in 1PP trial.

associated with them and not because of the concrete details of embodied and situated experiences attached to the pleasure of eating them and that are supposed to be emphasized in 1PP. However, evidence does not show either that viewing healthy foods from a 3PP (vs. 1PP) [HF3PP–HF1PP], which is more abstract than a 1PP (Libby & Eibach, 2011; Libby et al., 2009), can lead to increased activity in brain areas associated with taste and reward. Second, another explanation might be that, given their low-calorie content while palatability and enjoyment are often tied to energy density (Drewnowski & Almiron-Roig, 2010), the pleasure of eating healthy foods should also be enhanced by messages to allow the effect of visual perspective (Petit et al., 2016a; Rennie, Uskul, Adams, & Appleton, 2014). This remains to be further investigated in future studies.

3) Increased activity positively correlated with BMI in taste and reward areas when viewing unhealthy foods from first-person perspective.

Regression analyses confirm that visual perspective significantly modulates activity correlated with BMI in taste and reward areas when participants are presented with videos featuring a hand grasping unhealthy and healthy foods (vs. objects). More specifically, contrary to the 3PP [F3PP–O3PP], viewing foods (vs. objects) from a 1PP [F1PP–O1PP] leads to activations positively correlated with BMI in the right amygdala as well as in the right AI/IOFC that represents taste property information and feeding-relevant interoceptive states (Small, 2010; Veldhuizen et al., 2011) and in the VS and left medial OFC/gyrus rectus (extending into the caudate nucleus) that both support food reward processing (Haber, 2011; Kringelbach, 2005; Shott et al., 2015). A similar but attenuated pattern is observed for unhealthy foods: contrary to the 3PP [UF3PP–O3PP], viewing unhealthy foods (vs. objects) from a 1PP [UF1PP–O1PP] leads to activations positively correlated with BMI in the right AI/IOFC and the VS.

As aforementioned, the extant literature documents that the anterior insular cortex (AI/IOFC) activity depends on attentional resources available for processing of the reward cue (Rothkirch et al., 2014). Findings further showed that BMI correlates positively with activation in brain regions related to attention and food reward, including the AI/IOFC (Yokum, Ng, & Stice, 2011). Increased activity in the AI/IOFC may thus indicate that, in 1PP trials, higher-BMI participants pay more attention to the unhealthy foods (vs. objects) presented, which are incidental to the shape identification task. To the contrary, it has been shown that the VS responds to reward information even when participants' attention is

diverted (Rothkirch et al., 2014). Increased activity in the VS suggests that they also simulate eating the unhealthy foods (vs. objects) more strongly. Taken together, these findings indicate that viewing unhealthy foods (vs. objects) from 1PP leads to heightened attention and reward responses amongst higher-BMI participants.

Interestingly, increased activity when viewing food from 1PP (vs. 3PP) [F1PP–F3PP] is positively correlated with BMI in the right amygdala and VS. Consistently, ventral striatal activity is also positively correlated with BMI when viewing unhealthy foods from 1PP (vs. 3PP) [UF1PP–UF3PP]. However, in both contrasts of interest, we did not observe significant activity in the AI/IOFC. This pattern of activity indicates that, even if higher-BMI participants pay similar attention to unhealthy foods in 1PP and 3PP trials, the simulation of the reward associated with them is stronger in 1PP (vs. 3PP).

In this vein, regression analyses further reveal that ventral striatal activity correlated with BMI when viewing unhealthy (vs. healthy) food in 1PP trials [UF1PP–HF1PP] but not in 3PP trials [UF3PP–HF3PP]. This confirms that the 1PP makes unhealthy food more rewarding amongst high-BMI participants; whereas a 3PP contributes to reducing the reward activity associated with unhealthy (vs. healthy) food amongst high-BMI participants.

Overall, our results show that the 1PP increases brain activity in regions associated with taste and reward processing amongst higher-BMI participants when viewing (unhealthy) food items. This extends the aforementioned results from behavioral studies that have suggested that, when compared with the first-person imagery, the third-person imagery is characterized by fewer sensory components (e.g., of taste, smell and touch) and is less likely to produce the feelings of reward that heighten motivation to consume unhealthy foods (Christian et al., 2016). We might speculate that the 1PP (vs. 3PP) is actually making unhealthy foods more “available” to higher-BMI participants, which could be tested in a specific fMRI setting where food could be eaten during and after the experiment (Blechert, Klackl, Miedl, & Wilhelm, 2016).

However, it is noteworthy that viewing healthy food items from 1PP or 3PP does not give rise to any activity significantly correlated with BMI. In a set of exploratory analyses (including a separate regression analysis with BMI as regressor), we also tested whether visual perspective interacts with taste and reward, so that the 1PP (vs. 3PP) could actually offset the effect of the low-calorie content of healthy (vs. unhealthy) foods [H1PP–UF3PP]. These analyses did not reveal any significant activation above threshold criteria and failed to support the idea that a 1PP could help promote healthy food (while a 3PP could help attenuate the appraisal of

unhealthy food), especially amongst overweight individuals. Thus, this study indicates that the sole visual perspective cannot improve healthy food perception amongst higher-BMI people. Again, a complementary solution to visual perspective seems to be necessary to promote healthy food products. As suggested, one potentially promising avenue in this regard for future work would be to highlight the pleasure (vs. health benefits) of eating healthily with messages. When associated with a 1PP (vs. 3PP), this strategy could lead higher-BMI participants to stronger eating simulations and to healthier food choices (Petit et al., 2016a; Petit et al., 2016c).

Conclusions, perspectives and limitations. Collectively, these findings suggest that visual perspective (1PP or 3PP) modulates brain activity in motor-related and taste and reward areas when viewing food items. More specifically, our results indicate that unhealthy foods yielded activations in the superior parietal gyrus and the bilateral amygdala when viewed from 1PP (vs. 3PP) [UF1PP–UF3PP]. This supports the assumption that 1PP (vs. 3PP) can heighten the feelings of the rewarding experience associated with unhealthy food intake. In this vein, ventral striatal activity was positively correlated with BMI during exposure to unhealthy foods from 1PP (vs. 3PP) [UF1PP–UF3PP]. To the contrary, we did not observe any increased insular (AI/IOFC), amygdalar or ventral striatal activity correlated with BMI in 3PP trials, even when unhealthy foods were compared with healthy foods [UF3PP–HF3PP] or objects [UF3PP–O3PP]. These patterns of activity are thus aligned with previous results in the literature and also suggest that presenting unhealthy foods from 3PP can reduce temptation (Christian et al., 2016), especially amongst higher-BMI participants.

By manipulating camera angles, our research further shows that visual perspective can operate implicitly when participants are viewing unhealthy food cues. So far, it has been proposed to explicitly use visual imagery, and to encourage people to imagine themselves from a 3PP to regulate food intake (Christian et al., 2016). Yet, this would actually require a pre-existing level of self-regulation. In other words, to resist food temptation, people would have to think about themselves from a 3PP, which is different from their common experience that is usually in 1PP. In light of our study, it appears that simply depicting unhealthy food items from a 3PP can contribute to reducing food temptation amongst high-BMI participants by attenuating the non-conscious eating simulations that reenact sensory and bodily states associated with appetitive experiences (Barsalou, 2011; Papies & Barsalou, 2015; Papies, Best, Gelibter, & Barsalou, 2017).

As such, the current study also complements the larger existing literature in neuroscience that relied on mental imagery as a deliberate process to show that first-person simulations are more embodied and situated than their third-person counterparts (Christian et al., 2015; Lorey et al., 2009; Macrae, Raj, Best, Christian, & Miles, 2013). In light of our results, it nonetheless appears that a 1PP (vs. 3PP) is not the solution to enhance the perception of healthy food taste and to capture overweight people's attention in order to make it more rewarding [HF1PP–H3PP]. As stated above, future research might explore whether visual perspective interacts with messages that highlight the pleasure or the health benefits of healthy food products to reflect the value associated with eating healthily (Petit et al., 2016a; Petit et al., 2016c).

These empirical findings come with limitations that could serve as a basis for future research. First of all, as aforementioned, the shape identification task might have diverted participants' attention away from the food cues. Also, viewing stationary objects grasped from a plate in the control condition is unusual. This might have attenuated the brain response, especially in the anterior insular cortex. One cannot exclude either the possibility that performing the localizer task before the experimental runs might have induced habituation effects that are known to attenuate the brain response in taste and reward areas (LaBar, Gitelman, Mesulam, & Parrish, 2001).

Moreover, even though BMI operates as an index of cumulative energy dense food intake (Giuliani et al., 2014) and is an anthropometric measure widely used to assess excess body fat (Yokum, Ng, & Stice, 2012), future studies incorporating complementary measures such as adiposity (Rapuano, Huckins, Sargent, Heatherton, & Kelley, 2016), or waist circumference (Wallner-Liebmann et al., 2010), could also be utilized.

Furthermore, this study includes participants who can be categorized as healthy weight (18.50–24.99 kg/m²) and overweight (25.00–29.99 kg/m²), based on BMI ranges (World Health Organization (WHO) international classifications). As such, higher-BMI participants in this study are overweight but not obese. It might be worthwhile to try to replicate our findings in a group of obese (vs. non-obese) participants (>30.00 kg/m²) (Rothenmund et al., 2007).

Last, future studies could also investigate whether visual perspective affects the extent to which desire (Kavanagh, Andrade, & May, 2005; Papiés & Barsalou, 2015) or hunger (Cheng et al., 2007; LaBar, Gitelman, Parrish, et al., 2001) modulate neural responses to viewing food items, in lean, overweight and obese populations. An additional research avenue is to explore whether visual perspective can modulate activity in the dorsal control pathway that regulates

neural and behavioral responses to food cues, and help achieve eating and health goals (Chen et al., 2016; Kaye, Fudge, & Paulus, 2009).

Overall, these results contribute to the literature on the extent to which visual perspective modulates brain activity associated with taste and reward processing (Christian et al., 2016). Our findings show that merely viewing unhealthy food cues from a 1PP leads to brain activations that underlie representations of rewarding (appetitive) experiences, while the 3PP attenuates such neural activity, especially amongst higher-BMI participants. These findings are noteworthy in the current digital environments, where increasing exposure to appetizing food images (e.g., on Instagram, Facebook, Twitter) stimulates activity in brain regions contributing to taste and reward processing (Petit et al., 2016b; Spence et al., 2016). They encourage public health authorities to control (or even to manipulate) the visual perspective of unhealthy food images to nudge overweight consumers towards healthy options. However, the promotion of healthy food products through first- or third-person (video) images requires further investigation to focus attention and become more appetitive. To help fight obesity more efficiently, it might be worthwhile to test whether emphasizing the pleasure of eating (or, conversely, the health benefits) interacts with visual perspective to improve healthy food perception (Petit et al., 2016a, 2016c).

Last, our findings point to the more general issue of the extent to which bodily characteristics (higher-BMI) modulate how people experience the real-world and result in different responsiveness to the same cues (Chen et al., 2016; Papies & Barsalou, 2015). In this perspective, the video cameras used in the present research are similar to those used to collect subjective evidence in first-person ethnography, so our results could inform qualitative field studies on overweight and obese participants in social sciences (Lahlou, Le Bellu, & Boesen-Mariani, 2015).

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Authors' contributions

Conceived and designed the experiment: FB OP SLB SL. Performed the experiment: FB OP helped by SLB JLA AC. Analyzed the data: FB helped by OP JLA. Contributed reagents/materials/analysis tools: FB helped by OP SLB. Wrote the article: FB with contributions from all co-authors. Revised the article: FB.

Financial disclosure

The authors declare that no competing interests exist.

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Supplementary material

Supplementary methods

Participants and procedure. Before entering the fMRI scanner, each participant completed measures of weight and height, and visual analogue scales (VAS) of appetite (hunger: “How hungry do you feel right now?”; and pleasure: “How pleasant would it be to eat right now?”) (Goldstone et al., 2009; Wren et al., 2001). They performed a brief pre-fMRI scanning task familiarization session in which they were presented with 12 static pictures (with no hand grasping) and videos depicting items (food utensils: mugs, cups, forks, knives) grasped from 1PP and 3PP. These pictures and videos were different from the stimuli used in the study. After the fMRI session (i.e. outside the scanner), explicit measures were collected using the Qualtrics survey software. Participants reported stimuli valence on a 5-point rating scale (smiley faces ranging from very negative to very positive through neutral). They completed the two VAS of appetite (hunger, pleasure) again, in addition to the 9-point explicit belief in the unhealthy=tasty intuition (Raghunathan, Naylor, & Hoyer, 2006). Each participant was then offered to drink and to eat sweet and/or salty food, and was debriefed by the experimenter.

Stimuli selection. We selected 12 healthy (e.g., cherry tomato, white grape, banana) and 12 unhealthy (e.g., pizza, brownie, cookies), sweet and salty food items that match in terms of grasping affordances, from 500 food pictures rated for tastiness and healthiness by 236 participants on 7-item Likert scales (Pavlicek, 2013). The scores on tastiness and healthiness ranged from 1 (=not at all) to 7 (=very much so), with 4 as the midpoint of the scale. Items were considered to be tasty (not tasty), or healthy (unhealthy), when the mean scale score was significantly above (below) the scale midpoint (nonparametric one-sample *t*-test: Wilcoxon signed rank test). Stimuli selected were rated as tasty ($M_{\text{Healthy_food}}=5.07$, $SD=.52$, $Z=2.94$, $p<.005$; $M_{\text{Unhealthy_food}}=4.85$, $SD=.73$, $Z=2.75$, $p<.01$) and as different regarding healthiness ($M_{\text{Healthy_food}}=5.46$, $SD=.57$, $Z=3.06$, $p<.005$; $M_{\text{Unhealthy_food}}=2.65$, $SD=.33$, $Z=-3.06$, $p<.005$). Nonparametric paired sample *t*-tests (Mann-Whitney *U* test) showed that both categories (healthy and unhealthy food items) did not differ regarding tastiness ($Z=-.98$, $p=.347$), but, as intended, differed regarding healthiness ($Z=-4.16$, $p<.001$).

To ensure that unhealthy (healthy) food items were high- (low-) calorie foods, we controlled calories per serving and per plate so that unhealthy food servings ($M_{\text{Healthy_Food}}=21$ Kcal, $SD=21.43$; $M_{\text{Unhealthy_Food}}=89.29$ Kcal, $SD=41.21$; Mann-Whitney *U* test, $Z=3.55$, $p<.001$) and plates ($M_{\text{Healthy_Food}}=137.83$ Kcal, $SD=85.08$; $M_{\text{Unhealthy_Food}}=446.25$ Kcal, $SD=120.00$; Mann-Whitney *U* test, $Z=4.04$, $p<.001$) were at least three times more caloric than healthy food.

Stimuli preparation. Food and non-food items are listed in Table A1. For the localizer run, we edited 4:3 format (640×480) static pictures of an empty plate and the 36 (non grasped) food and non-food items (e.g. stationary objects such as pencils, scotch tape, post-its) taken from a lateral perspective, perpendicular to the 1PP and the 3PP in a controlled setting (i.e., under professional lighting, on black tablecloth). For the experimental runs, we edited 36 videos of the 24 food items and 12 non-food items, while two cameras on tripods filmed their grasping from a 1PP and a 3PP in a controlled setting (i.e., under professional lighting, in white mat plates, on black tablecloth, hands with black sleeves). High definition videos were in 4:3 format (640×480), 30 frames per second (fps), and were standardized in length (2,000ms) and timing (Cheng, Meltzoff, & Decety, 2007; Oosterhof, Tipper, & Downing, 2012) using Adobe After Effects CC (Adobe Systems Incorporated, San Jose, CA). Luminosity and contrast were controlled using Adobe Premiere Pro CC (Adobe Systems

Incorporated, San Jose, CA).

These stimuli featured one of three different geometric shapes (circle, rectangle and triangle) that appeared exactly 1,000ms after their beginning. In the localizer run, the geometric shape was depicted among food or non-food items on the plate or at 12 different locations on the empty plate. In total, there were 144 static pictures used in the localizer run (1 empty plate×3 geometric shapes×12 different locations per shape (=36); 12 healthy foods×3 geometric shapes (=36); and so on for unhealthy foods (=36) and stationary objects (=36)). In the experimental runs, reaching and grasping the item (food or object) lasted 1,000ms, and taking off revealed the geometric shape appearing under the grasped item for the remaining 1,000ms. In total, there were 216 videos used in the experimental runs (108 from 1PP: 12 healthy foods (from 1PP)×3 geometric shapes (=36); and so on for unhealthy foods (=36) and stationary objects (=36); 108 from 3PP (=36×3)).

Unhealthy foods	Healthy foods	Non-food objects
Brownies with nuts	Bananas	Chalk
Cheese pizza	Carrots	Clips
Cheeseburger	Cherry tomatoes	Elastic bands
Chicken nuggets	Clementine	Erasers
Crisps	Dried prunes	Mechanical pencils
Cookies	Dried apricots	Paperclips
Crackers	Maki	Pencil sharpeners
Frankfurters	Radishes	Pencils
Chocolate digestive biscuits	Apples	Pens
Mini muffins	Strawberries	Post-its
Shortbreads	Sushi	Sellotape rolls
Waffles	White grapes	USB cables

Table A1. Food and non-food items included in the present study.

Data acquisition and preprocessing

Neuroimaging was performed on a 3-Tesla BRUKER MEDSPEC 30/80 functional MRI scanner equipped with a circular polarized head coil. A fieldmap acquisition (3D FLASH sequence inter-echo time 4.552ms) was first collected in order to estimate and correct the B0 inhomogeneity. The fieldmap was followed by the acquisition of functional data which consisted of one functional localizer run, in which we acquired 205 volumes, and three experimental runs, in which we acquired 301 volumes. The functional slices acquisition was axial oblique, angled -30° relative to the AC-PC plane. This setting limited frontal distortions but prevented the collection of data at the cerebellar level. Changes in blood oxygenation level-dependent (BOLD) T2*- weighted magnetic resonance signal were measured using an echo planar sequence with 30 sequential 3 mm-thick/.5 mm-gap slices (repetition time=2,000ms, echo time=30ms, flip angle=78.4°, field of view=192 mm, 64×64 matrix of 3×3×3 mm voxels). After the functional session, whole brain anatomical MRI data was acquired using a high-resolution structural T1-weighted image (MPRAGE sequence, resolution 1×1×1 mm).

Six dummy scans in each of the four functional runs were discarded so that the longitudinal relaxation time equilibration was achieved. Data was pre-processed and analyzed using SPM8 (Wellcome Department of Cognitive Neurology, London, UK). First, processing started with the realign and unwarp procedure for distortion and motion correction, including the voxel displacement map (VDM) computed using the fieldmap toolbox. Given that the fieldmap was missing for two participants, their data went through the realign (estimate & reslice)

procedure. Second, the structural T1-weighted image was coregistered to the mean EPI image. Third, images were slice timed to correct for time differences in image acquisition between slices. Fourth, functional volumes were processed with SPM8's New Segment option to generate gray matter (GM) and white matter (WM) images. Fifth, a DARTEL template was generated and spatially normalized to MNI space. Sixth, functional data of each participant was normalized to the DARTEL template and, last, spatially smoothed using an 8 mm full-width at half isotropic Gaussian kernel.

Supplementary results

Scales

Given the Wilcoxon signed-rank tests, unhealthy foods ($M=3.98$, $SD=.46$) were rated more positively than healthy foods ($M=3.87$, $SD=.48$), but not significantly ($Z=-.70$; $p=.481$). Both foods were rated significantly more positively than objects ($M=2.78$, $SD=.59$; both $Zs < -3.70$; both $ps \leq .001$).

Participants had a low belief that what is healthy is not tasty ($M_{\text{Unhealthy=Tasty}}=2.97$, $SD=2.07$). Nonparametric paired sample t -tests (Wilcoxon signed-rank tests) on visual analogue scales (VAS) ratings showed that participants were significantly hungrier after ($M=73.30$, $SD=25.39$) than before ($M=52.10$, $SD=33.92$; $Z=-3.68$; $p < .001$) the fMRI session. They would also find eating significantly more pleasant after ($M=81.80$, $SD=18.19$) than before ($M=66.45$, $SD=29.99$; $Z=-3.29$; $p < .001$) completing the experiment. After the fMRI session, each participant ate spontaneously when offered food.

Neuroimaging results

Localizer run

Table A2

Peak	# of voxels	Coordinates			T value
		x	y	z	
UF-O					
L Lingual gyrus	180	-24	-51	-6	9.33***
R Superior occipital gyrus	196	27	-72	33	8.9***
L Superior occipital gyrus	217	-24	-87	21	8.47***
L Amygdala	85 ^a	-27	-6	-15	8.07***
R Hippocampus	102	21	-30	0	7.47***
R Insula	49 ^b	33	27	-3	7.29***
L Temporal pole: superior temporal gyrus	33	-51	12	-12	6.90***
R Amygdala	24	33	0	-15	6.67***
L Cuneus	31	0	-81	42	6.44***
R Caudate	46	9	0	3	6.41***
L Brainstem	59	-3	-18	-24	6.28***
L Middle frontal gyrus	27	-24	3	54	5.68***
Cingulate gyrus	19	0	-33	24	5.56***
R AI/IOFC	75	27	0	-18	5.27*
L AI/IOFC	46	-27	18	-18	4.55*
VS	32	6	0	-3	4.34*
HF-O					
L OFC (Inferior frontal gyrus, orbital part)	71 ^c	-27	27	-9	8.08**
L Superior parietal gyrus	188	-21	-72	57	5.95**
L Precentral gyrus	47	-36	0	51	5.47**
R Superior parietal gyrus	47	15	-69	63	5.09**
R Middle occipital gyrus	48	30	-75	24	4.84**
R AI/IOFC	51	42	15	-12	4.71*

L Amygdala	19	-18	0	-27	4.68*
R AI/IOFC	10	57	12	-9	3.6*

^a Seventy-six voxels of this cluster are located in the left amygdala ROI.

^b This cluster of voxels is not included in the right AI/IOFC ROI.

^c Sixty-one voxels of this cluster are located in the left AI/IOFC ROI.

Table A2. Brain regions obtained by a random effect model showing significant activations when viewing unhealthy foods (vs. objects) [UF–O] and healthy foods (vs. objects) [HF–O] in the localizer run (x, y and z refer to spatial coordinates in the MNI space; (*) ROI analysis, $p < .005$ uncorrected, cluster size $k > 5$ contiguous voxels; (**) whole-brain analysis, $p < .001$ uncorrected at voxel level and $p < .05$ FWE corrected for multiple comparisons at cluster level; (***) whole-brain analysis, $p < .0001$ uncorrected at voxel level and $p < .05$ FWE corrected for multiple comparisons at cluster level).

Table A3

Peak	# of voxels	Coordinates			T value
		x	y	z	
L Lingual gyrus extending into bilateral hippocampus/parahippocampal gyrus	1560	-18	-60	0	8.69**
R Middle temporal gyrus	120	57	-48	9	6.99**
L Amygdala extending into L hippocampus/parahippocampal gyrus	171 ^a	-21	-6	-15	4.39**
R Amygdala	19	18	-6	-21	4.54*
R AI/IOFC	6	36	27	0	3.36*

^a Thirty-five voxels of this cluster are located in the left amygdala ROI.

Table A3. Brain regions obtained by a random effect model showing significant activations when viewing unhealthy foods is contrasted with viewing healthy foods [UF–HF] in the localizer run (x, y and z refer to spatial coordinates in the MNI space; (*) ROI analysis, $p < .005$ uncorrected, cluster size $k > 5$ contiguous voxels; (**) whole-brain analysis, $p < .005$ uncorrected at voxel level and $p < .05$ FWE corrected for multiple comparisons at cluster level).

Experimental runs

Table A4

Peak	# of voxels	Coordinates			T value
		x	y	z	
F1PP–O3PP					
L Amygdala	12	-15	-3	-21	4.00
VS	7	0	-3	-15	3.73
R Amygdala	5	12	0	-21	3.33
UF1PP–O3PP					
L Amygdala	42	-24	-6	-18	3.94
R Amygdala	15	24	-3	-18	3.85
VS	2	0	-3	-15	3.17

VS	1	9	3	-21	2.91
HF1PP–O3PP					
VS	5	0	-3	-15	3.62
L Amygdala	4	-15	-3	-21	3.59

Table A4. Brain regions obtained by a random effect model showing significant activations when viewing unhealthy and/or healthy foods from 1PP is compared with viewing objects from 1PP ([F1PP–O3PP], [UF1PP–O3PP] and [HF1PP–O3PP]) in the experimental runs (x, y and z refer to spatial coordinates in the MNI space; ROI analysis, $p < .005$ uncorrected).

Significant activity in motor and visuomotor areas

In the experimental runs, the Food vs. Objects [F–O] and the Unhealthy food vs. Objects [UF–O] contrasts yielded a significant cluster of activations in the right middle occipital gyrus (extending into parieto-occipital areas: cuneus and superior parietal gyrus). The Healthy food vs. Objects [HF–O] contrast yielded a significant cluster of activations in the right cuneus (extending into the precuneus and superior parietal gyrus).

In 1PP trials, the Food vs. Objects [F1PP–O1PP] and the Unhealthy food vs. Objects [UF1PP–O1PP] contrasts increased activity in the right cuneus (extending from the right middle occipital gyrus to parieto-occipital areas: precuneus and superior parietal gyrus). When compared with objects, viewing healthy foods from 1PP [HF1PP–O1PP] did not reveal any significant activity above threshold criteria at the whole-brain level.

In 3PP trials, viewing (healthy) foods (vs. objects; [F3PP–O3PP] and [HF3PP–O3PP]) did not yield any significant cluster of activations. However, when compared with objects, viewing unhealthy foods from 3PP [UF3PP–O3PP] led to a significant cluster of activations in the right middle temporal gyrus (stretching from the right superior occipital gyrus to parieto-occipital areas: cuneus, precuneus and superior parietal gyrus).

Viewing unhealthy and/or healthy foods from 1PP (vs. 3PP) ([F1PP–F3PP], [UF1PP–UF3PP] and [HF1PP–HF3PP]) revealed significant clusters of activations in the left superior parietal gyrus (extending into the postcentral gyrus). Viewing unhealthy and/or healthy foods from 3PP (vs. 1PP) ([F3PP–F1PP], [UF3PP–UF1PP] and [HF3PP–HF1PP]) also led to activations in motor areas (located in the right postcentral gyrus and extending into the superior parietal gyrus).

Discussion

1) Increased activity in motor-related and taste and reward areas when viewing pictures and videos of foods (vs. objects).

As expected, in the localizer run, pictures of foods (vs. objects) lead to increased activity within the (bilateral) amygdalar and ventral striatal structural ROIs, in addition to the bilateral cluster of activity in the AI/IOFC identified as functional ROI. Exposure to food items from the present study is thus associated with activations located in the ventral reward pathway of the core eating network underlying taste and reward representations, i.e. the simulation of appetitive experiences (Chen, Papies, & Barsalou, 2016). In this vein, we also found that viewing pictures of foods (vs. objects) leads to a large network of neural activations including limbic structures (thalamus, amygdala) that are involved in both hedonic and homeostatic networks (Berthoud, 2006; Kaye, Fudge, & Paulus, 2009), and to contribute to taste and reward representations when participants are presented with visual food cues (Chen et al., 2016; Killgore et al., 2003). The thalamus, at the top of the brainstem through which interoceptive signals travel, is known to be involved in the recollection processes that make the experience of retrieval vivid (Carlesimo, Lombardi, Caltagirone, & Barban, 2015). Interestingly, the simulation of food consumption is multimodal and is supposed to re-enact not only sensory and bodily states but also motor behaviour and settings (Barsalou, 2011; Niedenthal, Barsalou, Winkielman, Krauth-Gruber, & Ric, 2005). In this perspective, we found that viewing pictures of foods (vs. objects) leads to significant activations in motor (precentral gyrus, middle frontal gyrus) and visuomotor areas (around the inferior and superior parietal lobules, and the superior occipital gyrus). It is most likely increased because the depicted food items were processed and displayed on a plate, and afforded grasping (i.e., they have the affordance of graspability) and eating (Vingerhoets, 2014). This is consistent with material obtained from verbal association tasks on the term “eating”, which also evokes desire, grasping and filling up (Lahlou, 2017, pp. 248–253).

Along the same line of argument, in the experimental runs, watching videos featuring a hand grasping (unhealthy and/or healthy) foods (vs. objects) leads to increased activity in parieto-occipital areas, which constitute the somatosensory association cortex that is involved in reaching and grasping objects in space (Vingerhoets, 2014). Activations in the right precuneus (BA7) are associated with visuomotor coordination (Vingerhoets, 2014). Activations in the right middle occipital gyrus, in the vicinity of the precuneus and at the junction of BA7 and BA40, are known to contribute to the feeling of observed movements (Costantini et al., 2005). Located in the dorsal pathway that interacts with the ventral pathway of the core eating network, this increased sensorimotor activity could facilitate the simulation of food consumption and result in approach (‘eat’) behaviors (Chen et al., 2016). We can thus speculate that activity in the motor and visuomotor areas also supported eating simulations.

2) Increased activity in motor-related areas when viewing unhealthy foods, but not healthy foods, from first- versus third-person perspective.

In the experimental runs, as suggested in the literature on motor simulation (Shmuelof & Zohary, 2005; Vingerhoets et al., 2012), a direct comparison between 1PP and 3PP trials shows increased activity in the superior parietal gyrus and the postcentral gyrus. As primary cortex, the postcentral gyrus is known to contribute to haptic imagery (Jacobs, Baumgartner, & Gegenfurtner, 2014; Lederman, Gati, Servos, & Wilson, 2001) and to be sensitive to visual food cues (Cornier et al., 2009; Killgore & Yurgelun-Todd, 2005). When viewing unhealthy foods from 1PP (vs. 3PP), activations are located in motor areas (left superior parietal gyrus, extending into the postcentral gyrus) contralateral to the observed grasping hand ([F1PP–F3PP], [UF1PP–UF3PP], and [HF1PP–HF3PP]). Reciprocally, the opposite contrasts reveal

activations in the right postcentral gyrus (extending into the superior parietal gyrus), i.e. in motor areas ipsilateral to the observed grasping hand ([F3PP–F1PP], [UF3PP–UF1PP], and [HF3PP–HF1PP]) (Shmuelof & Zohary, 2005; Vingerhoets et al., 2012).

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