Activity in the left amygdala in response to foods differs depending on the emotional context

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Abstract

Previous research has shown that emotions can influence our eating behaviors. Facing an acute stressor or being in a positive mood state are examples of situations that tend to modify appetite. However, the question of how the brain integrates food processing and emotional processing remains largely elusive. Here we designed an emotional priming fMRI task to test if amygdala activity in response to food pictures differs depending on the emotional context. We recruited 58 female participants and administered an emotional priming task, which displayed emotional photographs (depicting negative, neutral and positive situations) followed by either pictures of foods or objects. After priming in each trial, participants rated foods and objects according to how much they liked them. We focused on the contrast “foods > objects” and observed if/how this difference changed according to the emotional context. We also examined the potential effect of abdominal fat (i.e., waist circumference) on the results. We observed a higher difference between liking scores for foods and objects after positive priming than after negative priming. In the left amygdala, activity in the contrast “foods > objects” was higher after neutral and positive priming relative to negative priming. Waist circumference however, did not affect these results. Our results suggest that emotional context alters food processing, both in terms of liking scores and with regards to engagement of the left amygdala. The saliency of food is not a stable attribute, and our findings indicate that emotional context might have an impact on food processing, possibly affecting eating behavior.

Key words

Emotional priming; eating; neuroimaging; amygdala; food cue reactivity

Abbreviations

BMI, body mass index; fMRI, functional magnetic resonance imaging; MRI, magnetic resonance imaging; ROI, region of interest; SNc, substantia nigra pars compacta; vmPFC, ventromedial prefrontal cortex; VTA, ventral tegmental area

Introduction

Emotions can influence eating behaviors (Geliebter and Aversa, 2003). Specifically, it is well established that *negative* emotions can disturb our food perception and appetite (Evers et al., 2010; Macht, 2008). These effects of negative emotions on eating behavior are nevertheless largely heterogeneous, where around 30% of the population experience increases in appetite, 48% decreases in appetite and food consumption, and the rest is not changing their eating motivation (Macht, 2008). In addition to negative emotionality, some studies suggest that positive emotions might influence food intake as well. Compared to a neutral condition, when individuals are in a positive mood state, they tend to rate foods as being more pleasant (Bongers et al., 2013; Greimel et al., 2006) and they tend to increase the amount of food that they eat (Evers et al., 2013; Paquet et al., 2003).

Individuals with obesity seem to show different eating behavior in response to emotion than lean individuals. Studies have reported that psychosocial events associated with negative emotional states, such as work stress, predict weight gain in participants with high BMI (Block et al., 2009; Fujishiro et al., 2015; Kivimäki et al., 2006). In lean participants, conversely, psychosocial stress seems to be linked with weight loss or with no weight changes (Block et al., 2009; Fujishiro et al., 2015; Kivimäki et al., 2006). Individuals with high BMI also report more frequent use of eating and drinking as a stress coping strategy (Laitinen et al., 2002). These results suggest that emotions influence eating behavior differently in individuals with obesity compared to lean individuals.

In the brain, the amygdala is one of the regions that might strongly reflect changes in food processing according to emotions. Functional fMRI studies have reported a specially robust engagement of the bilateral amygdala in response to negative emotional stimuli (García-García et al., 2016). This brain region is frequently selected as Region of Interest (ROI) in emotional priming studies (Pichon et al., 2012). The amygdala has also been widely implicated in the processing of food and other rewarding stimuli (Sescousse et al., 2013; Tang et al., 2012; van der Laan et al., 2011). Moreover, altered amygdala activity might have clinical significance, since both individuals with obesity and patients with substance use disorders were shown to exhibit *enhanced* activity of this region in response to food and drug stimuli (García-García et al., 2014).

The amygdala exhibits widespread connections with the rest of the brain. Its basolateral subdivision is bilaterally connected with the hippocampus, medial prefrontal cortex and orbitofrontal cortex, and these connections seem to sustain habit-based behavior, cognitive control and reward processing, respectively (Janak and Tye, 2015). The central nucleus of the amygdala projects efferent signals to the ventral tegmental area (VTA) and to the substantia nigra pars compacta (SNc), possibly modulating the computation of reward signals (Watabe-Uchida et al., 2012). Researchers in the neurobiology of emotion and eating behavior have also emphasized the importance of the interactions between the amygdala and the ventromedial prefrontal cortex (vmPFC). This circuit is critically involved in the processing of subjective value, emotion regulation and fear extinction (Clithero and Rangel, 2013; Phelps et al., 2004; Seo et al., 2016). Studies have shown that animals with lesions in the amygdala-vmPFC pathways show altered decision making (Baxter et al., 2000; Fiuzat et al., 2017; St. Onge et al., 2012). In a similar vein, initial evidence in humans with amygdala lesions suggest that these patients exhibit altered activity in the vmPFC during reward expectation and behavioral choices (Hampton et al., 2007).

In sum, the amygdala has been implicated in the processing of both emotional stimuli and food, and it is widely connected with other reward and salience areas. This makes the amygdala a plausible structure engaged in the modulation of food processing according to the emotional context. However, to date there is no study directly addressing the role of the amygdala in this modulation.

In the present study we examine how emotional stimuli modify the subsequent processing of food cues in the brain. We designed an *fMRI emotional priming task* where we displayed sets of food and non-food (i.e., objects) pictures right after the presentation of emotional stimuli (negative, neutral, and positive). The first step was to test whether the emotional images were able to elicit a pattern of brain activity that is in line with the existing literature. Second, we examined the contrast "foods > objects" across the different emotional conditions. We hypothesized that both liking scores and activity in the amygdala in response to food stimuli would vary depending on the emotional context. We also hypothesized that body weight status, measured with waist circumference, would have an effect on the fMRI signal and liking rates. Finally, we examined the correlation between amygdala and vmPFC across the different emotional conditions.

Methods

Participants

The final sample consisted on 58 participants with their body mass index (BMI) ranging from 17.67 to 46.83 kg/m^2. We recruited participants from the volunteers' pool of the Max Planck Institute for Human Cognitive and Brain Sciences (Leipzig, Germany). We only included women in the study to reduce potential sex-related heterogeneity in the responses to emotional stimuli and food stimuli. The study was performed in compliance with the Declaration of Helsinki and was approved by the local ethics committee of the University of Leipzig.

Prior to the study, potential participants completed a screening interview by telephone. Inclusion criteria were female gender and age of 20-35 years old. Exclusion criteria comprised a history of neuropsychiatric disorders –such as depression (Beck Depression Inventory, BDI > 18) – medical disorders such as hypertension, hyper- or hypothyroidism, cancer, and diabetes, as well as left-handedness and MRI incompatibilities.

During the recruitment process, two additional participants had to be excluded due to pathologies not detected during the screening interview, one additional participant declined to perform the MRI session, and six additional participants were removed from the fMRI analysis due to excessive head movements. All subjects gave written informed consent prior to taking part in the study and received a compensation for their time in the study.

Anthropometric measures

On the day of the fMRI acquisition, we measured participants' weight, height, waist circumference and hip circumference. We used waist circumference as a surrogate measure of adiposity in our analyses. Nevertheless, we repeated all the analyses using BMI instead of waist circumference and the results did not change (data not shown).

Self-report questionnaires

A week before the date of the MRI acquisition, participants received an internet-based survey (with Limesurvey platform, www.limesurvey.org). The data collection for the present project was coordinated with a second independent project aimed at tackling social processing in obesity, whose results will be presented elsewhere. Participants completed several questionnaires that addressed social support and withdrawal as well as personality and eating behavior. We additionally evaluated chronic stress with the Trierer Inventar zum Chronischen Stress (TICS) (Schulz et al., 2004). The total time estimated for the completion of the Internet survey was 45 minutes.

Emotional priming task

Participants completed an fMRI event-related food processing task, in which we presented food and object photographs preceded by priming emotional stimuli. The task consisted of 6 conditions, combining 3 types of priming (negative, neutral, and positive) and 2 types of stimuli (food and objects).

Participants viewed an emotional picture (negative, neutral or positive) for 4 seconds. After a 2 seconds inter-stimuli interval with a blank screen, we presented either a food photograph or an object photograph for another 2 seconds. Subsequently, participants were asked to rate how much they liked the food/object on a -5 to +5 Likert scale, by utilizing a button box placed in their right hand. The Likert scale was programmed to last 8 seconds maximum, but as soon as the participants performed the rating, a fixation cross appeared on the screen for the remainder of the 8 seconds (Figure 1). Each condition consisted of 15 trials, and the order of the conditions was semi-randomized across participants – i.e., to ensure that the same condition would not appear more than twice for every 10 trials.

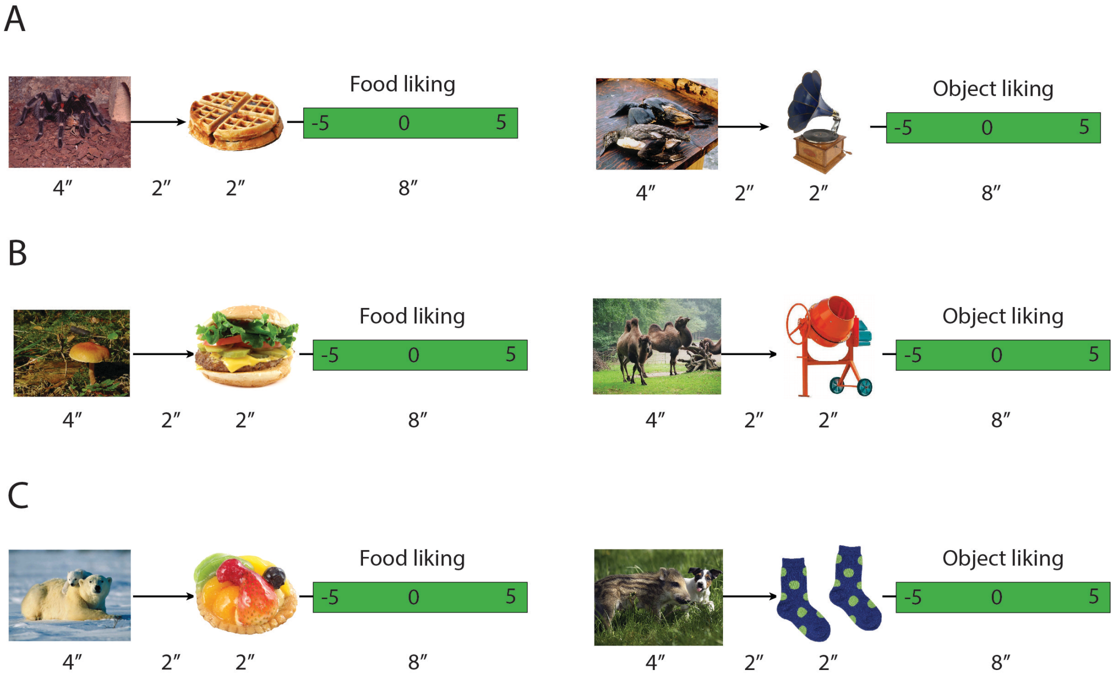

Figure 1: Schema of the fMRI task. We presented pictures of foods and objects preceded by emotional priming images. A) Negative emotional priming. B) Neutral emotional priming. C) Positive emotional priming.

Before the task we collected hunger rates (rated from 1 to 10, with higher values representing higher hunger) and number of hours before their last meal.

The emotional stimuli were extracted from the Emotional Picture Set (Wessa, M., Kanske, P., Neumeister, P., Bode, K., Heissler, J., & Schönfelder, 2010), a dataset that provides normative data from emotional images rated by German population in terms of valence and arousal. We selected the images rated as lowest, neutral, and highest in terms of valence for the negative, neutral, and positive emotional categories respectively. Repeated measures ANOVAS showed that the three image categories were similar in terms of luminosity, contrast, and color saturation (lowest Bonferroni corrected p = 0.9). Similar to the population ratings, the valence of the images was significantly different between the three groups (all Bonferroni corrected p<0.001).

We selected food and object photographs from the FoodCast Research Image Database (FRIDa) (Foroni et al., 2013). Food and objects were not significantly different in spatial frequency, brightness or size (lowest p = 0.065 after Bonferroni correction). However, and similar to the population ratings, valence and arousal of food items were higher than of objects (Bonferroni corrected p=0.005 for both tests). After the MRI session, participants rated each image regarding valence and arousal using a 1-9 Likert scale.

MRI acquisition

Images were acquired on a 3 Tesla Skyra scanner (Siemens, Erlangen, Germany). Eight hundred seventeen whole brain fMRI volumes were acquired using a multi-slice gradient-echo EPI sequence during 27.20 minutes [echo time (TE): 22 ms; repetition time (TR): 2000 ms; 2.5 mm slice thickness; 40

slices per volume; 20% interslice gap; 90º flip angle; 192 mm field of view (FOV); voxel size 3.0 x 3.0 x 2.5 mm^3].

For each participant, we also acquired a T1-weighted anatomical image with an MPRAGE ADNI protocol with 9.14 minutes of duration (T1: 900 ms; TE: 2.01 ms.; TR: 2300 ms.; 1-mm slice thickness; 50% interslice gap; 9º flip angle; 256 mm FOV; bandwidth: 240 Hz/pixel; sagittal orientation; voxel size: 1.0 x 1.0 x 1.0 mm^3).

FMRI analysis

We preprocessed and analyzed MRI data using SPM12 (Wellcome Trust Centre for Neuroimaging, UCL, London, UK), implemented in Matlab (The MathWorks Inc., Sherborn, MA). First, fMRI volumes were unwarped and spatially aligned to the first image of the session. Realignment parameters (motion parameters) were calculated and later used as nuisance regressors. We then performed slice-timing correction to the anatomical middle slice and coregistered the fMRI data to the high-resolution anatomical image. The reference image was segmented into gray matter, white matter and cerebrospinal fluid, and the MRI images were normalized to Montreal Neurological Institute (MNI) standard space. Finally, we applied an isotropic Gaussian kernel of 8 mm FWHM to smooth the normalized images.

For each participant, we modeled on the first level (a) the onset of each category of emotional stimuli (b) the onset of food and objects. That is, our design had 3 regressors modeling priming stimuli (negative, neutral and positive) and 6 regressors modeling the events of interest: (i) food presented after negative priming; (ii) objects presented after negative priming; (iii) food after neutral priming; (iv) objects after neutral priming; (v) food after positive priming; (vi) objects after positive priming. All six-motion parameters were modeled as nuisance regressors. Fixation trials and the time corresponding to perform the liking rates for foods/objects were left unmodeled.

First, we tested if priming stimuli elicited brain activity in coherence with what has been previously described in the literature. For that, we included the contrasts “negative emotional images > neutral images” and “positive emotional images > neutral images”. We did not include the comparison between negative images and positive images since this contrast does not usually yield a robust pattern of brain activity (Lindquist et al., 2015).

Our main contrast of interest was the difference in fMRI activity between foods and objects. We assessed this contrast (i.e., foods > objects) for each category of emotional priming (e.g., negative priming: foods > objects).

In a second-level analysis, we performed one-sample t-tests to examine the effect of each contrast; and we tested for the effects of obesity by including waist circumference as a regressor of interest. We included framewise displacement, calculated from the movement parameters (Power et al., 2012), as a nuisance regressor. Statistical threshold was set at FWE corrected $p<0.05$ at the voxel level.

Amygdala analysis

We tested whether amygdala activity for the contrast “food stimuli > objects” was influenced by emotional priming stimuli. We used the MarsBaR (MARSeille Boîte À Région d’Intérêt) toolbox from SPM to extract data from the amygdala. The amygdala ROI was defined with the Harvard-Oxford Atlas. In brief, MarsBaR allows calculating the mean for all the voxels included in the ROI. This produces time-course values for each subject and for each regressor specified in the first level analysis. We extracted the time courses associated with our events of interest (6 events that are the combination of 3 emotional priming (negative, neutral, positive) and the 2 types of stimuli (food, objects)). With these values, we run the statistical model in R.

Since we were primarily interested in the contrast “food stimuli > objects”, we subtracted the values of foods and objects in the amygdala separately for each emotional priming condition.

Statistical analysis: liking rates and amygdala activity

We tested whether emotional priming modifies liking rates and amygdala activity in response to foods compared to objects. We performed a repeated measures design with a multilevel linear model and compared three conditions (i.e., (1) negative priming: foods – objects; (2) neutral priming: foods – objects; (3) positive priming: foods – objects) using the R function lme() (package nlme). We performed post-hoc tests by applying Tukey's correction.

Correlation between percentage of signal change in the amygdala and in the ventromedial prefrontal cortex (vmPFC)

With the same procedure used for the amygdala, we extracted fMRI activity in the ventromedial prefrontal cortex (vmPFC). We analyzed the correlation between amygdala activity for the contrast “food stimuli > objects” and activity in the vmPFC for the same contrast during the different emotional priming conditions. We used the MarsBaR toolbox from SPM and defined the ROI in the vmPFC according to the meta-analysis from Clithero and Rangel (Clithero and Rangel, 2013). Specifically, we built the vmPFC ROI by drawing a 10mm sphere around the coordinates 2, 28 and -18.

Results

Demographical characteristics

We included fifty-eight female participants in the analyses; see Table 1 for a distribution of the demographic and clinical variables.

Table 1. Demographic characteristics and psychological measures.

	Minimum	Maximum	Mean	Std. Deviation
Age	20.0	35.0	26.33	3.69
BMI (kg/m^2)	17.67	46.83	25.63	5.84
Waist circumference (cm)	61	104	76.57	10.44
Waist-to-hip ratio	.69	.93	.81	.05
Subjective hunger (1-10)	1	7	2.1	1.66
Hours fasting	0.1	12	2.16	2.45
BDI	.0	12.0	4.05	3.48
Chronic stress (TICS)	13	162	81.72	28.40

Post-scan ratings for valence and arousal

In line with the population rating scores, priming emotional images (negative, neutral and positive) differed both in valence ($X^2(2)=403.19$; $p<0.001$) and arousal ($X^2(2)=156.11$; $p<0.001$) ratings in our sample. Likewise, foods and objects differed in valence ($X^2(1)=8.91$; $p<0.003$) and arousal ($X^2(1)=41.80$; $p<0.001$) ratings, with food stimuli obtaining higher scores for both measures (Figure 2).

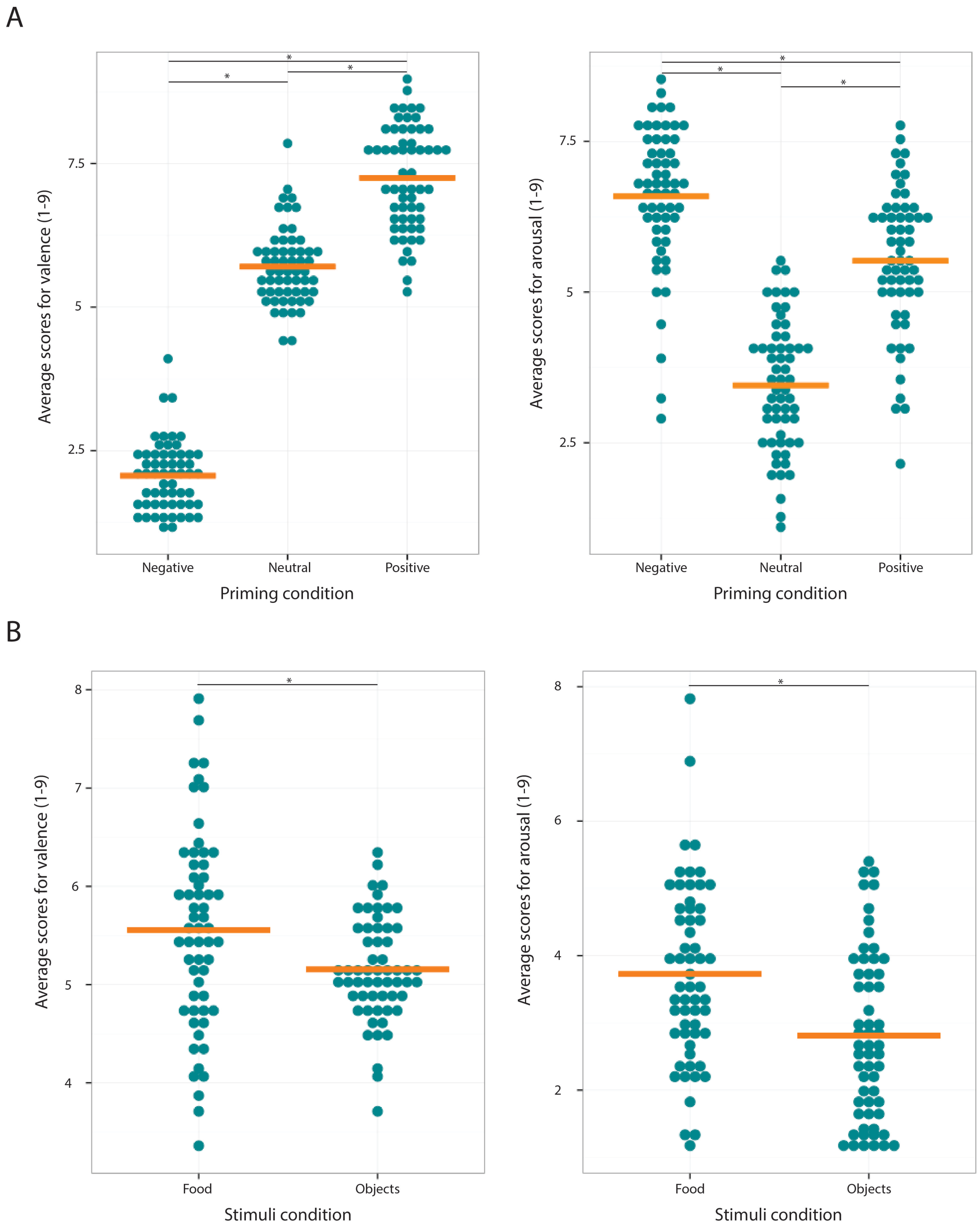

Figure 2. Average scores for valence and arousal provided after the MRI scan. (A) Scores for each priming emotional stimuli (negative, neutral and positive). (B) Average scores for food and object stimuli. Asterisks depict significant post-hoc differences.

Liking rates

The multilevel model for repeated measures showed that priming condition had an effect on the difference between liking scores for food and objects $X^2(2)=6.286$; $p=0.0432$. Post-hoc tests indicated that the difference between liking scores for foods and objects was higher during the positive priming condition compared to the negative priming condition ($z=2.48$; $p=0.0355$) (Figure 3). Participants' waist circumference had no effect on the liking rates, $X^2(3)=0.01$; $p=0.945$.

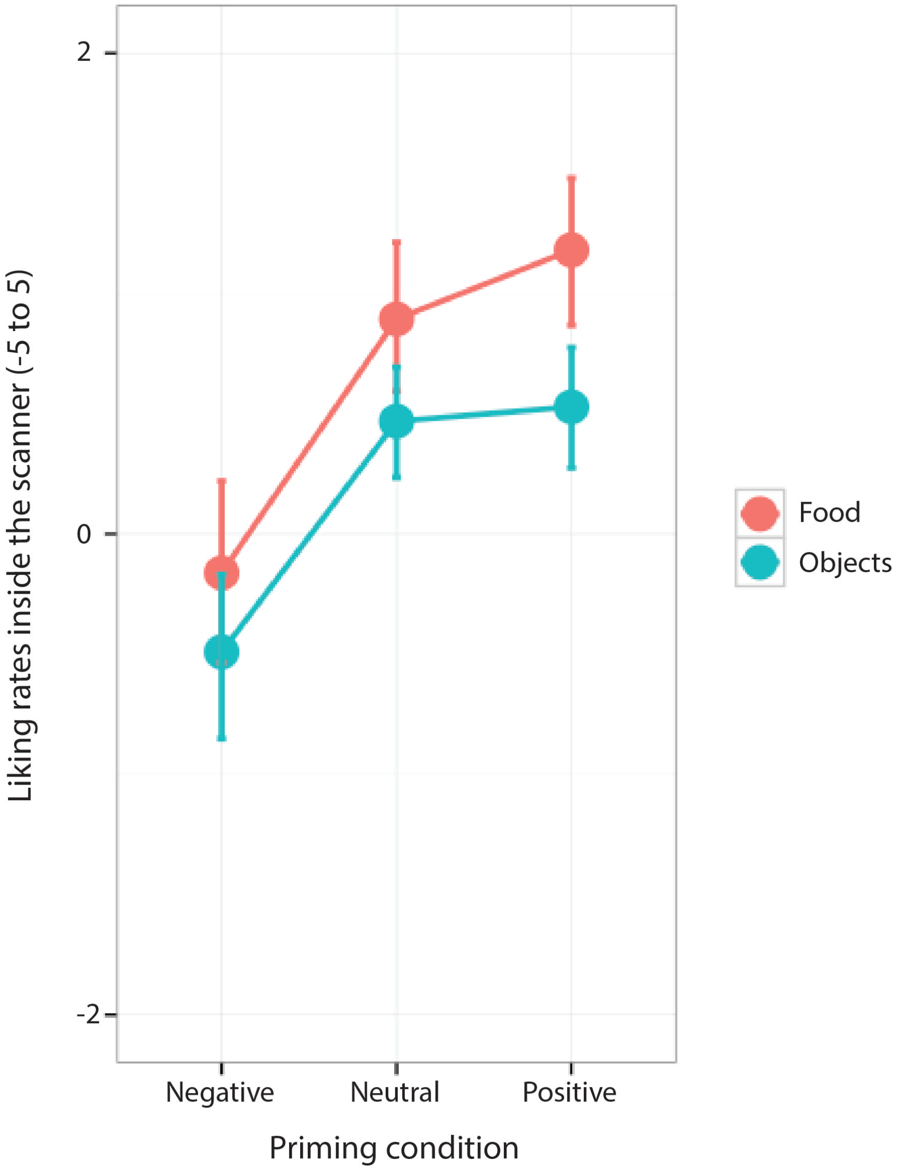

Figure 3. Liking rates for food and objects during the negative, neutral and positive priming condition. The error bars represent 95% confidence intervals.

Neuroimaging results

The emotional priming task contained two sets of images: emotional images (priming stimuli) and the events of interest (foods and objects under each emotional priming condition).

0. Effects of emotional images

In order to test that the emotional images were able to yield a pattern of activity in line with what it has been described in the literature, we first examined the contrasts “negative emotional stimuli > neutral stimuli” and “positive emotional stimuli > neutral stimuli”. Relative to neutral stimuli, negative emotional images activated the left amygdala, bilateral temporal occipital fusiform, brainstem right precentral gyrus, right inferior frontal gyrus, left OFC and left lateral occipital cortex. The contrast positive > neutral stimuli activated the bilateral lateral occipital cortex and the precuneus (Table 2).

Table 2. Whole brain results for the emotional priming stimuli

Brain region	MNI Coordinates			Cluster size	T
	X	Y	Z		
Negative emotional stimuli > Neutral stimuli					
Left amygdala	-20	-6	-12	654	9.90
Right temporal occipital fusiform	46	-42	-18	1027	9.44
Left temporal occipital fusiform	-40	-50	-16	734	9.18
Brain stem	-6	-28	-10	370	8.76
Right precentral gyrus	44	8	28	239	8.09
Right inferior frontal gyrus	50	34	8	244	7.68
Left OFC	-28	12	-18	61	7.11
Left lateral occipital cortex	-46	-64	16	107	6.79
Positive emotional stimuli >Neutral stimuli					
Right lateral occipital cortex	44	-80	-10	1147	11.01
Left lateral occipital cortex	-38	-86	-10	913	10.38
Precuneus	0	-60	32	63	5.98
Results are FWE corrected at the voxel level p<0.05; minimum cluster size: 50 voxels.					

1. The contrast foods > objects: differences depending on the emotional priming condition

Under negative priming, the contrast foods > objects yielded activity in the occipital pole and lateral orbitofrontal cortex (OFC) bilaterally. After the presentation of neutral images, we found that the contrast foods > objects engaged bilateral activity in the occipital pole, lateral occipital cortex, insula and amygdala. Finally, during the positive priming condition, the contrast foods > objects was associated with bilateral activity in the lateral OFC, occipital pole, insula, as well as with left lateralized activity in the amygdala (Table 3; Figure 4).

Table 3. Whole brain results for the events of interest

Brain region	MNI Coordinates			Cluster size	T
	X	Y	Z		
Negative priming condition: Foods > Objects					
L occipital pole	-12	-94	-2	588	9.18
R occipital pole	12	-90	-4	581	8.44
R lateral OFC	20	30	-16	83	8.31
L lateral OFC	-26	34	-14	96	7.92
Neutral priming condition: Foods > Objects					
R occipital pole	14	-92	0	2414	11.82
R insula	38	8	-12	148	8.71
L lateral OFC	-26	34	-14	94	8.69
L amygdala	-22	-6	-12	245	8.13
R amygdala	20	-2	-16	113	8.13
L insula	-36	-4	10	90	7.86
R lateral OFC	24	30	-16	53	7.20
Positive priming condition: Foods > Objects					
R lateral OFC	22	28	-16	132	10.05
L lateral OFC	-26	32	-16	130	9.53
L occipital pole	-12	-94	-8	694	9.33
R insula	38	4	-12	132	8.21
R occipital pole	16	-92	2	663	8.20
L insula	-38	-6	10	67	7.32
L amygdala	-18	-4	-22	79	7.30

Results are FWE corrected at the voxel level p<0.05; minimum cluster size: 50 voxels.

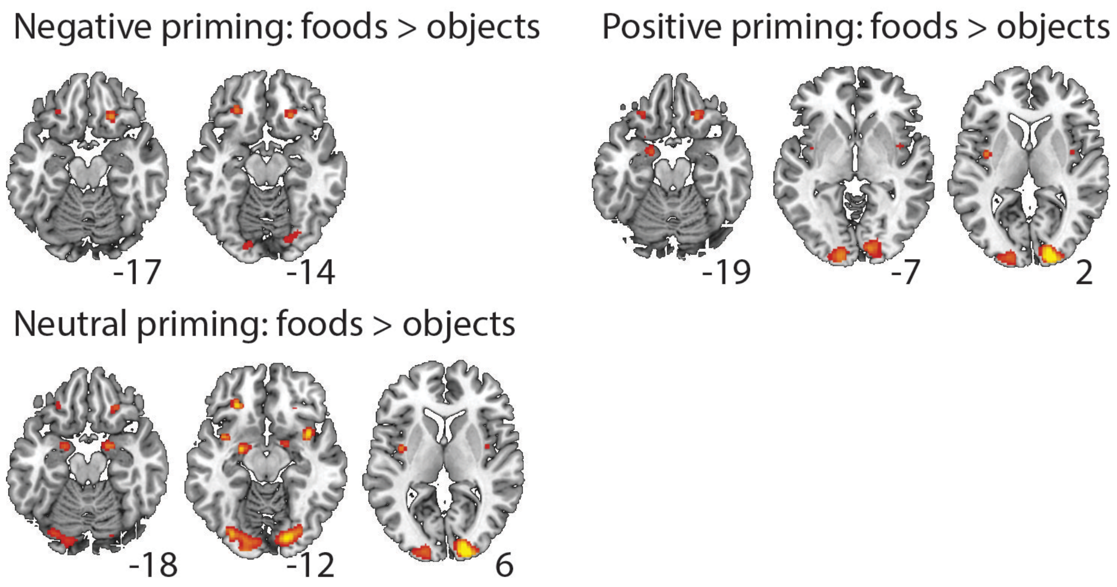

Figure 4. Whole brain fMRI results for the contrast “foods > objects” during the different priming conditions.

2. Interactions in the amygdala

Emotional priming had a significant effect on the difference between fMRI activity in the left amygdala in response to food stimuli and objects, $X^2(2)=6.374$; $p=0.041$. Orthogonal contrasts showed that differences in fMRI activity between foods and objects were significantly higher during neutral and positive priming compared to negative priming, $b=0.015$; $t_{(114)}=2.509$; $p=0.014$ (Figure 5). There was no effect of priming in the right amygdala.

Waist circumference had an additional effect on fMRI activity in the left amygdala $X^2(4)=4.754$; $p=0.029$. A closer examination into this effect indicated that, during the neutral priming condition, waist circumference was inversely related to the difference in left amygdala activity between food stimuli and objects (r=-0.40; Bonferroni corrected p=0.006). There was no effect of waist circumference in the other conditions.

Finally, we tested if the difference between foods and objects in terms of liking scores was correlated with the difference between foods and objects in terms of amygdala activity. The results of the correlations were not significant.

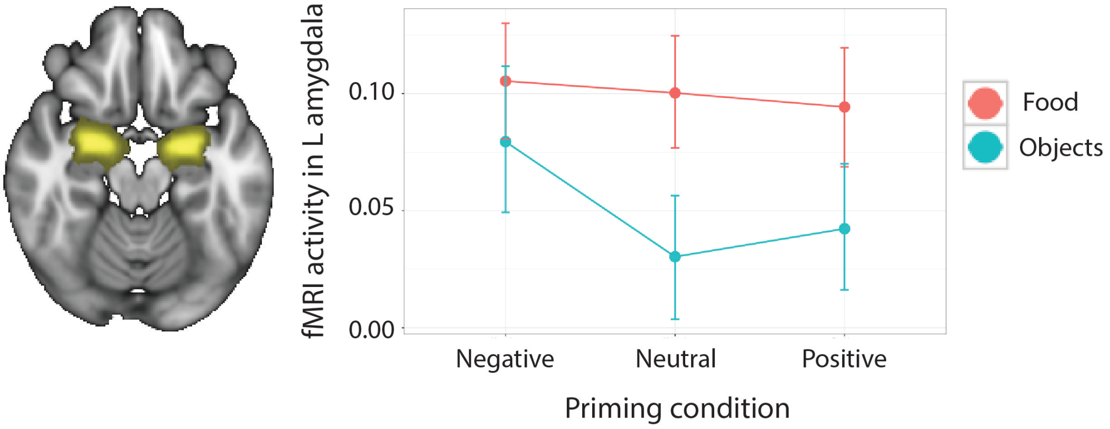

Figure 5. Emotional priming shows a significant effect on the difference between fMRI activity in the left amygdala in response to foods and objects.

3. Correlations between average activity in the left amygdala and average activity in the ventromedial prefrontal cortex

Activity in the left amygdala was significantly correlated with activity in the vmPFC for the contrast “foods > objects” during the 3 emotional conditions (negative priming: r=0.464, Bonferroni corrected p<0.001; neutral priming: r=0.423, p=0.003; positive priming: r=0.518; p<0.001). That is, between 18% and 27% of the variance on activity in the vmPFC was explained by activation in the left amygdala.

Discussion

The current study examined whether emotional context can influence the neural processing of food stimuli. To this aim, we designed an fMRI task that displayed emotional priming stimuli (photographs representing negative, neutral and positive situations) followed by the presentation of foods and objects. We obtained subjective liking rates for foods and objects and examined the contrast “foods > objects” across the different emotional contexts. We found that the difference between foods and objects in terms of liking scores was higher after the positive priming condition than after the negative priming condition. Likewise, the difference in amygdala activity between foods and objects was higher after the neutral and the positive emotional prime than after the negative emotional prime. Waist circumference, however, did not have an effect on emotional food processing. Our results suggest that food processing is not a rigid mechanism and that it seems to change according to the emotional context. Specifically, and given the role of the amygdala in salience processing, negative emotional context could potentially induce a decrease of saliency in food stimuli.

Neurobehavioral effects of emotional context on food processing

Eating is a potent pleasant and rewarding behavior. The rewarding value of food arises from signals in the mesolimbic dopamine circuit, a brain system that drives approach responses towards food and other rewards (Haber and Knutson, 2010). The processing of food, however, might not be rigid. Hunger, for instance, is a factor that can impact on the way that mesocorticolimbic areas process food (Charbonnier et al., 2018). In the current study, we have focused on emotional context, a variable that might putatively impact on eating behaviors.

Participants in our study rated foods higher than objects in terms of liking. This difference between food and objects, however, was higher after positive priming and lower after negative priming. Our findings thus suggest that emotional context modifies food liking.

Emotional experiences seem to play complex roles in the perception of reward and pleasure. For instance, anhedonia –i.e., decreases in the ability to experience pleasure – might occur as a consequence of negative emotional states. Using a threat-of-shock task, a behavioral study in healthy women showed that acute stress impaired responsiveness on a monetary decision making task (Bodgan and Pizzagalli, 2016). In a similar vein, a behavioral study on music suggested that, when participants listened to music that they disliked, they rated chocolate ice cream as being less pleasant. When the same participants listened to music that they liked, they rated chocolate ice cream as being more pleasant (Kantono et al., 2016).

Across all the emotional priming conditions, the contrast “foods > objects” yielded a pattern of brain activity that was closely in line with previous findings. This pattern included the occipital cortex, lateral OFC, insula and amygdala. Similar to our findings, a meta-analysis on 17 studies examined the neural correlates of food pictures and reported a consistent engagement of the posterior fusiform gyrus, lateral OFC and the insula. The same paper found that the amygdala was additionally engaged when participants were in a hungry condition, possibly reflecting the role of the amygdala in salience processing (van der Laan et al., 2011).

The amygdala is a brain region highly involved in the processing of emotional stimuli as well as in food processing. For this reason, we chose the amygdala as our main ROI. In line with our hypothesis, fMRI activity in the left amygdala in response to food stimuli showed differences according to the emotional context. Specifically, food processing was decreased during negative priming as compared to positive and neutral priming. Our results also indicate that a substantial proportion of variance on activity in the vmPFC was explained by activation in the left amygdala, speaking for a high functional connectivity between vmPFC and amygdala when food reward is processed (Seo et al., 2016).

Detecting and processing negative emotional stimuli in an efficient manner is crucial for survival. One possible interpretation for our findings in the amygdala is that a negative emotional condition might decrease the relevance of food. Hypothetically speaking, when an organism perceives negative emotional stimuli, it might elicit a general state of alertness to provide appropriate responses to the stimuli (such as fight or flight). This general state of alertness might overshadow other important stimuli, like food, that are comparatively less crucial. This way, foods and objects might be assigned a similar amount of salience resources. Conversely, when the emotional context is neutral or positive, the organism might be in a more favorable position to discriminate between the processing of rewarding stimuli (e.g., food) and neutral stimuli such as objects. In this vein, acute stressors seem to suppress appetite responses by engaging the hypothalamic-pituitary-adrenal axis (Sominsky and Spencer, 2014). An interesting possibility here is that the similar processes might apply when replacing the food stimuli with another motivating stimuli, such as monetary reward. While we could not find direct evidence supporting this hypothesis, a previous study suggests that emotional cues enhances monetary loss aversion responses in the amygdala and striatum in individuals reporting low levels of anxiety (Charpentier et al., 2016).

The current study is, to our knowledge, the first one to use an emotional priming task to test for neurobehavioral interactions between emotional context and food processing. However, previous studies have applied stress paradigms (a condition associated with negative emotionality) to evaluate the role of the amygdala and other corticolimbic areas on food-related behaviors. In this vein, two studies have suggested that, under stress, the amygdala and other mesocorticolimbic areas are *less engaged* in response to food. The first study, conducted in healthy female participants, suggested that, relative to a neutral condition, participants in a stressful condition exhibited lower activation in amygdala, cingulate cortex, and hippocampus while performing a food choice task (Born et al., 2009). A second study, which examined women with bulimia nervosa symptoms, showed that being in an experimental stressful situation was associated with decreases in BOLD signal in the anterior cingulate cortex, amygdala and ventromedial prefrontal cortex in response to food cues, as compared to a non-stressful control condition (Fischer et al., 2017). Moreover, these decreases in BOLD signal seemed to act as mediators on the relationship between increased negative affect and binge eating episodes (Wonderlich et al., 2018). However, evidence for the opposite effect, and findings that activity in the amygdala is *higher* during stress, also exist. Using an fMRI food choice paradigm, a study on male participants reported that, compared with participants in a neutral condition, subjects assigned to a stressful condition put greater weight on the taste of the food items presented. In parallel, bilateral amygdala and right nucleus accumbens reflected the relative taste value of chosen options more strongly in stressed compared to control participants. The authors interpreted these findings as suggesting that stress may increase the effect of the rewarding attributes of the stimuli (Maier et al., 2015).

Finally, another study examined fMRI activity in response to food stimuli in university students (both sexes) during final exam period and during a non-exam period. Personality differences in stress reactivity, as measured by the behavioral inhibition scale, predicted increases in perceived stress during the final exam period. Moreover, higher scores in the behavioral inhibition scale were associated with increased fMRI activity during exam versus non-exam period in the amygdala and vmPFC in response to foods (Neseliler et al., 2017).

Methodological heterogeneities between studies limit the comparability between the current studies and previous fMRI studies in stress. The most obvious one is that stress paradigms and emotional priming paradigms might not produce equivalent emotional reactivity. Sex is another factor that compromises the generalizability of our results, since we only recruited women in our study.

Weight status does not have an effect on the interaction between emotional context and food processing

Overweight and obesity may play an important role in the interplay between emotions and food consumption. Previous studies have reported that participants' body mass affects food intake and weight gain during chronic stress (Fujishiro et al., 2015; Kivimäki et al., 2006). In our statistical models, however, waist circumference did not have an impact on liking scores. In the case of the amygdala analysis, the effect of waist circumference was driven by the neutral (non-emotional) condition. Our findings thus do not support the hypothesis that waist circumference has a differential influence on food processing according to the emotional context. However, more studies are needed before this statement is conclusive.

Conclusions

In the present study we have addressed two main questions: (i) how does emotional context (negative, neutral and positive) influence the neurobehavioral processing of food and non-food stimuli; and (ii) whether waist circumference (a surrogate measure of abdominal fat) affects the interplay between emotional stimuli and food processing. Our findings suggest that liking scores seem to change in coherency with the valence of the emotional context. Liking scores for both food and non-food stimuli were lowest after negative priming and increased after neutral and positive priming, with overall higher scores for food compared to non-food stimuli. Most importantly, during the negative emotional context, the difference in liking scores between foods and objects was lower than during the positive emotional context. That is, positive priming had a stronger effect on food compared to non-food stimuli. Similar to this, the difference in amygdala activity between foods and objects was lower during the negative emotional context than during the neutral and positive emotional context. This is the first time that the interactions between emotional priming and food processing have been observed both behaviorally and with fMRI. Our findings emphasize the importance of emotional experiences in the context of food processing, and might inform clinical research and interventions. Future lines of research should extend these findings to patients with eating disorders.

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