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Title: Do food odors differently influence cerebral activity depending on weight status? An electroencephalography study of implicit olfactory priming effects on the processing of food pictures

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Abstract: Attentional automatic processes and cerebral activity may differ between individuals with different weight statuses in the presence of food stimuli (e.g. odors, pictures). In the present study, we used an implicit olfactory priming paradigm to test the influence of non-attentively perceived food odors on the cerebral activity underlying the processing of food pictures, in normal-weight, overweight, and obese adults. A pear odor and a pound cake odor were used as primes, respectively priming sweet low-energy-density foods and high-energy-density foods. Event-related potentials were recorded while the participants passively watched pictures of sweet low and high-energy-density foods, under the two priming conditions plus an odorless control condition. The amplitude and latency of several peaks were measured (P100, N100, P200, N400). As a major result, we found that weight status influences the cerebral activity underlying the processing of food cues outside of consciousness, as early as the first detectable P100 peak.

Keywords: obesity, food, odor, priming, event-related potentials, EEG

Introduction

Overweight and obesity are defined by the World Health Organization as 'abnormal or excessive fat accumulation that may impair health' (World Health Organization, 2020). In general, excess weight is characterized by a body mass index (BMI) between 25 and 30, and a person is considered as obese if her/his BMI is above 30. Across the world in 2016, 39% of adults aged 18 years and over were overweight, and 13% were obese. Moreover, the worldwide prevalence of obesity nearly tripled since 1975. This is a major public health concern given that obesity is a significant risk factor for several conditions that can reduce the quality of life and life expectancy, such as cardiovascular diseases, diabetes, and cancer (Abdelaal, Roux, & Docherty, 2017; Kumanyika, Jeffery, Morabia, Ritenbaugh, & Antipatis, 2002; Meegan, Perry, & Phillips, 2017; Rahati & Shahraki, 2014; Walker, 2013).

Excess weight appears when there is an energy imbalance between the calories consumed and expended. According to the World Health Organization, this imbalance is mostly due to an increased intake of high-energy-density foods coupled with a decrease in physical activity, favored by the sedentary nature of our modern lifestyles. Several public health interventions have been developed to promote a healthier lifestyle, with a particular focus on diet (Hill, Peters, Catenacci, & Wyatt, 2007). However, evidence suggests that providing the population with explicit dietary guidelines or nutritional information may have little effect on food choices, as obesity rates keep increasing (Mozaffarian, Angell, Lang, & Rivera, 2018). The poor efficiency of such interventions may rely on the fact that they target explicit food-choice behavior, while food choices may be mainly guided by non-conscious and automatic processes (Cohen, 2008; Jacquier, Bonthoux, Baciu, & Ruffieux, 2012; Papies, 2016; Sheeran & Gollwitzer, 2012). To develop more efficient interventions to improve people's diet, a better understanding of the non-conscious mechanisms underlying food choices and weight gain is needed.

In this context, it has been suggested that particular patterns of cognitive functioning and cerebral activity in the presence of food stimuli may be involved in food choices, and may differ depending on weight status. Current data showed indeed that overweight and obese individuals present greater attentional biases toward visual food stimuli (e.g. pictures, words), compared with normal-weight individuals (for a review, see Hendrikse et al., 2015). "Attentional bias" refers to the process by which a person's attention is automatically oriented toward certain types of stimuli, that are more salient for her/him. Increased salience of food stimuli in the environment enhances the probability of the food to be chosen (Cohen, 2008), and the intensity of the attentional bias toward food cues may be a predictor of weight gain (Yokum, Ng, & Stice, 2011). Therefore, an automatic and increased allocation of attention toward food cues in individuals with higher BMIs may contribute to overeating and weight gain. This phenomenon may partly explain why some individuals fail to respond to explicit dietary interventions to maintain or lose weight (Hendrikse et al., 2015).

Moreover, there is evidence that the cerebral activity underlying attentional processes may also differ as a function of BMI, starting from early stages of the cerebral processing of food cues (for reviews, see Carbine et al., 2018; Hendrikse et al., 2015). Studies using electroencephalography (EEG) to record event-related potentials (ERPs) reported a greater amplitude of the P200 peak elicited by visual food stimuli in obese individuals, compared with normal-weight individuals (Hume, Howells, Rauch, Kroff, & Lambert, 2015; Nijs, Franken, & Muris, 2010). Both of these studies used modified Stroop tasks, one with food pictures (Hume et al., 2015), and the other with food words (Nijs, Franken, et al., 2010). The P200 is a mid-latency component of the ERP waveform peaking around 200 ms after stimulus presentation, and reflecting preconscious attentional processing: the greater its amplitude, the greater the involvement of automatic attentional resources to process the stimuli. Therefore, individuals with higher BMIs may allocate more cerebral resources to process food cues, at early and automatic stages of attention orientation. However, no effect of BMI was reported on the amplitude of earlier peaks such as the P100 and N100, which are associated with pre-attentive sensory processing (Hume et al., 2015). Analyses focusing on later peaks associated with conscious maintained attention, such as the P300 and the *Late Positive Potential* (LPP), generally reported larger amplitudes for food than non-food stimuli, but also no differences depending on BMI (Hanlon, Larson, Bailey, & Lecheminant, 2012; Nijs, Franken, & Muris, 2008; Nijs, Franken, et al., 2010; Nijs, Muris, Euser, & Franken, 2010). These studies used passive-viewing tasks (Hanlon et al., 2012; Nijs et al., 2008), a Stroop task (Nijs, Franken, et al., 2010), and a counting task (Nijs, Muris, et al., 2010). These observations overall support the idea that weight status influences cerebral activity at specific steps of processing, and the modulation of the P200 peak in particular highlights the special role that automatic processes may play when individuals with higher BMIs are in the presence of food stimuli.

However, all foods are not equivalent in terms of energetic value. High-energy-density (HED) foods are more likely to contribute to weight gain than low-energy-density (LED) foods. Less healthy diets (i.e., more HED foods) may be one of the factors contributing to weight gain in overweight and obese populations. Thus, we can hypothesize that attentional and cerebral differences based on BMI may exist concerning the perception of foods with different energetic contents. Nevertheless, most ERP studies compared food stimuli to other types of stimuli (e.g., furniture, flowers; see Hendrikse et al., 2015), and little is known about a possible interaction of energetic value and BMI on cerebral activity. One research measured the N100 peak while female participants watched LED and HED food pictures, under the instructions to imagine either the immediate or long-term effects of consumption ("perspective" factor; Meule, Kübler, & Blechert, 2013). The results showed that LED food pictures elicited a larger N100 amplitude than HED food pictures, independently from perspective. The effect of BMI was not tested in this study, although the experimental group included underweight, normal-weight, and overweight participants (BMI range: 17.60 – 27.80). Other authors used a go/no-go task to assess inhibitory control for food pictures with various energetic values, in individuals with different BMIs (Carbine, Christensen, et al., 2017). The N200 peak was measured as an index of inhibition. When the participants had to refrain from answering (no-go trials), the results showed a greater N200 amplitude for HED than LED food pictures for all participants. This suggests that HED foods required increased recruitment of inhibitory control processes than LED foods, but with no differential effect of BMI. The impact of energetic value on the P200 peak is yet unknown but appears particularly interesting to test, as there is already evidence of its sensitivity to weight status.

To better understand food choices, it seems also necessary to assess the factors that may modulate these attentional and neurophysiological processes in favor of particular foods (i.e., LED or HED foods). In this context, interesting results have been provided with priming paradigms using food odors as cues. Priming is a paradigm that consists in exposing individuals to one stimulus (prime) to influence a response to a subsequent stimulus (target). The target can be either congruent (related) or incongruent (unrelated) to the prime. Zoon, De Graaf, & Boesveldt (2016) reported that exposing normal-weight subjects to food odors (e.g., HED-sweet odors) increased their appetite for the congruent products (e.g., HED-sweet foods). Moreover, implicit olfactory priming paradigms showed that the food odors do not need to be attentively perceived to cause a priming effect on behavior. A couple of studies showed indeed that in the presence of low LED food odors (e.g., pear, melon), normal-weight adults chose significantly more vegetable-based plates and fruits from a buffet than in a non-odorized condition (Gaillet, Sulmont-Rossé, Issanchou, Chabanet, & Chambaron, 2013, 2014). Similar results were observed when the subjects were primed with a HED, fatty-sweet odor: they tended to choose more HED desserts (Chambaron, Chisin, Chabanet, Issanchou, & Brand, 2015). In these studies, the olfactory priming was implicit, which means that all participants declared that they did not attentively perceive the olfactory primes. Therefore, the presence of a non-attentively perceived food odor may influence the subsequent food-choices, at least in normal-weight individuals.

As overweight and obese persons present an enhanced reactivity to food cues (Hendrikse et al., 2015), we can expect that olfactory priming effects may be stronger for them, at least on attentional processes. To bring some answers to this question, a recent study compared the impact of implicit and explicit olfactory priming on attention toward food pictures, in subjects with different weight statuses (Mas, Brindisi, Chabanet, Nicklaus, & Chambaron, 2019). By using a visual-probe task, they reported greater attentional biases toward pictures of sweet foods (vs. non-food pictures) in obese subjects primed with a HED food odor (pound-cake), than when primed with a LED food odor (pear). The trend was reversed in normal-weight subjects, and no significant effects were observed in overweight subjects. Interestingly, the priming effect in obese individuals was only present when the exposure to olfactory primes was implicit. Obese individuals may thus be particularly sensitive to non-attentively perceived HED food cues from the environment, which may automatically direct their attention toward available foods, and contribute to a tendency to overeat. These results also suggest that overweight and obese persons perform differently on cognitive tasks, highlighting the interest of distinguishing these two populations, which is not systematically done (Babiloni, Del Percio, Valenzano, et al., 2009; Nijs, Muris, et al., 2010).

The impact of priming on cerebral activity has been well documented for various types of stimuli (e.g. visual, auditive, olfactory), although few studies used food-related stimuli. In ERP research, the N400 peak is usually measured as an index of priming effects. The N400 is a negative ERP component that peaks between 300 and 600 ms after stimulus presentation. It is associated with meaning processing, and its amplitude reflects the degree of semantic incongruency between the prime and the target (Kutas & Federmeier, 2011). Indeed, previous research showed that N400 amplitude was consistently larger for incongruent prime-target pairs than for congruent pairs, for a variety of stimuli and across different sensory modalities (e.g., words, pictures, sounds, odors; Castle, Toller, & Milligan, 2000; Cook et al., 2017; Deacon, Mehta, Tinsley, & Nousak, 1995; Goto, Ando, Huang, Yee, & Lewis, 2010; Grigor, Toller, Behan, & Richardson, 1999; Hamm, Johnson, & Kirk, 2002; Holcomb, Anderson, & Grainger, 2005; Kowalewski & Murphy, 2013; Sarfarazi, Cave, Richardson, Behan, & Sedgwick, 1999). It has been hypothesized that N400 effects could be obtained with any stimuli from any sensory modality, as long as an associative relationship between primes and targets exists (Sarfarazi et al., 1999). In particular, previous investigations suggested that olfactory primes were effective in eliciting a cross-modal N400 peak in the presence of incongruent pictures (Castle et al., 2000; Grigor et al., 1999; Kowalewski & Murphy, 2013; Sarfarazi et al., 1999). Most of these studies used non-food odors (e.g. laundry, flowers) or combinations of food and non-food odors (Kowalewski & Murphy, 2013). Finally, longer N400 latencies for incongruent prime-target pairs were also observed but less frequently (Deacon et al., 1995). To our knowledge, the differential effect of LED and HED food odors on the N400 peak remains to be tested, as well as the impact of weight status on this measure. Considering the increased reactivity of obese individuals to food stimuli, we can wonder whether the BMI would modulate the N400 effect in a cross-modal paradigm using food odors as primes and food pictures as targets.

Further research is needed to better understand the cerebral processing of food stimuli in adults of different weight statuses. Thus, the present study aimed to investigate the priming effects of non-attentively perceived food odors on the ERPs elicited by HED and LED food pictures in normal-weight, overweight, and obese individuals, during a passive viewing task. Passive viewing is effective in eliciting various peaks associated with attentional processing, including the P200 (Becker, Flaisch, Renner, & Schupp, 2016; Blechert, Feige, Hajcak, & Tuschen-caffier, 2010; Carbine, Larson, et al., 2017; Schwab, Giraldo, Spiegl, & Schienle, 2017; Stockburger, Hamm, & Schupp, 2008), and is also commonly used in priming paradigms to elicit the N400 (Grigor et al., 1999; Kowalewski & Murphy, 2013). Based on previous implicit olfactory priming paradigms (Marty, Bentivegna, Nicklaus, Monnery-Patris, & Chambaron, 2017; Mas, Brindisi, Chabanet, & Chambaron, 2020; Mas et al., 2019), we selected the two odors that had already proven to be efficient as primes: a fruity odor (pear, priming sweet LED foods), and a fatty-sweet odor (pound cake, priming sweet HED foods). Consequently, we used pictures of sweet LED and HED foods as targets, congruent to either one of the odors (e.g., various fruits, cakes). ERPs were recorded while the participants passively watched the pictures on a computer screen, under the two priming conditions plus an odorless control condition. We measured the P100, N100, P200, and N400 peaks of the ERPs elicited by the pictures. The P100 and N100 were assessed rather for exploratory purposes, as little data is available on the subject. Both peaks are associated with pre-attentive sensory processing and seem not modulated by BMI, but one study reported an effect of energy density on the N100. Thus, we made the hypothesis that these early peaks may be modulated by the energy density of the stimuli, but not by BMI. The P200 peak was chosen because it is associated with automatic attentional processes and has proven to be influenced by BMI, and the N400 because it is a robust index of priming effects. For all participants, we expected: 1/ a greater P200 amplitude and a shorter P200 latency for congruent odor-picture pairs (e.g., pound-cake odor and HED food pictures), and 2/ a greater N400 amplitude and a longer N400 latency for incongruent odor-picture pairs (e.g., pound-cake odor and LED food pictures). Considering the increased reactivity for food cues in obese individuals, we expected these effects to be more pronounced with increasing BMI, and particularly when the pound cake odor was used as a prime.

Materials and Methods

Participants

The study was conducted in accordance with the Declaration of Helsinki, and was approved by the Comité d'Evaluation Ethique de l'Inserm (CEEI, File number IRB 0000388817-417). All participants provided written informed consent, and received a 20 euros voucher in return for their participation. All participants were french speakers, right-handed, aged between 20 and 50 years old, and free from known psychiatric conditions (bipolar disorder, schizophrenia), neurological disorders (epilepsy, stroke, intracranial hypertension, memory loss, coma), neurodegenerative diseases (Parkinson, Alzheimer's disease), and metabolic diseases associated with excess weight (diabetes, cardiovascular diseases). The other exclusion criteria were: past or current eating disorders (anorexia, bulimia), food allergies, bariatric surgery, pregnancy, or a vegan diet, as some of the pictures used in the study displayed desserts made from eggs or dairy products. We also controlled that participants met EEG requirements for the recording (no metallic implants on the head, dreadlocks, or braided hair).

Eighty-four participants took part in the study. After data acquisition, 14 participants were excluded because they declared to have been attentively detecting the olfactory primes, and

8 for having fewer than 10% useable ERP trials in at least two conditions. The final sample included 62 participants, split in three groups based on their BMI: 23 normal-weight (NW; BMI between 18.5-25 kg/m^2), 19 overweight (OW; BMI between 25 kg/m^2-30 kg/m^2) and 20 obese individuals (OB; BMI>30 kg/m^2; see **Table 1** for the characteristics of the sample). Mean age was not significantly different between groups (*F*(2, 59) = 0.10, *p* = .90), as well as the number of years of higher education (*F*(2, 59) = 2.74, *p* = .07).

Table 1. Mean characteristics (*SD*) of the 62 participants included in the study, by group (normal-weight = NW; overweight = OW; obese = OB).

	NW	OW	OB
N	23	19	20
***N* female/male**	17/6	13/6	17/3
Age (*SD*)	39.1 (6.4)	38.2 (5.6)	38.4 (8.1)
***N* years of education (*SD*)**	2.78 (1.93)	2.68 (2.16)	1.55 (1.47)
BMI (*SD*)	22.4 (1.9)	27.7 (1.1)	34.4(3.7)

Questionnaires

At the beginning and at the end of the experiment, the participants indicated the intensity of their hunger on a 10-point scale going from 1–*not hungry at all* to 10–*very hungry*. This measure was done to control that the groups did not differ on hunger levels while doing the experiment, because hunger can influence attention toward food cues and cerebral activity (Nijs, Muris, et al., 2010).

The Dutch Eating Behavior Questionnaire (DEBQ; Van Strien et al., 1986) was used to control whether our three groups of participants differed on eating behavior, with a particular interest in restrained eating, which can influence neurophysiological activity associated with food stimuli (Kong, Zhang, & Chen, 2015). The DEBQ is a self-report questionnaire with 33 items, measuring three aspects of eating behavior: emotional eating, external eating, and restrained eating (for details, see Van Strien et al., 1986). Higher scores indicate greater endorsement of the eating behavior.

To control that the participants had a proper sense of smell while priming them with low concentrated odors, they also performed the European Test of Olfactory Capabilities (ETOC; Thomas-Danguin et al., 2003). The ETOC is a standardized test designed to assess olfactory capacities in the European population. The subjects are asked to detect odorous vials among non-odorized vials, and to identify the odors (e.g., vanilla, garlic; for methodological details, see Thomas-Danguin et al., 2003). All included subjects had a total score above 80% and were considered normosmic. This test was also used to control that olfactory capacities did not differ between the groups, as they seem to reduce with increasing BMI (Peng, Coutts, Wang, & Cakmak, 2019).

Finally, the participants completed an investigation questionnaire in which they had to guess the aim of the experiment, and indicate whether they noticed anything particular during the task that could have influenced their performance. This questionnaire was successfully used on previous studies on implicit olfactory priming (Chambaron et al., 2015; Marty et al., 2017; Mas et al., 2020, 2019). Participants reporting odors or headsets were excluded from the study (*N* = 14). This step ensured that no odor or headset change was perceived, validating the implicit quality of the priming.

Stimuli

Pictures

To select pictures depicting foods contrasted in terms of energy density, but equivalent in terms of liking, we conducted an online pilot study. We pre-selected 56 pictures from the FoodPics database, which features food pictures with simple figure-ground compositions (Blechert, Meule, Busch, & Ohla, 2014; www.food-pics.sbg.ac.at). All pictures had a size of 577*433 pixels, and a 120 ppp resolution. Our selection included 28 sweet HED foods (e.g. cookies, chocolate, ice cream), and 28 sweet LED foods (various whole and cut fruits). We created an online questionnaire with the survey website LimeSurvey (https://www.limesurvey.org/fr/) to assess these food pictures in terms of liking and healthiness. For each food displayed, participants were asked to indicate: 1/ how much they liked the taste of the food (answer from 1–*I do not like it at all*, to 10–*I like it a lot*), and 2/ how much they thought this food was good for their health (answer from 1–*very bad for my health*, to 10–*excellent for my health*).

Sixty-two participants, different from those included in the EEG experiment, completed the questionnaire. We excluded 6 participants because of their particular diet (no dairy products (*N* = 2), no sugar (*N* = 1), veganism (*N* = 1), or on a weight-loss diet (*N* = 2)). We did not exclude the vegetarians (*N* = 5), as the picture selection did not represent any meat or fish products. We also excluded the subjects who had 50% or more of their liking scores below 5, for at least one category of foods (HED and/or LED), suggesting they did not like this category of foods in general (*N* = 5). Thus, the final sample included 51 individuals (32 female, 19 male), with a mean age of 37.35 years old (*SD* = 10.53).

Based on the mean scores obtained on the liking scale, we selected 12 HED food pictures and 12 LED food pictures with a mean liking score above 6, to ensure that the foods depicted were generally liked. We carefully selected pictures representing different foods, to ensure variety in both categories. We performed *t*-tests with R-3.6.3 software (R Development Core Team) to control that liking was statistically equivalent between the LED and HED categories (mean liking scores (*SD*): LED = 7.48 (1.01), HED = 7.01 (1.38); *t*(22) =

1.94, *p* = .06), and that LED foods were perceived as significantly more healthy than HED foods (mean healthiness scores (*SD*): LED = 8.57 (1.13), HED = 2.80 (1.10); *t*(22) = -27.50, *p* = .01). We also used several informations provided by FoodPics to control that pictures from both categories were similar according to: object size (*t*(22) = 0.71, *p* = .48), brightness (*t*(22) = -0.41, *p* = .68), contrast (*t*(22) = - 0.46, *p* = .65), visual complexity (*t*(22) = - 0.27, *p* = .78), spatial frequencies (*t*(22) = - 1.75, *p* = .09), and familiarity (*t*(22) = 1.41, *p* = .17). Finally, we also controlled that the LED foods were indeed less caloric than the HED foods (mean Kcal (*SD*), LED = 28.50 (50.16), HED = 230.41 (98.36); *t*(22) = - 5.50, *p* < .001).

Odors and olfactory priming device

The olfactory priming device was based on the method developed by Marty, Bentivegna, Nicklaus, Monnery-Patris, & Chambaron (2017), which was successfully used in other studies since (Mas et al., 2020, 2019). In these studies, the participants successively wore different headsets, whose microphone foams had been odorized beforehand. We used three different odors as priming conditions: a pear odor (fruity odor, priming LED foods), a pound cake odor (fatty-sweet odor, priming HED foods), and a control condition (no odor).

For the olfactory primes, we selected the pear and pound cake aromas sold by Meilleur du Chef© (Bassussarry, France), because they have proven to be efficient as implicit olfactory primes (Marty et al., 2017; Mas et al., 2020, 2019). Both odors were also rated as equivalent in terms of liking (*t*(40) = 1.14, *p* = .26) and hedonicity (*t*(40) = 0.38, *p* = .70) by 42 adults volunteers, in a pilot study done for a previous research on olfactory priming (Marty et al., 2017).

We tested five different flavor concentrations, by using dipropylene glycol for dilution: pure, 1/5, 1/15, 1/20, 1/25. Ten adult subjects rated their intensity in a pilot study, in order to select iso-intense odors. The pure pear odor and the 1/25 diluted pound cake odor were rated as isointense, thus we used these concentrations for the study. For the olfactory priming, we placed 15 µL of each dilution (pear, pound cake) inside disposable microphone foams. For the non-odorized control condition, we used 15 µL of dipropylene glycol. The microphone was cleaned with ethanol between participants and the foams were changed.

EEG recording

Visual ERPs, time-locked to picture onset, were recorded using a 32-channel EEG with Ag–AgCl active electrodes, positioned on an elastic cap according to the BioSemi designed equiradial system with ABC layout and then translated with 10-20 annotations. ERPs were recorded with a 24-bit resolution and a sampling rate of 1000 Hz running Acqknowledge 4.1 software, and the signal was amplified using an Active Two amplifier system (BioSemi, Amsterdam, Netherlands). The reference electrodes were fixed on the left and right earlobes, and the ground electrodes on the left and right mastoids. Two additional electrodes were placed above and below the right eye to record the vertical electro-oculogram, and two other electrodes were placed on the outer corners of the left and right eyes to record the horizontal electro-oculogram. Electrode impedance was kept below 5 kΩ with the help of a saline gel that maximized contact between the electrodes and the scalp. Throughout the experiment, triggers were sent with E-Prime 2.0 (Psychology Software Tools) and recorded as events on the EEG signal at the onset of each food picture. Participants received instructions to not touch their heads and to try not to move during the presentation of the pictures.

Procedure

The experimental sessions were individual and lasted 1h45. To ensure the absence of residual odors, the sessions took place in a positive pressure room, which allowed the complete renewal of the air every two minutes. The participants were invited to the laboratory under a false pretext that did not mention food odors, in order to keep the olfactory priming implicit. To control hunger levels, the participants were instructed not to eat anything during the 3 hours before the session. They were also instructed not to wear perfume and hair products, to avoid interference with the olfactory primes.

Upon arriving at the laboratory, each participant gave her/his informed consent. She/he was seated in front of the computer, and the EEG electrodes and cap were installed by the experimenter. A first headset microphone, odorized according to one of the 3 priming conditions (pear, pound cake, none), was placed above the EEG cap. The experimenter was careful not to press any electrodes with the headset, and the microphone was always placed at a 4 cm distance from the upper lip. The participant indicated the time of her/his last meal and the intensity of her/his hunger on a scale going from 1–*not hungry at all* to 10–*very hungry*. Then, the EEG recording started and the participant completed the passive viewing task.

The passive viewing task was programmed with E-Prime 2.0 (Psychology Software Tools). In this task, the participants were instructed to pay close attention to the pictures that would be presented on the computer screen (passive viewing without responses). One trial consisted of a fixation cross (presented for 1600 ± 100 ms) followed either by a LED or HED food picture (presented for 200 ms) on a silver grey background (see **Figure 1, A**). The task was divided into three identical blocks, each one corresponding to a different olfactory priming condition (pear, pound cake, no odor). The 12 LED food pictures and the 12 HED food pictures selected in the pilot study were presented 8 times by block in a randomized order, resulting in 192 trials by block (96 LED and 96 HED trials; see **Figure 1, B**). To maintain attention throughout the experiment and minimize alpha waves due to boredom (Luck, 2005), we included a short game randomly appearing 10 times by block. The game consisted in finding a “Q” letter hidden among numerous “O” letters. The participant was instructed to find and click with the mouse on the “Q” letter when such a game was appearing on the computer screen. Between the blocks, the participants had 4-minutes breaks where they were offered to do a “connect-the-dots” game on a sheet of paper. The purpose of these breaks was to distract the participants while the experimenter switched the odorized headset microphones out of their sight, in order to alternate the three olfactory priming conditions. All participants did the 3 priming conditions in a counterbalanced order.

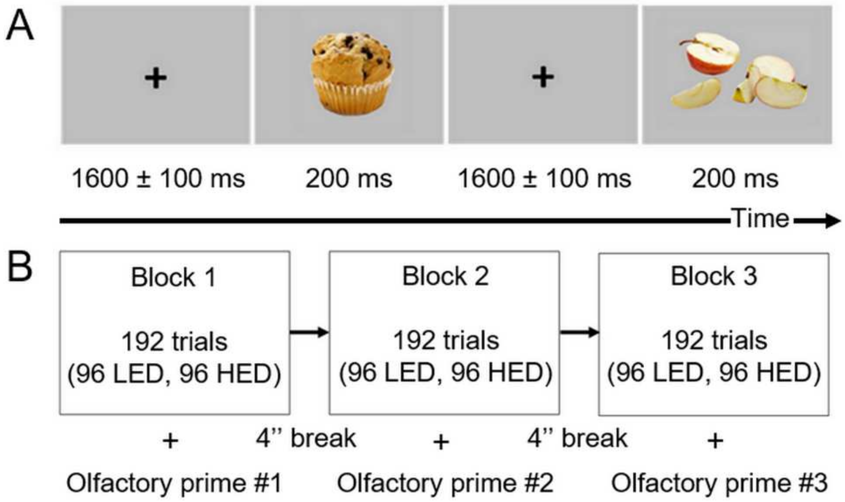

Figure 1. (A) Example of a “HED” trial followed by a “LED” trial; (B) Design of the passive viewing task and the olfactory priming paradigm.

During the blocks, a white noise was continuously played in the headset, and the participants were instructed to use the microphone to call the experimenter when the words *“break time”* would appear on the screen at the end of each block. These two aspects justified the presence of the headset microphone. EEG was continuously recorded during each block. After the last block, the participants indicated again their level of hunger on the 10-points scale, and the EEG cap was removed.

Finally, the participants answered the questionnaires (DEBQ, ETOC, investigation questionnaire), and anthropometric measurements were conducted by the experimenter to calculate BMI (weight in kg/height in m^2). Height was assessed with a measuring rod (Leicester Height Measure©) and weight with a digital scale (Soehnle©). The participants were asked to remove their shoes before both measurements. To correct for the weight of clothing, we substracted 1.2 kgs to the measured weight before calculating BMI.

ERP data: Signal extraction and pre-processing

Offline data analysis was performed with Letswave 6, the open-source EEG signal processing toolbox, implemented in MATLAB R2018b. For drift correction, the EEG data were first offline filtered with a 0.1-Hz low cutoff filter. Data were then epoched starting at 200 ms before picture onset and ending 1000 ms after picture onset. They were filtered (Butterworth, bandpass filter: 0.01-30Hz, filter order 4) and baseline corrected [yi=xi-mean(bl)] using the 200 ms before the stimulus. The epochs contaminated by eye blinks, eye movements, or any peaks exceeding |90| µV at any electrode were automatically excluded from the average. Each subject's dataset was also visually inspected. After removal of the artifacts, participants who presented fewer than 10% valid trials for at least two conditions were excluded from further analysis (*N* = 8). The remaining epochs were then averaged for each participant and each electrode, by priming condition (control, pear, pound cake) and type of food picture (HED, LED), resulting in six conditions (control-HED, control-LED, pear-HED, pear-LED, pound cake-HED, pound cake-LED).

Grand-average waveforms were generated by group. Based on the literature (Castle et al., 2000; Grigor et al., 1999; Hume et al., 2015; Nijs, Franken, et al., 2010), we determined specific peak windows search and shorten them when necessary, i.e. when an adjacent peak was computed instead of P100, N100, P200 or N400. Thus, for all conditions, we extracted amplitude (µV) and latency (ms) values in a 10–100 ms window for the P100 peak, a 30–130 ms window for the N100, a 130–230 ms window for the P200, and in a 310–460 ms window for the N400 (see **Figures 2 and 3** for the grand-averages highlighting the measured peaks).

To simplify the statistical model, we selected subsets of relevant electrodes for further analysis of each component. As the P100 peak was previously observed in parieto-occipital areas, we performed a Tukey's Range Test on P100 amplitude to assess the homogeneity of recording in the 5 parieto-occipital electrodes (PO3, PO4, O1, Oz, O2). The pairwise comparisons showed that O1 and O2 had the highest amplitudes and did not differ significantly (*p* > .05), which is a relevant cue for a non-artifactual brain response. Thus, we performed the statistical analysis on the amplitude and latency values from these electrodes. We followed the same procedure to select electrodes for the analysis of all the peaks. For the N100, which is frequently reported in fronto-central areas, we kept 4 electrodes for further analysis (Cz, Fz, FC1, FC2), selected among the 12 fronto-central electrodes (F7, F3, Fz, F4, F8, FC5, FC1, FC2, FC6, C3, Cz, C4). For the P200, which is usually observed in fronto-central and parietal areas, we kept 3 electrodes (CP1, CP2, Cz) selected among the 11 fronto-central and centro-parietal electrodes (FC5, FC1, FC2, FC6, C3, Cz, C4, CP5, CP1, CP2, CP6). The N400 component has been observed in different cortical areas depending on the paradigm and the type of stimuli used to generate ERPs (for a discussion, see Kutas & Federmeier, 2011). Priming paradigms using pictures (Hamm et al., 2002; Holcomb & Mcpherson, 1994), or pictures and odors (Sarfarazi et al., 1999), report N400 effects mainly at frontal and central sites. Thus, we performed a Tukey's Range Test on the N400 amplitude to assess the homogeneity of the 12 frontal, fronto-central, and central electrodes

(F7, F3, Fz, F4, F8, FC1, FC2, FC5, FC6, C3, Cz, C4). For further analysis, we kept the two electrodes with the highest amplitudes that did not differ significantly (FC2 and Fz).

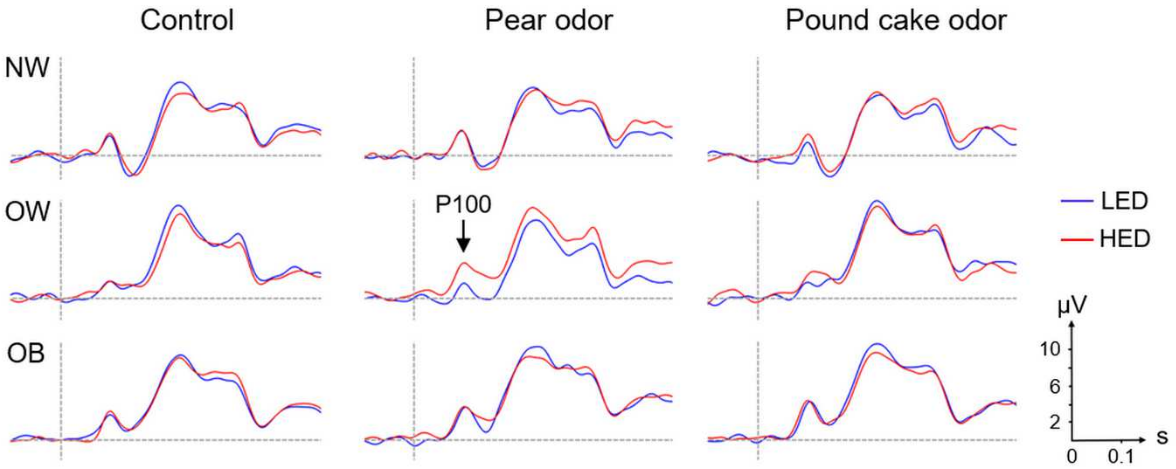

Figure 2. Grand-average ERP highlighting the P100 peak at the O1 electrode, by group (NW, OW, OB), priming condition (control, pear odor, pound cake odor), and type of food picture (LED, HED).

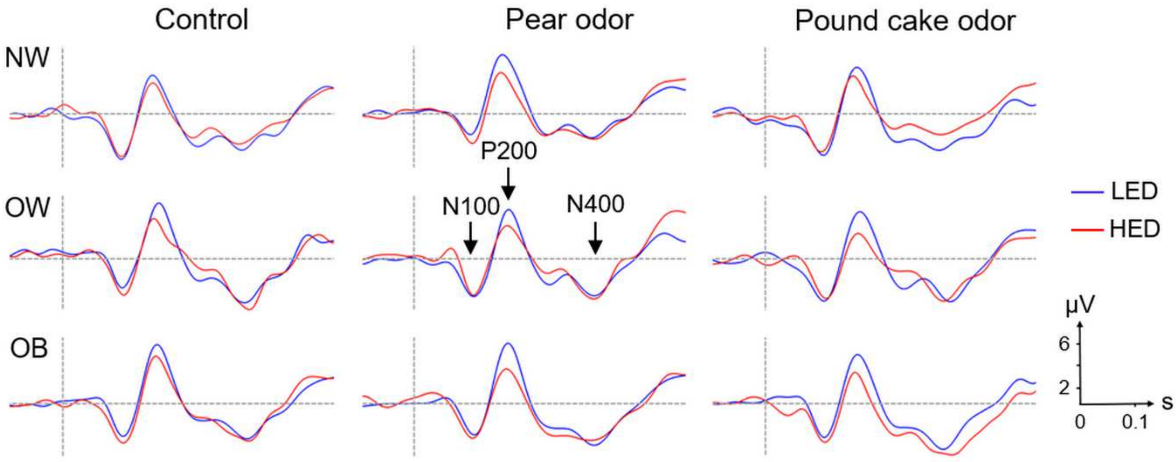

Figure 3. Grand-average ERP highlighting the N100, P200, and N400 peaks, at the Cz electrode, by group (NW, OW, OB), priming condition (control, pear odor, pound cake odor), and type of food picture (LED, HED).

Data analysis and results

Statistical analysis of the questionnaires

All the statistical analyses below were conducted with R-3.6.3 software. We performed several one-way ANOVAs to compare the groups on the level of hunger throughout the experiment, the total ETOC score, and the three DEBQ scores (see **Table 2** below for the mean scores by group).

For testing differences of hunger between groups, we first calculated an index of hunger evolution by substracting the level of hunger reported before and after EEG recording. Results showed no significant group differences for the evolution of hunger through the task

(*F*(2, 59) = 0.37, *p* = .69). To test differences in olfactory capacities, we compared the groups on the ETOC total score, expressed in percentage ([(identification score + detection score)/32]*100). Again, no significant differences were observed between groups on olfactory capacities (*F*(2, 59) = 0.25, *p* = .78). To assess potential differences in eating behavior by BMI status, we performed three distinct one-way ANOVAs to compare the groups on each score of the DEBQ. No significant between-group differences were observed on the restrained eating scale (*F*(2, 59) = 1.33, *p* = .27), the emotional eating scale (*F*(2, 59) = 0.43, *p* = .65), or the external eating scale (*F*(2 , 59) = 1.49, *p* = .23).

Table 2. Mean scores (*SD*) to the questionnaires by group (NW, OW, OB).

	NW	**OW**	**OB**
Evolution of hunger (*SD*)	1.26 (1.32)	1.32 (1.11)	1.65 (2.11)
ETOC total score (*SD*)	91.71 % (5.93)	91.28 % (6.88)	90.31 % (6.94)
DEBQ Restriction (*SD*)	2.76 (0.75)	3.10 (0.71)	2.84 (0.63)
DEBQ Emotivity (*SD*)	2.67 (0.68)	2.58 (0.67)	2.80 (0.89)
DEBQ Externality (*SD*)	3.16 (0.50)	2.92 (0.59)	2.94 (0.43)

EEG data analysis

To study the impact of food odors on the cerebral processing of food pictures in individuals with different BMIs, we used a linear mixed-effects model (LME model; “lme” function in the R package “nlme”, R-3.6.3 software, R Development Core Team) to analyze the amplitude and latency of each peak separately (P100, N100, P200, and N400), calculated on the individual averages. For each subject and condition, these measures were weighted by the number of trials included in individual averages. The model included the *group* (NW, OW, OB) as a between-subjects factor, the *priming condition* (pear odor, pound cake odor, no odor) and the *type of food picture* (HED, LED) as within-subjects factors. The *subjects* were added as a random factor. The subsets of electrodes that we selected for the analysis of each peak did not differ statistically; therefore, we did not include an “electrode” factor in the model. For all datasets, the normality of the random effects and the residuals was controlled with quantile–quantile plots (“qqnorm” and “qqline” functions in R), and the homogeneity of residual variance was tested between groups with Levene’s test (“leveneTest” function in R). All datasets presented normal distributions and equal variances (*p* > .05). Main effects and interactions are detailed below and were considered as significant for *p* < .05. When significant interactions were found, the data were split based on levels of one or two factors, and tested independently with the LME model (*p* < .05).

P100 results

P100 amplitude. The interaction between group, priming condition, and type of food picture was significant (*F*(4, 659) = 2.56, *p* = .04). Data were split by group and by priming conditions, and independant LME models were performed to test the differences in amplitude between LED and HED food pictures, for each priming condition by group separately (see **Figure 4**). In NW subjects, P100 amplitude was larger for HED than LED food pictures when they were primed with the pound cake odor (*F*(1, 65) = 4.61, *p* = .04). The difference in P100 amplitude by type of food picture was not significant when NW subjects were primed with the pear odor (*F*(1, 68) = 0.34, *p* = .56) or in the odorless control condition (*F*(1, 68) = 0.01, *p* = .94). In OW subjects, P100 amplitude was larger for HED than LED food pictures in the presence of the pear odor (*F*(1, 56) = 22.34, *p* < .001), but no significant differences were observed with the pound cake odor (*F*(1, 54) = 0.10, *p* = .76) or the control condition (*F*(1, 56) = 0.08, *p* = .77). OB individuals presented no differences in P100 amplitude by type of food pictures when primed with the pear odor (*F*(1, 58) = 0.34, *p* = .56), the pound cake odor (*F*(1, 59) = 1.61, *p* = .21), and in the non-odorized condition (*F*(1, 58) = 0.73, *p* = .40).

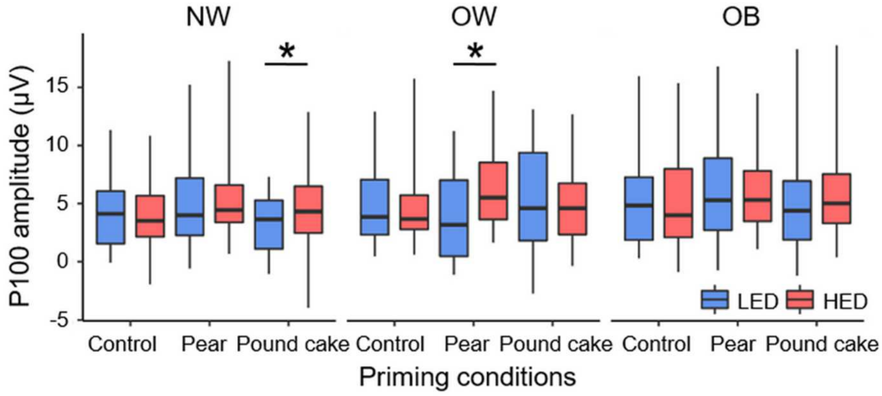

Figure 4. P100 amplitude (µV) by group (NW, OW, OB), priming condition (control, pear, pound cake), and picture type (LED, HED). The significant differences are represented with a threshold set to **p* < .05.

P100 latency. The interaction between group, priming condition, and type of food picture was significant (*F*(4, 659) = 3.60, *p* = .006). An independant LME model testing the effect of picture type for each priming condition by group separately revealed that OB subjects presented a longer P100 latency for HED than LED food pictures in the odorless control condition (*F*(1, 58) = 12.53, *p* < .001, mean latency ± 95% CI: HED = 48.94 ± 4.63, LED = 39.17 ± 4.51). No significant differences in P100 latency were observed by type of food pictures when the OB subjects were primed with the pear odor (*F*(1, 58) = 0.34, *p* = .54) or the pound cake odor (*F*(1, 59) = 2.62, *p* = .11). No significant results were observed in NW subjects for any of the priming conditions (pear odor: *F*(1, 68) = 0.21, *p* = .65; pound cake odor: *F*(1, 65) = 1.20, *p* = .28; control condition: *F*(1, 68) = 0.58, *p* = .45), as well as in OW subjects (pear odor: *F*(1, 56) = 0.05, *p* = .83; pound cake odor: *F*(1, 54) = 0.00006, *p* = .99; control condition: *F*(1, 56) = 0.02, *p* = .89).

N100 results

N100 amplitude. The interaction between group, priming condition, and type of food picture was significant (*F*(4, 1397) = 6.94, $p < .001$). Data were split by group and by priming conditions, and independent LME models were used to test the differences in amplitude between LED and HED food pictures for each condition (see **Figure 5**). As the N100 is a negative peak, larger amplitudes are more negative, whereas smaller amplitudes are less negative. In NW subjects, N100 amplitude was significantly larger for HED than LED food pictures when the subjects were primed with the pear odor (*F*(1, 160) = 7.51, $p = .007$). No significant differences were observed with the pound cake odor (*F*(1, 156) = 0.19, $p = .67$) and in the odorless control condition (*F*(1, 160) = 0.02, $p = .90$). In OW subjects, N100 amplitude was larger for HED food pictures in the control condition (*F*(1, 132) = 13.54, $p < .001$), and for LED food pictures in the pear-odorized condition (*F*(1, 128) = 17.90, $p < .001$). OW subjects presented no differences in N100 amplitude by type of food picture when primed with the pound cake odor (*F*(1, 132) = 0.95, $p = .33$). In OB subjects, N100 amplitude was larger for HED than LED food pictures when primed with the pear odor (*F*(1, 138) = 6.01, $p = .01$) and in the control condition (*F*(1, 138) = 10.87, $p = .001$). In the presence of the pound cake odor, N100 amplitude of OB subjects was larger for LED than HED food pictures (*F*(1, 135) = 5.07, $p = .03$).

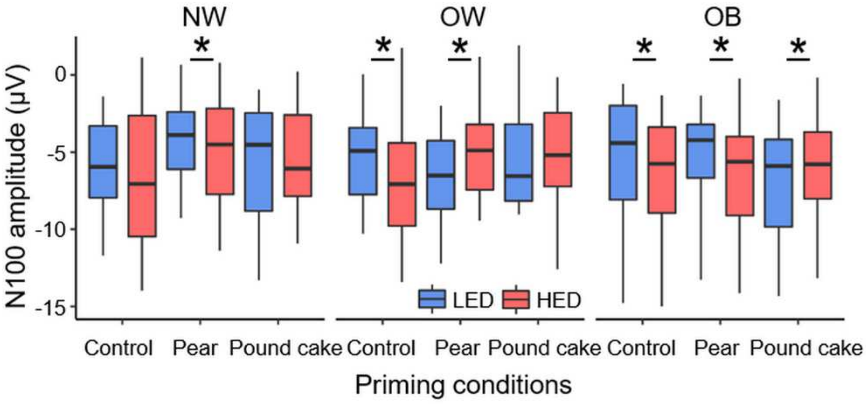

Figure 5. N100 amplitude (µV) by group (NW, OW, OB), priming condition (control, pear, pound cake), and picture type (LED, HED). The significant differences are represented with a threshold set to *$p < .05$.

N100 latency. The interaction between group, priming condition, and type of food picture was not significant for the latency of the N100 (*F*(4, 1397) = 1.74, $p = .14$). However, the main effect of the type of picture was significant, showing longer N100 latencies for HED than LED food pictures independently from group and priming condition (*F*(1, 1397) = 52.76, $p < .001$, mean latency ± 95% CI: HED = 64.45 ± 1.08, LED = 60.41 ± 0.95).

P200 results

P200 amplitude. Results showed a main effect of the type of picture (*F*(1, 1036) = 54.93, *p* < .001), showing a higher amplitude of the P200 for LED than HED food pictures, independently from group and priming conditions.

The interaction between group, priming condition, and type of food picture was also significant (*F*(4, 1036) = 2.99, *p* = .02). Similarly to the P100 and N100, independant LME models were performed to test the differences in amplitude between LED and HED food pictures, for each priming condition by group separately (see **Figure 6**). In NW individuals, the P200 amplitude was greater for LED than HED food pictures in the control condition (*F*(1, 114) = 4.53, *p* = .03), and when they were primed with the pear odor (*F*(1, 114) = 6.81, *p* = .01). NW subjects presented no differences in P200 amplitude by type of food picture when they were primed with the pound cake odor (*F*(1, 114) = 2.21, *p* = .14). OW individuals presented a greater P200 amplitude for LED than HED food pictures in all conditions: without odors (*F*(1, 94) = 21.70, *p* < .001), when primed with the pound-cake odor (*F*(1, 94) = 10.65, *p* = .001), and with the pear odor (*F*(1, 94) = 13.46, *p* < .001). OB individuals had a greater P200 amplitude for LED than HED food pictures when primed with the pear odor (*F*(1, 96) = 26.56, *p* < .001), and also with the pound cake odor (*F*(1, 99) = 34.01, *p* < .001). In the non-odorized condition, we observed no differences in amplitude by type of food picture (*F*(1, 99) = 0.03, *p* = .86).

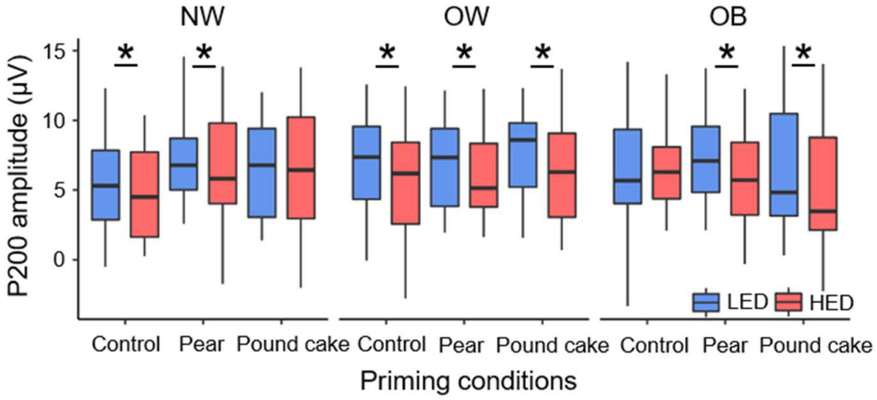

Figure 6. P200 amplitude (µV) by group (NW, OW, OB), priming condition (control, pear, pound cake), and picture type (LED, HED). The significant differences are represented with a threshold set to **p* < .05.

P200 latency. The interaction between priming condition and type of food picture was significant, independently from BMI (*F*(2, 1036) = 3.76, *p* = .02). To analyze this interaction, data were split by priming condition, and we used independent LME models to test the difference in P200 latency between LED and HED food pictures for each priming condition separately. No significant differences by type of food picture were observed neither in the control condition (*F*(1, 309) = 0.78, *p* = .38), nor in the presence of the pear odor (*F*(1, 306) =

0.77, *p* = .38). However, the P200 latency was longer for LED than HED food pictures when the subjects were primed with the pound cake odor (*F*(1, 309) = 18.61, *p* < .001, mean latency ± 95% CI: LED = 179.09 ± 3.10, HED = 171.62 ± 3.36). The interaction between group, priming condition, and type of food picture, was not significant (*F*(4, 1036) = 1.86, *p* = .11).

N400 results

N400 amplitude. The interaction between group, priming condition, and type of food picture was also significant (*F*(4, 666) = 3.55, *p* = .01). Independant LME models were performed to test the differences in amplitude between LED and HED food pictures, for each priming condition by group separately (see **Figure 7**). NW subjects presented a larger (more negative) N400 amplitude for HED than LED food pictures in the odorless condition (*F*(1, 68) = 7.41, *p* = .01). With the pound cake odor, we observed the opposite effect; namely, a larger N400 amplitude for LED than HED food pictures (*F*(1, 68) = 11.31, *p* = .001). The difference in N400 amplitude by type of food picture was not significant when NW subjects were primed with the pear odor (*F*(1, 68) = 0.90, *p* = .35). OW individuals presented a greater N400 amplitude for HED than LED food pictures in the non-odorized condition (*F*(1, 56) = 4.56, *p* = .04). No significant differences in N400 amplitude by type of food picture were observed when OW subjects were primed with the pear odor (*F*(1, 56) = 1.85, *p* = .18) or the pound cake odor (*F*(1, 56) = 0.13, *p* = .72). OB individuals had no differences in N400 amplitude by type of food picture when primed with the pear odor (*F*(1, 59) = 0.07, *p* = .78), as well as in the control condition (*F*(1, 59) = 1.38, *p* = .24). However, in the presence of the pound cake odor, the N400 amplitude was larger for HED than LED food pictures (*F*(1, 59) = 9.79, *p* = .002).

N400 latency. No significant effects were observed.

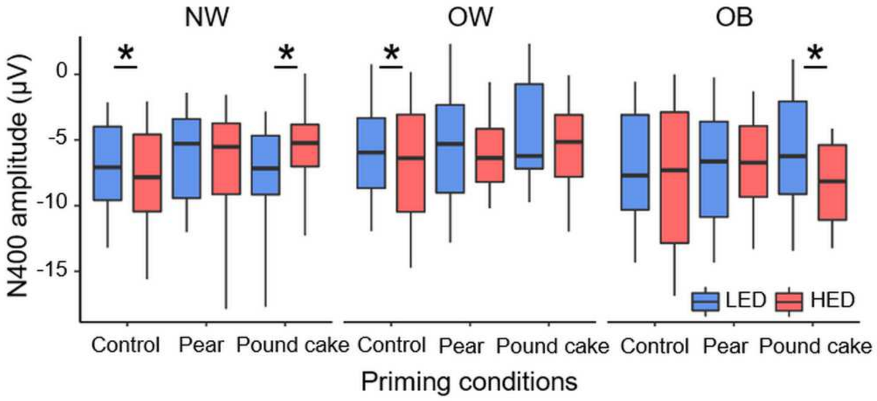

Figure 7. N400 amplitude (µV) by group (NW, OW, OB), priming condition (control, pear, pound cake), and picture type (LED, HED). The significant differences are represented with a threshold set to *$p < .05$.

Amplitude analysis: summary of the results

The interaction between group, priming condition, and type of food picture was significant for the amplitude of all the peaks measured. For each peak, several LME models were modeled to compare the amplitude between LED and HED food pictures, by priming condition and group separately. The **Table 3** below is provided to simplify the reading of these numerous comparisons, by highlighting the significant and non-significant results.

Table 3. Summary table of the statistical comparisons performed between low-energy-density (LED) and high-energy-density (HED) food pictures, by priming condition and group (NW = normal-weight; OW = overweight; OB = obese).

Peak	**P100**			**N100**		
Priming condition	*Control*	*Pear*	*Pound cake*	*Control*	*Pear*	*Pound cake*
NW	*NS*	*NS*	LED < HED	*NS*	LED < HED	*NS*
OW	*NS*	LED < HED	*NS*	LED < HED	LED > HED	*NS*
OB	*NS*	*NS*	*NS*	LED < HED	LED < HED	LED > HED
Peak	**P200**			**N400**		
Priming condition	*Control*	*Pear*	*Pound cake*	*Control*	*Pear*	*Pound cake*
NW	LED > HED	LED > HED	*NS*	LED < HED	*NS*	LED > HED
OW	LED > HED	LED > HED	LED > HED	LED < HED	*NS*	*NS*
OB	*NS*	LED > HED	LED > HED	*NS*	*NS*	LED < HED

Discussion

The main objective of the current study was to better understand the cerebral differences underlying the processing of food cues between individuals with various weight statuses. For the first time, we used an implicit olfactory priming paradigm to assess the effect of non-attentively perceived food odors on the ERPs elicited by HED and LED food pictures in NW, OW, and OB individuals. The BMI was expected to modulate the impact of food odors on the P200 and N400 peaks elicited by the food pictures. Earlier peaks (P100 and N100) were expected to be modulated by the energy density of the food stimuli (LED vs. HED), but not BMI. Overall, the results suggested strong differences between groups with different BMIs on the amplitude (but not latency) of all components, starting from the P100. For the discussion of the results, we will compare the groups by following the time course of the ERP (P100-N100-P200-N400), before highlighting limits and perspectives.

P100

The P100 was the first detectable peak on the ERPs elicited by the food pictures, and it reflects the early cerebral activity associated with pre-attentive sensory processing. The P100 is sensitive to the visual parameters of the stimuli (e.g. contrast, brightness; Luck, 2005), but our selection of LED and HED food pictures did not statistically differ on these aspects. Thus, any amplitude or latency differences reported on the P100 is likely due to the conceptual content of the pictures, and not to perceptual differences. This idea is supported by the fact that in the odorless control condition, the P100 was not modulated by the energy density of the food pictures in any group.

Cerebral differences between the groups appeared in the presence of the olfactory primes. Indeed, a larger P100 amplitude for HED than LED food pictures was observed: 1/ in NW subjects when they were primed with the pound cake odor, and 2/ in OW subjects when they were primed with the pear odor. These results suggest that the initial sensory processing of food cues can be enhanced in favor of HED food pictures in the presence of food odors, at least in NW and OW individuals, and even when the odors are not consciously perceived. This effect does not seem to depend on a food odor in particular, as both the congruent odor (pound cake) and the incongruent odor (pear) led to an increased processing of HED food pictures. However, the subjects reacted to one type of odor or the other depending on their BMI, suggesting an influence of weight status on the reactivity to particular food odors. The fact that the early cerebral processing increased specifically for HED food pictures rather than LED food pictures may be partly explained by the more appealing nature of HED foods, which makes them more salient in the environment (Alonso-alonso et al., 2015; Cohen, 2008).

OB subjects presented no significant differences in P100 amplitude between the two categories of food pictures, in any of the priming conditions. The only significant effect observed in OB subjects concerned the P100 latency, which was longer for HED than LED foods in the control condition. Therefore, food odors seem to have little impact on the P100 peak in OB individuals.

N100

The N100 follows the P100 on the ERP, and is also associated with pre-attentive processes and perception (Meule et al., 2013). Both OW and OB subjects presented a larger (more negative) N100 amplitude for HED than LED food pictures in the odorless control condition, suggesting a spontaneous enhanced processing of HED food stimuli in individuals with higher BMIs. Thus, HED foods may be particularly salient in the environment for OW and OB individuals, compared with NW individuals. This tendency is reversed with the pear odor in OW subjects, in the presence of which they present a larger N100 for LED than HED food pictures. We can assume that LED food odors (such as pear) may increase the early sensory processing of the congruent LED food pictures, at least in OW subjects. However, the HED food odor (pound cake) modulated neither the N100 nor the P100 of OW individuals, suggesting a reduced early reactivity to this odor for this population.

OB subjects were reactive to both odors, but we observed the opposite of the priming effects that were expected: the N100 amplitude was larger for HED food pictures in the presence of the LED food odor (pear), and larger for LED food pictures in the presence of the HED food odor (pound cake). In NW subjects, N100 amplitude was also larger for the HED food pictures in the presence of the incongruent LED food odor. These findings support the few available data showing that the N100 component may be modulated by the congruency between stimuli, by presenting larger amplitudes in incongruent situations (Atkinson, Drysdale, & Fulham, 2003; Lu, Zhang, Hu, & Luo, 2011; Zinchenko et al., 2018). To the best of our knowledge, our study is the first to suggest that the N100 can be modulated by the congruency between odors and pictures, in a cross-modal priming paradigm.

No effects of BMI were observed on N100 latency. A main effect of the type of pictures was reported, showing longer N100 latencies for HED than LED foods. Although the visual complexity was not significantly different between LED et HED food pictures, the HED foods depicted (e.g. biscuits, chocolates, cakes) may be conceptually more complex than the LED foods (fruits only). We can wonder whether the HED foods may have been cognitively more demanding to process, leading to longer N100 latencies.

P200

Following the N100 on the ERP, the P200 is thought to reflect automatic attentional processes (Hume et al., 2015; Nijs, Franken, et al., 2010). A significant main effect of the type of food pictures showed that the P200 was generally larger for LED than HED food pictures. This effect was however tempered by the BMI of the subjects and the priming conditions. The OW subjects presented a larger P200 for LED food pictures in all priming conditions. Thus, we can assume that OW subjects tend to automatically engage more attentional resources toward LED food pictures, whether olfactory cues are present or not. Unlike OW and NW subjects, the P200 of OB subjects was not modulated by the energy density of the food pictures in the control condition, suggesting that they do not automatically engage their attention toward one type of food stimuli in the absence of olfactory cues. These observations suggest that environmental food odors may be a greater source of influence for OB individuals (at least on attentional processes), compared with OW or NW individuals.

In OW and OB subjects, the presence of a HED food odor (pound cake) did not lead to the expected priming effect, which would have been an increased attentional processing of the congruent HED food pictures. An explanation of this interesting result may rely on contextual factors, and in the very nature of the priming effect. For a priming effect to occur, the existence of mental representations linking the prime to the target stimulus is mandatory. It has been suggested that the non-attentive perception of a food odor may activate the concept of the associated categories of food, but also a concept of the context of consumption (Gaillet et al., 2013). In our study, both odors may have activated the concept of “sweet foods” independently from the energy density of the foods. Moreover, it is assumed that attentional resources (reflected by P200 amplitude here) orient toward the most appropriate choice based on each person's motivations (Schomaker, Walper, Wittmann, & Einhäuser, 2017; Vuilleumier, 2015). As our experimental sessions took part in summer (from June to September), fruits may have been more attractive than fatty-sweet foods, leading to a larger P200 amplitude for this category of foods. The hypothesis of such a "seasonality effect" depending on the energy density of the foods remains to be tested.

About P200 latency, the only significant effect showed longer latencies for LED than HED food pictures in the presence of the pound cake odor, independently from BMI. This HED food odor may have interfered with the automatic engagement of attention toward LED food pictures. Based on the reasoning developed earlier, we can also wonder whether the concept of "LED foods" may be activated more slowly in the presence of a HED food odor, which would appear as mismatched multimodal information.

N400

The N400 peak was measured as an index of priming effects, since its amplitude is known to be modulated by the congruency between a prime and a target (Kutas & Federmeier, 2011). We expected larger N400 amplitudes when the food pictures were incongruent with the odorous prime (e.g. HED food pictures primed with the LED food odor).

Surprisingly, in NW and OW subjects, larger N400 amplitudes were observed for HED than LED food pictures but in the absence of olfactory primes. As the N400 is generally elicited by unexpected stimuli (Kutas & Federmeier, 2011), the HED foods may have been considered as more "unexpected" than LED foods in this particular context, at least for NW and OW subjects. No differences in N400 amplitude were observed between HED and LED food pictures when the subjects were primed with the pear odor. In the presence of the pound cake odor, NW subjects presented a larger N400 amplitude for the incongruent category of food pictures (LED), as expected. On the contrary, the pound cake odor was associated with an increased N400 amplitude for the congruent HED food pictures in OB subjects. No latency effects were observed, in line with the numerous studies showing that this peak latency is rather constant (for a review, see Kutas & Federmeier, 2011).

Overall, we observed the expected N400 effect only in NW subjects, who presented a larger N400 amplitude for LED food pictures in the presence of the incongruent pound cake odor. This lack of incongruency effects reported on the N400 could be explained by the implicit nature of our olfactory primes. To our knowledge, most studies assessing the effect of odors on the N400 peak elicited by pictures used explicit olfactory primes (Castle et al., 2000; Grigor et al., 1999; Kowalewski & Murphy, 2013; Sarfarazi et al., 1999). In at least one study, the attention of the subjects was not explicitly directed toward the odors (Sarfarazi et al., 1999), but the subjects were informed that odors would be presented from time to time.

Therefore, the olfactory priming was not really implicit as the odors may have been attentively perceived. In our study, we used odors at very low-intensity levels and carefully controlled that the participants did not attentively perceive them. Our results then suggest that the olfactory primes may need to be consciously detected to modulate the N400 component elicited by visual stimuli. Further research is needed to explore this hypothesis.

Limitations and perspectives

The current study has some limitations. We selected a fruity odor (pear, priming sweet LED foods) and a fatty-sweet odor (pound cake, priming sweet HED foods) as olfactory primes, because their effectiveness as primes has already been proven in previous works (Marty et al., 2017; Mas et al., 2020, 2019). However, some of our results suggested that both odors may have activated a general “sweet food” concept in our study, that did not differentiate between LED and HED foods. Thus, the increased cerebral activity that we observed in favor of one type of food picture may depend on parameters other than the difference in energy density between the odors (e.g. context, motivations, personal taste), and also on the step of cerebral processing (e.g. P100, P200).

As target stimuli, we made two selections of pictures based on the energy density of the foods depicted: fruit pictures were selected as LED foods, and various fatty-sweet desserts as HED foods (e.g. biscuits, chocolate). These two selections may also differ on other parameters than just energy density. First, in everyday life, sweet HED foods are more diverse and conceptually more complex than fruits (Mas et al., 2020), and that could have made the latter easier to categorize. Second, the LED food pictures depicted only raw fruits, while the HED food pictures showed manufactured sweet desserts. This could have also induced a bias, as the concepts of raw and manufactured foods may be differently represented in the brain (Rumiati & Foroni, 2016). Finally, as we used odors and pictures depicting only sweet foods, it is difficult to generalize our results to other food types (e.g. savory foods, vegetables).

Another limitation of our study concerns the design that we used for the passive-viewing task. For each priming condition, there were 96 trials for each type of food picture (LED, HED). This number of trials was selected in order to be optimal for the statistical analysis of the ERP peaks, but also to minimize boredom, which can influence cerebral activity (Luck, 2005). However, early peaks such as the P100 and N100 may require more trials (at least 300) per condition to be reliably measured (Woodman, 2010). Thus, our results concerning these peaks need to be interpreted with caution and replicated.

From our study, several directions may be taken for future research. We highlighted cerebral differences between individuals with various BMIs when they perceive visual food cues primed by food odors. However, the impact of such differences on behavior remains to be tested. They may result in the orientation of attention toward specific foods (e.g. LED or HED foods), and thus influence the subsequent food choices. The effect of BMI on attention orientation toward food cues in the presence of food odors has already been tested (Mas et al., 2019), but the impact on food choices is yet unknown. We can make the hypothesis that particular patterns of cerebral activity in the presence of food cues may lead to food choices that contribute to weight gain. Further research linking brain activity, cognitive function, and behavioral outcomes is then needed to better understand the non-conscious mechanisms leading to food choices in populations with various weight statuses. In particular, a relevant line of research would be to study the link between brain activity (in presence of food cues) and real food choices. Such studies would provide valuable information on the effect of the environment on eating behavior, and may help develop efficient interventions to improve people's diet and reduce weight gain.

We also wanted to highlight the interest of pursuing studies using priming paradigms to assess the impact of non-attentively perceived food cues on brain activity and behavior. A priming effect occurs when an environmental stimulus influences cognitive processing and behavioral outcomes, in an automatic and non-conscious way (Smeets & Dijksterhuis, 2014). In everyday life, we all experience priming effects outside of our consciousness. For example, the presence of food cues (such as food odors) increases the salience of food stimuli in the environment, enhancing the probability of some foods to be chosen as a meal (Cohen, 2008). It has been suggested that the individuals should not be aware of the priming effects for the priming to be successful, and since humans are generally unaware of the presence of odors in the environment, odors may be particularly useful as primes (Smeets & Dijksterhuis, 2014). Thus, we can make the hypothesis that non-attentively perceived food odors may have a particularly strong influence on food choices compared to other food cues (e.g. visual or auditory food cues). It would be interesting to compare the influence of primes from different sensory modalities on cerebral activity and behavioral outcomes. As individuals with higher BMIs may be more reactive to food cues (Hendrikse et al., 2015), differences depending on weight status might be expected.

Our results also suggest that OW and OB individuals present different cerebral patterns when processing food cues, in line with the idea that the cognitive profile of these subjects may differ (Mas et al., 2020, 2019). This highlights the need to systematically distinguish OW and OB subjects in future studies, which is not always done as they are sometimes gathered in one "overweight" or "high BMI" category (Babiloni, Del Percio, Valenzano, et al., 2009; Nijs, Muris, et al., 2010).

Finally, further ERP research comparing different types of foods is needed (e.g. LED vs. HED foods, sweet vs. savory foods), because it is more representative of what happens in everyday life when we chose what to eat (Carbine et al., 2018). In general, original paradigms providing a better simulation of real-life situations should be developed, in order to provide more ecological observations.

In summary, our study showed for the first time that non-attentively perceived food odors influence the cerebral activity associated with the perception and attentional processing of food pictures, and that this influence is modulated by the weight status of the subjects and the energy density of the food stimuli. These effects were mainly observed on the amplitude of the ERP peaks measured, as very few effects were obtained on latency. Our results also suggest that the same odor can have different effects on ERP components over time. Contrary to our hypothesis, BMI effects were observed very early on the ERP (P100 and N100 peaks). The food odors influenced the cerebral activity of NW and OW individuals earlier (P100) than OB individuals (N100). Moreover, the early perceptive processing was mainly enhanced for HED food pictures in the presence of both odors. This trend reversed over the time course of the ERP, as the results on the P200 peak showed an increased involvement of attentional resources for LED than HED food pictures. The P200 of OW and OB subjects was modulated by both odors, while it was not modulated by the pound cake odor in NW subjects, suggesting an enhanced reactivity to odors in persons with higher BMIs. Finally, the N400 peak was modulated by the pound cake odor in NW and OB subjects only. No effects of the pear odor were reported on this peak. This study brought some new elements on the relationship between cerebral activity, reactivity to food cues, and BMI. Further research should be pursued to characterize the cerebral and cognitive features of individuals with different weight statuses, to better understand how these features may influence their subsequent food choices.

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