Appetite 133 (2019) 83–92

Contents lists available at ScienceDirect

Appetite

journal homepage: www.elsevier.com/locate/appet

Watching happy faces potentiates incentive salience but not hedonic reactions to palatable food cues in overweight/obese adults

Robert Soussignan[a,*], Benoist Schaal[a], Tao Jiang[b]

[a] Developmental Ethology and Cognitive Group, Centre des Sciences du Goût et de l'Alimentation, CNRS (UMR 6265), Université de Bourgogne, INRA, 9E boulevard Jeanne D'arc, Dijon, France

[b] Centre de Recherche en Neurosciences de Lyon, CNRS (UMR 5292), Université Claude Bernard Lyon 1-INSERM, Lyon, France

ARTICLE INFO

Keywords:
Wanting
Liking
Incentive salience
Social reward
Overweight
Facial expression

ABSTRACT

'Wanting' and 'liking' are mediated by distinct brain reward systems but their dissociation in human appetite and overeating remains debated. Further, the influence of socioemotional cues on food reward is little explored. We examined these issues in overweight/obese (OW/OB) and normal-weight (NW) participants who watched food images varying in palatability in the same time as videoclips of avatars looking at the food images while displaying facial expressions (happy, disgust or neutral) with their gaze directed only toward the food or consecutively toward the food and participants. We measured heart rate (HR) deceleration as an index of attentional/incentive salience, facial EMG activity as an index of hedonic or disgust reactions, and self-report of wanting and liking. OW/OB participants exhibited a larger HR deceleration to palatable food pictures than NW participants suggesting that they attributed greater incentive salience to food cues. However, in contrast to NW participants, they did not display increased hedonic facial reactions to the liked food cues. Subjective ratings of wanting and liking did not differentiate the two groups. Further, OW/OB participants had more pronounced HR deceleration than NW participants to palatable food cues when they watched avatars' happy faces gazing at the food. In line with the "incentive-sensitization" hypothesis, our data suggest that incentive salience attribution and not hedonic reactivity is increased in OW/OB individuals and that happy faces, as social reward cues, potentiate implicit wanting in OW/OB people.

1. Introduction

In industrialized and recently westernized societies, the abundance of palatable and energy dense foods high in fat and sugar exposes people to attractive cues triggering urges to obtain and consume their rewards, which can foster the development of overweight/obesity (Boswell & Kober, 2015; Werthmann, Roefs, Nederkoorn, Mogg, Bradley & Jansen, 2011). Animal models and human neuroimaging studies demonstrate that palatable food and learned associated cues activate not only neural mechanisms regulating metabolic needs, but also the reward circuitry (e.g., nucleus accumbens, ventral pallidum, orbitofrontal cortex), which encodes food cues as attractive and pleasurable (Beaver, Lawrence, van Ditzhuijzen, Davis, Woods & Calder, 2006; Berridge, 2009; Jiang, Soussignan, Schaal, & Royet, 2015; Stoeckel, Weller, Cook, Twieg, Knowlton & Cox, 2008; Yokum, Ng, & Stice, 2011). Further, electrophysiological and psychopharmacological evidence from animal research supports the view that food reward is a dissociable process involving the mesocorticolimbic dopaminergic circuitry mediating incentive motivation (i.e., 'wanting', the attribution of incentive salience to a reward and the effort to obtain it) and opioid/endocannabinoid striatopallidal hotspots mediating the hedonic impact of the reward (i.e., 'liking') (Berridge, 1996; Berridge & Robinson, 1998; Peciña, Cagniard, Berridge, Aldridge, & Zhuang, 2003). Although the implications of this dual process model of food reward have been stressed for characterizing overweight/obesity and eating disorders in humans, it remains unclear how food 'liking' and 'wanting' interact (the quotation marks refer to implicit components of reward, Berridge & Robinson, 2003), whether they can be disentangled in humans, and whether they constitute an independent risk factor for overweight/obesity (Berridge, 2009; Finlayson & Dalton, 2012; Finlayson, King, & Blundell, 2007; Havermans, 2011; Peciña & Smith, 2010). Further, it is debated whether the incentive-sensitization theory, which posits an excessive amplification of the motivational salience of cues previously associated with hedonic reward, but without a concomitant enhancement of 'liking' is relevant to explain hyper-responsivity to, and overeating of, food in overweight/obesity (Berridge, 2009; Filbey, Myers &

* Corresponding author.
E-mail addresses: robert.soussignan@u-bourgogne.fr, soussignan.robert@bbox.fr (R. Soussignan).

https://doi.org/10.1016/j.appet.2018.10.024
Received 5 September 2018; Received in revised form 19 October 2018; Accepted 21 October 2018
Available online 24 October 2018
0195-6663/

Dewitt, 2012; Finlayson & Dalton, 2012; Havermans, 2011; Peciña & Smith, 2010). So far, although a greater motivation to react to food-associated cues and to overeat palatable food has been associated with overweight/obesity (Castellanos et al., 2009; Doolan, Breslin, Hanna, Murphy & Gallagher, 2014; Giesen, Havermans, Douven, Tekelenburg & Jansen, 2010; Mela, 2006; Ouwehand & de Ridder, 2008; Saelens & Epstein, 1996; Temple, Legierski, Giacomelli, Salvy & Epstein, 2008), there are also studies showing that food hedonics/pleasantness may influence consumption, or is associated with overeating/obesity (De Graaf, 2008; Dressler & Smith, 2013; Drewnowski, Krahn, Demitrack, Nairn, & Gosnell, 1992; Ricketts, 1997; Soussignan, Schaal, Boulanger, Gaillet, & Jiang, 2012; Yeomans, Blundell, & Leshem, 2004). Although these mixed findings suggest that overweight/obese (OW/OB) persons may be similarly sensitive to these two rewarding aspects of food, they may reflect the difficulty of disentangling food reward because wanting and liking usually co-vary, cannot be differentially manipulated in the human brain as in animal models, and have been partially operationalized in core/implicit processes of food reward (Finlayson & Dalton, 2012; Havermans, 2011). For example, previous research used either subjective ratings of wanting/liking (e.g., conscious processes), or objective behavioral/psychophysiological measures (e.g., via eye-tracking technique, event-related potential (ERP), progressive ratio schedules of reinforcement) for one reward component only (Doolan, Breslin, Hanna, Murphy, & Gallagher, 2014; Giesen, Havermans, Douven, Tekelenburg, & Jansen, 2010; Hume, Howells, Rauch, Kroff, & Lambert, 2015; Nijs, Muris, Euser, & Franken, 2010; Saelens & Epstein, 1996; Werthmann et al., 2011), but to our knowledge, no research used psychophysiological indices measuring these two reward components simultaneously in OW/OB individuals. The objective assessment of wanting and liking in humans constitutes an important step for capturing core processes of food reward because brain, autonomic, and behavioral reactivity may be affected by reward cues without being available to conscious introspection (Anselme & Robinson, 2016; Berridge & Kringelbach, 2008) and are less susceptible to demand characteristics/social desirability effects than are self-report data. Thus, the first aim of the present study was to investigate whether electrophysiological indices of incentive salience attribution and hedonic reactions to food-related visual cues can be dissociated as a function of food palatability and participants' BMI status. More specifically, based on the incentive-sensitization hypothesis (Berridge, 2009; Robinson & Berridge, 2001), we firstly examined whether OW/OB individuals, as compared to normal-weight (NW) controls, attribute an incentive salience to palatable food pictures in the absence of increased hedonic reaction/subjective pleasure to rewarding stimuli. The attribution of incentive salience to a reward-related cue makes the stimulus perceptually attractive and attention grabbing (Berridge, 2009; Berridge & Robinson, 2016). This motivational property of reward cues indexed by their attractiveness and their ability to capture attention can be measured using behavioral (e.g., gaze duration, reaction time) or psychophysiological (e.g., ERP, heart rate deceleration) variables. For example, eye movement-tracking technology combined with a visual probe task revealed that OW/OB people showed a greater attentional bias to food cues (*vs*. non-food images, high-energy *vs*. low-energy food images) compared to NW individuals (Castellanos et al., 2009; Doolan et al., 2014; Werthmann et al., 2011). In the current study, we used heart rate (HR) deceleration as an index of attentional/incentive salience in participants exposed to food images varying in palatability. Previous research revealed that HR deceleration, occurring 3–6 s after visual fixation, index sustained/focused attention characterized by active information processing and interest for both positive and negative stimuli (Graham & Clifton, 1966; Lansink & Richards, 1997; Richards, 2008). Indeed, individuals showed HR deceleration when exposed to palatable food pictures (Davids et al., 2010), happy and fear faces (Peltola, Leppänen & Hietanen, 2011; Soussignan, Schaal, Boulanger, Garcia, & Jiang, 2015), pleasurable sexual readings (Fehr & Schulman, 1978), and pleasant odorants (Delplanque et al., 2009; Soussignan, Schaal, Rigaud, Royet, & Jiang, 2011). Further, adults with Williams syndrome characterized by a strong interest for human faces showed more HR deceleration than the controls when watching emotional faces (Plesa Skwerer et al., 2009).

We also recorded facial reactions to food cues using facial electromyography (fEMG), because this technique is sensitive to capture covert and dynamic changes of muscle activity indexing affective valence (i.e., pleasantness-unpleasantness dimension) or emotion-specific reactions (Lang, Greenwald, Bradley, & Hamm, 1993; Larsen, Norris, & Cacioppo, 2003; Soussignan et al., 2013). Indeed, subtle contraction of the *zygomaticus major* muscle (i.e., not necessarily visible) may reflect a positive affective reaction to non-social rewarding cues (Soussignan et al., 2011) even if overt expression of smiles are signals serving a communicative function (e.g., a signal of affiliation) (Schrammel, Pannasch, Graupner, Mojzisch, & Velichkovsky, 2009; Soussignan et al., 2013). For example, EMG activity over the *zygomaticus* muscle region increases in NW adults exposed to pictures of palatable food (Soussignan et al., 2011, 2015) or to pleasant odors (Pichon et al., 2015), and in smokers women watching affective slides while exposed to nicotine compared with placebo spray (Robinson, Cinciripini, Carter, Lam, & Wetter, 2007). In contrast, EMG activity over the *levator labii* muscle region (underlying upper lip raising in disgust faces) increases in adults experiencing negative hedonic sensations to different tastes (Hu et al., 1999), imagining disgust situations (Vrana, 1993), or looking at disliked food pictures (Soussignan et al., 2015). In line with the incentive-sensitization hypothesis, we tested whether OW/OB participants, relative to NW participants, exhibit a larger HR deceleration (i.e., focused attention) to palatable food pictures without an increased zygomatic responsivity (hedonic reaction) to these cues.

Secondly, because human eating behavior is often embedded in social contexts, we examined whether looking at happy/smiling faces toward food prompted the participants to smile automatically in a similar way, and thus to display facial mimicry (Soussignan et al., 2013) that has been proposed to foster affiliative interactions (Hess & Fischer, 2014). Further, we examined whether watching a happy face in a feeding context acts as a social reward, namely a social cue that potentiates incentive salience and hedonic reactions to palatable food cues according to participants' BMI. Indeed, human smiles/happy faces are usually perceived as attractive and intrinsically high in reward value (Martin, Rycholwska, Wood, & Niedenthal, 2017; Otta, Folladore, & Hoshino, 1996). For example, someone's smiles activate reward-related brain regions (O'Doherty et al., 2003; Strathearn, Li, Fonagy, & Montague, 2008) and reinforce decision making and social approach (Averbeck & Duchaine, 2009; Furl, Gallagher, & Averbeck, 2012). To our knowledge, no empirical research has addressed this issue in NW or OW/OB individuals. Previous research mainly focused on the influence of social facilitation, impression management, or social modeling on eating behavior (Cruwys, Bevelander & Hermans, 2015; Herman, Roth, & Polivy, 2003). Studies also examined the mediators of social influence on eating and food liking/desire ratings (e.g., imitation, positive/negative feedback, conformity to social norms) (Barthomeuf, Rousset & Droit-Volet, 2010; Bevelander, Aschoff-Lichtwarck, Anschütz, Hermans, & Engels, 2013; Herman et al., 2003). In the current study, we tested the modulating role of socio-emotional cues from virtual characters on incentive salience attribution and hedonic reactivity to liked/disliked food cues in OW/OB participants using a joint attention paradigm already validated in NW adults (Soussignan et al., 2015). Participants were exposed to video-clips of avatars looking at food images and displaying facial expressions (of happiness, disgust or neutrality) with their gaze directed either toward the food cues only or alternating between the food and participant. This paradigm bears a high ecological validity as people are often exposed in everyday life to visual food cues embedded in socio-emotional contexts via many forms of media including television, the internet, and print (e.g., advertisements showing persons smiling while looking/eating a food). In a previous study, we showed that avatars' happy faces increased the participants' zygomatic reactions and subjective food liking, with mutual eye contact boosting attentional responses (Soussignan et al., 2015). In the current study, we investigated whether happy faces (i.e., a social reward) interact with food palatability to increase attention to food cues in OW/OB participants. More specifically, we examined whether the avatars' happy faces have a greater effect on HR deceleration (focused attention) to palatable food cues in OW/OB than in NW participants. Further, we investigate whether emotional communication through facial expressions and mutual eye contact affects implicit and explicit (e.g., subjective wanting/desire and subjective pleasure) components of food reward in OW/OB participants.

2. Methods

2.1. Participants

The samples comprised 30 NW (15 women) and 30 OW/OB (15 women) Caucasian French adults. The study was conducted in accordance with the 1964 Declaration of Helsinki, revised in 2008. Participants were recruited by local advertisements and selected from a survey on their self-reported height and weight. Before inclusion, all participants provided written consent indicating that they approved the collection, anonymous storage, and analysis of the data. The final allocation of participants to the NW and OW/OB groups was based on the accurate measurement of their height and weight at the beginning of the test session (see procedure). Participants with a body mass index (BMI) between 18 and 25 kg/m^2 were classified as NW, while those with a BMI ≥ 25.3 and ≤ 34.6 kg/m^2 were classified as OW/OB, respectively (Doolan et al., 2014). We regrouped individuals with a BMI of 25.3–34.6 kg/m^2 to render our data comparable to previous literature. It can be stressed that preliminary statistical analyses conducted only on the OW sample (n = 25) without the OB participants provided the same pattern of findings. The characteristics of both groups are presented in Table 1. A questionnaire screened: 1) normal or corrected-to-normal vision; 2) absence of neurological diseases, substance abuse or medication, and sensory alteration; and 3) absence of eating disorders and dietary restraint. Dietary restraint was assessed using the restraint scale of the Dutch Eating Behavior Questionnaire (DEBQ-R) (Van Strien, Frijters, Bergers, & Defares, 1986), which revealed no significant difference between NW (M = 2.52, SD = 2.85) and OW/OB (M = 2.85, SD = 0.66) groups. Further, participants completed French versions of the i) Behavioral Inhibition and Activation System Scales (BIS/BAS) (Carver & White, 1994); ii) Temporal Experience of Pleasure Scale (TEPS) (Gard, Gard, Kring, & John, 2006), and iii) Interpersonal Reactivity Index (IRI) (Davis, 1983) assessing multiple dimensions of empathy.

Table 1
Variable characteristics of normal-weight and overweight-obese participants.

Variable characteristics	NW* (n = 30) *M* (*SD*)	OW/OB* (n = 30) *M* (*SD*)	*t*	*P*
Age	27.40 (10.12)	29.27 (11.27)	0.68	NS
BMI*	22.11 (2.18)	27.84 (2.24)	10.08	< 0.0001
Level of education	4.13 (1.22)	4.47 (0.82)	1.24	NS
Behavioral inhibition/activation scale (BIS/BAS)				
Drive	10.10 (2.23)	10.67 (2.29)	0.97	NS
Fun Seeking	8.77 (2.16)	8.20 (1.99)	1.06	NS
Reward Responsiveness	8.57 (1.77)	8.83 (2.51)	0.47	NS
Inhibition	15.10 (3.90)	14.60 (3.39)	0.53	NS
Temporal Experience of Pleasure Scale (TEPS)				
Anticipatory pleasure	41.07 (5.33)	41.67 (7,93)	0.34	NS
Consummatory pleasure	35.80 (6.69)	38.33 (6.71)	1.46	NS
Interpersonal Reactivity Index Scale (IRI)				
Empathic Concern	18.4 (5.82)	17.97 (5.25)	0.32	NS
Perspective Taking	15.8 (3.84)	16.6 (5.12)	0.68	NS
Personal Distress	13.6 (5.084)	15.03 (4.57)	1.14	NS
Fantasy	17.47 (5.56)	18.7.8 (5.50)	0.86	NS

*Abbreviations: NW, normal-weight; OW/OB, overweight-obese; BMI, body-mass index. Level of education ranging from 1 to 5 (1: Junior high school, 2: 2 years technical degree, 3: High school graduation, 4: Associate's degree, 5: Bachelor's/Master's degree).

2.2. Stimuli and joint attention paradigm

As the details of the procedure of validation of food stimuli, facial stimuli, and of the joint attention paradigm were presented in a previous paper (Soussignan et al., 2015), we only summarize here the description of stimulus materials. Nine food pictures (336 × 208 pixels) were selected from a set of 245 standardized food pictures presented on white plates, following a pre-test in 32 adults. Using a 9-point rating scale, 3 foods were most often disliked (Brussels sprouts, black pudding, and red cabbage), 3 were moderately liked (pâté, white bean, and zucchini) and 3 were the most liked (French fries, hamburger, and chocolate pastry). These food images were presented to the participants of the study to assess their individual preferences (food palatability index).

The facial stimuli consisted of 5-s movie clips depicting two animated virtual characters (a male or a female avatar, 603 × 598 pixels) displaying (or not) a facial expression (happy, disgust, or neutral face) and eye movement (see joint attention scenario) using the Poser 9 software (Smith Micro Software, Watsonville, Ca). The validation of facial stimuli was based on both the Facial Action Coding System (FACS, Ekman & Friesen, 1978) and on a pilot study on the recognition of avatars' facial expressions. A certified FACS coder (R.S.) manipulated the actions units (AUs) corresponding to prototypical facial expressions by using the following codes: AUs 6 + 12 + 25 for happy faces and AU 9 for disgust faces.

The joint attention script that assembled facial expressions movies and food pictures was created using the SuperLab 4.5 software (Cedrus Corporation, San Pedro, CA, USA). This script was presented on a 17-inch TFT screen of an eye-movement tracking system (Tobii T120, Danderyd, Sweden). Each trial began with a warning signal on the screen ('are you ready?'), followed by a 1000-ms cross placed centrally to fixate the participant's gaze. This cross was immediately replaced by an avatar face (onset of the trial, 0 ms) with eyes gazing straight ahead toward the participant. At 500-ms, a food picture appeared either to the left or to the right of the avatar (to counterbalance conditions). At 1000–1100 ms, the avatar shifted his (her) gaze from the participant to the food image with the gaze directed toward the target for 400 ms (1100–1500 ms). At 1500 ms, the avatar either maintained a neutral face or displayed an expression (happy or disgust) beginning at 1500-ms and reaching its apex at 2000-ms, and maintained the expression until the end of video clip (5000 ms). The avatar's gaze was either maintained toward the food (averted gaze, 1100–5000 ms) or redirected to the participants (mutual eye contact, 3000–5000 ms). For each male or female avatar, 12 video-clips of 5 s were created so that all conditions were counterbalanced in a 3 × 2 × 2-factorial design [expressed emotion (happy, disgust, or neutral) × gaze direction (averted or direct) × side (left or right)]. The validity of the joint attention script was assessed between 3000 and 5000 ms by showing that participants increased their gaze duration toward food cues when the avatar looked toward food cues (joint attention condition) than when s/he redirected its attention toward the participants (Soussignan et al., 2015).

2.3. Procedure

Participants were tested in the pre-prandial state between 11:30 a.m. and 1:00 p.m. They were asked to have a breakfast before 8:00 *a.m.* and to abstain from eating or drinking (except water) afterwards. Their hunger state was measured at the beginning and end of each session using a 9-point scale ranging from 1 (not at all hungry) to 9 (extreme hunger). Hunger self-perception, calculated by averaging these two scores, revealed no significant differences between NW ($M = 6.65$, $SD = 1.42$) and OW/OB ($M = 6.28$, $SD = 1.34$). On arrival, the participants' height (cm) and weight (kg) were measured using a portable scale (SECA, Leicester, UK) and a digital weight scale (accuracy: 100 g; Teraillon, Valence, France). Then, the participants were seated in a comfortable chair in a dimly lit, sound-attenuated room. During the placement of sensors, a cover story was used for the fEMG to minimize demand characteristics and to avoid the voluntary control of facial muscles. The participant's head was stabilized on a headrest and positioned at about 60 cm in front of the screen of the eye tracker (1280 × 1024 pixels), with the eyes at the level of the center of the screen. They were instructed to keep their head motionless while looking attentively at the video clips. A Hi-speed USB Webcam was placed on the eye-tracker screen to record visible facial movements of the participants to enable inspection of movement artifacts during fEMG recording. Before data acquisition, 3 stimuli served as training trials. The participants read the instructions on the screen and were informed that they would see videos showing an avatar and food pictures and that after each trial, they had to rate their own actual wanting and liking of the pictured foods [ranging from “I do not want to eat it at all” and “I do not like it at all”, respectively, to “I want to eat it very much” and “I like it very much”, respectively] on a 1000 × 250-pixel digital scale by clicking with the mouse at the chosen point on the scale. A complete trial comprises a 1-s warning signal + 5-s joint attention script and the time necessary to score the two rating scales (liking and wanting). Thus the duration of a complete trial varied in function of the time taken to score the scales (5–10 s). When the last scale was scored, the warning signal of the following trial was immediately launched. Following the familiarization trials, they were exposed to 54 trials of the joint attention test (9 food stimuli × 3 facial expressions × 2 gaze conditions). Using SuperLab software, the order of trials was randomized and the presentation side of food pictures was counterbalanced across participants. The presentation order of the rating scales (food wanting and liking) was also counterbalanced across participants as well as the type of avatar (male vs. female).

At the end of the experiment, the participants performed two post-tests comprising of the presentation the 9 food pictures on the monitor screen, but without any avatar. These post-tests were designed to assess the actual preferences of participants (i.e., food palatability). First, they had to rate the 9 food pictures one after another on a 9-point scale [ranging from “I do not like it at all” (1) to “I like it very much” (9)]. For each participant the order of the 9 stimuli was presented at random using the randomization function of the SuperLab Pro software. Then, the 9 food pictures were presented together on the screen, with each picture associated with a distinct letter. The participants had to press on a keyboard the letters corresponding to the 3 most liked/preferred foods and the letters corresponding to the 3 least liked/disliked foods. The location of each food picture on the screen was counterbalanced across participants. The order of presentation of the two post-tests was also counterbalanced across the participants. An ANOVA performed on the liking scores during the post-test, using food palatability (3 most preferred/liked, 3 moderately liked, and 3 least liked/disliked) as the within-subjects factor, and BMI group as the between-subjects factor, revealed that the liking scores discriminated the three categories of foods as a function of palatability ratings, $F(2,112) = 542.30$, $p < 0.0001$, $\eta_p^2 = 0.906$ (liked foods: $M = 7.96$, $SD = 0.716$; moderately liked foods: $M = 5.83$, $SD = 1.20$; disliked foods: $M = 2.96$, $SD = 1.02$). The interaction between BMI group and food palatability was not significant. From this analysis, food palatability of participants was used as a within-subjects factor in the results reported below.

2.4. Psychophysiological measures

The facial and autonomic measures were recorded using a 16-channel Power Lab system (ADInstruments Pty Ltd., Bella Vista, Australia) connected to a PC computer. The bioelectrical signals were filtered, amplified, and sampled at a rate of 2000 Hz under the control of the LabChart 7 software. The onset of the stimuli delivered by the SuperLab software was automatically labeled on one of the LabChart channels via a digital I/O device (USB-6501, National Instruments, France). As part of the LabChart software, the Video Capture module was used with a Webcam to record visible facial movements of the participants to enable later inspection of movement artifacts. Before attaching the electrodes, the target sites of the skin of the left side of the face were cleaned with alcohol and gently rubbed, and then 2 pairs of 4-mm shielded Ag/AgCl electrodes filled with electrolyte gel were placed and secured using adhesive collars and sticky tape. A ground electrode was placed on the upper part of the forehead. Both electrodes of a pair were placed at a distance of approximately 1.5 cm over muscle regions associated with emotion expressions. To assess whether the participants differentially reacted to liked/disliked food pictures and to determine whether they displayed facial mimicry to avatars’ happy and disgust faces, the activity of the *zygomaticus major* muscle region (which elicits a smile) and of the *levator labii superioris* muscle region (which deepens the nasiolabial fold/wrinkles the nose) were used as indices of hedonic reactivity and disgust expressions, respectively. The EMG signals were recorded with a 10- to 500-Hz band pass filter and with a 50-Hz notch filter, rectified and smoothed online using a 500-ms time constant. HR was measured using Ag/AgCl electrodes and a standard lead I electrode configuration. A low-pass filtering of 50 Hz was used with the bioamplifier to eliminate high-frequency components. A computer input command allowed a threshold control to detect R wave pulses and to display heart rate in beats per minute (bpm) on a separate channel.

2.5. Data analysis

The digital values (1000 × 250 pixels) of self-report scales of food wanting and liking were converted to scores varying from 1 to 9. Then, 4-way ANOVAs (food palatability × avatars' emotion × avatars' gaze direction × BMI group) were performed using food palatability (liked, moderately liked, or disliked), avatars' emotions (disgust, happy, and neutral), and avatars' gaze (direct, averted) as within-subjects factors, and BMI group (NW, OW/OB) as a between-subjects factor. Following the significance of any overall F test, we used Tukey's HSD tests to compare differences between means. For the psychophysiological measures, because of electrical noise in fEMG, data of 2 ($n = 58$) and 3 ($n = 57$) participants were excluded for the *zygomaticus* and *levator labii* muscle regions, respectively. Then, the movies of participants' facial reactivity were visually inspected to verify the presence of movements unrelated to the activity of the target muscle regions. Less than 1% of trials showing irrelevant movements (e.g., mouth movement) were dropped from subsequent analyses. Following visual inspection, EMG amplitudes and HR were calculated during the 500-ms window preceding stimulus onset (baseline) and during 10 time intervals of 500-ms trial presentations. The data of HR changes and EMG amplitudes during the subsequent 500-ms intervals were expressed as the percentage change from the baseline. Percentage scores were used to standardize the widely differing absolute EMG amplitudes of the participants and to enable meaningful comparisons among individuals and across sites (Soussignan et al., 2015). Five-way ANOVAs (food palatability × avatars' emotion × avatars' gaze × time × BMI group) were performed on the psychophysiological data. We performed planned contrasts to compare means when significant interactions involving the time factor were detected. Because HR deceleration to visual stimuli may be detected at about 3–5 s after stimulus onset (Soussignan et al., 2013, 2015), planned contrasts were performed between the first 5 time periods (T1–T5) and the last 5 time periods (T6-T10) of 500 ms. For *zygomaticus* and *levator labii* muscles activity, participants' facial reactions to food cues and avatars' emotional expressions were assessed by comparing T1-T3 to T4-T6 (four-six 500-ms time bins) because facial EMG reactions to food cues or others' facial expressions can occur rapidly (Soussignan et al., 2013). We also used Tukey's HSD tests to compare significant differences between means when the time factor was not involved.

3. Results

3.1. Self-report measures

Food wanting. As expected, the ANOVA revealed a main effect of food palatability on the subjective rating of wanting, (F[2116] = 254.09, $p < 0.0001$, $\eta_p^2 = 0.81$) with the preferred food evoking a higher wanting to eat ($M = 6.98$, $SD = 3.52$) compared to the other food categories (moderately liked food: $M = 5.25$, $SD = 4.14$; disliked food: $M = 2.77$, $SD = 2.59$). However, the other factors (BMI group, avatars' emotion, avatars' gaze) yielded no significant effects.

Food liking. As expected, we also found a main effect of food palatability on the subjective rating of liking, (F[2116] = 159.81, $p < 0.0001$, $\eta_p^2 = 0.73$), indicating that the participants rated more positively the preferred food ($M = 8.18$, $SD = 5.23$) than the other food categories (moderately liked food: $M = 6.61$, $SD = 3.13$; disliked food: $M = 3.81$, $SD = 3.51$). However, the other factors (BMI group, avatars' emotion, avatars' gaze) did not significantly affect food liking ratings.

Eating behavior and socio-affective personality. The mean ratings of approach/avoidance motives (BAS/BIS), pleasure experience (TEPS) and of multi-dimensional assessment of empathy (IRI) are shown in Table 1. As can be seen, the t tests did not detect significant differences between OW/OB participants and NW participants.

3.2. Psychophysiological measures

HR deceleration to food cues as in index of incentive salience attribution. The ANOVA performed on HR changes yielded significant main effects for the BMI group (F[1,58] = 4.72, $p = 0.03$, $\eta_p^2 = 0.07$) and Time (F[9522] = 17.69, $p < 0.0001$, $\eta_p^2 = 0.23$), qualified by a BMI group by Time interaction (F[9522] = 3.27, $p = 0.0006$, $\eta_p^2 = 0.05$). As expected, both NW and OW/OB participants revealed a significant HR decrease between 2.5 and 5 s (T6 to T10) compared to the initial phase of stimulus exposure (0–2.5 s: T1 to T5), all $ps < 0.05$). The BMI group × Time interaction indicated that OW/OB participants showed a larger HR deceleration than the NW participants at T6-T10 (F(1,58) = 7.27, $p = 0.009$), whereas no significance difference was detected between groups during the initial phase of stimulus exposure (T1-T5). There was also an effect of the avatars' expressed Emotion, F(2, 116) = 3.46, $p = 0.03$, $\eta_p^2 = 0.05$, as well as a significant avatar's Emotion × Time interaction, (F[18,1044] = 1.63, $p = 0.04$, $\eta_p^2 = 0.03$). This indicates that the disgust (F(1,58) = 4.25, $p = 0.04$) and happy (F(1,58) = 5.19, $p = 0.03$) faces of avatars induced a larger deceleration at T6-T10 (2.5–5 s) as compared with the avatars' neutral faces (Table S1). Interestingly, significant interactions were detected between BMI group, avatars' Emotion, Food palatability, and avatars' Gaze, (F[4232] = 2.67, $p = 0.03$, $\eta_p^2 = 0.04$), as well as between BMI group, avatars' Emotion, Food palatability, Time, and avatars' Gaze, (F[36,2088] = 1.60, $p = 0.013$, $\eta_p^2 = 0.03$). To clarify the meanings of these interactions 4-way ANOVAs (Emotion x Gaze x Time x BMI) were performed for each category of food palatability (disliked food, moderately liked food, liked food). The BMI group significantly interacted with Time, F[9, 522] = 4.05, $p < 0.0001$, $\eta_p^2 = 0.065$, avatars' Emotion x Time (F[18,1044] = 1.92, $p = 0.01$, $\eta_p^2 = 0.03$), and avatars' Emotion x Gaze x Time (F[18,1044] = 1.59, $p = 0.05$, $\eta_p^2 = 0.03$) for the palatable foods, whereas no significant interactions were found between the BMI group and the other factors for the disliked or the moderately liked foods. As illustrated in Fig. 1, the BMI × Time interaction reflects the fact that regardless of the avatars' social cues, the most liked food elicited a larger HR deceleration in OW/OB than NW participants at T6-T10, F(1, 58) = 6.55, $p = 0.013$. Further, the OW/OB participants, but not the NW participants, showed a significant decrease of HR between T1-T5 and T6-T10 when exposed to palatable food pictures, F(1, 58) = 29.99, $p < 0.0001$.

As illustrated in Fig. 2, the BMI group x avatars' Emotion × Time interaction indicates that the palatable food associated with the avatars' happy faces induced a larger HR deceleration in OW/OB than in NW participants during T6-T10 compared to the first phase of exposure (T1-T5), (F(1,58) = 14.53, $p = 0.0003$).

The BMI group x avatars' Emotion x avatars' Gaze x Time revealed that the avatars' happy faces with averted gaze associated with the liked foods induced a larger HR deceleration in OW/OB than in NW participants during T6-T10 than T1-T5 phases, (F(1,58) = 17.05, $p = 0.0001$), whereas no significant difference was found between the two groups when the avatars' happy expressions were directed toward the participants (Fig. 3).

Zygomatic reactivity to food cues as an index of 'liking'. The ANOVA on zygomatic activity resulted in significant main effects for avatars' Emotion (F[2, 112] = 4.10, $p = 0.02$, $\eta_p^2 = 0.07$) and Time (F[9504] = 6.20, $p < 0.0001$, $\eta_p^2 = 0.10$), qualified by an avatars' Emotion × Time interaction (F[18,1008] = 1.71, $p = 0.03$, $\eta_p^2 = 0.03$). The latter effect indicated that the avatars' happy faces elicited a greater zygomatic reactivity than the avatars' neutral (F(1,56) = 5.37, $p = 0.02$) or disgust (F(1,56) = 5.27, $p = 0.02$) faces at T4-T6 (Table S2). Significant effects were also found for Food palatability (F(2, 112) = 8.09, $p = 0.0005$, $\eta_p^2 = 0.13$), as well as for the interactions between Food palatability and Time (F[18,1008] = 2.79, $p = 0.00009$, $\eta_p^2 = 0.05$), and between BMI group, Food palatability, and Time (F[18,1008] = 1.80, $p = 0.02$, $\eta_p^2 = 0.03$). As illustrated in Fig. 4, the three-way interaction reflects the fact that the palatable foods elicited greater zygomatic activity in NW participants at T4-T6 as compared to T1-T3 (F(1,56) = 8.37, $p = 0.005$), whereas no significant difference were found in OW/OB participants. The NW participants also revealed greater zygomatic activity at T4-T6 as compared to T1-T3 when exposed to the palatable food than to the moderately liked (F(1,56) = 6.96, $p = 0.01$) or disliked foods (F(1,56) = 8.25, $p = 0.006$).

Levator labii reactivity to food cues as an index of disliking. Significant two-way interactions were found between BMI group and Food palatability (F[2110] = 3.51, $p = 0.03$, $\eta_p^2 = 0.06$), Food palatability and Time (F[18,990] = 2.66, $p = 0.0002$, $\eta_p^2 = 0.05$), avatars' Emotion and Time (F[18,990] = 3.14, $p < 0.0001$, $\eta_p^2 = 0.05$), and avatars' Gaze and Food palatability (F[2110] = 4.11, $p = 0.02$, $\eta_p^2 = 0.07$). The avatars' Emotion × Food palatability × Time interaction (F[36,1980] = 1.89, $p = 0.001$, $\eta_p^2 = 0.03$) and the Food palatability × avatars' Gaze × Time interaction (F[18,990] = 2.19, $p = 0.004$, $\eta_p^2 = 0.04$) were also significant. Tukey post-hoc test revealed that NW participants displayed increased *levator labii* muscle activity in response to disliked foods (M = 4.0%, $SD = 1.93$) than to the moderately liked ($M = 1.34\%$, $SD = 1.18$, $p = 0.03$) or liked foods ($M = 1.67$, $SD = 1.44$, $p = 0.09$), whereas no significant differences were detected in OW/OB participants (Fig. 5). Planned contrasts performed on the facial expression × food preference × time interaction indicated that disliked foods associated with the avatars' disgust faces elicited a greater activity increase in the *levator labii* muscle as compared with those foods associated with the avatars' neutral (T4–T6 vs T1-T3, F(1,55) = 8.19, $p = 0.006$) and happy faces (T4–T6 vs T1-T3, F(1,55) = 7.36, $p = 0.009$) (Fig. S1).

4. Discussion

The first aim of this study was to investigate whether psychophysiological markers of incentive salience attribution (objective wanting) and hedonic reactivity (objective liking) to food reward-related cues may be disentangled in OW/OB adults compared to NW adults. In line with the incentive sensitization hypothesis, OW/OB participants exhibited a larger HR deceleration to palatable food pictures than NW participants suggesting that they allocated more sustained attention to salient food cues, while at the same time, they did not reveal an

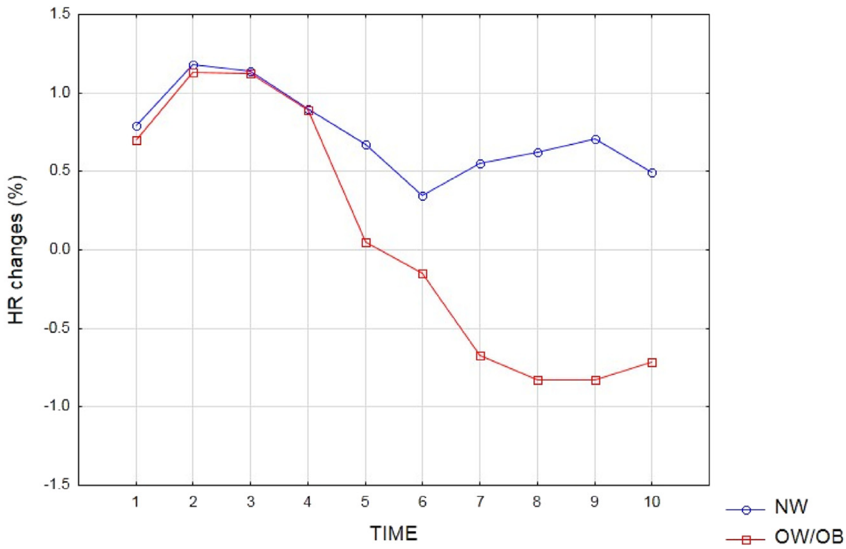

Fig. 1. Time course of heart rate (HR) changes (% changes from baseline) in normal weight (NW) and overweight/obese (OW/OB) participants exposed to pictures of liked food in the joint attention paradigm. Each point of the abscissa represents the average activity during each 500-ms time interval.

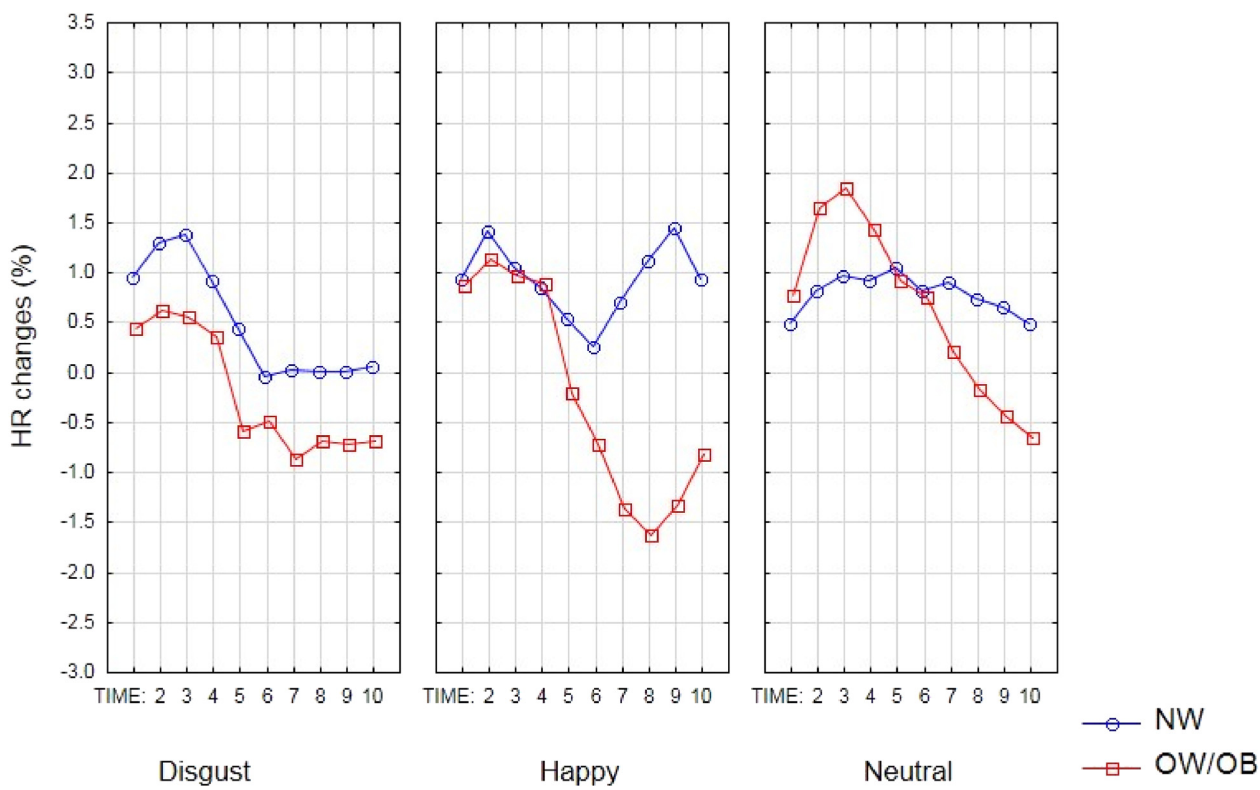

Fig. 2. Time course of HR changes (% changes from baseline) in the normal weight (NW) and overweight/obese (OW/OB) participants exposed to pictures of liked food associated with the avatars' facial expressions of emotion (disgust, happy, and neutral) in the joint attention paradigm. Each point of the abscissa represents the average activity during each 500-ms time interval.

increase of positive hedonic facial reactions to visual cues of liked foods. Indeed, only the NW group displayed an increase in zygomatic activity to the pictures of the most liked food than to those of the moderately liked, or disliked foods. In addition, they showed an increase in disgust reactions (as indexed by greater *levator labii* muscle activity) to disliked foods than to the moderately liked or most liked foods. Taken together, our autonomic and facial EMG data suggest that OW/OB people reacted more to the motivational salience of food-related cues (as reflected by their attention-grabbing properties) than to their affective valence. To our knowledge, this is the first evidence of a dissociation between implicit components of food 'wanting' and 'liking' in OW/OB participants using two psychophysiological indices of incentive salience and affective valence. In contrast, we did not find a dissociation for their explicit counterparts as a function of BMI status because the participants of the two groups reported similar scores for subjective food wanting and liking.

The present findings add to the existing literature because previous studies in OW/OB individuals used only implicit measures of attentional processing of food-related visual cues (e.g., eye movements, ERP P200 amplitude, ERP P300 latency), but not facial EMG measures of

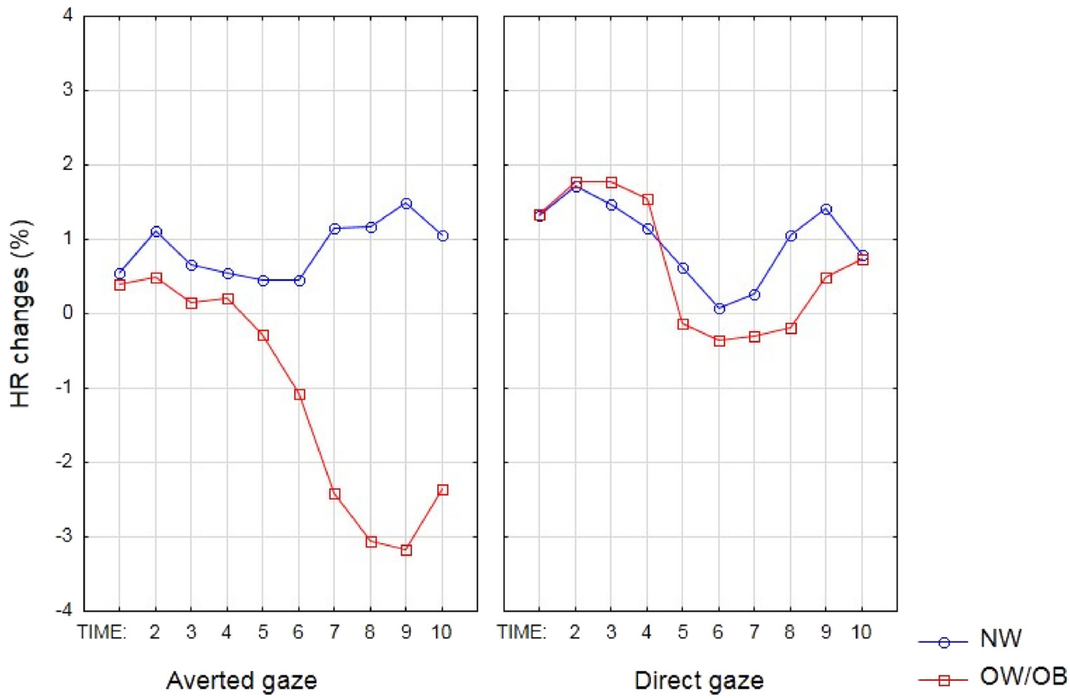

Fig. 3. Time course of HR changes (% changes from baseline) in the normal weight (NW) and overweight/obese (OW/OB) participants exposed to pictures of liked food and to avatars' happy faces with averted gaze (directed only toward the food) or direct gaze (consecutively directed toward the food and participants). Each point of the abscissa represents the average activity during each 500-ms time interval.

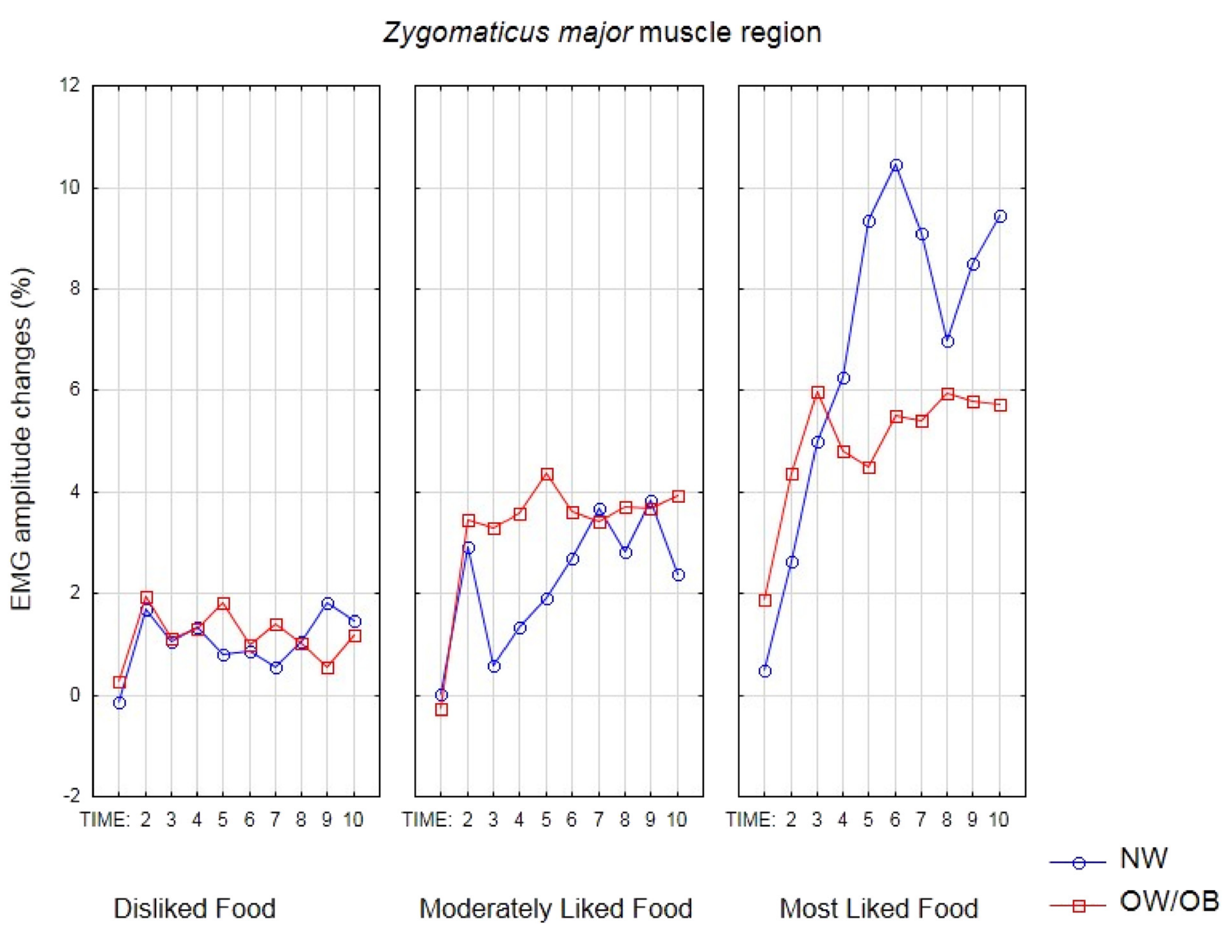

Fig. 4. Time course of mean amplitude changes of *zygomaticus major* muscle region activity (% changes from baseline) as a function of food palatability in normal weight (NW) and overweight/obese (OW/OB) participants. Each point of the abscissa represents the average activity during each 500-ms time interval.

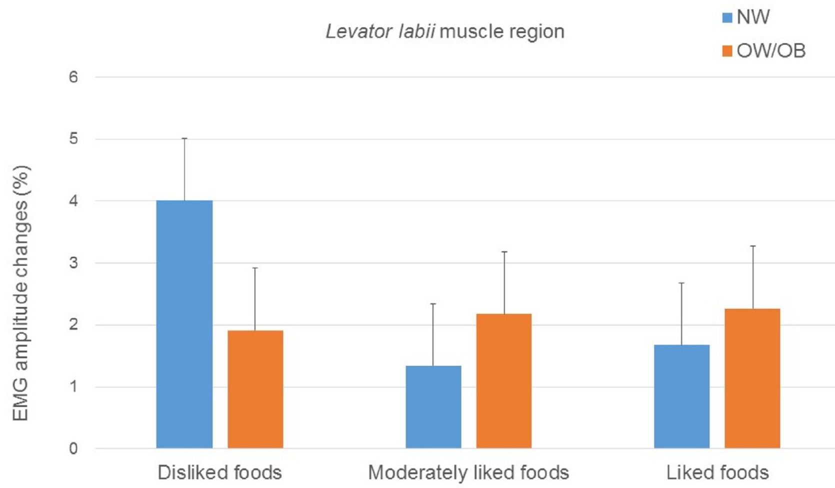

Fig. 5. Changes in the mean amplitude of *levator labii* muscle region activity (% from baseline) as a function of food palatability in normal weight (NW) and overweight/obese (OW/OB) participants.

hedonic reactivity. For example, OW/OB participants increased their gaze duration to food compared to non-food images in a sated condition (Castellanos et al., 2009), or maintained greater attention towards high energy dense compared to low-energy-density food images regardless of hunger condition (Doolan et al., 2014). Studies also showed that OW/OB participants directed their initial gaze more often toward high-fat food (Werthmann et al., 2011), or displayed ERP indices of enhanced attentional processing to food pictures (Hume et al., 2015). Concerning liking, previous research mainly used pleasantness rating (explicit liking) during food taste/intake in OW/OB individuals. However, self-report studies found discrepancies about the relationships between food liking, BMI and food consumption/choice (Bobroff & Kissileff, 1986; De Graaf, 2008; Fisher & Birch, 1995; Giesen et al., 2010; Le Noury, Lawton, & Blundell, 2002; Ouwehand & de Ridder, 2008; Ricketts, 1997; Saelens & Epstein, 1996). Given the limitations of subjective reports and as objective 'wanting' and 'liking' also depend on mechanisms acting below the level of consciousness (Anselme & Robinson, 2016; Berridge & Robinson, 2003), our findings support the view that excessive attribution of incentive salience, but probably not objective 'liking', might contribute to overeating or overweight/obesity. It should be noted that the construct of liking has often been operationalized during the consummatory phase of reward processing (Berridge & Robinson, 2003; Pool, Sennwald, Delplanque, Tobias Brosch, & Sander, 2016). Thus, our study highlights the necessity to take into account this construct during anticipatory reward processing (*i.e.*, anticipated liking/pleasure) as people exposed to the smell or the sight of palatable food cues can display pleasure faces (Armstrong, Hutchinson, Laing, & Jinks, 2007; Soussignan et al., 2011, 2015) and experience the feeling of pleasure in association with the brain reward circuitry activation (Born et al., 2011; Jiang et al., 2015). For example, sensory cues (smell, sight) while cooking can grasp a person's attention (incentive salience attribution) and trigger positive hedonic facial reactions even in the absence of food consumption.

The second aim of our study was to examine whether a rewarding social context, such as watching happy faces and establishing eye contact while engaging in eating behavior, modulates electrophysiological correlates of incentive salience and hedonic reactions to food cues in OW/OB participants. The present study provides interesting contributions to current knowledge on the relationship between positive social cues and food reward as a function of BMI status. First, HR deceleration in response to palatable food cues, as an index of incentive salience attribution, was more pronounced in OW/OB than in NW participants when palatable food cues were associated with avatars' happy faces, whereas zygomatic EMG activity, as an index of hedonic reactivity, was not modulated by the interaction between this social reward and food palatability. Rather, regardless of food palatability, both groups of participants displayed a greater zygomatic activity to avatars' happy faces compared to the other avatars' facial expressions. This latter finding probably reflects an automatic tendency to display positive facial mimicry when someone looks at a happy face (Schrammel et al., 2009; Soussignan et al., 2013, 2018). The fact that the avatars' happy faces had a powerful effect on attention, but not on hedonic reactivity, to palatable food cues in OW/OB individuals suggests that positive cues of the social environment potentiate the rewarding value of food 'wanting' probably by acting on the brain reward circuitry, which is known to mediate the evaluation of both social and non-social rewards (Beaver et al., 2006; Bhanji & Delgado, 2014; Burger & Stice, 2011). In line with a previous study (Barthomeuf, Rousset, & Droit-Volet, 2010), we did not find that happy faces of avatars modified the subjective desire of participants to eat liked food as a function of BMI. In contrast, we provided evidence that avatars' happy faces as an index of a social reward cue influenced incentive salience (objective wanting) in OW/OB persons. The demonstration of an effect of others' happy faces on incentive salience attribution to food images is ecologically relevant because people in societies with industrialized marketing are intensively exposed, via advertising media (*e.g.*, television, internet, print), to happy/smiling faces of persons watching or eating foods. Second, our data revealed that avatars' happy faces gazing at palatable food (averted gaze condition) produced a more pronounced effect on HR deceleration in OW/OB than in NW participants. Although the meaning of this result remains to clarify, it may reflect that seeing a happy face with a gaze directed toward a palatable food, by focusing the attention' participants to attractive cues, increased the rewarding value/incentive salience of food cues, and consequently, increased HR deceleration in OW/OB participants.

This study has several limitations. First, although our findings of a dissociation between incentive salience and hedonic reactivity in OW/OB persons is compatible with an "incentive sensitization" view, they do not necessarily reflect a process of neural sensitization of the dopaminergic mesolimbic pathway because our psychophysiological measures were not designed to reflect the underlying brain processes. Second, in the incentive-sensitization theory of addiction, neural sensitization leads to compulsive patterns of reward-seeking (Robinson & Berridge, 2001). Overweight/obesity comprises distinct phenotypes (e.g., polymorphisms of the dopamine D2 receptor and dopamine transporter genes; binge eating subtype) with some individuals being more compulsive than others (Dalton, Blundell & Finlayson, 2013; Epstein, Temple, Neaderhiser, Salis & Leddy, 2008). As we assessed only the perceptual component of food 'wanting' (incentive salience), it is unclear whether our findings can be generalized to distinct phenotypes of overweight/obesity. Third, as in a number of previous studies, both overweight and obese participants were included in a single group. Thus, future studies on larger samples should examine whether overweight and obese participants may be differentiated in terms of incentive salience attribution and hedonic reactivity when exposed to palatable food cues. However, despite these limitations, the present study has several strengths. First, using for the first time two electrophysiological indices of attentional/incentive salience and hedonic reactivity within an innovative and ecologically relevant paradigm, we provide evidence that objective components of 'wanting' and 'liking' may be dissociated in OW/OB individuals, but not for their explicit counterparts. Second, our paradigm strengthens the view that a social reward, such as looking at happy faces in a feeding context, may automatically potentiate incentive salience attribution to palatable food cues in OW/OB people. This finding stresses the need to take greater account in future studies that food reward is intertwined within affiliative and reinforcing cues in the social context which likely contribute to overeating and overweight by increasing the activity of the brain reward system.

Author contributions

R.S, B.S. and T.J. designed the study; T.J. conducted the experiment and collected the data; R.S. conceived the paradigm, analyzed the data, interpreted the results and wrote the paper; R.S, B.S. and T.J. reviewed the final version of the manuscript.

Additional information

The authors declare no competing financial interests.

Acknowledgements

We greatly thank the persons who accepted to participate in this research which was financially supported by a grant from the French National Research Agency (ANR 11 EMCO 00902).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.appet.2018.10.024.

References

Anselme, P., & Robinson, M. J. (2016). "Wanting", "liking", and their relation to consciousness. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 42*, 123–140.
Armstrong, J. E., Hutchinson, I., Laing, D. G., & Jinks, A. L. (2007). Facial electromyography: Responses of children to odor and taste stimuli. *Chemical Senses, 32*, 611–621.
Averbeck, B. B., & Duchaine, B. (2009). Integration of social and utilitarian factors in decision making. *Emotion, 9*, 599–608.
Barthomeuf, L., Rousset, S., & Droit-Volet, S. (2010). The desire to eat in the presence of obese or normal-weight eaters as a function of their emotional facial expression. *Obesity, 18*, 719–724.
Beaver, J. D., Lawrence, A. D., van Ditzhuijzen, J., Davis, M. H., Woods, A., & Calder, A. J. (2006). Individual differences in reward drive predict neural responses to images of food. *Journal of Neuroscience, 26*, 5160–5166.
Berridge, K. C. (1996). Food reward: Brain substrates of wanting and liking. *Neuroscience & Biobehavioral Reviews, 20*, 1–25.
Berridge, K. C. (2009). Liking' and 'wanting' food rewards: Brain substrates and roles in eating disorders. *Physiology & Behavior, 97* 537-950.
Berridge, K. C., & Kringelbach, M. L. (2008). Affective neuroscience of pleasure: Reward in humans and animals. *Psychopharmacology, 199*, 457–480.
Berridge, K. C., & Robinson, T. E. (1998). What is the role of dopamine in reward: Hedonic impact, reward learning, or incentive salience? *Brain Research. Brain Research Reviews, 28*, 309–369.
Berridge, K. C., & Robinson, T. E. (2003). Parsing reward. *Trends in Neurosciences, 26*, 507–513.
Berridge, K. C., & Robinson, T. E. (2016). Liking, wanting, and the incentive-sensitization theory of addiction. *American Psychologist, 71*, 670–679.
Bevelander, K. E., Lichtwarck-Aschoff, A., Anschütz, D. J., Hermans, R. C. J., & Engels, R. C. M. E. (2013). Imitation of snack food intake among normal-weight and overweight children. *Frontiers in Psychology, 4*, 949.
Bhanji, J. P., & Delgado, M. R. (2014). The social brain and reward: Social information processing in the human striatum. *Wiley Interdisciplinary Reviews: Cognitive Science, 5*, 61–73.
Bobroff, E. M., & Kissileff, H. R. (1986). Effects of changes in palatability on food intake and the cumulative food intake curve in man. *Appetite, 7*, 85–96.
Born, J. M., Lemmens, S. G., Martens, M. J., Formisano, E., Goebel, R., & Westerterp-Plantenga, M. S. (2011). Differences between liking and wanting signals in the human brain and relations with cognitive dietary restraint and body mass index. *The American Journal of Clinical Nutrition, 94*, 392–403.
Boswell, R. G., & Kober, H. (2015). Food cue reactivity and craving predict eating and weight gain: A meta-analytic review. *Obesity Review, 17*, 159–177.
Burger, K. S., & Stice, E. (2011). Variability in reward responsivity and obesity: Evidence from brain imaging studies. *Current Drug Abuse Reviews, 4*, 182–189.
Carver, C. S., & White, T. L. (1994). Behavioral inhibition, behavioral activation, and affective responses to impending reward and punishment: The BIS/BAS Scales. *Journal of Personality and Social Psychology, 67*, 319–333.
Castellanos, E. H., Charboneau, E., Dietrich, M. S., Park, S., Bradley, B. P., Mogg, K., et al. (2009). Obese adults have visual attention bias for food cue images: Evidence for altered reward system function. *International Journal of Obesity, 33*, 1063–1073.
Cruwys, T., Bevelander, K. E., & Hermans, R. C. (2015). Social modeling of eating: A review of when and why social influence affects food intake and choice. *Appetite, 86*, 3–18.
Dalton, M., Blundell, J., & Finlayson, G. (2013). Effect of BMI and binge eating on food reward and energy intake: Further evidence for a binge eating subtype of obesity. *Obesity Facts, 6*, 348–359.
Davids, S., Lauffer, H., Thoms, K., Jagdhuhn, M., Hirschfeld, H., Domin, M., et al. (2010). Increased dorsolateral prefrontal cortex activation in obese children during observation of food stimuli. *International Journal of Obesity, 34*, 94–104.
Davis, M. H. (1983). Measuring individual differences in empathy: Evidence for a multidimensional approach. *Journal of Personality and Social Psychology, 44*, 113–126.
De Graaf, C. (2008). The development of sensory preferences in children in relation to food intake and obesity. *Enfance, 60*, 281–288.
Delplanque, S., Grandjean, D., Chrea, C., Coppin, G., Aymard, L., Cayeux, I., et al. (2009). Sequential unfolding of novelty and pleasantness appraisals of odors: Evidence from facial electromyography and autonomic reactions. *Emotion, 9*, 316–328.
Doolan, K. J., Breslin, G., Hanna, D., Murphy, K., & Gallagher, A. M. (2014). Visual attention to food cues in obesity: An eye-tracking study. *Obesity, 22*, 2501–2507.
Dressler, H., & Smith, C. (2013). Food choice, eating behavior, and food liking differ between lean/normal and overweight/obese, low-income women. *Appetite, 65*, 145–152.
Drewnowski, A., Krahn, D. D., Demitrack, M. A., Nairn, K., & Gosnell, B. A. (1992). Taste responses and preferences for sweet high-fat foods. Evidence for opioid involvement. *Physiology & Behavior, 51*, 371–379.
Ekman, P., & Friesen, W. V. (1978). *Facial action coding system: A technique for the measurement of facial movement.* Palo Alto, CA: Consulting Psychologists Press.
Epstein, L. H., Temple, J. L., Neaderhiser, B. J., Salis, R. J., Erbe, R. W., & Leddy, J. J. (2008). Food reinforcement, the dopamine D2 receptor genotype, and energy intake in obese and nonobese humans. *Behavioral Neuroscience, 122*, 877–886.
Fehr, F. S., & Schulman, M. (1978). Female self-report and autonomic responses to sexually pleasurable and sexually aversive readings. *Archives of Sexual Behavior, 7*, 443–453.
Filbey, F. M., Myers, U. S., & Dewitt, S. (2012). Reward circuit function in high BMI individuals with compulsive overeating: Similarities with addiction. *NeuroImage, 63*, 1800–1806.
Finlayson, G., & Dalton, M. (2012). Current progress in the assessment of 'liking' vs. 'wanting' food in human appetite. Comment on "'You say it's liking, i say it's wanting . . .". On the difficulty of disentangling food reward in man. *Appetite, 58*, 373–378.
Finlayson, G., King, N., & Blundell, J. E. (2007). Liking vs. wanting food. Importance for human appetite control and weight regulation. *Neuroscience & Biobehavioral Reviews, 31*, 987–1002.
Fisher, J. O., & Birch, L. L. (1995). Fat preferences and fat consumption of 3- to 5-year-old children are related to parental adiposity. *Journal of the American Dietetic Association, 95*, 759–764.
Furl, N., Gallagher, S., & Averbeck, B. B. (2012). A selective emotional decision-making bias elicited by facial expressions. *PloS One, 7*(3), e33461.
Gard, D. E., Gard, M. G., Kring, A. M., & John, O. P. (2006). Anticipatory and consummatory components of the experience of pleasure: A scale development study. *Journal of Research in Personality, 50*, 1086–1102.
Giesen, J. C., Havermans, R. C., Douven, A., Tekelenburg, M., & Jansen, A. (2010). Will work for snack food: The association of BMI and snack reinforcement. *Obesity, 18*, 966–970.
Graham, F. K., & Clifton, R. K. (1966). Heart-rate change as a component of the orienting response. *Psychological Bulletin, 65*, 305–320. http://psycnet.apa.org/doi/10.1037/h0023258.
Havermans, R. C. (2011). "You Say it's Liking, I Say it's Wanting . . .". On the difficulty of disentangling food reward in man. *Appetite, 57*, 286–294.
Herman, C. P., Roth, D. A., & Polivy, J. (2003). Effects of the presence of others on food intake: A normative interpretation. *Psychological Bulletin, 129*, 873–886.
Hess, U., & Fischer, A. (2014). Emotional mimicry: Why and when we mimic emotions. *Social and Personality Psychology Compass, 8*, 45–57.
Hume, D. J., Howells, F. M., Rauch, H. G., Kroff, J., & Lambert, E. V. (2015).

Electrophysiological indices of visual food cue-reactivity. Differences in obese, overweight and normal weight women. *Appetite, 85*, 126–137.
Hu, S., Player, K. A., Mcchesney, K. A., Dalistan, M. D., Tyner, C. A., & Scozzafava, J. E. (1999). Facial EMG as an indicator of palatability in humans. *Physiology & Behavior, 68*, 31–35.
Jiang, T., Soussignan, R., Schaal, B., & Royet, J. P. (2015). Reward for food odors: An fMRI study of liking and wanting as a function of metabolic state and BMI. *Social Cognitive and Affective Neuroscience, 10*, 561–568.
Lang, P. J., Greenwald, M. K., Bradley, M. M., & Hamm, A. O. (1993). Looking at pictures: Affective, facial, visceral, and behavioral reactions. *Psychophysiology, 30*, 261–267.
Lansink, J. M., & Richards, J. E. (1997). Heart rate and behavioral measures of attention in six-, nine-, and twelve-month-old infants during object exploration. *Child Development, 68*, 610–620.
Larsen, J. T., Norris, C. J., & Cacioppo, J. T. (2003). Effects of positive and negative affect on electromyographic activity over zygomaticus major and corrugator supercilii. *Psychophysiology, 40*, 776–785.
Le Noury, J., Lawton, C. L., & Blundell, J. (2002). Food choice and hedonic responses: Difference between overweight and lean high fat phenotypes. *International Journal of Obesity, 26*, S125.
Martin, J., Rychlowska, M., Wood, A., & Niedenthal, P. (2017). Smiles as multipurpose social signals. *Trends in Cognitive Sciences, 21*, 864–877.
Mela, D. J. (2006). Eating for pleasure or just wanting to eat? Reconsidering sensory hedonic responses as a driver of obesity. *Appetite, 47*, 10–17. https://www.ncbi.nlm.nih.gov/pubmed/16647788.
Nijs, I. M., Muris, P., Euser, A. S., & Franken, I. H. (2010). Differences in attention to food and food intake between overweight/obese and normal-weight females under conditions of hunger and satiety. *Appetite, 54*, 243–254.
O'Doherty, J., Winston, J., Critchley, H., Perrett, D., Burt, D. M., & Dolan, R. J. (2003). Beauty in a smile: The role of medial orbitofrontal cortex in facial attractiveness. *Neuropsychologia, 41*, 147–155.
Otta, E., Folladore, A. F., & Hoshino, R. L. (1996). Reading a smiling face: Messages conveyed by various forms of smiling. *Perceptual & Motor Skills, 82*, 1111–1121.
Ouwehand, C., & de Ridder, D. T. (2008). Effects of temptation and weight on hedonics and motivation to eat in women. *Obesity, 16*, 1788–1793.
Peciña, S., Cagniard, B., Berridge, K. C., Aldridge, J. W., & Zhuang, X. (2003). Hyperdopaminergic mutant mice have higher "wanting" but not "liking" for sweet rewards. *Journal of Neuroscience, 23*, 9395–9402.
Peciña, S., & Smith, K. S. (2010). Hedonic and motivational roles of opioids in food reward: Implications for overeating disorders. *Pharmacology Biochemistry and Behavior, 97*, 34–46.
Peltola, M. J., Leppänen, J. M., & Hietanen, J. K. (2011). Enhanced cardiac and attentional responding to fearful faces in 7-month-old infants. *Psychophysiology, 48*, 1291–1298.
Pichon, A. M., Coppin, G., Cayeux, I., Porcherot, C., Sander, D., & Delplanque, S. (2015). Sensitivity of physiological emotional measures to odors depends on the product and the pleasantness ranges used. *Frontiers in Psychology, 6*, 1821.
Plesa Skwerer, D., Borum, L., Verbalis, A., Schofield, C., Crawford, N., Ciciolla, L., et al. (2009). Autonomic responses to dynamic displays of facial expressions in adolescents and adults with Williams syndrome. *Social Cognitive and Affective Neuroscience, 4*, 93–100.
Pool, E., Sennwald, V., Delplanque, S., Tobias Brosch, T., & Sander, D. (2016). Measuring wanting and liking from animals to humans: A systematic review. *Neuroscience & Biobehavioral Reviews, 63*, 124–142.
Richards, J. E. (2008). Attention in young infants: A developmental psychophysiological perspective. In C. A. Nelson, & M. Luciana (Eds.). *Handbook of developmental cognitive neuroscience* (pp. 479–497). Cambridge, MA, US: MIT Press.
Ricketts, C. D. (1997). Fat preferences, dietary fat intake and body composition in children. *European Journal of Clinical Nutrition, 51*, 778–781.
Robinson, T. E., & Berridge, K. C. (2001). Incentive-sensitization and addiction. *Addiction, 96*, 103–114.
Robinson, J. D., Cinciripini, P. M., Carter, B. L., Lam, C. Y., & Wetter, D. W. (2007). Facial EMG as an index of affective response to nicotine. *Experimental and Clinical Psychopharmacology, 15*, 390–399.
Saelens, B. E., & Epstein, L. H. (1996). Reinforcing value of food in obese and non-obese women. *Appetite, 27*, 41–50.
Schrammel, F., Pannasch, S., Graupner, S., Mojzisch, A., & Velichkovsky, B. (2009). Virtual friend or threat? The effects of facial expression and gaze interaction on psychophysiological responses and emotional experience. *Psychophysiology, 46*, 922–931.
Soussignan, R., Chadwick, M., Leonor, P., Conty, L., Dezecache, G., & Grèzes, J. (2013). Self-relevance appraisal of gaze direction and dynamic facial expressions: Effects on facial electromyographic and autonomic reactions. *Emotion, 13*, 330–337.
Soussignan, R., Dollion, N., Schaal, B., Durand, K., Reissland, N., & Baudouin, J. Y. (2018). Mimicking emotions: How 3-12-month-old infants use the facial expressions and eyes of a model. *Cognition & Emotion, 32*, 827–842.
Soussignan, R., Schaal, B., Boulanger, V., Gaillet, M., & Jiang, T. (2012). Orofacial reactivity to the sight and smell of food stimuli. Evidence for anticipatory liking related to food reward cues in overweight children. *Appetite, 58*, 508–516.
Soussignan, R., Schaal, B., Boulanger, V., Garcia, S., & Jiang, T. (2015). Emotional communication in the context of joint attention for food stimuli: Effects on attentional and affective processing. *Biological Psychology, 104*, 173–183.
Soussignan, R., Schaal, B., Rigaud, D., Royet, J. P., & Jiang, T. (2011). Hedonic reactivity to visual and olfactory cues: Rapid facial electromyographic reactions are altered in anorexia nervosa. *Biological Psychology, 86*, 265–272.
Stoeckel, L. E., Weller, R. E., Cook, E. W., Twieg, D. B., Knowlton, R. C., & Cox, J. E. (2008). Widespread reward-system activation in obese women in response to pictures of high-calorie foods. *NeuroImage, 41*, 636–647.
Strathearn, L., Li, J., Fonagy, P., & Montague, P. R. (2008). What's in a smile? Maternal brain responses to infant facial cues. *Pediatrics, 122*, 40–51.
Temple, J. L., Legierski, C. M., Giacomelli, A. M., Salvy, S. J., & Epstein, L. H. (2008). Overweight children find food more reinforcing and consume more energy than do nonoverweight children. *The American Journal of Clinical Nutrition, 87*, 1121–1127.
Van Strien, T., Frijters, J. E., Bergers, G. P., & Defares, P. B. (1986). The Dutch Eating Behavior Questionnaire (DEBQ) for assessment of restrained, emotional, and external eating behavior. *International Journal of Eating Disorders, 5*, 295–315.
Vrana, S. R. (1993). The psychophysiology of disgust: Differentiating negative emotional contexts with facial EMG. *Psychophysiology, 30*, 279–286.
Werthmann, J., Roefs, A., Nederkoorn, C., Mogg, K., Bradley, B. P., & Jansen, A. (2011). Can(not) take my eyes off it: Attention bias for food in overweight participants. *Health Psychology, 30*, 561–569.
Yeomans, M. R., Blundell, J. E., & Leshem, M. (2004). Palatability. Response to nutritional need or need-free stimulation of appetite? *British Journal of Nutrition, 92*, S3–S14.
Yokum, S., Ng, J., & Stice, E. (2011). Attentional bias to food images associated with elevated weight and future weight gain: An fMRI Study. *Obesity, 19*, 1775–1783.