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Brain dynamics of meal size selection in humans

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ABSTRACT

Although neuroimaging research has evidenced specific responses to visual food stimuli based on their nutritional quality (e.g., energy density, fat content), brain processes underlying portion size selection remain largely unexplored. We identified spatio-temporal brain dynamics in response to meal images varying in portion size during a task of ideal portion selection for prospective lunch intake and expected satiety. Brain responses to meal portions judged by the participants as 'too small', 'ideal' and 'too big' were measured by means of electroencephalographic (EEG) recordings in 21 normal-weight women. During an early stage of meal viewing (105-145 ms), data showed an incremental increase of the head-surface global electric field strength (quantified via global field power; GFP) as portion judgments ranged from 'too small' to 'too big'. Estimations of neural source activity revealed that brain regions underlying this effect were located in the insula, middle frontal gyrus and middle temporal gyrus, and are similar to those reported in previous studies investigating responses to changes in food nutritional content. In contrast, during a later stage (230-270 ms), GFP was maximal for the 'ideal' relative to the 'non-ideal' portion sizes. Greater neural source activity to 'ideal' vs. 'non-ideal' portion sizes was observed in the inferior parietal lobule, superior temporal gyrus and mid-posterior cingulate gyrus. Collectively, our results provide evidence that several brain regions involved in attention and adaptive behavior track 'ideal' meal portion sizes as early as 230 ms during visual encounter. That is, responses do not show an increase paralleling the amount of food viewed (and, in extension, the amount of reward), but are shaped by regulatory mechanisms.

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1. Introduction

The sight of food triggers a range of physiological and psychological anticipatory responses based on knowledge acquired through past experiences. These responses not only prepare the body for ingestion but serve to guide food choice and intake with little conscious effort. At the neural level, the simple viewing of energy-dense foods elicits strong activations in visual, homeostatic and reward-related areas in comparison to low-energy foods (Frank et al., 2010; Killgore et al.,

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2003: Siep et al., 2009: Toepel et al., 2009). The most consistent activations across functional magnetic resonance imaging (fMRI) studies are found in the middle occipital gyrus, inferior temporal gyrus, hypothalamus, ventral striatum and middle frontal gyrus (van der Laan et al., 2011). These activations were obtained in normal-weight individuals while viewing food items with high vs. low caloric content with no explicit evaluation of foods requested. Detecting foods rich in energy is essential to ensure nutrition as those foods help to achieve satiety faster and for longer periods than foods poor in energy (Drewnowski and Almiron-Roig, 2010). Responses to the sight of energy-dense foods, especially in the prefrontal region, may further reflect the expected pleasantness of these foods because this brain region is highly responsive to the pleasant taste or flavor of foods (Kringelbach et al., 2003; Kringelbach, 2005; Ohla et al., 2012; Small et al., 2003b; Tzieropoulos et al., 2013). Yet, the practical implications of the greater activations to energy-dense foods on food intake control and in particular on portion size selection remain so far elusive. For example, the abovementioned neuroimaging studies (Frank et al., 2010; Killgore

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Abbreviations: CG, cingulate gyrus; EEG, electro-encephalographic; fMRI, functional magnetic resonance imaging; GFP, global field power; IOG, inferior occipital gyrus; IPL, inferior parietal lobe; INS, insula; LAURA, local autoregressive average; MFG, middle frontal gyrus; MTG, middle temporal gyrus; FCQ-S, momentary craving state questionnaire; SPL, superior parietal lobule; STG, superior temporal gyrus; TFEQ-R 18, Three-Factor-Eating questionnaire; VEPs, visual evoked potentials.

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et al., 2003; Siep et al., 2009; Toepel et al., 2009; van der Laan et al., 2011) did not systematically control food portion sizes (Frank et al., 2010; Killgore et al., 2003; Siep et al., 2009; Toepel et al., 2009; van der Laan et al., 2011).

Portion size is yet a crucial determinant of energy balance and weight management (Rolls et al., 2002; Wansink et al., 2005; Wansink and Kim, 2005). Using computer-based tasks with food pictures, a number of studies showed that decisions on portion size are not driven by food energy density or food liking as such, and that participants do not necessarily select the largest portion sizes as their ideal ones (Brogden and Almiron-Roig, 2010; Brunstrom et al., 2010; Brunstrom and Rogers, 2009; Brunstrom and Shakeshaft, 2009; Forde et al., 2011). In other words, it seems that individuals do not select meal portion sizes only for calories or for pleasure. Instead, other factors related to expected post-ingestive effects appear to be key motivators for meal size selection, namely 'expected satiation' (anticipated fullness after consumption) and 'expected satiety' (anticipated fullness between meals). Along these lines, Wilkinson et al. (2012) showed that portion size selection and expected satiety are good predictors of energy intake, thus establishing the practical relevance of computer-based assessments to food intake behavior.

The primary objective of the current study was to identify the spatiotemporal brain dynamics mediating portion size judgment to gain further insight into food intake behavior and control. Responses to visually presented meals of varying portion size were assessed by means of electro-encephalographic (EEG) recordings in 24 normalweight women during a task of portion size judgment for expected satiety. Stimuli were pictures of 19 meals presented on a computer screen in a range of 11 different portion sizes. EEG data were analyzed using an electrical neuroimaging approach (Michel and Murray, 2012) as a function of individuals' judgments on the presented portion size among the three following forced-choice options: 'too small', 'ideal' and 'too big'. Under an assumption that only the increasing quantity of food viewed modulates brain responsiveness, one would expect to find an incremental increase of responses in the temporo-occipital brain regions involved in visual analysis and categorization within 200 ms after image onset (Busch et al., 2004; Puce et al., 2013), likely paralleled by similar response directions in prefrontal regions due to the reward value to food (Frank et al., 2010; Killgore et al., 2003; Siep et al., 2009; Toepel et al., 2009; van der Laan et al., 2011). In contrast, we hypothesized that an at least partially distinct network of brain regions would be involved in adaptive portion size selections (i.e., greatest responses to the portions judged as 'ideal' relative to those judged as 'non-ideal'). Due to the high temporal resolution of EEG, such response dissociations might not only be observed along a spatial dimension as in functional neuroimaging studies, but also along a temporal dimension with EEG modulations differing in the time domain for the expected effects (i.e., incremental increase vs. highest response to the portions judged as 'ideal'). Secondary objectives of the study were to explore associations between individual's responses to self-selected portion sizes with food intake attitudes such as dietary restraint and tendencies to overeat in emotionally challenging situations. These factors, known to influence brain responses to visual food cues (Meule et al., 2013; Toepel et al., 2012) and decisions on portion size (Brunstrom et al., 2008) in normal-weight individuals may reveal further insights into the brain mechanisms mediating portion size selection.

2. Material and methods

2.1. Study participants

Twenty-four normal-weight women participated in the study. Women were chosen to avoid confounding factors linked to gender differences in eating behavior and neural responses to food cues (Cornier et al., 2010; Rolls et al., 1991; Toepel et al., 2012). They completed the Three-Factor-Eating questionnaire (TFEO-R 18) (Karlsson et al., 2000) and momentary craving state questionnaires (FCO-S) (Nijs et al., 2007). Data from the standardized questionnaires were used for secondary data analyses as factors relating to food intake attitudes. All participants were healthy, with no prior history of selfreported head trauma, neurological disorder or diabetes, and were not under medication. All reported not having any history of eating disorders, current diet attempts, food allergies or intolerances and food restriction such as vegetarianism. Other exclusion criteria were pregnancy, breast-feeding, illicit drug consumption and the consumption of more than one alcoholic drink per day. Due to low EEG signal quality of three participants, only the data of 21 women entered the final analyses and their characteristics are summarized in Table 1. The study was approved by the Ethics Committee of the Faculty of Biology and Medicine of the University of Lausanne. All subjects gave written informed consent and received financial compensation for their participation.

2.2. Stimuli

Stimuli were pictures of 19 test meals commercially available and used previously in a consumer study (Forde et al., 2011). Each stimulus was photographed on a standard white plate. Fifty-one color pictures of different 'physical' portions for each meal were used during a prior familiarization session during which pictures were presented with a description label. A subset of 11 pictures for each meal was used for the subsequent EEG session (Fig. 1A). For a given meal, the central picture #25 corresponds to 100% of the portion size as sold. Picture #1 and picture #50 respectively represent 33% and 300% the kcal content of picture #25. Across this range, the portion size and, by extension, the caloric content of pictures, increase in equal logarithmic steps (0.3 log series) based on the originally published method for quantifying expectations of satiety and satiation (Brunstrom and Shakeshaft, 2009).

2.3. Study design and procedure

Participants completed two experimental sessions on different days. They were instructed to have their usual breakfast between 7:00 and 8:00 am and to refrain from eating any food and drinking caffeinated beverages until they arrived in the laboratory between 9:00 and 10:00. Participants were tested individually in a sound-attenuated booth.

During the prior familiarization session, participants performed a computer-based task comprising sequentially: Thirst and hunger ratings, matched fullness task (expected satiation), selection of portion size to stop feeling hungry until an evening meal (expected fullness), food consumption frequency (times per day/week/month/year), food familiarity and expected liking ratings. The exclusive purpose of this session was to familiarize participants with the views of the 19 meals used in the subsequent EEG session. A report on the outcome data is not in the scope of the current report.

During the EEG session, participants first received the following instructions: "You will be presented with a number of food pictures.

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Participants'	BMI and food	intake	attitudes	(N =	21).

Table 1

		Mean (\pm s.e.m.)	Range
BMI (in kg/m ²)		21.3 (±0.4)	17.5-26
TFEQ-R 18	Uncontrolled eating score	$40.4(\pm 3.1)$	19-67
	Emotional eating score	42.3 (±5.1)	0-78
	Restrained eating score	27.0 (±4.1)	0-56
FCQ-S score		31.8 (±2.0)	16-49

A)

Four cheese pizza

Beef and brocoli



B)



Fig. 1. Exemplar stimuli and study design. A) Portion size range of two test meals used in the EEG session. For each meal, every fifth portion size was chosen out of the full picture set with #25 being current portion of the meal as sold (100%), #1 being the smallest (33%) and #50 the largest (300%). B) Experimental design of the EEG session. The 209 stimuli (19 meals * 11 portion sizes) were presented once during each experimental block in a pseudo-random order. For each stimulus participants had to judge the size of the meal portion presented relative to their expected satiety for prospective lunch intake by choosing between 'too small', 'ideal' and 'too big'.

Imagine you are about to eat that food at lunchtime. No other foods are available. Judge the size of the portion relative to the size that you would select yourself for lunch today to stop feeling hungry until an evening meal." They were further instructed not to respond in cases where they completely disliked a meal so that the related data did not enter the subsequent analysis. They then completed five blocks of trials of approximately 6 min each and separated by a 2 min break (Fig. 1B). One block of trials consisted of the presentation of all 209 stimuli (19 meals \times 11 portion sizes) in a pseudo-random order, differently arranged in each block. The order of blocks was counter-balanced across participants to avoid position effects. During one trial, a meal picture was presented for 500 ms in the center of a 21" CRT monitor screen with a gray background, which was followed by a question mark presented for 2500 ms. Starting from stimulus presentation onset, participants had 3000 ms for judging the size of the meal portion relative to expected satiety according to a 3-alternative forced-choice: 'too small', 'ideal' or 'too big'. Behavioral responses and response times were recorded via a response box controlled by E-Prime with stimulus presentation (Psychology Software Tools Inc., Pittsburgh, USA; www. pstnet.com/eprime). Inter-trial intervals varied between 500 and 1000 ms during which participants had to fixate a central cross to avoid eye movements. The EEG session lasted between 60 and 75 min including electrode preparation.

EEG was continuously recorded at a 512 Hz digitization rate using a Biosemi ActiveTwo system (Biosemi, Amsterdam, The Netherlands) from 64 head-surface electrodes, arranged according to the expanded 10–20 positions. This system uses a pair of electrodes (common mode sense and driven right leg) as a feedback loop driving the average potential across the montage as close as possible to the amplifier zero. Details of this circuitry, including a diagram can be found on the Biosemi website (http://www.biosemi.com/pics/zero_ref1_big.gif). In the beginning and at the end of the session, participants rated their hunger level using 100 mm rating scales anchored from 'not hungry at all' to 'extremely hungry' to check for changes in food motivation

along the procedure. Overall, hunger level increased in all participants (mean change \pm s.e.m. = 42.8 \pm 5.5), indicating that the task did not have a detrimental impact on food motivation due to repeated exposure to visual food cues.

2.4. Data analysis

2.4.1. Behavioral data analysis

In a first descriptive step, the distribution of portion size judgments ('too small', 'ideal', 'too big') for the 11 physical portion sizes was assessed by averaging response frequency across meals and participants. In a second step, the frequency of portion size judgments and related reaction times were averaged across meals, physical portion sizes and participants. These data were submitted to one-way ANOVAs with the factor of portion judgment ('too small', 'ideal', 'too big'). Posthoc paired t-tests were computed when justified by the ANOVAs. Results were considered significant when $p \leq 0.05$.

2.4.2. EEG data analysis

Visual evoked potentials (VEPs) were computed by averaging EEG epochs from -100 ms to 500 ms relative to stimulus onset, separately for each participant as a function of individual portion judgment ('too small', 'ideal', 'too big'). The number of trials obtained for each portion judgment was examined individually and adjusted when necessary by randomly removing trials. As a result, the final number of trials for VEP analyses did not statistically differ between portion judgment conditions ($F_{2.60} = 0.55$; p = 0.58; mean \pm s.e.m.: 'too small' = 312 ± 4 , 'ideal' = 290 ± 10 , 'too big' = 300 ± 16). To avoid data contamination by artifacts such as eye blinks and drifts, an automatic trial rejection criterion of \pm 80 μ V was applied and followed by a trialby-trial visual inspection. The EEG was filtered (2nd order Butterworth with -12 dB/octave roll-off; 0.1 Hz high-pass; 30 Hz low-pass; 50 Hz notch). The filters were computed linearly in both the forward and backward directions to eliminate phase shifts. Artifact-corrupted electrodes were interpolated using 3-D splines (Perrin et al., 1987). Group average VEPs were next computed against the average reference.

The impact of portion size judgments on the spatio-temporal brain dynamics was then quantified by assessing modulations in the strength of the global electric field amplitude at the scalp (global field power, GFP) and in the underlying activity of neural sources using the CarTool (http://sites.google.com/site/fbmlab/cartool) and the STEN software packages (http://unil.ch/line/home/menuinst/about-the-line/softwareanalysis-tools.html). GFP was derived from VEP responses and calculated as the square root of the mean of the squared amplitude values recorded at each electrode (vs. the average reference), representing by definition the spatial standard deviation of the electric field (Brunet et al., 2011; Murray et al., 2008). That is, GFP yields larger amplitudes for stronger electric fields, and GFP maxima are indicative of maximally synchronous neural sources underlying the scalp-recorded activity (Michel and Murray, 2012; Skrandies, 1990). We identified GFP maxima from the group-averaged VEPs and verified their occurrence in single-subject data. These GFP maxima (spanning 40 or 60 ms, respectively, to encompass the latencies of GFP peaks in each individual's data) delineated time windows of interest for further analyses. Mean GFP amplitudes were calculated in each time window, for each participant and portion judgment condition separately, resulting in one data-point per subject and condition. Mean amplitude values were submitted to one-way ANOVAs with the factor of portion judgment ('too small', 'ideal', 'too big'). Post-hoc paired t-tests were conducted when a main effect had been attested by the ANOVA. Results were considered significant when $p \leq 0.05$.

The same averages across time windows of GFP maxima were the basis for neural source estimations using the local autoregressive average (LAURA) distributed linear inverse solution (Grave de Peralta et al., 2001, 2004). The solution matrix consists of 3005 nodes equally distributed within the gray matter of the Montreal Neurological Institute average brain. This implementation of LAURA was generated with the Spherical Model with Anatomical Constraints (SMAC; Spinelli et al., 2000). As output, LAURA provides current density values (in μ A/mm³) at each solution point (node). Mean current density values at each node and over each time window were submitted to one-way ANOVAs with the factors of portion judgment ('too small', 'ideal', 'too big'). The effect of portion judgment was considered significant when the statistical threshold of $p \le 0.05$ was exceeded within a cluster of \geq 10 contiguous nodes of the inverse solution matrix to correct for multiple measures. This spatial extension criterion was based on AlphaSim randomizations (http://afni.nimh.nih.gov) which has been similarly applied in prior works from our group (Lietti et al., 2012; Toepel et al., 2009, 2012). Prior basic and clinical researches have documented and discussed in detail the spatial accuracy of this inverse solution, which is in the order of the grid size of the solution points (here $\sim 6 \times 6 \times 6$ mm) (Gonzalez Andino et al., 2005a, 2005b; Grave de Peralta et al., 2004; Michel et al., 2004). Within the statistically defined regions of interest based on whole-brain analyses, post-hoc paired t-tests (two-tailed) and correlation analyses were conducted, i.e., on the mean value of the node (plus its six immediate neighbors) for which the ANOVA had revealed the maximal F-value. Results were considered significant when p-values ≤ 0.05 .

2.4.3. Correlation analysis

Pearson's correlation coefficients were computed to explore associations between neural source activity elicited by portion size judgments and food intake attitudes (cognitive restraint of eating score, emotional eating score and uncontrolled eating score from the subscales of the TFEQ-R18 and food craving score from FCQ-S) and BMI. Results were considered significant when $|r19| \ge 0.433$; $p \le 0.05$ (two-sided).

3. Results

3.1. Behavioral responses to meal portion sizes

Fig. 2A displays the distribution of portion size judgments ('too small', 'ideal', 'too big') for the 11 physical portion sizes across meals and participants. The frequency of portions judged as 'too small' progressively decreases from pictures #1 to #50; that is from the smallest to the largest portion size presented (see Fig. 1). Portions judged as 'too big' follow the opposite pattern. After plotting the behavioral data across portion sizes, the statistical analysis on response frequencies revealed a significant effect of portion judgment ($F_{2,40} =$ 6.58; $p \le 0.01$). Meal portions were more often judged as 'too small' (40.8%) relative to 'ideal' (28.4%; $t_{20} = 4.27$; $p \le 0.01$) and 'too big' (30.6%; $t_{20} = 4.27$; $p \le 0.05$) for expected satiety. Portion judgment also had a significant effect on response times ($F_{2.40} = 8.83$; $p \le 0.01$). Participants responded significantly faster when portions were judged as 'ideal' (942 ms \pm 49 s.e.m.) than 'too small' (998 ms \pm 50 s.e.m.; $t_{20} = 2.08$; $p \le 0.05$) or 'too big' (1038 ms \pm 48 s.e.m.; $t_{20} = 5.08$; $p \le 0.01$) (Fig. 2B).

3.2. GFP modulations by portion size judgment

In the group-averaged data, the GFP waveform showed three maxima, in turn delineating three time intervals of interest for statistical analyses on single-subject responses (Fig. 3A). Over the first time interval (105–145 ms), the ANOVA revealed an effect of judgment ($F_{2,40} = 30.19$; $p \le 0.01$) driven by a significant increase of the GFP as portion size increases (Fig. 3B, left panel). Over the second time interval (230–270 ms), portion size judgment had a significant effect on mean GFP ($F_{2,40} = 4.33$; $p \le 0.05$), with larger responses for the 'ideal' than for the 'too small' and 'too big' portion sizes (Fig. 3B, middle panel). Over the third time-interval (350–410 ms), the effect of portion size judgment ($F_{2,40} = 4.33$; $p \le 0.05$) was due to a linear decrease of the GFP while portion size increased (Fig. 3B, right panel).



Fig. 2. Behavioral data collected during the EEG session. A) Distribution of the behavioral responses given to the different portion sizes across meals. B) Mean response times for portion size judgments. Error bars, standard error of the mean; $*p \le 0.05$; $**p \le 0.01$.

3.3. Neural source modulations by portion size judgment

Over the first time interval (105–145 ms), the ANOVA revealed a distributed impact of portion judgment on neural source activity in the right middle frontal gyrus (MFG), right insula (INS) and bilaterally in the middle temporal gyrus (MTG) (Fig. 4A). Within these regions of interest, post-hoc t-tests showed that this effect was due to an incremental increase of neural activity as portion size increases (Fig. 4B).

The ANOVA on neural source activity over the second time interval (230–270 ms) revealed effects of portion judgment on responses in the frontal, temporal, parietal, and occipital regions (Fig. 5A). Two directions of responses were found therein (Fig. 5B): (1) incremental increases of activity in the MFG and inferior occipital gyrus (IOG) as portion size increases, and (2) maximal activity in response to portions judged as 'ideal' compared to 'non-ideal' (i.e., 'too small' and 'too big') in the inferior parietal lobe (IPL), cingulate gyrus (CG) and superior temporal gyrus (STG).

Over the last time interval (350–410 ms), portion size judgment was found to modulate neural activity in the temporal, parietal and occipital regions (Fig. 6A) with mixed effects (Fig. 6B). On the one hand, portions judged as 'ideal' induced higher neural activity in the STG and superior parietal lobule (SPL) relative to 'too small' portions. On the other hand, portions judged as 'too small' went along with lower neural activity in the IOG and higher neural activity in the MTG than portions judged as 'ideal' or 'too big'.

3.4. Associations between neural activity and food intake attitudes

Significant correlations between neural source activity and food intake attitudes as assessed by the TFEQ-R18 scores were observed over the second (Fig. 7A) and third (Fig. 7B) time intervals (i.e., 230–270 ms and 350–410 ms during meal viewing). Neural activity in the cingulate gyrus was negatively associated with cognitive eating restraint when portion sizes were judged as 'too big' ($r_{19} = -0.44$;



Fig. 3. GFP analysis as a function of portion size judgment over time. A) GFP waveform with three time intervals of maxima highlighted by a gray frame with dotted lines. B) Mean GFP computed for the three time intervals. 0, stimulus presentation onset; $*p \le 0.05$; $**p \le 0.01$; error bar, standard error of the mean.



Time interval 105-145ms





Time interval 230-270ms

Fig. 5. Differences in neural source activity as a function of portion size category during 230–270 ms post-stimulus onset. A) Color-coded p-values of the ANOVA on portion size judgment plotted on axial brain sections with maxima indicated. B) Results of post-hoc t-tests in brain regions showing the portion judgment effect with Talairach coordinates of maxima (x,y,z). * $p \le 0.05$; ** $p \le 0.01$; error bar, standard error of the mean; CG, cingulate gyrus; IOG, inferior occipital gyrus; IPL, inferior parietal lobe; MFG, middle frontal gyrus; STG, superior temporal gyrus.



Time interval 350-410ms

Fig. 6. Differences in neural source activity as a function of portion size category during 350–410 ms post-stimulus onset. A) Color-coded p-values of the ANOVA on portion size judgment plotted on axial brain sections with maxima indicated. B) Results of post-hoc t-tests in brain regions showing the portion judgment effect with Talairach coordinates of maxima (x,y,z). * $p \le 0.05$; ** $p \le 0.01$; error bar, standard error of the mean; IOG, inferior occipital gyrus; MTG, medial temporal gyrus; SPL, superior parietal lobule; STG, superior temporal gyrus.



Fig. 7. Correlations between neural response and factors relating to eating style. Significant correlations obtained during A) 230–270 ms and B) 350–410 ms post-stimulus onset in response to meal portions judged as 'ideal' or 'too big'. CG, cingulate gyrus; IOG, inferior occipital gyrus; MFG, middle frontal gyrus; MTG, middle temporal gyrus; SPL, superior parietal lobule.

 $p \leq 0.05$). Activity in the ventral prefrontal MFG, SPL and IOG was positively linked with emotional eating. The later associations were obtained in the MFG in response to 'ideal' portions ($r_{19}=0.44$; $p \leq 0.05$), in the SPL to both 'ideal' ($r_{19}=0.49$; $p \leq 0.05$) and 'too big' ($r_{19}=0.60$; $p \leq 0.01$) portions, and in the IOG to 'too big' portions ($r_{19}=-0.50$; $p \leq 0.05$).

4. Discussion

This is the first study to investigate brain responses to meal images presented in different portion sizes. While female participants were judging the size of the foods presented relative to their expected satiety, we identified spatio-temporal brain dynamics underlying ideal portion selection and disentangled effects due to the increase in food quantity (i.e., from portions judged as 'too small' to 'too big').

4.1. Portion size judgments

The distribution of response frequencies across physical portion sizes shows that portions judged as 'too small', 'ideal' and 'too big' largely overlap with the smallest, intermediate and largest portions, respectively. This result is well aligned with previous work showing that the portion chosen as ideal for satiety is not necessarily the largest portion available (Brunstrom et al., 2010; Brunstrom and Rogers, 2009; Brunstrom and Shakeshaft, 2009; Forde et al., 2011). Response times show that portions considered as 'ideal' for prospective lunch intake and satiety were judged faster than 'non-ideal' meal portions. This result confirms that incremental increases in food quantity and/or visual complexity are not the key drivers in portion size decisions and are in line with those previous results on portion selection (Brunstrom et al., 2010; Brunstrom and Rogers, 2009; Brunstrom and Shakeshaft, 2009; Forde et al., 2011). Studies on the visual perception of non-food objects have established that the higher the reaction times the more complex the stimuli and task requirements are (O'Shea and Bashore, 2012). In contrast, our study shows longer reaction times for both 'too small' and 'too big' portion sizes as compared to 'ideal' ones, likely indicating the influence of additional variables in these judgments like the weighing between energetic needs and hedonic drives for food intake control.

4.2. Dissociable brain dynamics to meal portions and ideal portion selection

EEG responses to the meal portion sizes presented were quantified by assessing modulations in the GFP which is derived from the visually evoked potentials and which represents the strength of electric potentials concurrently recorded at all electrodes (Michel and Murray, 2012; Skrandies, 1990). Three periods of GFP maxima were identified and results revealed differential modulations of the GFP within these periods as a function of portion size judgment (see Fig. 3). Over the first time interval (105-145 ms), GFP increased incrementally from viewing portions judged as 'too small', 'ideal', and 'too big'. The opposite effect was observed over the late time interval (350-410 ms) as GFP decreased from viewing meal portions judged as 'too small', 'ideal' and 'too big'. In contrast, over the second time interval (230–270 ms), the largest electric field strength was observed in response to portions judged as 'ideal'. Because global GFP maxima are indicative of greatest synchronization of underlying neural sources (Michel and Murray, 2012), not excluding the contemporaneous possibility of differences between conditions (here: responses to selected portion sizes), we conducted neural source estimations over these three time intervals of interest.

4.3. Brain regions showing incremental increase with meal portions

Over the earliest time interval, we observed incremental increases of activity in the insula, MFG and the MTG from portions judged as 'too small', 'ideal' and 'too big'. Over the later time windows, similar modulations in neural activity were observed in the MFG (230-270 ms) and IOG (230–270 ms and 350–410 ms). These findings resemble previous results from EEG and fMRI studies comparing brain responses to pictures of high- versus low-caloric foods (Asmaro and Liotti, 2014; Garcia-Garcia et al., 2013; van der Laan et al., 2011). Changes in the physical size or number of non-food visual stimuli have been shown to induce similar incremental increases in neural activity, yet confined to occipito-temporal and intraparietal regions as observed for instance with numbers/letters (Pinel et al., 2004), cubes (Kornmeier et al., 2011) or faces (Puce et al., 2013). However, our data show food portion size-related increases also in the insula and lateral prefrontal areas. The insula is involved in the detection of stimulus salience and serves to integrate information provided by varying functional systems (Kurth et al., 2010; Menon and Uddin, 2010). Lateral prefrontal regions are usually associated with cognitive influences on sensory processes and reward valuation, such as pricing information on product preferences and choices (Knutson et al., 2007), and control over food intake (see review of Garcia-Garcia et al., 2013). Yet, other studies have also shown that the lateral prefrontal cortex is positively associated with the evaluation of appetitive rewarding goals (Plassmann et al., 2008). Current data thus suggest that responses to food quantity (as reflected by incremental increase in activity in response to portions judged as 'too small', 'ideal' and 'too big') are mediated by brain regions involved in visual analysis and categorization as well as in salience attribution and reward valuation.

4.4. Brain regions showing greatest responsiveness to 'ideal' meal portions

Higher neural activity to 'ideal' meal portion as compared to 'nonideal' portions was observed during the later stages of responses to meal viewing, with the largest effects at 230–270 ms post-stimulus onset and residual effects at 350–410 ms post-stimulus onset. GFP responses to meal images judged as 'ideal' portion sizes were significantly stronger than those to images judged as 'too small' or 'too big' over the 230–270 ms time interval. In particular, three brain regions showed an 'ideal'-preferring response pattern: the inferior-to-posterior parietal region, the superior temporal gyrus and the mid-posterior cingulate cortex, suggesting that these areas are influenced by cognitive processes in order to weigh adaptive food choices (i.e., 'ideal' portion sizes) against non-adaptive ones.

The temporo-parietal junction is a key region in attentional processes mediating the selection of behaviorally relevant stimuli (Corbetta and Shulman, 2002). In the context of food perception, responses to highcaloric foods in a network of brain regions encompassing the parietal lobule have been for instance associated with weight management success (Murdaugh et al., 2012). The posterior cingulate cortex is a region believed to act as a hub integrating diverse types of information through a dense connectivity pattern with prominent connections to the frontal and limbic regions (Hagemann et al., 2003). This region has been associated with a large number of functions in relation to conscious awareness, cognitive control and adaptive behavior (Leech and Sharp, 2014; Pearson et al., 2011; Vogt and Laureys, 2005). In particular, it is involved in the allocation of attentional resources to relevant stimuli (Leech et al., 2011, 2012; Small et al., 2003a) and in the subjective valuation of a selected option relative to the outcomes of a choice (Kable and Glimcher, 2007). In a task of visual spatial attention, activity in the posterior cingulate was found to be higher for the detection of food cues when participants were hungry compared to being sated (Mohanty et al., 2008). In the same study, this effect was not observed for non-food cues, thus highlighting a role of this region in the motivational modulation of attention to food stimuli based on homeostatic needs. Taken together, a distributed network of brain regions likely mediating the motivational and attentional relevance of complex food cues subserves the elevated responsiveness to 'ideal' as opposed to 'non-ideal' portion sizes.

4.5. Associations between meal portion responses and food intake attitudes

With respect to the second objective of our study, we found several associations between individuals' food intake attitudes (as assessed by the subscales of the TFEQ-R18; Karlsson et al., 2000) and the neural activity patterns in the brain regions discussed above. Neural responses to meal portions judged as 'ideal' or as 'too big' for prospective lunch intake in the middle frontal gyrus (interval 230-270 ms), as well as in the superior parietal lobule and the inferior occipital gyrus (350-410 ms) co-varied with emotional eating scores. A similar correlation was found by Meule et al. (2013) between emotional eating and the amplitude of the late ERP component (350-550 ms). Emotional eating can be defined by the inability to resist emotional cues where eating is triggered by feelings of anxiety, sadness or loneliness. As a consequence, emotional eaters indulge more snack foods rich in energy and have a higher energy intake than other individuals (de Lauzon et al., 2004; Lahteenmaki and Tuorila, 1995). Our current data indicate that the responsiveness to food in lateral prefrontal to occipital regions is influenced by tendencies to overeat in emotionally challenging situations, but further research is certainly needed to investigate such links in more detail. Results of the current study revealed an inverse relationship between neural activity level in the CG and cognitive restraint scores when meal size was judged as 'too big' (see Fig. 7A). Dietary restraint is defined by the cognitive effort made to consciously limit food intake to avoid weight gain or promote weight loss (Karlsson et al., 2000). This self-regulation leads to the selection of low- over high-energy foods and to a lower energy intake in restrained than non-restrained eaters (de Castro, 1995; de Lauzon et al., 2004; Sunday et al., 1992). The motivational value of food modulated by cognitive control for weight management is mediated by a set of brain regions encompassing the posterior cingulate cortex (Harris et al., 2013; Yokum and Stice, 2013). From this, the diminished neural activity level in the CG by cognitive restraint when large portions are presented may reflect a lessened cognitive load engaged for self-regulation by participants with already high dietary restraint to reject those inadequate 'too big' meal portion sizes.

4.6. Conclusion

In conclusion, results of the present study provide the first evidence that the selection of the ideal portion size relies on specific spatiotemporal brain dynamics. We propose that incremental increases in early brain response - in visual, salience and reward-related regions to portion size increases (from portions judged as 'too small' to 'too big') likely reflect an assessment of the general amount of food available for ingestion (i.e., a quantitative evaluation). Only during a subsequent information processing stage, marked by greatest responsiveness to the portions judged as 'ideal', brain regions involved in attention and adaptive behaviors subserve the choice of a meal size portion assumed by the individual as adequate to reach satiety. Future studies investigating the impact of food intake attitudes and also other factors like hunger state, gender or weight status on the neural dynamics of portion size selection would certainly help gain further insight in the neural processes associated with portion selection and ultimately food intake regulation.

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