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Does my brain want what my eyes like? – How food liking influences choice and impacts spatio-temporal brain dynamics of food viewing

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Abstract

How food valuation affects decision-making, and how both influence the perception of food, is of major interest to better understand food intake behavior and, by extension, body weight management. Our study investigated behavioral responses and spatio-temporal brain dynamics by means of visual evoked potentials (VEPs) in twenty-two normal-weight participants when viewing pairs of food photographs. Participants rated how much they liked each food item (valuation) and subsequently chose between the two alternative food images.

Unsurprisingly, strongly liked foods were also chosen most often. Foods were rated faster as strongly liked than as mildly liked or disliked irrespective of whether they were subsequently chosen over an alternative. Moreover, strongly liked foods were subsequently also chosen faster than the less liked alternatives. Response times during valuation and choice were positively correlated, but only when foods were liked; the faster participants rated foods as strongly liked, the faster they were in choosing the food item over an alternative.

VEPs modulated according to the level of liking attributed as well as the subsequent choice as early as 135-180ms after food image onset. Analyses of neural source activity patterns over this time interval revealed an interaction between liking and the subsequent choice within the insula, dorsal frontal and superior parietal regions. Only when foods were chosen did the attributed level of liking modulate neural responses to food viewing. Therein, the responses to disliked foods were generally greater than those to foods that were liked more. Moreover, the responses to disliked but chosen foods were greater than responses to disliked foods which were subsequently dismissed for an alternative offer. Our findings show that the spatio-temporal brain dynamics to food viewing are immediately influenced both by how much encountered foods are liked, and in parallel by choices participants have to take. These valuation and choice processes are subserved by brain regions involved in salience and reward attribution as well as in

decision-making processes, which are likely to influence prospective dietary choices in everyday life.

Introduction

A better understanding of how humans evaluate foods and make choices about them, particularly if associated with objective brain markers underlying decision-making processes, are of great interest because eating-related disorders and especially obesity figures are still increasing world-wide. In daily life, decisions on what to eat are determined by hunger (homeostatic needs),and also by hedonic drives that can even override homeostatic needs (Berthoud, 2011; Kenny, 2011). The latter have been strongly associated with the propensity of food indulgence, leading to overweight and detrimental health consequences like cardiovascular disease and diabetes. In light of such developments, it is critical to better understand how food choice decisions are shaped as well as the underlying neural mechanisms, with the long-term goal to potentially being able to affect maladaptive choices in favor of health-beneficial ones.

A core concept in research on human economic and food-related choice-making states that when several choices are presented at the same time, they are assigned abstract and often subjective values. These values, and especially between-value weighing, serves to enable decisions in favor of a (a more highly valued) choice option (Economides et al., 2015; Hare et al., 2009; Kable and Glimcher, 2009). Several functional neuroimaging studies have revealed that in particular the ventromedial prefrontal cortex (vmPFC) subserves the computation of an overall subjective value of choice options and thereby biases decisions (Kable and Glimcher, 2009). Dorsal and ventrolateral PFC (dlPFC and vlPFC, respectively) have been shown to modulate vmPFC activity and are involved in inhibitory control processes (Hare et al., 2009; Hutcherson et al., 2012) as well as emotional self-regulation (Ochsner and Gross, 2008). For example, activity of the vmPFC was found to be modulated by lateral PFC activity in individuals who are successful (self-) controllers of their dietary choices (Hare et al., 2009). In the study of Hare and colleagues (2009), the success of self-control on dietary choices (meaning that study participants successfully considered the health aspects of food in their dietary choices) was

positively associated with the activity in the dlPFC, subsequently influencing food value attribution as reflected by vmPFC modulations. Other neuroimaging studies have further shown that the brain tracks the energy content of foods (García-García et al., 2013; Killgore et al., 2003; Van der Laan et al., 2011). Responses to varying food types (Toepel et al., 2009) and food portion sizes (Toepel et al., 2015) have been shown to differ already within 200ms after image exposure; reflected by activity modulations in temporo-occipital and frontal brain regions (e.g. orbitofrontal cortex, anterior cingulate cortex, lateral prefrontal cortex, and the insula).

To date, only few neuroimaging studies have investigated modulations in brain responses during food viewing according to valuation or liking, respectively, including the impact of valuation on subsequent food choices. In nutrition sciences and research on human food choice behavior, a prominent concept posits a dissociation of processes related to food 'liking' as opposed to 'wanting', as well as how 'liking' and 'wanting' impact food choices and intake (Berridge, 2009). Consequently, foods that are not necessarily 'liked' can nevertheless trigger implicit 'wanting' mechanisms (e.g. when adequate alternatives are lacking) and thus impact food choices and intake (Berridge, 2009; Finlayson et al., 2007). By contrast, 'liking' is not necessarily coupled with 'wanting' since this would be maladaptive for dietary choices given the abundance of foods with strong hedonic impact in everyday life.

Our study aimed to determine how food liking and successive choices shape the spatio-temporal brain dynamics during food image viewing. Visual evoked potentials (VEPs) were analyzed within an electrical neuroimaging framework (Murray et al., 2008; Koenig et al., 2014). This approach not only includes the analysis of VEPs at the head-surface, but also intracranial source estimations. We have successfully employed this method when investigating uni- and multisensory responses to food (Lietti et al., 2012; Ohla et al., 2012; Toepel et al., 2009, 2012, 2014, 2015). We hypothesized that the level of liking attributed to foods directly impacts VEPs

and neural source activity during food viewing. Moreover, we questioned whether participants' successive choices (i.e. whether food items were subsequently chosen or dismissed for an alternative offer) would differentially impact brain responses during food viewing or not given that choices between food alternatives only had to be taken subsequent to, but not during, viewing.

Materials and Methods

Participants in the EEG study

Twenty-two (11 female) normal-weighted volunteers, aged 21–38 yrs (mean ± s.e.m. = 27.23 ± 0.98 yrs; mean BMI ± s.e.m. = 22.72 ± 0.61 kg/m^2), participated in the study. Twenty of these participants were right-handed, and two were ambidextrous according to the Edinburgh Handedness Inventory (Oldfield, 1971). None of the participants reported current or prior neurological or psychiatric illnesses or self-reported eating disorders, and all participants had normal or corrected-to-normal vision. All participants completed the Three-Factor-Eating questionnaire TFEQ-R 18 (Karlsson et al., 2000) and the momentary craving state questionnaires (FCQ-S) (Nijs et al., 2007). The EEG recording sessions started between 15:00 and 16:00h to control for circadian modulations of hunger. Furthermore, participants were instructed (and also themselves reported) to have eaten lunch ~2h before the recording sessions. The volunteers provided written, informed consent to the procedures, which were approved by the Ethics Committee of the Faculty of Biology and Medicine of the University of Lausanne and the Vaudois University Hospital Center (CHUV).

Procedure of the EEG study

Participants sat comfortably inside a dimly lit, sound-attenuated booth and completed 704 trials (structure as schematized in Figure 1). Images were presented on a 21″ CRT monitor. On each trial, participants were successively presented with two food items and rated each during a 'valuation phase' on a 5-point Likert according to how much they liked each food item presented (Literal translation from French: 1= The item does not seem pleasant to me.; 5= The item seems very pleasant to me.). Following each image pair, participants were presented with a question mark indicating the 'choice period'. They were told to decide by button press whether they preferred the first (button press 1) or the second food (button press 2) viewed. All behavioral responses were given by button-presses on a serial response box using the index finger. Responses were allowed during the presentation of the food image and 2000ms after image/ question mark offset. Participants were instructed not to respond at all in case they encountered unknown food items. Stimulus presentation and response recordings were controlled by E-Prime (Psychology Software Tools Inc., Pittsburgh, USA; www.pstnet.com/eprime).

Image pairs consisted of foods from a similar product category (e.g. milk products, meat products, desserts, salty snacks, fruits, vegetables) and were adapted in energy content (Toepel et al., 2009) to prevent effects from general preferences for e.g. only sweet or high-energy foods. Each food image pair was presented twice to each participant with inversed image order to avoid position effects of foods within a trial. Images were controlled for low-level visual features, including luminance and spatial frequency (Knebel et al., 2008).

- *Insert Figure 1 about here -*

Behavioral data analyses

First, we analyzed participants' behavioral responses to each food item given during the valuation phase. By using customized MATLAB scripts, individuals' responses to each food were sorted by the level of liking participants had attributed, as well as by whether the food items were subsequently "chosen" vs. "dismissed". Since extreme ratings were low in number, food items scored with "1" and "2" were pooled together, as well as those rated with "4" and "5". That is, overall six conditions entered the analyses, i.e. chosen food items that had been rated as rather disliked, as mildly liked and rather strongly liked, as well as dismissed food items which had been rated as rather disliked, as mildly liked and strongly liked. For each condition, the frequency of responses and reaction times were first averaged within and then across subjects. 2x3 ANOVAs with the factors of choice (chosen vs. dismissed) and liking (rather disliked, mildly and strongly liked) were conducted on response frequencies as well as response times. When appropriate, separate one-way ANOVAs for each choice option as well as paired post-hoc t-tests (two-tailed) were conducted.

Second, we analyzed participants' response times to the chosen food item during the 'choice period' of each trial. Therein, responses to chosen foods were (this time retrospectively) sorted depending on whether the respective food item had been rated as rather disliked, mildly liked or strongly liked. A one-way ANOVA including the three liking levels was conducted to investigate liking-related differences in food choices, as well as paired post-hoc t-tests when appropriate.

Third, we conducted Pearson correlation analyses (two-tailed) between individuals' response times in the valuation and choice period to investigate whether decisions about food liking (as assessed by response times) are predictive of food choice decisions. The outcomes of all performed analyses were only considered significant when $p \leq 0.05$.

Electroencephalography (EEG) acquisition and preprocessing

Continuous EEG was acquired at 512 Hz through a 128-channel Biosemi ActiveTwo system (Biosemi, Amsterdam, The Netherlands) referenced to a ground circuitry (common mode sense and driven right leg electrodes or CMS–DRL). This circuitry functions 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). All data pre-processing steps and VEP averaging were done using the Cartool software (http://sites.google.com/site/fbmlab/cartool; (Brunet et al., 2011). All statistical analyses were conducted using the Statistical Toolbox for Electrical Neuroimaging (STEN) developed by Jean-François Knebel (http://www.unil.ch/line/home/menuinst/about-the-line/software--analysis-tools.html).

To calculate VEPs, epochs of EEG from 98 ms pre- to 488 ms post-food image onset (i.e. 50 data points before and 250 data points after stimulus onset) were separately averaged for each response condition and each participant. In addition to an automatic ±80 μV artifact rejection criterion, EEG epochs containing eye blinks or other noise transients were removed by trial-to-trial inspection of the data. Data were high-pass and low-pass filtered during single-subject averaging (second order Butterworth with -12db/octave roll-off; 0.1Hz high-pass; 40Hz low-pass; 50Hz notch) and baseline corrected using the 98 ms pre-stimulus period. Data from artifact electrodes of each participant were interpolated using 3-D splines (Perrin et al., 1987), and single-subject EEG epochs were averaged into VEPs depending on the behavioral response of each participant on each trial (see above). EEG responses were thus sorted into six conditions, i.e. responses to (subsequently) chosen food that had been rated as rather disliked, as mildly liked and strongly liked, as well as responses to (subsequently) dismissed foods that had been rated as rather disliked, as mildly liked and rather strongly liked. Single subject's responses were then group-averaged and recalculated against the average reference. The average number of accepted VEP epochs ranged from 60 (s.e.m. ± 12) to 175 (s.e.m. ± 16) per condition. Due to the differing number of epochs per condition, VEP epochs were normalized by

the mean instantaneous Global Field Power (GFP) at each sampling point (Lehmann and Skrandies, 1980) during group averaging. GFP is calculated as the square root of the mean of the squared amplitude value recorded at each electrode of the 128-channel montage we used (vs. the average reference and represents the spatial standard deviation of the electric field measured on the head surface (Koenig and Melie-Garcia, 2010).

Analyses of VEP data

The influence of liking and choices on brain responses was quantified by assessments of modulations in the VEPs at the head-surface and in estimations of the underlying neural activity (Brunet et al., 2011; Murray et al., 2008). Periods of interest were determined by a time-point and electrode-wise 2x3 ANOVA with the factors of choice (chosen vs. dismissed) and liking (disliked, mildly and strongly liked). Only periods showing a significant interaction of liking x choice ($p \leq 0.05$) for longer than 20ms on more than 10% of all channels were considered significant, so as to account for temporal and spatial auto-correlation (e.g. Guthrie and Buchwald, 1991).

In parallel, we assessed the electric field strength field at the scalp surface for each response condition, viz. Global Field Power (GFP; (Lehmann and Skrandies, 1980) in the VEP responses. GFP is calculated as the square root of the mean of the squared amplitude value recorded at each electrode of the 128-channel montage (vs. the average reference) and represents the spatial standard deviation of the electric field at the scalp. That is, GFP yields larger amplitudes for stronger electric fields, and GFP peaks are indicative of maximally synchronized neural sources underlying the scalp-recorded activity (Michel and Murray, 2012). Over the periods of interest (i.e. showing an interaction between the factors of choice and liking at the VEP level), mean GFP values were computed for individuals and used for statistical analyses. First, 2x3 ANOVAs with the factors of choice (chosen vs. dismissed) and liking (rather disliked, mildly and strongly liked) were conducted. When appropriate, separate one-way

ANOVAs for each choice option condition as well as t-tests (two-tailed) were conducted to detail the impact of each level of liking attributed on subsequent food choice. All these results were only considered significant when $p \leq 0.05$.

To assess whether and which neural sources (i.e. brain regions) revealed activity patterns modulated by liking and choices, we then estimated the active sources over the GFP maxima in each condition using the local autoregressive average (LAURA) distributed linear inverse solution (Grave de Peralta Menendez et al., 2001, 2004). As input for these estimations, single subject VEP responses at each electrode were averaged over the (overlapping) interval of the GFP maxima and electrode-wise VEP differences, by this generating a single value for each participant and each response condition to increase the signal to noise ratio. The LAURA algorithm then serves to estimate the neural sources of the electric signal recorded at the 128 head-surface sensors by using an inverse solution matrix consisting of 3005 nodes equally distributed within the grey matter of the Montreal Neurological Institute (MNI) 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 mA/mm^3) at each node. The spatial accuracy attained, which is on the order of the grid size (here: 6x6x6mm; (Gonzalez Andino et al., 2005a, 2005b; Michel et al., 2004), has been documented and discussed in detail in prior fundamental and clinical research.

Modulations in neural source activity over each GFP maximum were assessed by means of 2x3 ANOVAs on each node of the solution point matrix with the factors of choice (chosen vs. dismissed) and liking (rather disliked, mildly and strongly liked). Activity in brain regions where a significant interaction of both factors was found served as regions of interest for post-hoc analyses. These regions of interest were considered significant when the statistical threshold of $p \leq 0.05$ (two-tailed) was exceeded within a cluster of ≥ 10 contiguous nodes of the inverse solution matrix. This spatial extension criterion was based on AlphaSim randomizations (http://afni.nimh.nih.gov) and also used in previous publications of our group (Lietti et al., 2012;

Toepel et al., 2009, 2012, 2014). Post-hoc comparisons (separate one-way ANOVAs for responses to chosen and dismissed foods as well as t-tests between) were conducted on the averaged scalar values (in $\mu A/mm^3$) of the node revealing the minimal p-value within a region of interest plus its six immediate neighbors. The results analyses were rendered on the MNI template brain with the Talairach and Tournoux (1988) coordinates of the maximal statistical differences indicated.

Results

Behavioral results

Figure 2a shows the mean response frequencies (in percent) to chosen and dismissed food items as a function of the liking level attributed. A 2x3 ANOVA revealed an interaction of liking and choice ($F_{2,42}$=46.93; p≤0.01; η_p^2= 0.69) indicating that the number of food items rated as rather disliked, mildly or strongly liked substantially differed depending on whether they were subsequently chosen over an alternative or dismissed. Separate one-way ANOVAs for each choice condition revealed an effect of liking for chosen ($F_{2,42}$=17,88; p≤ 0.01; η_p^2= 0.46), but not for dismissed food items. Within the chosen foods items, paired t-tests showed that strongly liked ones were preferred more often over an alternative than mildly liked (t_{21}=3.57; p≤0.01) and disliked ones (t_{21}=4.54; p≤0.01). Also, food items rated as mildly liked were chosen more often than disliked ones (t_{21}=2.09; p≤0.05). Paired t-tests between the two choice options (chosen vs. dismissed) revealed that rather disliked foods were chosen less often than dismissed (t_{21}=6.30; p≤0.01), but that strongly liked foods were indeed more often chosen than dismissed (t_{21}=8.12; p≤0.01). Figure 2b displays mean reaction times of participants (in milliseconds) to food items as a function of how much they were liked. A 2x3 ANOVA with the factors of choice (chosen vs.

dismissed food items) and liking (rather disliked, mildly or strongly liked) only revealed a main effect of liking ($F_{2,42}$=307.62; p≤ 0.01;η_p^2= 0.94). For post-hoc comparisons, responses were thus collapsed across choices (chosen and dismissed). Paired t-tests between liking levels showed that food items rated as strongly liked were rated faster than mildly liked (t_{21}=25.08; p≤0.01) and disliked ones (t_{21}=14.20; p≤0.01).

Figure 2c illustrates reaction times of participants over the period of choice between the two presented food alternatives in each trial. A one-way ANOVA revealed a main effect of liking ($F_{2,42}$=5.883; p≤0.01; η_p^2=0.22). Post-hoc paired t-tests between liking levels revealed that participants were faster when choosing food images that had previously been rated as strongly liked as compared to mildly liked (t_{21}=2.26; p≤0.05) and rather disliked (t_{21}=3.25; p≤0.01). Figure 2d illustrates the associations between participants' response times in the food valuation phase and the subsequent food choice period. When participants were fast in rating foods as mildly or strongly liked, they were likewise faster in making a decision in favor of these foods over the choice period (mildly liked foods: r_{20}= 0.46; p≤0.05; strongly liked foods: r_{20}= 0.54; p≤0.01). Supplementary Table 1 provides a comprehensive numerical overview of participants' responses given during the valuation phase and the food choice period.

- *Insert Figure 2 about here* -

Modulations of head-surface responses to food viewing by liking and choices

The electrode-wise 2x3 ANOVA on the head-surface VEPs over time revealed an interaction between liking and subsequent choice over the 135-180ms post-image onset interval (Figure 3a). The effect was particularly prominent at frontal electrodes, though we would remind the reader that analyses of voltage waveforms are dependent on the choice of the reference electrode, including also when the average reference is used. We therefore also analyzed a

reference-independent measure – GFP – taking a mean value over the time window identified above (i.e. 135-180ms; bar graph in Figure 3b). The 2x3 ANOVA conducted revealed an interaction of liking and choice ($F_{2,20}$=4.84; p≤0.05; η_p^2= 0.33). Separate one-way ANOVAs for each choice condition (chosen and dismissed) revealed that the GFP was only modulated by the level of liking attributed when later chosen foods were viewed ($F_{2,20}$=3.72; p≤0.05; η_p^2= 0.27), but not when later dismissed foods were viewed (p=0.09; η_p^2= 0.21). Within chosen foods, post-hoc t-tests then showed that the electric field strength when viewing strongly liked foods was higher than when mildly liked foods were viewed (t_{21}=2.78; p≤0.01). Paired t-tests between responses to equally liked chosen and dismissed foods showed that the GFP was higher for successively chosen strongly liked foods as opposed to their dismissed counterparts (t_{21}=3.19; p≤0.01).[1]

- *Insert Figure 3 about here* -

Modulations in neural source activity to food viewing by liking and choice

A whole-head 2x3 ANOVA with the factors of liking (rather disliked, mildly and strongly liked) and choice (chosen vs. dismissed) served to define regions of interest for post-hoc contrasts (Figure 4). An interaction of the factors liking and choice (visualized in Figure 3a) was observed in the right dorsolateral PFC (dlPFC; Max: 57, -5, 35), the insula of the left hemisphere (INS; Max: x=-34, y=-11, z=14), and in the right superior parietal cortex (SPC; Max: x=22, y=-40, z=65). Neural activity in these regions was modulated by whether foods are liked and whether they are successively chosen or dismissed for an alternative.

[1] Note: We did not find correlations between participants' behavioral data, anthropometric characteristics or food intake attitudes with the GFP responses.

Separate one-way ANOVAs on neural activity in the abovementioned areas to foods that were either chosen or dismissed revealed modulations only when subsequently chosen foods were viewed, but not when later dismissed foods had been encountered (dlPFC: $F_{2,42}$=3.25; p=0.05 INS: $F_{2,42}$=5.42; p≤0.01; SPC: $F_{2,42}$=3.28; p≤0.05). Post-hoc t-tests on the neural activity pattern in these regions showed the following results. In the dlPFC, the difference in neural activity was most pronounced when subsequently chosen mildly liked foods were viewed as opposed to their dismissed counterparts (t_{21}=2.67; p≤0.05). Moreover, the activity when viewing mildly liked subsequently chosen foods was higher than when strongly liked later chosen foods were viewed (t_{21}=2.49; p≤0.05). In the insula, neural activity when viewing rather disliked foods was higher when they were subsequently chosen as when they were later dismissed for an alternative (t_{21}=3.00; p≤0.01), and also greater as when mildly liked foods were viewed that were later chosen (t_{21}=3.29; p≤0.01). In the superior parietal region, neural activity was found greater when rather disliked foods were viewed that were subsequently chosen as compared to when disliked foods were later dismissed for an alternative (t_{21}=3.71; p≤0.01). Activity was also greater when comparing the neural responses to disliked subsequently chosen foods and strongly liked chosen foods (t_{21}=2.48; p≤0.05).

The whole-head 2x3 ANOVA we conducted additionally revealed a main effect of liking (visualized in Figure 4b) in the dorsomedial prefrontal region (Max: x=-20, y=30, z=42) indicating that this region's responsiveness is modulated by food liking rather independent of whether foods are subsequently chosen or dismissed for an alternative. For post-hoc comparisons, data points for chosen and dismissed foods were thus collapsed, and revealed stronger activity to the viewing of rather disliked as opposed to mildly (t_{21}=2.33; p≤0.05) and strongly liked foods (t_{21}=2.17; p≤0.05).

Moreover, the whole-head 2x3 ANOVA showed an additional main effect of choice (visualized in Figure 4c) in the right dorsolateral prefrontal cortex (Max: x=27, y=49, z=20) indicating that activity in this region is in particular modulated by food choices, independent of

how much the viewed foods were liked. For post-hoc comparisons, data points were thus collapsed across liking levels, and revealed stronger activity to the viewing of subsequently chosen as opposed to dismissed foods (t_{21}=2.37; p≤0.05).[2]

- *Insert Figure 4 about here* -

Discussion

Our study identified the impact of food liking on successive choices and on the spatio-temporal brain dynamics during food viewing in normal-weight participants. Behaviorally, our results showed (unsurprisingly) that strongly liked food items were more frequently chosen than dismissed, and that disliked items were more frequently dismissed than chosen. Nonetheless and regardless of the subsequent choice (i.e. whether food items were chosen or dismissed), participants were faster in rating food items as strongly liked (vs. disliked or mildly liked). Moreover, they were faster in making a choice in favor of foods that had been rated as strongly liked as opposed to mildly liked and disliked ones. Response times in both behavioral tasks, food valuation and food choice, were positively correlated when foods had been rated as mildly or strongly liked, showing that a fast decision about food liking is predictive of a fast decision in favor of a food item, but only when foods are liked.

These findings are in line with previous literature reporting decreased response times to highly valued visual items (Kahnt et al., 2014). Given that in our study liked items were more often chosen by participants in general, this association is likely due to the inherent parallel assessment of 'liking' and 'wanting' aspects during preference building (Finlayson et al., 2008).

[2] Note: We did not find correlations between participants' behavioral data, anthropometric characteristics or food intake attitudes with the neural source estimation measures.

We would nonetheless note that the food choice task we employed in our study is not appropriate to investigate deliberate 'wanting' (Berridge, 2009) and to thus enable assertions on a clear dissociation of 'liking' and 'wanting' processes. Participants were not given the opportunity of 'free' choices between food options, but they had to perform forced decisions between two alternatives. We will further refer to this issue in the discussion on elevated brain responses to disliked foods that were still chosen over an alternative.

With respect to spatio-temporal brain dynamics, VEP modulations during food viewing as a function of liking and subsequent choice were apparent within the first 150ms after image onset. The timing of these modulations converges with previously reported effects of food categorization in terms of energy content (Toepel et al., 2009) and effects of judging meal portion sizes for expected satiety (Toepel et al., 2015). Estimations of neural source activity over the time interval from 135-180ms showed an interaction of liking and choice in the neural activity patterns of the dorsolateral PFC, the insula and the superior parietal lobe. Only brain responses to foods that were successively chosen were modulated by the level of liking, whereas no modulation was observed for responses to foods that were later dismissed for an alternative. Within responses to chosen foods, the strongest neural response was often associated with the viewing of disliked foods that were nevertheless preferred over an alternative. Statistics analyses of neural source activity additionally identified two brain areas whose activity was either modulated by food liking only, independent of whether the viewed foods were subsequently chosen or dismissed for an alternative (i.e. dorsomedial PFC), or was altered by choice only, independent of how much the viewed foods had been rated as liked (i.e. lateral PFC).

Modulations in neural activity during food viewing by the level of liking attributed and subsequent choices thus involved a network of regions associated with salience-related attentional and cognitive control processes (Menon and Uddin, 2010; Mitchell, 2011). Harris and colleagues (2013) showed that the dlPFC is involved in the early top-down modulation of

attention when participants had to perform a decision-making task and exercise self-control while viewing appetizing food images. This electrical neuroimaging study reported higher neural activity over the time interval between 150-200ms when participants successfully chose healthy foods for prospective consumption while dismissing unhealthy food alternatives. These effects converge with the time interval (135-180ms) during which we observed pronounced modulations of neural activity by the level of liking attributed to foods that were successively chosen over an alternative. The viewing of chosen, yet disliked foods, elicited the greatest activity.

The prefrontal cortex has consistently been found to be involved in decision-making and emotion regulation in different experimental paradigms and modalities (Mitchell, 2011; Shenhav and Buckner, 2014). The dorsomedial PFC is believed to be involved in the encoding of reward-related information, i.e. stimulus values, in the context of decision-making (Camus et al., 2009). In contrast, the dorsolateral prefrontal cortex is particularly recruited when choice options have to be weighed and self-control has to be exerted (Hare et al., 2009; Kober et al., 2010; McClure et al., 2007). When facing conflicts between choice options, the activity of the dmPFC and dlPFC often increases in parallel, allowing for an adjustment of cognitive control and rendering of most relevant stimulus features as salient in order to guide choice behavior (Egner and Hirsch, 2005; Mitchell, 2011; Mitchell et al., 2009; Walton et al., 2007). In direct relation to food decisions, increased dlPFC activity was reported in successful rather than in unsuccessful dieters (Hare et al., 2009).

The insula, as second region found to be modulated, is known to be directly involved in task-related signaling in the context of food valuation (Born et al., 2011). Middle-to-posterior insular regions are further related to the exertion of self-control over food intake (Harris et al., 2013) and the integration of interoceptive sensations (Craig, 2002). Due to its high connectivity with the dlPFC and the vmPFC (Carmichael and Price, 1996; Craig, 2002), the insula is thought to be a key player enabling the interactions between regions for stimulus valuation and choice (Harris et al., 2013). Prior electrical neuroimaging studies have further shown that insular activity

is elevated within 150ms when participants view meal portion sizes judged as inappropriate for prospective intake (Toepel et al., 2015) further indicating its role in the integration of homeostatic and hedonic information.

A third region showing modulations of neural activity during food viewing by liking and choices is in the superior parietal cortex. The region has been ascribed a role in attentional processes (Bisley and Goldberg, 2010), e.g. when non-food objects are viewed (Levy et al., 2011). However, the superior parietal cortex has also been reported to be involved in the abstract coding of stimulus values in order to mediate goal-directed behaviors and to maximize the outcome of choices taken (Kahnt et al., 2014), as well as to enable choices between several alternative options (Kable and Glimcher, 2009; McClure et al., 2007). Electrical neuroimaging results have shown its involvement in such operations within 200ms after visual cues are encountered whose values need to be coded in an abstract form in order to enable decisions between choice alternatives (Harris et al., 2011).

In our study, both the insula and the posterior parietal region showed elevated responses in particular when foods rated as rather disliked were viewed, yet subsequently chosen likely since the alternative option was not considered more tempting. That is, an interpretation of our findings in terms of increased stimulus valuation mediating decision-making seems rather counter-intuitive. On the other hand, an alternative explanation of the observed response patterns might be a particularly strong choice conflict when both food alternatives presented in one experimental trial were rated as rather disliked, but a choice had to nonetheless be indicated despite of the low liking level attributed to both images. In order to query this interpretation possibility, we computed indices of choice coherence in individuals (Supplementary figure), and also questioned the potential association of individuals' choice coherence with neural source activity.

To do so, we calculated the %response to foods that were chosen among the two alternatives presented per experimental trial *and* had been attributed the highest level of liking in

each individual (coherent choice). In addition, individuals' %response to foods chosen although *not* attributed the highest level of liking in the respective experimental trials were computed (incoherent choice). Moreover, neutral choices were defined as instances were both food items had been attributed the identical level of liking. In a next step, the percentage of incoherent choices was subtracted from the percentage of coherent choices in each participant and for each level of liking to obtain 'choice coherence indices'. A one-way ANOVA on participants' choice coherence including the three levels of liking (disliked, mildly liked and strongly liked) revealed a significant effect of liking. Yet, choice coherence was not found to be correlated with neural source activity during the viewing of disliked, yet chosen, food items in any of the previously discussed brain regions. That is, the additional analysis provided no indication of a relation between a strong choice conflict (assumed for disliked yet chosen foods) and elevated neural responses when foods were viewed that were rated as disliked, yet subsequently chosen over an alternative option.

Still, these additional analyses certainly cannot fully exclude the possibility of a strong choice conflict for disliked food items induced by the forced-choice task in our design. A recent EEG study of Harris and colleagues (2013) proposed that top-down influences of attentional filtering can impact responses during food viewing within 200ms under conditions where controlled decisions need to be taken. In their experiment, participants viewed appetizing food products under varying tasks. In one part of the experiment, participants were asked to make random food choices without constraints, while they had to exert self-control during food viewing in a second part of the study with the goal to receive monetary incentives for longitudinal body weight loss. Over the 150-200ms interval during food viewing, successful self-control trials (which were defined as accepting healthy, but disliked, foods or rejecting unhealthy, but liked, foods) elicited stronger activity in the insula, the dorsolateral PFC and the ventrolateral PFC.

In this vein, we would thus like to propose that brain responses to foods rated as disliked, although not ultimately chosen, are impacted by attentional filtering mechanisms already during the valuation phase. Such attentional filtering, in our study mostly subserved by the insula and the superior parietal cortex, in turn likely rendered those food images more salient than the disliked yet dismissed counterparts, and helped to lower the choice conflict between two similarly valued choice options. Future investigations are yet needed to further disentangle the influences of valuation and choice on the spatio-temporal brain dynamics to food viewing. With the current design, the decisive information for value comparison between two food choices only became available upon the presentation of the second food image. That is, restricting analyses to the responses to the 'choice-decisive' food item might provide still more detailed insights regarding the contribution of valuation and choice in food perception.

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Figure captions

Figure 1: Trial structure. Participants were asked to rate how much they liked each of two presented food items per trial on a 1-5 Likert scale during the valuation phase. Over the choice period they had to choose whether they prefer the first or second presented food item.

Figure 2: Behavioral results. a) Mean response frequencies (± s.e.m.) and (b) mean response times to disliked (red), mildly liked (blue) and strongly liked food items (green) during the valuation phase. c) Response times (± s.e.m.) over the choice period where participants had to choose in each trial one of two food alternatives. d) Associations between response times during the food valuation phase and the choice period. * $p \leq 0.05$, ** $p \leq 0.01$.

Figure 3: Results of head-surface VEP analyses. a) Interaction obtained by an electrode and time-point-wise 2x3 ANOVA with the factors of liking and choice, b) GFP waveforms to food viewing as modulated by liking and subsequent food choices as well as bar graphs visualizing the mean GFP to each food viewing condition over the time window 135-180ms. ** $p \leq 0.01$

Figure 4: Neural source modulations by liking and subsequent food choice over the 135-180ms interval following food image onset. a) Brain areas showing an interaction of the factors Liking and Choice b) main effect of Liking. c) Main effect of Choice. * $p \leq 0.05$, ** $p \leq 0.01$.

Figure 1

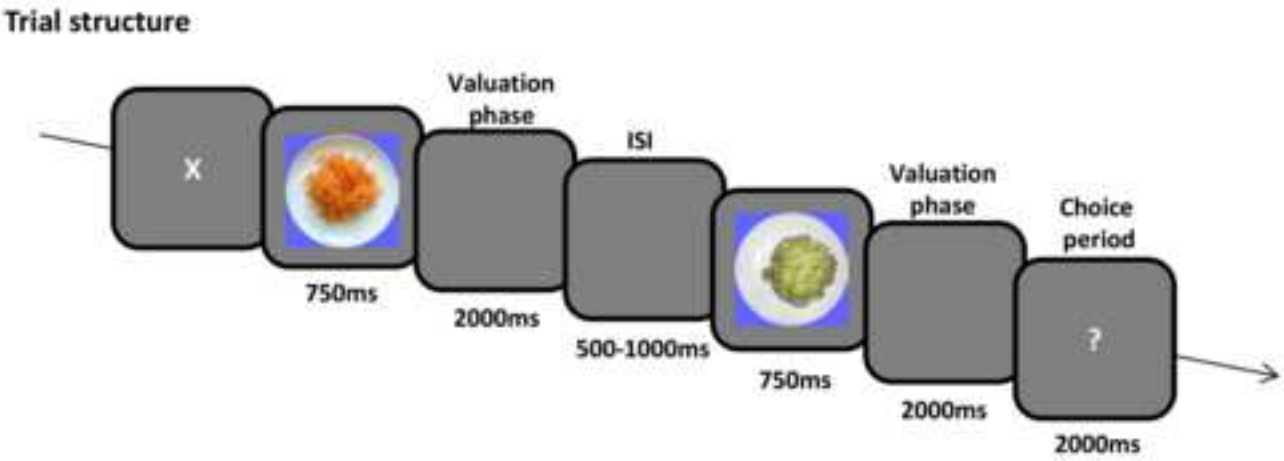

Trial structure
X
750ms
Valuation phase
2000ms
ISI
500-1000ms
750ms
Valuation phase
2000ms
Choice period
?
2000ms

Figure 2

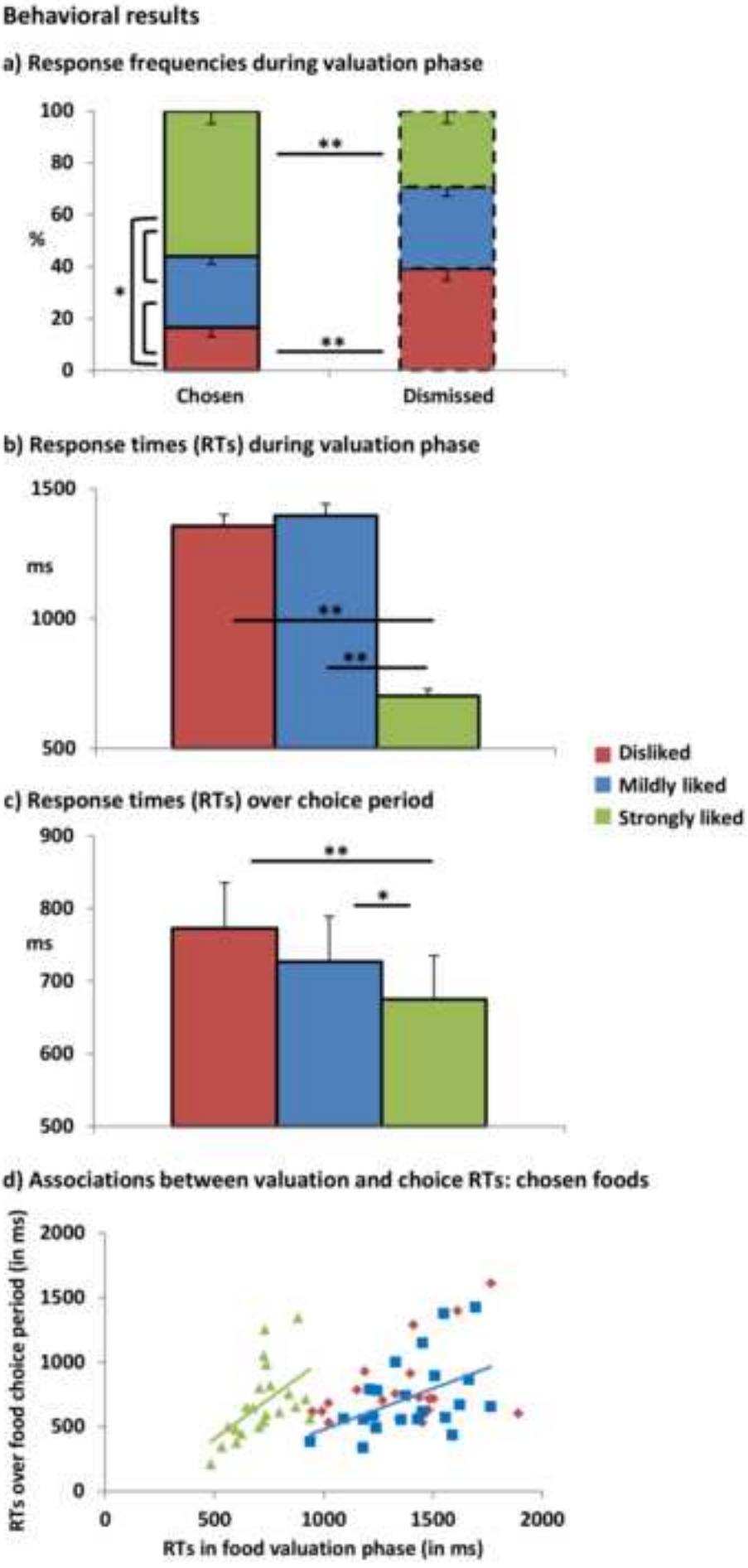

Behavioral results
a) Response frequencies during valuation phase
100
80
60
%
40
20
0
**
**
*
Chosen
Dismissed
b) Response times (RTs) during valuation phase
1500
ms
1000
500
**
**
Disliked
Mildly liked
Strongly liked
c) Response times (RTs) over choice period
900
800
ms
700
600
500
**
*
d) Associations between valuation and choice RTs: chosen foods
RTs over food choice period (in ms)
2000
1500
1000
500
0
0
500
1000
1500
2000
RTs in food valuation phase (in ms)

Figure 3

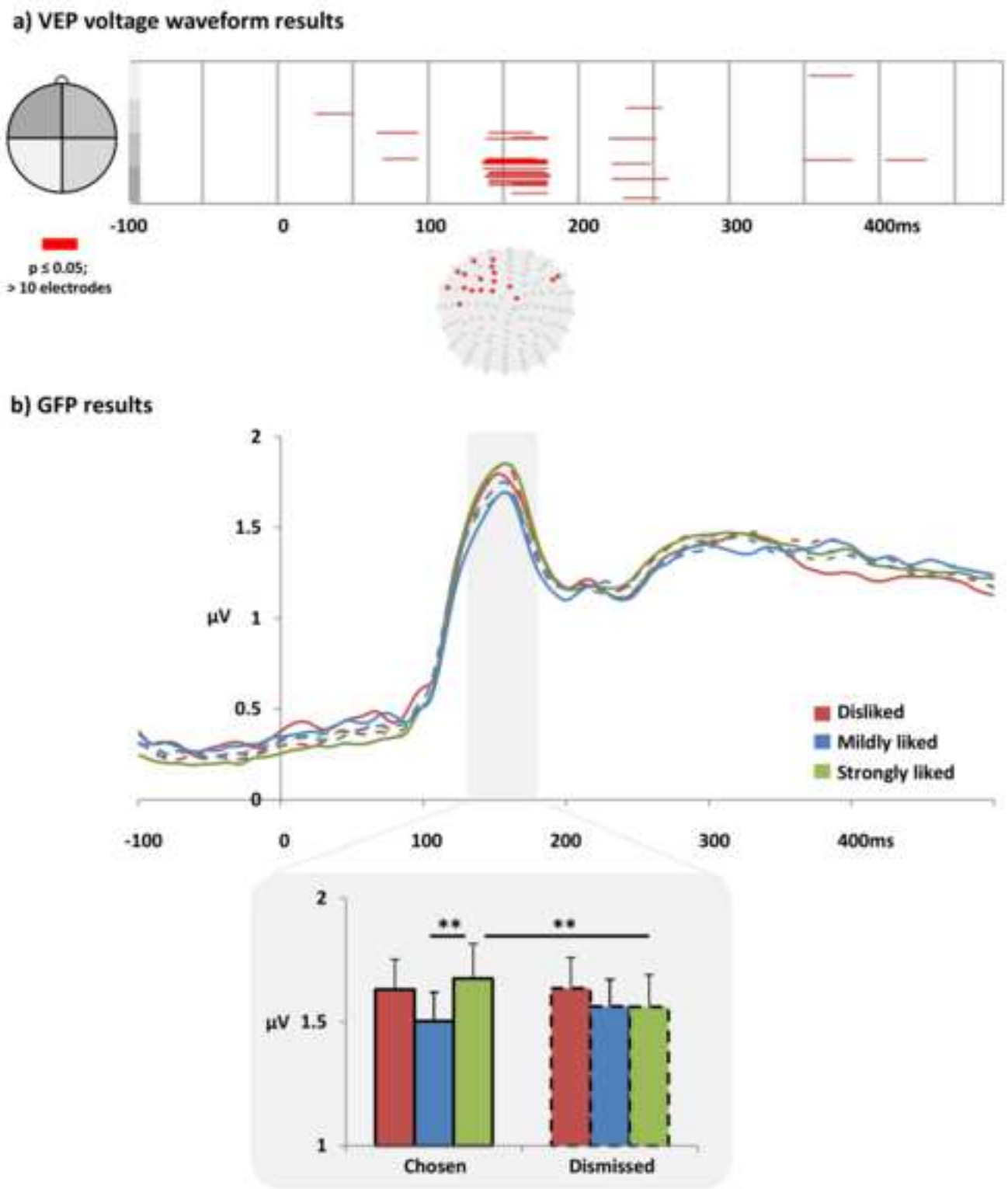
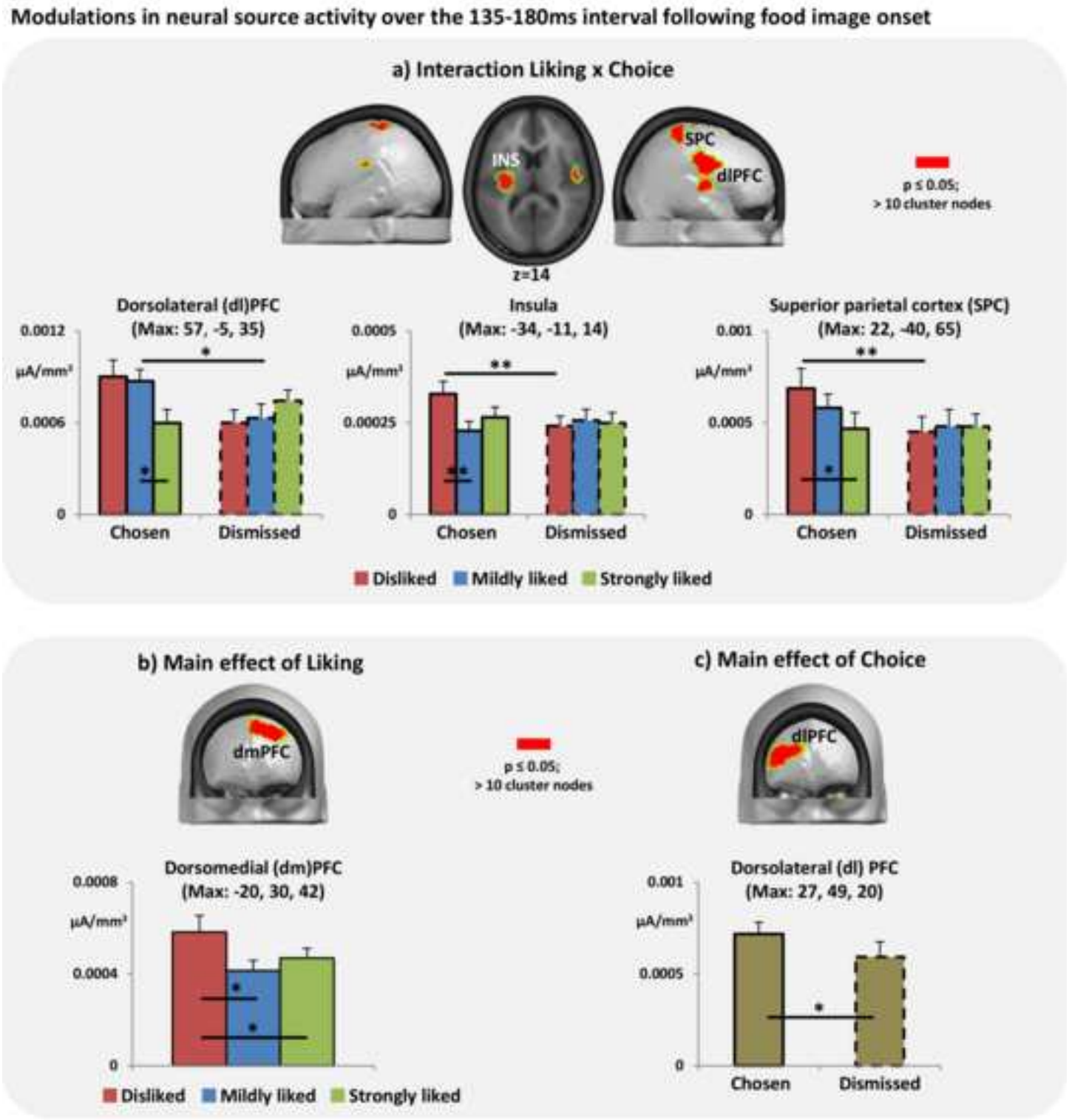

a) VEP voltage waveform results
-100
0
100
200
300
400ms
p ≤ 0.05;
> 10 electrodes
b) GFP results
2
1.5
μV 1
0.5
0
Disliked
Mildly liked
Strongly liked
μV 1.5
1
**
**
Chosen
Dismissed

Figure 4


Modulations in neural source activity over the 135-180ms interval following food image onset
a) Interaction Liking x Choice
INS
SPC
dlPFC
p ≤ 0.05;
> 10 cluster nodes
z=14
Dorsolateral (dl)PFC
(Max: 57, -5, 35)
Insula
(Max: -34, -11, 14)
Superior parietal cortex (SPC)
(Max: 22, -40, 65)
0.0012
0.0006
0
0.0005
0.00025
0.001
0.0005
µA/mm³
Chosen
Dismissed
Disliked
Mildly liked
Strongly liked
b) Main effect of Liking
dmPFC
Dorsomedial (dm)PFC
(Max: -20, 30, 42)
0.0008
0.0004
c) Main effect of Choice
dlPFC
Dorsolateral (dl) PFC
(Max: 27, 49, 20)