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Research report

The role of energetic value in dynamic brain response adaptation during repeated food image viewing

Claudia V. Lietti [b], Micah M. Murray [a,b,c], Julie Hudry [d], Johannes le Coutre [d,e], Ulrike Toepel [a,b,*]

[a] The Functional Electrical Neuroimaging Laboratory, Department of Clinical Neurosciences, Centre Hospitalier Universitaire Vaudois, Lausanne, Switzerland
[b] The Functional Electrical Neuroimaging Laboratory, Department of Radiology, Centre Hospitalier Universitaire Vaudois, Lausanne, Switzerland
[c] EEG Core, Center for Biomedical Imaging of Lausanne and Geneva, Switzerland
[d] Nestlé Research Center, Vers-chez-les-Blanc, Lausanne, Switzerland
[e] The University of Tokyo, Organization for Interdisciplinary Research Projects, 1-1-1 Yayoi, Bunkyo-ku, Tokyo 113-8657, Japan

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ABSTRACT

The repeated presentation of simple objects as well as biologically salient objects can cause the adaptation of behavioral and neural responses during the visual categorization of these objects. Mechanisms of response adaptation during repeated food viewing are of particular interest for better understanding food intake beyond energetic needs. Here, we measured visual evoked potentials (VEPs) and conducted neural source estimations to initial and repeated presentations of high-energy and low-energy foods as well as non-food images. The results of our study show that the behavioral and neural responses to food and food-related objects are not uniformly affected by repetition. While the repetition of images displaying low-energy foods and non-food modulated VEPs as well as their underlying neural sources and increased behavioral categorization accuracy, the responses to high-energy images remained largely invariant between initial and repeated encounters. Brain mechanisms when viewing images of high-energy foods thus appear less susceptible to repetition effects than responses to low-energy and non-food images. This finding is likely related to the superior reward value of high-energy foods and might be one reason why in particular high-energetic foods are indulged although potentially leading to detrimental health consequences.

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Introduction

The prevalence of obesity is increasing throughout the world population, causing long-term health problems such as diabetes or cardiac disorders. Obesity is linked to a loss in the ability to adjust food intake for maintaining the energetic balance of the body. Deviant eating behavior leading to obesity can, however, not be seen as a pure problem of food intake. There is increasing evidence that human food intake is not only controlled by brain areas involved in homeostatic control, but also by cortical and subcortical areas involved in the reward and cognitive aspects of hedonic feeding (Gibson, Carnell, Ochner, & Geliebter, 2010). Moreover, nutrition intake behavior is strongly based on pre-ingestion choices that can be driven by visual food appearance, including influences from marketing strategies such as prices (Knutson, Rick, Wimmer, Prelec, & Loewenstein, 2007) as well as repeated product exposure (Krajbich, Armel, & Rangel, 2010).

Our previous research has demonstrated that food images are readily differentiated according to their energetic content, resulting in power and topography modulations of the electric field when high-fat vs. low-fat foods are viewed (Toepel, Knebel, Hudry, le Coutre, & Murray, 2009). As low-level visual features were controlled for, this differentiation is likely related to the varying food reward properties of high- and low-energetic foods as well decision mechanisms related to their pre-ingestion valuation. Whether the repeated exposure to these food classes alters the brain processes underlying the differentiation of foods have, however, not yet been investigated.

So far, the adaptation of behavioral and neural responses to repeated object exposure has mainly been investigated by employing stimuli like familiar and unfamiliar objects and faces. Typically, behavioral effects manifest through facilitation of reaction times and accuracy rates for the discrimination and categorization of repeatedly as opposed to initially presented objects. Hemodynamic neuroimaging studies often report activation changes in prefrontal and ventral temporal cortex during repeated object exposure – an effect typically referred to as repetition priming (Dolan et al., 1997; George et al., 1999; Grill-Spector, Henson, & Martin, 2006; Henson, Shallice, & Dolan, 2000 for review). Electrophysiological

* Corresponding author.
E-mail address: Ulrike.Toepel@chuv.ch (U. Toepel).

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studies often show early amplitude modulations of the visual evoked potentials (VEP) around ~150–200 ms post-stimulus onset (George, Jemel, Fiori, & Renault, 1997; Guillaume et al., 2009; Henson, 2003; Henson, Rylands, Ross, Vuilleumier, & Rugg, 2004; Schendan & Kutas, 2003; Soldan, Mangels, & Cooper, 2006; Tacikowski, Jednoróg, Marchewka, & Nowicka, 2011). However, later repetition-induced VEP modulations are frequently observed as well around 250 and 400 ms (Henson, 2003; Schweinberger, Pfütze, & Sommer, 1995; Schweinberger, Pickering, Burton, & Kaufmann, 2002). Therein, the alterations in behavioral and neural response patterns are most often explained in terms of implicit memory processes (e.g. De Lucia et al., 2010; Henson, 2003; Murray, Camen, Spierer, & Clarke, 2008; Schacter, Dobbins, & Schnyer, 2004).

What previous studies leave open, however, is the question of whether repetition-induced neural and behavioral adaptation mechanisms are also effective when the viewed objects are potentially relevant for bodily energy homeostasis, i.e. food items. Moreover, when comparing response adaptations for food classes that differ in energetic content, varying perceptual and mnemonic mechanisms might be indexed as high- and low-energetic foods inherently differ with respect to their reward and hedonic properties. High-energy foods have, for example, been shown to be more pleasant even in normal-weighted adults (Finlayson, King, & Blundell, 2007) with such preferences already shaped during childhood (Birch, 1999). As lower food response adaptation or habituation, respectively, is associated with greater food intake (Temple, Giacomelli, Roemmich, & Epstein, 2007; Wisniewski, Epstein, & Caggiula, 1992), more invariant representations of high-energetic foods across repetitions (as compared with low-energy food items and non-food artifacts) might contribute to why especially high-energetic foods are indulged despite of potential long-term detrimental consequences (like obesity, and in turn, increased risk for cardiovascular disorders). For this purpose, raw data from our previous study (Toepel et al., 2009) were processed and analyzed with a focus on comparing VEPs and behavioral responses to the initial and repeated presentations of images depicting high- and low-energetic foods (in terms of fat content) as well as non-food kitchen utensils.

Material and methods

Participants

Twenty-one remunerated volunteers partook in the study (11 women, 10 men, aged 19–33 years [mean ± s.e.m. = 24.62 ± 1.01 - years]). All of these 21 individuals were from our original study (Toepel et al., 2009). 17 participants were right-handed, and four ambidextrous according to the Edinburgh Handedness Inventory (Oldfield, 1971). Data from one additional subject were excluded from the present analyses due to insufficient signal quality. All subjects had a BMI within the normal range (mean ± - s.e.m = 21.95 ± 0.53 kg/m^2) and no current or prior neurological or psychiatric illness or self-reported eating disorders. They all had normal or corrected-to-normal vision. Each EEG recording session started between 13h00 and 14h00 to control for circadian modulations of hunger. Moreover, all participants were instructed and also self-reported to have eaten lunch before the recording session. Participants 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.

Stimuli and procedure

The present analyses focused on the initial and first repetition of images presented in our previous experiment (Toepel et al., 2009). That is, the effects of repeated object exposure were studied on 100 photographs of foods and 50 non-food images (Fig. 1). The food images were subdivided into equi-sized high- and low-energy classes by means of their fat content (cf. Toepel et al., 2009) and are hereafter referred to as HiFat and LoFat categories, though we would emphasize that fat and energy content are highly correlated. The temporal lag between the initial and repeated presentation of an image was ~8–10 min due to image randomization within blocks.

All pictures were adapted in luminance at an individual image level (Knebel, Toepel, Hudry, le Coutre, & Murray, 2008; see Toepel et al., 2009 for further information). However, due to the predominant goal of our previous analyses, the spatial frequency distribution between the food categories and the non-food image category could not be fully adapted (Fig. 1, right panel).

The pictures measured 300 × 300 pixels, which corresponded to ~6° visual angle on the computer monitor and had been photographed using an identical background and top-view angle. Each image was presented for 500 ms in the center of a 21″ CRT monitor that participants viewed within an electrically shielded and sound attenuated booth. Immediately after the picture presentation, a question mark was presented on the screen as a request to decide via button-press if the preceding image had been a food or a non-food item. The question mark remained on the screen until a response was made, allowing participants to self-pace the experiment. In order to minimize eye movements, a crosshair was shown in the screen center whenever no image or question mark was present. The interval between crosshair and image onset varied randomly between 250 and 750 ms. Stimulus presentation and response recordings were controlled by E-Prime (Psychology Software Tools Inc., Pittsburgh, USA; www.pstnet.com/eprime).

EEG data acquisition and pre-processing

Continuous electroencephalogram (EEG) was acquired at 512 Hz through a 160-channel Biosemi Active Two system (Biosemi, Amsterdam, Netherlands) referenced to the common mode sense/driven right leg (CMS-DRL) ground. All data pre-processing and analyses were performed with the CarTool software (http://sites.google.com/site/fbmlab/cartool). VEP epochs from 98 ms pre- to 488 ms post-stimulus onset (i.e. 50 data points before and 250 data points after stimulus onset) were first separately averaged for each presentation (initial and repeated), image category (HiFat, LoFat and NoFood), and each participant. An ±80 μV artifact rejection criterion was applied to the dataset and EEG epochs containing eye blinks or other noise transients were removed through trial-by-trial visual inspection. Before performing the group averaging for each presentation and condition, data from artifact-contaminated electrodes were interpolated (Perrin, Pernier, Bertrand, Giard, & Echallier, 1987). The dataset was also baseline-corrected using the pre-stimulus period, band-pass filtered (0.1–40 Hz) and recalculated against the average reference. The number of VEP epochs (mean and s.e.m. given) per category entering the statistical analyses did not differ significantly between presentation phases (HiFat initial vs. repeated: 48.62 [±0.38] vs. 48.86 [±0.32]; $p = 0.51$; LoFat initial vs. repeated: 48.38 [±0.38] vs. 48.38 [±0.52]; $p = 1.00$; NoFood initial vs. repeated: 47.38 [±0.39] vs. 46.86 [±0.48]; $p = 0.17$).

EEG analyses

General analysis strategy

The electrophysiological analyses applied used both local and global measures of the electric field at the scalp. These so-called electrical neuroimaging analyses allow differentiating effects caused by modulations in the VEP strength or amplitude, respectively, from alterations in the VEP topography considering data

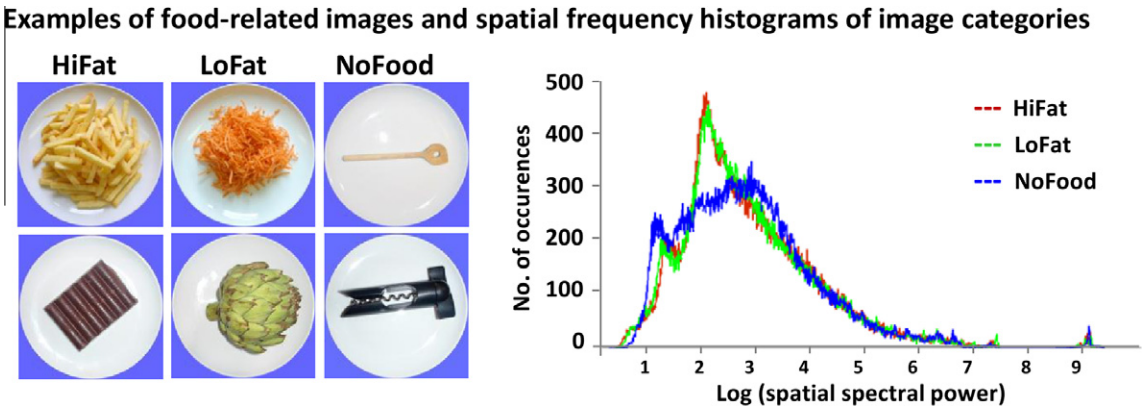

Fig. 1. (left panel) Exemplar stimuli from each image category; i.e. HiFat and LoFat foods, and NoFood kitchen utensils. (right panel) Histograms for each image category illustrating the similarity in spatial frequency distribution between HiFat and LoFat food images.

from all electrode sensors (here: 160) in a concurrent manner. Only fundamental information on the analyses is given here (see Michel et al., 2004 and Murray, Brunet, & Michel, 2008 for further details). For all local and global VEP analyses, only effects with *p*-values $\leqslant 0.05$ were considered statistically significant (with Greenhouse-Geisser correction applied when the sphericity assumption was violated) and temporal correlation was corrected through the application of a 15 contiguous data-point criterion (~30 ms; Guthrie & Buchwald, 1991).

As pure effects of image category in our design could be confounded by low-level visual feature differences between image categories (i.e. spatial frequencies; see right panel of Fig. 1) we will henceforth emphasize effects of presentation and interactions between image category and presentation phase.

VEP waveform analyses

The first analysis step included a 3×2 sample-wise ANOVA across all electrodes involving the factors presentation (initial, repeated) and category (HiFat, LoFat and NoFood). The output of the analysis is an intensity plot indicating time, electrode location and significant *p*-values at each data point. These analyses on local VEP modulations give a visual impression of effects within the dataset and provide a link between electrical neuroimaging and more traditional VEP analysis approaches. We would note, however, that our conclusions are based on reference-independent global measures of the electric field.

A global topographic cluster analysis was performed to identify the sequence of VEP topographies within and across categories and presentation phases (Murray, Brunet, et al., 2008; Murray, Camen, et al., 2008). Topographic VEP modulations indicate differences in the brain's underlying generators (Lehmann, 1987) independent from strength modulations of the electric field. The optimal number of topographic maps was determined using a modified Krzanowski-Lai criterion, which is a measure of the dispersion across clusters (see Murray, Brunet, et al., 2008; Murray, Camen, et al., 2008 for formulae). When map topographies were found to descriptively differ by presentation and/or category over a certain time period, the observed differences at the group level were statistically validated by comparing the map cluster appearance with the individuals' VEPs from each presentation phase and category over a given time period. This analysis is referred to as "fitting". During the fitting procedure, each time point of each single subject VEP was labeled in accordance to the group-average map topography with which it best correlated spatially (Murray, Brunet, et al., 2008; Murray, Camen, et al., 2008). The dependent measure is the global explained variance (GEV) in percent, indicating how well a certain map identified in the group-averaged data explains the VEP responses from a given individual participant and for each presentation phase (initial or repeated) or image category viewed (HiFat, LoFat and NoFood). Repeated measures ANOVAs with the factors presentation phase, category and map were performed to validate presentation- and category-related modulations in map topography presence. Post-hoc paired *t*-tests were conducted when appropriate.

Importantly, the fitting procedure does not test whether the electric field configurations of the best-correlating maps themselves statistically differ. This aspect was addressed by performing a time point-wise topographic ANOVA or T-ANOVA, respectively, that provides a direct index of global spatial VEP dissimilarity independent of electric field strength (Murray, Brunet, et al., 2008; Murray, Camen, et al., 2008). In detail, the T-ANOVA tested in 5000 randomizations per data sampling point whether the VEP topography to each image category and presentation statistically differs from the mean VEP topography across presentations and categories (Koenig, Melie-García, Stein, Strik, & Lehmann, 2008; Wirth et al., 2008).

In addition to the topographic analyses, modulations in the global VEP strength were assessed using global field power (GFP; Lehmann & Skrandies, 1980) at each data point. GFP is calculated as the square root of the mean of the squared value recorded at each electrode in the 160-channel montage (vs. the average reference) and represents the spatial standard deviation of the electric field at the scalp. It yields larger values for stronger electric fields. Statistical differences in GFP were assessed in a 3×2 ANOVA including the factors presentation (initial, repeated) and category (HiFat, LoFat and NoFood) and post-hoc paired *t*-tests when appropriate.

Estimation of neural sources underlying VEPs

We estimated the intracranial sources generating the VEPs for each image category and presentation phase using the local autoregressive average (LAURA) distributed linear inverse solution (Grave de Peralta, Gonzalez Andino, Lantz, Michel, & Landis, 2001; Grave de Peralta Menendez, Murray, Michel, Martuzzi, & Gonzalez Andino, 2004). The version of LAURA used here employs a realistic head model with 3005 nodes arranged within the gray matter of the Montreal Neurological Institute's (MNI) average brain, and was generated with the Spherical Model with Anatomical Constraints (SMAC; Spinelli, Andino, Lantz, Seeck, & Michel, 2000). As an output, LAURA provides current density value (in $\mu A/mm^3$) at each node. Prior fundamental and clinical research have documented and discussed in detail the spatial accuracy of this inverse solution, which are on the order of the grid size of the solution points (here $\sim 6 \times 6 \times 6$ mm, Gonzalez Andino, Michel, Thut, Landis, & Grave de Peralta, 2005; Gonzalez Andino, Murray, Foxe, & de Peralta Menendez, 2005; Grave de Peralta Menendez

et al., 2004; Michel et al., 2004; Michel, Seeck, & Murray, 2004). The time period for which intracranial sources were estimated and statistically compared between presentation phases (here: 125–164 ms post-image onset) was defined by the topographic cluster analysis. Statistics on the source estimations was performed by first averaging the VEP data over the 125–164 ms interval to generate a single data point for each participant to increase the signal-to-noise ratio. The inverse solution (21 participants × 3 image categories × 2 presentations) was then estimated for each of the 3005 nodes. An ANOVA was performed with the within-subject factors of image category (HiFat, LoFat and NoFood) and presentation (initial vs. repeated) at each source node. Post-hoc paired *t*-tests between initial and repeated image viewing were conducted for each image category separately (using the ANOVA output as inclusive mask). The results of these analyses were rendered on the MNI brain with the corresponding coordinates of Talairach and Tournoux (1988) and similarly the locus of the Brodmann area of the maximal *t*-value indicated. Only effects with *p*-values $\leqslant 0.05$ and present in at least 15 contiguous nodes were considered significant (cf. Toepel et al., 2009). This spatial criterion was determined using the AlphaSim program (available at http://afni.nimh.nih.gov). 10,000 Monte Carlo permutations were performed using the nodes of our lead field matrix and revealed a false positive probability of <0.005 for observing a cluster of at least 15 nodes. No additional correction for multiple comparisons was applied.

Results

Behavioral results

Table 1 provides a summary of accuracy rates and reaction times in the food vs. non-food discrimination task. A 3 × 2 ANOVA on the accuracy rates with the factors of presentation and category revealed main effects of category ($F_{(2,40)} = 9.69$; $p \leqslant 0.01$) and of presentation ($F_{(1,20)} = 9.52$; $p \leqslant 0.01$) as well as an interaction between these factors ($F_{(2,40)} = 9.69$; $p \leqslant 0.01$).

Post-hoc paired *t*-tests revealed significant improvements in accuracy between initial vs. repeated presentations for LoFat foods ($t_{(20)} = -2.29$; $p \leqslant 0.05$) and NoFood ($t_{(20)} = -4.08$; $p \leqslant 0.01$), but not for HiFat foods. Moreover, accuracy during initial presentations was found to be higher for HiFat foods than for NoFood ($t_{(20)} = 3.42$; $p \leqslant 0.01$), and higher for LoFat foods than for NoFood ($t_{(20)} = 3.58$; $p \leqslant 0.01$).

An 3 × 2 ANOVA on reaction times with the factors of presentation and category showed only a main effect of presentation ($F_{(1,20)} = 22.36$; $p \leqslant 0.01$). Participants' reaction times decreased reliably during the repeated viewing of all three image categories as compared to the initial presentation (HiFat: $t_{(20)} = 2.87$; $p \leqslant 0.05$; LoFat: $t_{(20)} = 4.72$; $p \leqslant 0.05$; NoFood: $t_{(20)} = 5.40$; $p \leqslant 0.05$). We would remind the reader that RT speed was not emphasized in the instructions to the participants or in the paradigm itself.

Results of the local and global VEP analyses

Figure 2a shows the results of the electrode- and time-point-wise ANOVA on all electrodes and Fig. 2b the group-averaged VEP waveforms at three exemplar electrodes. The ANOVA evinced an effect of presentation across a wide range of electrodes starting ~130 ms post-image onset and a sustained effect of category from ~190 ms. No significant interactions including neighboring electrodes were observed by the time-point wise ANOVA at the single waveform level.

As these local and reference-dependent VEP analyses cannot reveal the bases of the repetition-induced differences (i.e. whether they arise from alterations in strength or topography of the electric field), we conducted a common topographic cluster analysis on the group-averaged VEPs to all image categories (HiFat, LoFat and NoFood) and presentation phases (initial, repeated). This analysis identified periods of eight stable electric field topographic clusters (maps) that explained 98.78% of the variance in the collective group-average dataset. The sequence of topographic clusters was similar across object categories and presentation phases over the majority of the post-stimulus period. Differing map clusters were observed from 125 to 164 ms (see Fig. 3a), i.e. over the period that is in temporal agreement with the effect of presentation observed at single electrode level (see Fig. 2a).

Over the time interval from 125 to 164 ms, two map topographies (map A and B in the left panel of Fig. 3a) were first identified at the VEP group-average level. These maps were mainly characterized by a fronto-medial VEP maximum with negative amplitude in map A, and a more left-lateralized frontal negativity in map B (also apparent in the difference between map A and B). The occurrence of the maps as a function of image category and presentation phase was statistically validated in the VEPs from individual subjects by the fitting procedure using a 3 × 2 × 2 ANOVA. The analysis revealed a main effect of presentation ($F_{(1,20)} = 5.82$; $p \leqslant 0.05$) and an interaction of category × presentation × map ($F_{(2,40)} = 5.10$; $p \leqslant 0.05$). Such an interaction indicates that the extent to which a given template map accounted for the initial vs. repeated presentation of a particular image type itself significantly differed. This can more simply be understood as indicating that different patterns of response adaptation as expressed in the VEP topography were taking place for different image types. Post-hoc paired *t*-tests focusing on the impact of repetition revealed changes in the pattern of these map topographies when LoFat foods and NoFood images were viewed, but not when HiFat food images were viewed. In particular, during LoFat food viewing, map A (framed in black) was better representative of subjects' responses during repeated than initial presentations ($t_{(20)} = 2.15$; $p \leqslant 0.05$). By contrast, when NoFood images were viewed, map B (framed in gray) reliably better accounted for subjects' responses during repeated than initial presentations ($t_{(20)} = 2.87$; $p \leqslant 0.01$). That is, the VEP topographies elicited by viewing LoFat and NoFood objects were modulated by whether the images were seen for the first or second time. However, responses to HiFat foods did not result in altered VEP topographies.

The topographic map cluster analysis, although well suited to validate the contribution of single subjects to the group-average topographic VEP responses, does not test in how far the (descriptively) varying map topographies over a certain time period themselves differ. In order to test for global VEP dissimilarity, we thus performed a time-point wise topographic ANOVA over the post-stimulus epoch (T-ANOVA; see "Methods" section). The T-ANOVA revealed an effect of presentation between 125 and 193 ms and

Table 1
Response accuracy (in percent) and reaction times (in ms) in the behavioral object categorization task during initial and repeated image encounters.

	Initial presentation		Repeated presentation	
	RT in ms (±s.e.m.)	Accuracy in % (±s.e.m.)	RT in ms (±s.e.m.)	Accuracy in % (±s.e.m.)
HiFat	443.55 (29.45)	97.28 (1.60)	389.41 (24.13)	100.00 (0)
LoFat	452.71 (28.95)	96.50 (1.56)	372.44 (24.04)	100.00 (0)
NoFood	454.49 (30.46)	92.20 (1.96)	373.82 (26.32)	100.00 (0)

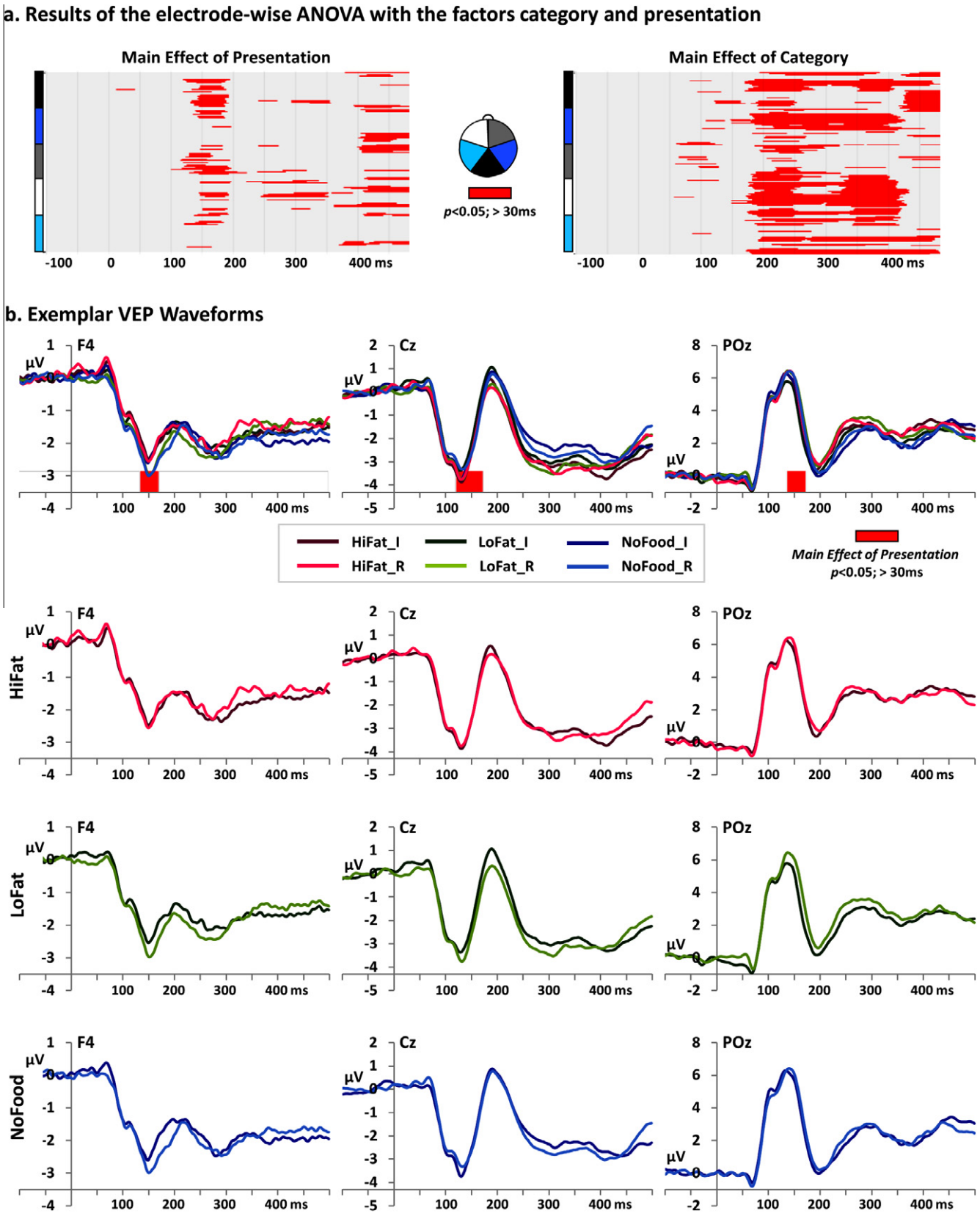

Fig. 2. (a) Results of the electrode- and time-point-wise 2 × 3 ANOVA. Spatially and temporally distributed effects of presentation began ~130 ms, while effects of image category started at ~190 ms post-image onset. (b) Top panel: Exemplar electrodes showing VEP waveforms jointly for all conditions with the latencies of the main effect of presentation indicated by red bars. I = initial presentation, R = repeated presentation. Lower panels: Separate electrode displays for each category (HiFat, LoFat and NoFood) illustrating the VEP waveforms during initial (I) and repeated (R) image presentations.

from 375 ms to the end of the computation period. A temporally sustained effect of image category, on the other hand, only became evident later, i.e. from 181 ms. In accordance with the previously obtained repetition-induced differences by image category at the

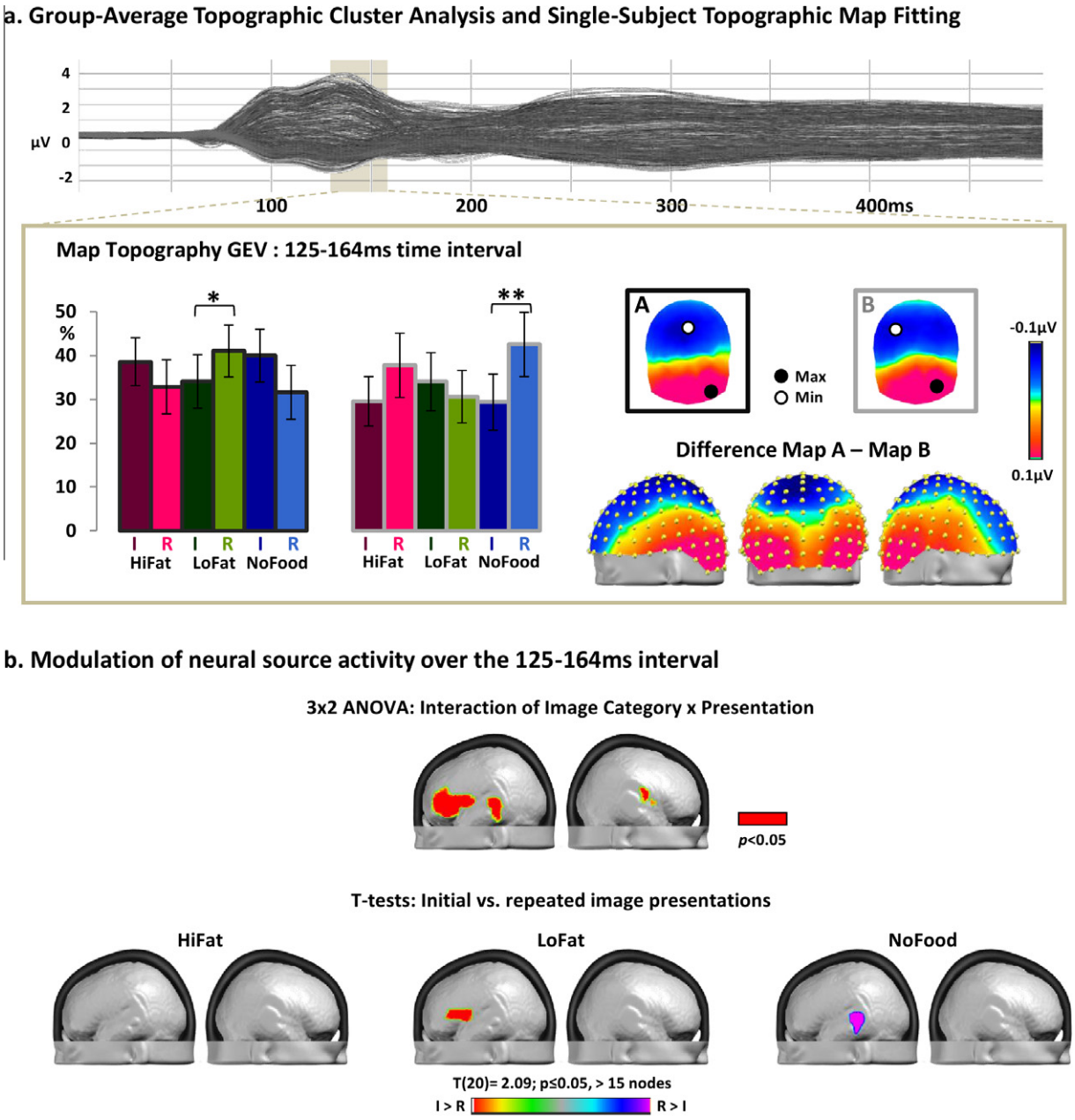

Fig. 3. (a) The topographic clustering on the collective group-averaged VEPs revealed a time interval of stable but varying VEP topographies (i.e. over the 125–164 ms post-stimulus interval). The bar graphs show the results of the fitting procedure for the interval, expressing the global explained variance (GEV in percent) a given map topography yielded a higher spatial correlation with the single-subject responses than an alternative one (±s.e.m. indicated). Bars framed in black illustrate the variance explained by map topography A (also framed in black), and bars framed in gray illustrate the variance explained by map topography B (also framed in gray). Asterisks above the bar graphs indicate significant values in the post-hoc paired *t*-tests between presentation phases within one image category; I = initial presentation, R = repeated presentation. Below the topographic map displays, the difference topography comparing map A–B is visualized. (b) Differences in neural source estimations underlying the observed VEPs as obtained by an ANOVA including the responses to all image categories and both presentations, and separate paired *t*-tests for each image category comparing the neural source activation during initial vs. repeated image presentations.

topographic map cluster level, separate T-ANOVAs were conducted for each category. These yielded reliable differences in global VEP topography between initial and repeated presentations of LoFat foods (144–187 ms) and NoFood images (142–158 and 175–189 ms), but not when HiFat foods were viewed.

As all the analyses on topographic VEP modulations are independent of electric field strength, we further analyzed global field power (GFP) to test whether VEP response differences are also reflected in modulations of response strength. A time-point wise ANOVA on GFP with the factors image category and presentation over the peri-stimulus epoch evinced only effects of category (i.e. between 218–291 and 330–408 ms) but no changes in global response strength as a function of presentation phase.

Results of the neural source estimations on VEP generators

The upper panel of Fig. 3b illustrates the interaction between image category (HiFat, LoFat and NoFood) and presentation (initial vs. repeated) on the neural source activity underlying the VEPs observed on the scalp-surface over the time interval from 125 to 164 ms. Significant interactions between image category and presentation were evident in the prefrontal and the middle temporal cortex, mostly restricted to the left hemisphere. Source nodes

showing significant interactions were rendered on the MNI average brain for visualization.

Separate post-hoc paired *t*-tests for each image category comparing the neural source strength between presentation phases (lower panel of Fig. 3b) showed that activity in the ventral prefrontal cortex of the left hemisphere was lower when LoFat images were viewed for the second as opposed to the first time (Max: −54 8 13; BA4; $t_{(20)} = 3.26$). In contrast, the viewing of NoFood images induced elevated activation in the middle temporal cortex (Max: −63 −27 0; BA21; $t_{(20)} = -3.68$) of the left hemisphere when items were encountered for the second as opposed to first time. When HiFat images were viewed, no reliable source estimation differences were observed between initial and repeated presentations.

Discussion

The results of our study reveal that visual processing of food and non-food objects is not uniformly affected by repetition. In terms of behavioral adaptation in the object categorization task, participants performed at near-ceiling level during initial image presentations and at ceiling level during repeated exposure. Reliable increases in accuracy following repetition were limited to objects depicting low-energy foods and non-food kitchen utensils. In contrast, no such improvement was observed during the repeated exposure to high-energy food images. During initial presentation, high-and low-energy foods were categorized with similar accuracy, indicating that the lack in response adaptation between the initial and repeated viewing of high-energy foods could not solely be attributed to a general recognition advantage for high-energy foods. Moreover, reaction times decreased between initial and repeated viewing of all three image categories, an effect frequently reported for repetition-induced behavioral modulations (Henson, 2003). Yet, we would like to emphasize that participants were cued to respond only after image onset (i.e. to avoid confounds of VEP modulations and motor-evoked brain responses), so that the observed decreases in reaction time have to be interpreted with caution.

The time-point wise analyses on VEP waveforms (Fig. 2a) indicated as a first result that repetition-induced modulations precede effects induced by image categorization. In this respect, our results are consistent with findings on repetition priming for faces, i.e. another class of biologically highly salient objects. Such studies either showed direct modulations of face-sensitive VEP components like the N170 (Eimer, Kiss, & Nicholas, 2010; Guillaume et al., 2009; Itier & Taylor, 2004) or even repetition-induced modulations preceding face-selective categorization effects (George et al., 1997; Michel, Seeck & Murray, 2004; Seeck et al., 1997).

Moreover, our data revealed differential effects depending on whether images of high-or low-energy foods or non-food objects were repeatedly presented. While wide-spread repetition-induced VEP modulations were observed for low-energy food and non-food images, the VEPs to high-energy food images were less altered during presentation phases. A topographic cluster analysis incorporating data points from all 160 electrode sensors across the full post-stimulus period then identified the time interval between 125 and 164 ms as bearing stable VEP topographic maps that differed, however, depending on whether low-energy foods or non-food items were seen for the first or the second time. No topographic modulation was, on the other hand, observed when high-energy food images were repeatedly viewed.

These repetition-induced topographic VEP differences immediately precede what we previously identified as the latency when images of high-energy and low-energy foods were incidentally discriminated from each other (i.e. at ~165 ms; Toepel et al., 2009). In our previous study, neural source estimations revealed the differential engagement of a network mostly encompassing prefrontal and temporo-occipital areas in the visual perception of high- vs. low-energy foods, i.e. brain regions that are implicated into object categorization, the assessment of food reward and decision-making (e.g. Killgore et al., 2003).

Our current study points to alterations in neural network recruitment imposed by repetition priming. Yet, the implicit memory processes that priming effects are usually associated with differed by the type of image category that was repeatedly encountered. Repeated viewing of non-food items led to enhanced responses in middle temporal cortex, a brain region proximate to inferior temporal areas often reported in imaging studies on face priming (see Grill-Spector et al., 2006; Henson, 2003 for reviews). On the other hand, the repeated encounter of images depicting low-energy foods resulted in response suppression in ventral prefrontal areas. In contrast, we did neither observe repetition enhancement nor suppression when images of high-energy foods were repeatedly viewed although high- and low-energy food images were closely matched in terms of low-level visual features (cf. Fig. 1), and both image categories comprised of commonly consumed and easily identifiable exemplars. Object repetition is often associated with response suppression, although response enhancement has previously been observed as well, i.e. during face perception. According to extant accounts, response enhancement is thought to indicate processes during item repetition that were not performed during initial exposure reflecting, e.g., a stabilization of mnemonic traces due to increasing stimulus familiarity or discrete item recognition within a category (Fiebach, Gruber, & Supp, 2005; Henson, 2003; Henson et al., 2000; Wiggs & Martin, 1998). On the other hand, response suppression supposedly reflects similar brain processes during initial and repeated exposure, e.g., an efficient reactivation or "sharpening" of representations of familiar objects. In keeping with these accounts, (low-energy) food and non-food objects likely undergo a differential treatment during repeated encounter. While the re-recognition of (low-energy) food objects seem to involve the efficient exploitation of a mnemonic trace established already during initial viewing, repeating non-food items likely leads to further mnemonic consolidation based, e.g., on the recognition of specific object-determining features. Notably, the finding of ventral prefrontal (for low-energy foods) vs. middle temporal (for non-food items) repetition modulations further indicates that food as a primary reinforcer and reward impacts implicit memory processes differently than non-food objects, but also other biologically salient stimuli like faces (Grill-Spector et al., 2006; Henson, 2003).

However, when bringing together our behavioral, global VEP and neural source findings, the representations of high-energy foods appear to be more invariant between initial and repeated viewing than those of low-energy foods. High-energy foods are known to have a strong impact on homeostatic body balance, to produce stronger hedonic drives than low-energy foods and are associated with higher reward (for overviews see Almiron-Roig & Drewnowski, 2003; Rolls, 2009) and greater motivational salience (Frank et al., 2010). That is, these properties likely render high-energetic foods mnemonically potent and stable, and, in turn, less susceptible to repetition-induced modulations than low-energetic foods, even when only perceived visually, i.e. evaluated for potential consumption. The more invariant representation of high-energetic foods throughout first and repeated encounters might be a contributing (but surely not exclusive) reason why especially high-energetic foods are eaten beyond energetic body homeostasis although bearing potentially detrimental long-term consequences for body weight and health. Another possibility, which we cannot fully discount, is that our analysis methods lacked sufficient sensitivity to detect differences between initial and repeated presentations of high-energetic foods. We consider this unlikely, as VEPs to this class of images were based on similar numbers of EEG epochs

as those to other classes of images. Additionally, because our electrical neuroimaging analyses entailed independent tests of topography and global field power, we had internal replication of positive effects for low-energetic and non-food images and replication of negative effects for high-energetic images. When coupled with additional analyses linked to the topographic cluster analysis as well as distributed source estimations (both of which also failed to reveal significant effects for high-energetic food images), a recurring pattern emerges.

Notwithstanding, our study only tapped into one aspect of memory for food and our analysis included only instances of first and second food item encounters. Thus, we cannot exclude that further visual encounters of high-energy foods would not lead to behavioral and neural repetition modulations as found for low-energy food items. Yet, also slower habituation to food has been associated with greater food intake (Wisniewski et al., 1992; Temple et al., 2007). Along these lines, weight gain is often related to generally altered responses in brain areas implicated in reward assessment, so that more extended investigations on memory processes for food in overweight women and men would be beneficial to better understand how to interact with hedonic food intake beyond homeostatic needs, i.e. in order to develop cognitive-behavioral weight management strategies.

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