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Distinct brain representations of processed and unprocessed foods

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Abstract

Among all of the stimuli surrounding us, food is arguably the most rewarding for the essential role it plays in our survival. In previous visual recognition research, it has already been demonstrated that the brain not only differentiates edible stimuli from non-edible stimuli but also is endowed with the ability to detect foods' idiosyncratic properties such as energy content. Given the contribution of the cooked diet to human evolution, in the present study we investigated whether the brain is sensitive to the level of processing food underwent, based solely on its visual appearance. We thus recorded visual evoked potentials (VEPs) from normal-weight healthy volunteers who viewed color images of unprocessed and processed foods equated in caloric content. Results showed that VEPs and underlying neural sources differed as early as 130 ms post-image onset when participants viewed unprocessed versus processed foods, suggesting a within-category early discrimination of food stimuli. Responses to unprocessed foods engaged the inferior frontal and temporal regions and the premotor cortices. In contrast, viewing processed foods led to the recruitment of occipito-temporal cortices bilaterally, consistently with other motivationally relevant stimuli. This is the first evidence of diverging brain responses to food as a function of the transformation undergone during its preparation that provides insights on the spatiotemporal dynamics of food recognition.

KEYWORDS

electrical neuroimaging, event-related potential, object categorization, object recognition

Abbreviations: BDI, Beck Depression Inventory; BMI, body mass index; EDI-3, Eating Disorder Inventory; EEG, electroencephalography; ERP, event-related potentials; GFP, global field power; GMD, global map dissimilarity; ITI, inter-trial interval; LAURA, local autoregressive average; M, mean; MNI, Montreal Neurological Institute; PF, processed food; RT, reaction times; SD, standard deviation; SE, standard error; UF, unprocessed food; VEPS, visual evoked potentials.

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1 | INTRODUCTION

Humans have evolved to be omnivores (Rozin, 1976). This predisposition together with the abundance and availability of foods in affluent countries makes the control over food intake and weight management challenging for the individual. Moreover, food intake behavior is largely guided by hedonic (or reward-based) regulation that increases the desire to eat beyond homeostatic needs to restore body energy balance (Berthoud, 2011; Lutter & Nestler, 2009).

Although experiencing and enjoying food is particularly enriched by the contribution of the different sensory modalities (Rolls, 2015), it is vision that mostly drives our everyday food recognition and choice (Linné, Barkeling, Rössner, & Rooth, 2002; Van der Laan, De Ridder, Viergever, & Smeets, 2011). To date, a handful of electrophysiological studies have provided insight about the types of information that are extracted during visual object recognition. For instance, already around 85 ms the brain is able to discriminate between edible and non-edible items (Tsourides et al., 2016), while between 100–200 ms post-image onset it detects differences in processing visually presented high- and low-energy food (Lietti, Murray, Hudry, le Coutre, & Toepel, 2012; Meule, Kübler, & Blechert, 2013; Toepel, Knebel, Hudry, le Coutre, & Murray, 2009); around the same time (100–200 ms), the brain distinguishes between natural items and artifacts, animate and inanimate items (Antal, Keri, Kovacs, Janka, & Benedek, 2000; Cichy, Pantazis, & Oliva, 2014; Proverbio, Del Zotto, & Zani, 2007; Thorpe, Fize, & Marlot, 1996).

In terms of underlying brain regions, visually presented food and non-food stimuli were shown to lead to activations in brain networks including occipital visual areas (i.e., fusiform gyrus, as in Adamson & Troiani, 2018; Grootswagers, Cichy, & Carlson, 2018) , orbitofrontal cortex (OFC), insula, and amygdala (García-García et al., 2013; Simmons et al., 2016; Van der Laan et al., 2011) , as well as fronto-striatal circuits (Hare, Camerer, & Rangel, 2009; Schur et al., 2009; Siep et al., 2012) . The energetic value of visual stimuli also reliably activates discrete brain regions, with higher prefrontal, hypothalamic, and striatal activation associated with high-energy foods (Beaver et al., 2006; Killgore et al., 2003; Rothemund et al., 2007). Given the importance of food for survival, a brain network preferentially responding to food stimuli relative to non-food stimuli resembles findings of other brain networks modulated by salience and reward (Seeley et al., 2007; Sescousse, Caldú, Segura, & Dreher, 2013). However, a highly specialized neural circuitry for food as, for instance, the one identified for faces (Kanwisher & Yovel, 2006; Grill-Spector & Weiner, 2014, for a review), has not been singled out to date.

Foods are complex and multidimensional stimuli. The aspect that has been mostly investigated is their energetic value, using calorie density and fat content as proxies. However, one aspect of food recognition that has received little attention in controlled studies is its level of transformation (see Rumiati & Foroni, 2016; Foroni & Rumiati, 2017). Human diets rely ubiquitously on food transformed through cooking, aggregation, or preservation procedures (Wrangham & Conklin-Brittain, 2003). Such procedures are argued to have played a fundamental role in human evolution, by reducing hominids' tooth and gut size, while body and brain size (Wrangham, 2013; Wrangham et al., 1999; Zink & Lieberman, 2016), and brain neurons increased (Herculano-Houzel, 2012). Moreover, according to the *cooking hypothesis,* the use of fire for cooking freed time for hominids to engage in activities other than gathering and chewing food (Wrangham, 2009). Studies of non-human primates suggest a preference for cooked food that is interpreted as reflecting a similar preference in early hominids (Warneken & Rosati, 2015; Wobber, Hare, & Wrangham, 2008). Being able to distinguish between raw and cooked food may well be an adaptive behavior, given that cooking increases the energy gain and reduces the risk of infections (Carmody & Wrangham, 2009). Processed foods are here defined as foods on which a sign of the human intervention can be traced. Such intervention changes the organoleptic state of such foods. Examples of transformations are the following: *cooking* (i.e., boiled/fried potatoes); *aggregation* (i.e., mayonnaise); or *preservation procedures* (i.e., cured meat; see also Foroni, Pergola, Argiris, & Rumiati, 2013). On the other hand, no modifications of this sort occur in the structure of unprocessed foods, that is, they are as they occur in nature. Recently, concepts about processed and unprocessed food have been found to be differently represented in both humans' episodic memory (Aiello et al., 2018) and semantic memory (Pergola, Foroni, Mengotti, Argiris, & Rumiati, 2017; Rumiati, Foroni, Pergola, Rossi, & Silveri, 2016; Vignando et al., 2018), similarly to what has been observed for natural and artificial categories (see Rumiati & Foroni, 2016, for a review).

The aim of the present study was to identify, in normal-weight participants, the spatiotemporal brain dynamics of the ability to discriminate between visually presented images of unprocessed and processed foods equated, on average, in caloric content. First, in analogy with other highly salient stimuli such as high-energy foods or emotional faces, we expected to find an early neural signature, within the 100–200 ms time window, of processed and unprocessed food discrimination as a result of the evolutionary pressure that shaped human food preferences. As mentioned above, this is the window within which the brain begins to extract salient information about food stimuli such as the calorie content (Lietti et al., 2012; Meule et al., 2013; Toepel et al., 2009) and teases a part other properties about stimuli such as naturalness and animacy (Antal et al., 2000; Cichy et al., 2014; Proverbio et al., 2007; Thorpe et al., 1996).

Consequently, viewing processed food was expected to chiefly activate regions associated with motivation

and reward, resulting in differential temporal dynamics and underlying brain regions associated when contrasted with unprocessed foods. Second, as unprocessed foods are rated by participants as more distant from edibility than processed foods which, in turn, are perceived as ready to be consumed (Foroni et al., 2013), we expected unprocessed foods to trigger distinct activities in the brain.

2 | MATERIALS AND METHODS

2.1 | Participants

Twenty (10 women) healthy Italian speakers participated in the experiment. Participants were aged between 18 and 35 years (M = 24.8, SD = 3.93), and their body mass index (BMI) was in the normal range (18.5 kg/m^2 < BMI < 25.0 kg/m^2; M = 21.61, SD = 1.80, range = 18.61–24.93). Participants were not included in the study if (a) they showed signs of aberrant eating behavior and/or behavioral symptoms in the 3 months previous testing (e.g., binge eating, vomiting, use of diuretics, or laxatives, assessed by the *Eating Disorder Inventory-3*, EDI-3, Garner, Olmstead, & Polivy, 1983); (b) they acknowledged prior neurological or psychiatric illness or the consumption of neurotropic substances; (c) they had severe dietary restrictions for medical (i.e., severe food allergies or intolerances) or personal reasons (both ethical or religious reasons, i.e., vegetarian, vegan, kosher diets), or (d) they presented traits of a severe depressed mood assessed by the *Beck Depression Inventory* (BDI-II; Beck, Steer, & Brown, 1996). All participants reported being right-handed (confirmed by the *Edinburgh Handedness Inventory*; Oldfield, 1971) and had normal or corrected-to-normal vision. The experiment began either at 9:00 a.m. or 2:00 p.m., and participants were asked to eat a meal 2-hr before the beginning of the recordings (upon arrival they reported at what time and the quantity of food eaten) in order to moderate the impact of the circadian modulations of hunger. Table 1 summarizes participants' demographic data.

TABLE 1 Participants' demographic, hunger level, and questionnaires data

	Mean	SD	Range
Age	*24.8*	*3.93*	*18–32*
BMI	*21.62*	*1.80*	*18.61–24.93*
Hunger	*39.26*	*28.65*	*5.33–97.63*
BDI-II	*6.1*	*6.96*	*0–29*
RS	*10.20*	*4.74*	*3–21*

In italics mean, standard deviations (SD) and range for each variable.
BMI, body mass index; BDI-II, Beck Depression Inventory; RS, Restraint Scale.

2.2 | Procedure and stimuli

Upon arrival, participants signed the written informed consent, completed the *Edinburgh Handedness Inventory* (Oldfield, 1971) and the *Beck Depression Inventory* (BDI-II; Beck et al., 1996). They were then prepared for the electroencephalogram (EEG) recordings and sat in front of a computer inside a sound-attenuated EEG cabin at 60 cm distance from the monitor. Stimulus presentation and registration of responses were controlled by Eprime 2.0 version (Psychology Tools Inc.; www.pstnet.com/eprime). Experiment completion required approximately 2 hr, and participants received 30 CHF in compensation. The study conformed to the Declaration of Helsinki and was approved by the Ethics Committee of the Vaudois University Hospital Center (CHUV) of Lausanne.

Before EEG recordings, participants also answered four questions regarding their current psycho-physiological state via *Visual Analog Scales* (VAS). The questions were the following (in brackets the anchored labels): (a) "How hungry are you at the moment?" ("Not at all hungry"—"very hungry"). (b) "How much would you like to eat at the moment?" ("Not at all"—"a lot"). (c) "How thirsty are you at the moment?" ("Not at all thirsty"—"very thirsty"). (d) "How tired are you at the moment?" ("Not at all tired"—" very tired").

During the EEG recordings, participants performed a categorization task (Figure 1a) involving full-color images. After a central cross appeared for a randomized period between 250 ms and 750 ms, images were presented centrally for 500 ms on a 21" CRT monitor. After image presentation, a question mark ("?") appeared, informing participants that they should respond whether the previously viewed image was a food or a non-food item via button press. The question mark disappeared as soon as participants responded or if a maximum period of 1,500 ms elapsed. Participants responded via a response box, which had two buttons, using the index and middle fingers of their dominant hand. This food versus non-food categorization was orthogonal to the discrimination between unprocessed and processed foods of interest for the behavioral and EEG analyses. During the EEG recordings, three blocks of trials of 350 color photographs each were presented in pseudo-randomized order. The 350 images per block consisted of 200 food images (see Appendix S1) and 150 non-food images (Figure 1b for exemplar stimuli). The 200 food stimuli were selected from three different food image databases: images used by Toepel and colleagues (Toepel et al., 2009), images from the FRIDa database (Foroni et al., 2013), and images from the FoodPics database (Blechert, Meule, Busch, & Ohla, 2014). Images were resized (300 × 300 pixels) and placed on a white background (plates in the background were removed) using the GNU Image Manipulation Program (GIMP; https://www.gimp.org). The 200 food images were equally divided in

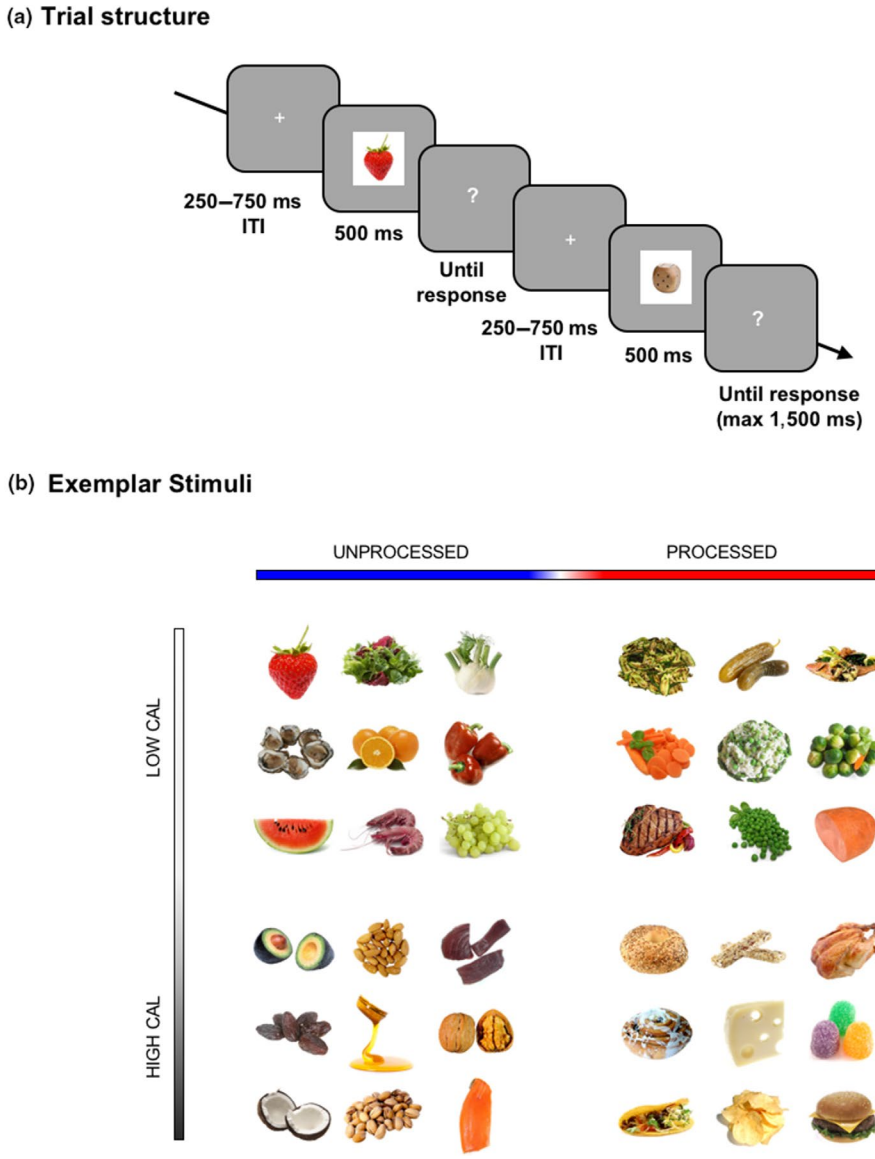

FIGURE 1 (a) Exemplar trial structure. Participants had to perform a food/non-food categorization task of each image responding via button press after the "?" appeared on the screen. Inter-trial interval (ITI) varied randomly between 250–750 ms; (b) Exemplar images of *unprocessed foods* (UF), *processed foods* (PF), equated on average on *caloric density* (kcal/100 g). [Colour figure can be viewed at wileyonlinelibrary.com]

100 unprocessed foods (UF; e.g., *avocado*, *strawberry*, *raw prawns*) and 100 processed foods (PF; e.g., *grilled zucchini*, *blue cheese*, *ice cream*). Within the 100 unprocessed foods, 50 images comprised low-calorie foods and 50 high-calorie foods, the same for the processed foods. Overall, food images were matched on various dimensions that were statistically tested with independent samples *t* tests. In particular, the unprocessed and processed images were matched in *caloric density* (kcal per 100 g portion; UF: M = 194.98 kcal/100 g *SE* = 21.37; PF: *M* = 201.66 kcal/100 g, *SE* = 16.15; $t(198) = -0.250$, $p = 0.803$), *valence* (UF: *M* = 60.61, *SE* = 1.04, PF: *M* = 59.74, *SE* = 0.84, $t(198) = 0.650$, $p = 0.516$, and *arousal* (UF: *M* = 42.44, *SE* = 1.66, PF: *M* = 42.18, *SE* = 1.21; $t(198) = 0.124$, $p = 0.901$). Non-food images were represented by three categories consisting of kitchen utensils (e.g., *knife, pan, and cup*), common objects (e.g., *dice, balloon, and book*), and natural entities that are not edible (e.g., *rose, coral, and leaf*). The images were matched in luminance and spatial spectral power following the analyses described by Knebel, Toepel, Hudry, Le Coutre, and Murray (2008).

After the end of the EEG recordings, participants again viewed all of the food images on the PC screen in pseudo-randomized order and rated them on VAS scales via a computer mouse. The images were rated along the following dimensions: *valence* "How negative/positive do you value the content of the picture?" ("Very negative" [0] and "Very positive" [100]), *wanting* "How much do you desire in this moment the food represented in the picture?" ("I do not desire it at all" [0] and "I desire it very much" [100]) and *frequency of consumption* "How frequently do you eat the food represented in the picture?" ("Never" [0] and "Every week" [50], "Every day" [100]).

Finally, participants filled in paper–pencil questionnaires regarding their health state (e.g., hours slept, time and quantity of food ingested, quantity of caffeine, cigarettes and

alcohol, habitual drugs, and other factors that could have influenced their performance). Moreover, they completed the *Eating Disorder Inventory-3* (EDI-3; Garner et al., 1983) and the *Restraint Scale* (RS; Herman & Polivy, 1980) questionnaires that provide information about individuals' dieting and eating habits.

2.3 | Electroencephalography acquisition and preprocessing

A 128-channel Biosemi ActiveTwo system (Biosemi; http://www.biosemi.com) acquired continuous EEG at 512 Hz sampling rate and referenced to the common mode sense (CMS; active electrode) and grounded to the driven right leg (passive electrode), which functions as a feedback loop driving the average potential across the electrode montage to the amplifier zero. Data preprocessing and the reported analyses were all performed using Cartool software (Brunet, Murray, & Michel, 2011).

Single participant's raw EEG data were inspected trial-by-trial using epochs from 98 ms pre- to 488 ms post-stimulus onset (corresponding to 50 data points pre- and 250 data points post-stimulus onset) using an artifact rejection criterion of ±80 μV at each channel. Epochs containing eye blinks and other movements, or non-stereotypic artifacts were rejected. During averaging, data were baseline corrected using the 98 ms pre-stimulus period, filtered (0.1 HZ high-pass, 40 Hz low-pass, and 50 Hz notch), and recalculated against the average reference. Data at artifact electrodes were interpolated using 3-D splines (Perrin, Pernier, Bertnard, Giard, & Echallier, 1987). On average, 6.4% (SE = 1.12) of trials were rejected during single subject preprocessing. Furthermore, only trials on which participants were accurate were further analyzed. Visual evoked potentials (VEPs) were first calculated for each participant and stimulus condition (i.e., unprocessed food and processed food images). Second, VEPs to each stimulus condition were group-averaged.

2.4 | EEG data analysis and source estimation

2.4.1 | General analysis strategy

In order to investigate whether VEPs to unprocessed and processed food images differed, we conducted VEP analyses at the single waveform level, on the global strength of the electric field at the scalp (viz. global field power [GFP]), on the topography of the VEP (viz. global map dissimilarity [GMD], as well as topographic clustering), and on the estimated intracranial sources of the VEP responses (viz. LAURA source estimations). Details of the analyses will be described in the following paragraphs; however, these methods have been extensively described elsewhere (Brunet et al., 2011; Michel & Murray, 2012; Murray, Brunet, & Michel, 2008). All analyses presented are based on paired contrasts between unprocessed and processed food viewing conditions.

2.4.2 | Analysis of VEPs waveform modulations

As first level of analysis, VEP group-averaged waveform data from all 128 electrodes were analyzed as a function of time. At each time point (millisecond-by-millisecond; Murray et al., 2004) pairwise comparisons (t tests) between the two conditions (unprocessed vs. processed) at each of the scalp electrodes were performed. Effects that did not last at least 20 ms (11 contiguous data points) were rejected in order to correct for temporal auto-correlation at individual electrodes (as in Toepel et al., 2009). Results of this analysis give a visual impression of the distribution of significant differences in time and space, minimizing the possibility of missed effects (type II errors).

2.4.3 | Global electric field analyses

The second level of analyses first assessed the modulations in the strength of the electric field at the scalp using GFP (Lehmann & Skrandies, 1980) over the post-stimulus period for each participant and stimulus condition using paired t tests. GFP is calculated as the square root of the mean of the squared value recorded at each electrode (vs. the average reference) and is equal to the spatial standard deviation across electrodes at a given instant in time (Michel & Murray, 2012). Larger GFP values are associated with greater synchronized neural activity.

Differences in the topography between electric fields in response to each stimulus condition were assessed through the analysis of GMD (Lehmann & Skrandies, 1980). Strength-normalized data were compared by dividing potentials at each electrode of a given map by its GFP. GMD is calculated as the root mean square of the difference between two normalized maps and can range from 0 to 2, where 0 indicates identical maps and 2 maps topographies inverted. A Monte Carlo nonparametric bootstrapping procedure (5,000 permutations per time point), referred to as "topographic ANOVA" or "TANOVA" (Murray et al., 2008), identified statistical differences in the GMD between two conditions by comparing the observed GMD with the empirical distribution obtained from the bootstrapping. Effects that lasted at least 11 contiguous data points (~20 ms; with a p-value below 0.05) were considered reliable (as in Toepel et al., 2009). Topographic differences are indicative of differences in the underlying neural generators. Time intervals in which the GMD differed between stimulus conditions were therefore used as time intervals of interest for the source estimation analysis (LAURA). Of note, analyses of GMD and GFP

are independent, and observations of time intervals with GFP modulations with a lack of differences in map topographies are interpreted as the modulation of statistically indistinguishable generators across stimulus conditions.

2.5 | Estimations of neural source activity

A distributed linear inverse solution was applied using the local autoregressive average (LAURA) regularization approach (Grave de Peralta Menendez et al., 2001; for a review, see Michel, Murray, et al., 2004). Distributed source models reconstruct the brain electric activity in each point of a 3D grid of solution points. LAURA selects the sources that better mimic the behavior of the electric vector fields using a realistic head model, which here included 3,005 solution point nodes of a 6 × 6 × 6 mm grid equally distributed within the gray matter of the Montreal Neurological Institute's (MNI) average brain. The time intervals in which differences in the GMD were found were used as time periods of interest regarding modulations in neural source activity between conditions. Paired t tests were calculated at each solution point node using the variance across participants. Only nodes with p-values < 0.05 and within clusters of at least 10 contiguous nodes were considered significant. The results were rendered on the MNI brain, and we report the Tailarach and Tournoux (1988) coordinates (as in Toepel et al., 2009; Brunet et al., 2011).

3 | RESULTS

3.1 | Psychophysical state

Participants' psychophysical state assessed via VAS scales ranging from 0 to 100. Participants reported a low hunger level ($M = 39.26$, $SD = 28.65$), a low desire to eat ($M = 37.04$, $SD = 25.53$), low thirst ($M = 42.93$, $SD = 23.28$), and a low level of tiredness ($M = 25.62$, $SD = 24.80$). As requested, participants reported that they ate a meal 2 hr before the beginning of the recordings.

3.2 | Behavioral results

3.2.1 | Accuracy and RTs

Participants' categorization accuracy, calculated as the percentage of correct answers, was at ceiling. On average (±*SEM*), participants correctly categorized 98.20 ± 0.2% of food images and 98.61 ± 0.2% of non-food images (paired t test: t (19) = −2.13; $p = 0.046$), consistently with the accuracy values reported in previous studies (Toepel, Knebel, Hudry, Le Coutre, & Murray, 2010; Toepel et al., 2009). Within the food images, 98.30 ± 0.2% of unprocessed foods and 98.03 ± 0.3% of processed foods were correctly categorized (paired t test: $t(19) = 1.38$; $p = 0.184$).

As participants were instructed to respond only after the question mark that appeared after the images presentation, reaction time data (RTs) are less informative. Specifically, RTs were time-locked to the appearance of the question mark and not to the onset of the image. Results showed that, on average (±*SEM*), participants were equally fast at categorizing food and non-food images (food: 342 ± 20 ms and non-foods: 331 ± 20 ms; paired t test: t (19) = 1.71; $p = 0.103$). Moreover, for within the food category, participants were faster with processed food (332 ± 20 ms) than unprocessed food (with 352 ± 20 ms) (paired t test: t (19) = 3.01; $p = 0.007$).

3.2.2 | Ratings

Participants' ratings of the images were averaged for each subject and each image category viewed. Results revealed that on average (±*SEM*), participants' ratings did not differ between unprocessed and processed foods in terms of valence (UF: 70.06 ± 3.04; PF: 65.83 ± 2.61; $t(19) = 1.66$; $p = 0.112$), wanting (UF: 50.89 ± 3.15; PF: 50.65 ± 3.75; $t(19) = 0.074$; $p = 0.941$), or frequency of consumption (UF: 49.43 ± 3.28; PF: 48.60 ± 2.77; $t(19) = 0.315$; $p = 0.756$).

3.3 | Results of VEP data analysis

3.3.1 | Waveform modulations at individual electrodes

Single electrode level analyses revealed VEP response differences between unprocessed and processed food images. Differences arose as early as around 130 ms at posterior electrodes and more widespread around 200 ms (Figure 2a). Group-averaged VEP waveforms per each condition at an exemplar midline occipital electrode (O_z) revealed a first peak with positive amplitude greater for unprocessed foods in the 130–175 ms interval and a second positive peak significantly greater for processed foods in the 195–240 ms interval (Figure 2a). These VEP peaks correspond to the traditional series of ERP components, including the P1, N1, and P2. Significant differences in amplitudes emerged in the posterior electrodes in both P1 and P2, whereas N1 component amplitude differences between our conditions were not significant at the midline occipital sites.

3.3.2 | Global measures of the electric field

Significant modulations in response to strength between conditions, assessed via GFP, were observed over the 207–341 ms interval and >400 ms post-stimulus onset (Figure 2b), wherein processed foods elicited stronger responses than

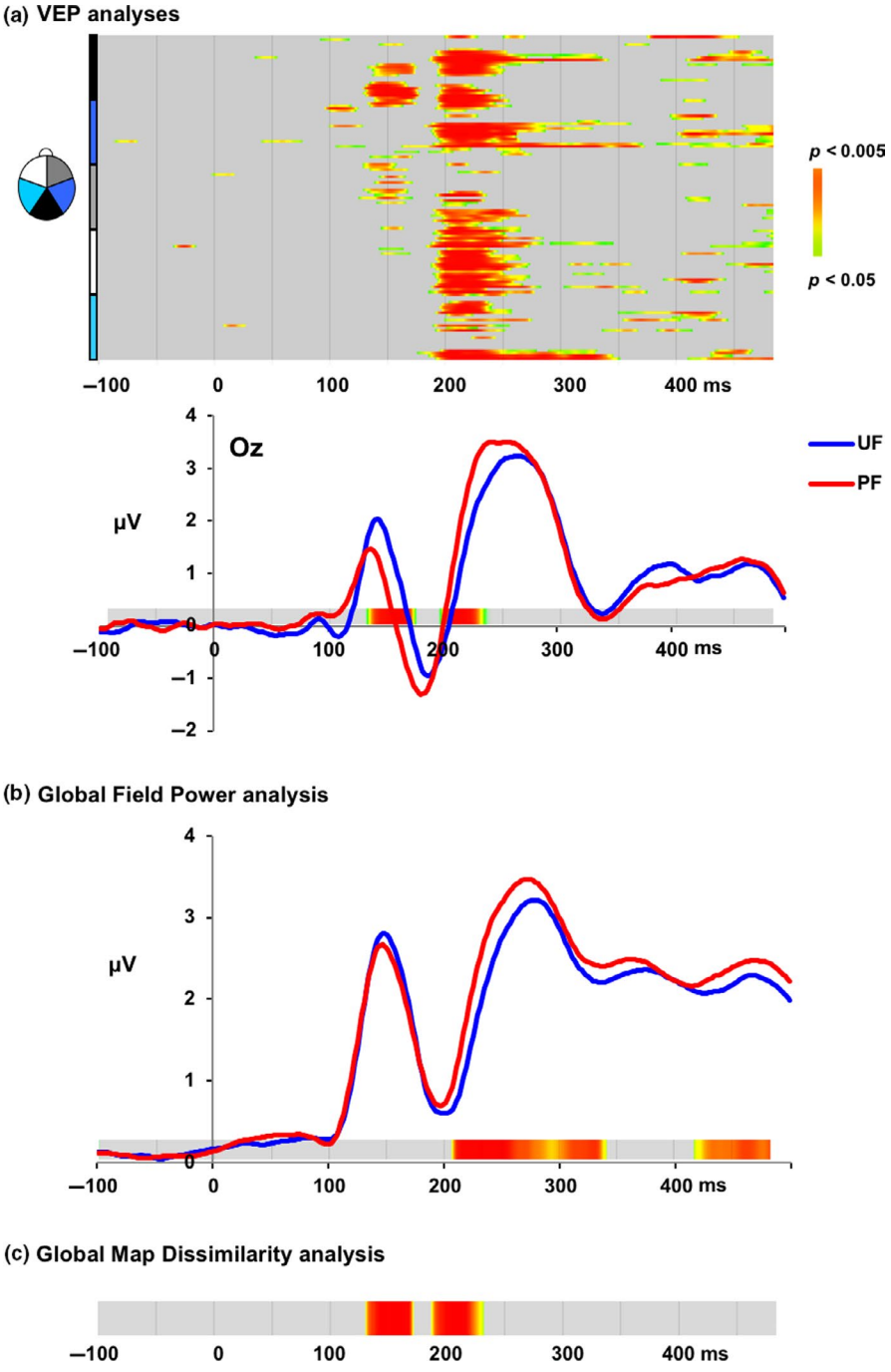

FIGURE 2 (a) Results of the electrode-wise and millisecond-by-millisecond paired *t* tests between unprocessed and processed conditions. Temporally sustained differences emerged around 150 ms post-stimulus onset. Exemplar midline occipital electrode (O_z) group-average waveforms are displayed. (b) Modulations in response strength assessed through global field power waveforms, differences between conditions emerged in the 207–341 ms and >400 ms post-stimulus onset intervals; (c) Modulations in response topography assessed through global map dissimilarity emerged in the 130–171 ms and 187–232 ms post-stimulus onset intervals. [Colour figure can be viewed at wileyonlinelibrary.com]

unprocessed foods in such time intervals. Significant modulations in response topography between unprocessed and processed foods assessed via GMD were observed over the 130–171 ms and 187–232 ms intervals post-stimulus onset (Figure 2c), indicating different configurations of brain sources over these intervals.

3.3.3 | Source estimations

For the time intervals revealed by the GMD analysis (130–171 ms and 187–232 ms), distributed source estimations were calculated for each condition and each individual participant. The reported coordinates represent the maximal *t*-values within a cluster and are based on the Tailarach and Tournoux (1988) system, and the corresponding Brodmann areas (BA) are reported. Over the 130–171 ms post-stimulus period (Figure 3a,c for the axial images), several brain regions showed different responses to unprocessed versus processed foods. The occipital cortex (BA 17/18/19; $x = 9$, $y = -69$, $z = 23$) and the posterior portion of the right inferior temporal cortex (BA 20; $x = 60$, $y = -7$, $z = -18$) showed stronger responses to processed foods than unprocessed

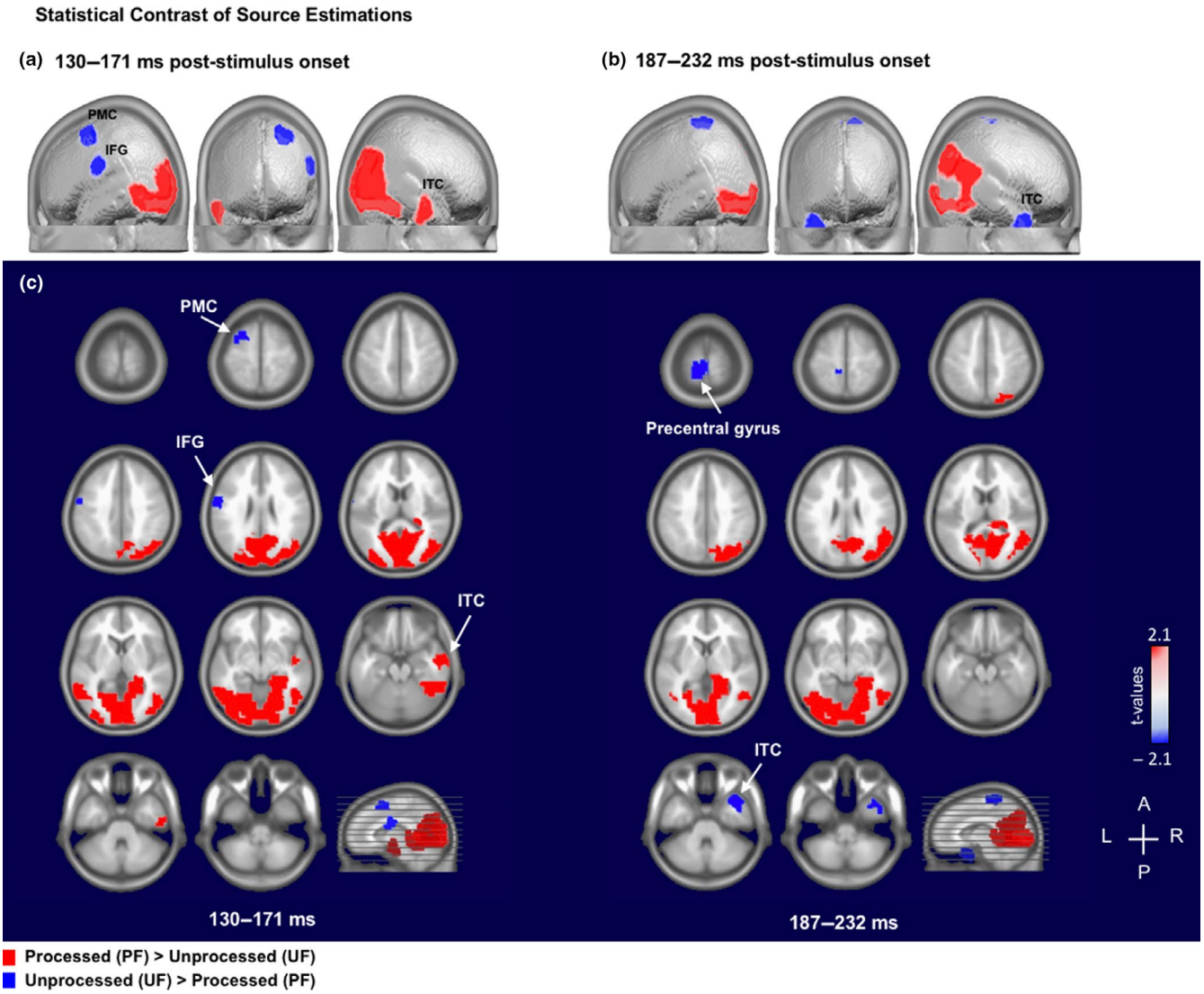

FIGURE 3 Statistical contrasts of source estimations performed over the 130–171 ms and 187–232 ms post-stimulus onset intervals (panels a and b, respectively). The color scale displays the *t*-values where positive values, indicating greater activation in response to processed foods versus unprocessed (in red), whereas negative values indicating greater activation of unprocessed foods versus processed (in blue). In panel c axial sections of the results are displayed (IFG, inferior frontal gyrus; ITC, inferior temporal cortex; PMC, premotor cortex). [Colour figure can be viewed at wileyonlinelibrary.com]

foods. In contrast, source estimations within the left lateral premotor cortex (BA 6, $x = -31$, $y = 7$, $z = 58$) and left inferior frontal gyrus (BA 47, $x = -60$, $y = -1$, $z = 23$) were significantly stronger in response to unprocessed foods than processed foods.

Over the 187–232 ms post-stimulus onset (Figure 3b,c for the axial images), distributed brain regions showed differential responses to unprocessed and processed foods. The occipital cortex (BA 17/18/19; $x = 33$, $y = -75$, $z = 35$), extending to the parietal cortex, responded significantly stronger to processed foods than unprocessed foods. In contrast, the left precentral gyrus (BA 4, $x = 40$, $y = 12$, $z = -27$) and the anterior portion of the right inferior temporal cortex (BA 20, $x = -9$, $y = -27$, $z = 71$) showed stronger responses to unprocessed foods than processed foods.

4 | DISCUSSION

Several lines of evidence led to suggest that food transformation impressed an acceleration on the making of humankind (Herculano-Houzel, 2012; Wrangham, 2009; Zink & Lieberman, 2016). Transformation procedures, such as cooking at high temperatures or boiling, increase the net energy gain after ingestion (for evidence in mice see Carmody, Weintraub, & Wrangham, 2011), reduce the risk of food infections (Carmody & Wrangham, 2009), and are argued to have produced morphological changes of the human body during evolution, leading to larger brains and smaller teeth and stomach (Wrangham, 2009).

In the present study, we investigated the neural signatures of the ability to discriminate between unprocessed and

processed foods. To this end, normal-weight participants viewed images of unprocessed and processed foods that were matched for physical characteristics such as brightness and spatial frequency, as well as for valence, arousal and, most importantly, for caloric density. Behaviorally, no differences between the two food subcategories were found either in participants' response accuracy or ratings. However, a significant difference in reaction times emerged, with participants being faster in categorizing processed foods as foods. Consistently, Aiello et al. (2018) found that, in a recognition memory task, healthy participants were significantly better at recognizing processed compared with unprocessed foods. Advantageous recognition of processed over unprocessed foods resembles the differences observed when high-fat and low-fat food items were compared (Toepel et al., 2009; see also Toepel et al., 2010).

In addition to being recognized more easily, processed foods might be characterized by higher reward value (*subjective value*) assigned by the participants (Sellitto, Ciaramelli, & di Pellegrino, 2011). *Temporal discounting* studies demonstrated that the reward value is affected by the cost of time: Humans tend to prefer immediate rewards to those that are delivered later (even when the latter are larger; Ainslie, 1975). Food as a primary reward (compared to secondary rewards i.e., money) is affected by intertemporal choices, triggering impulsive behaviors, as when the immediate consumption of a palatable food (usually smaller in quantity) is compared to the reward of a larger, but delayed in time, amount of the same food (Schiff et al., 2016). We hypothesize that unprocessed foods are associated with a lower subjective value as it usually takes a longer time to consume them; however, further investigations using the typical temporal discounting paradigm are necessary to test this interpretation.

The analyses of the spatiotemporal brain dynamics revealed the following significant effects. First, differences in the VEPs between unprocessed and processed foods were observed as early as 130 ms post-stimulus onset. An early timeframe was also reported in the studies by Toepel et al. (2009, 2010) and Meule et al. (2013), in which participants showed an implicit within-category discrimination of fat content of food. Second, our VEP results at the electrode level arise around 130 ms in a cluster of posterior electrodes, but they then spread across the scalp around 200 ms, with significant differences in the topography of the electric field in response to food categories. Our findings thus clearly demonstrate that the brain *readily* detects food properties such as the degree of processing, in addition to the already demonstrated ability to discriminate foods differing in energy content (Meule et al., 2013; Toepel et al., 2009).

Here we will focus on two aspects of our results, both concerning the *early emergence* of the unprocessed-processed discrimination effect. First, also in virtue of its timeframe, this ability to discriminate between unprocessed–processed food is argued to be adaptive, in line with the *cooking hypothesis* (Wrangham, 2009). The second aspect concerns the evidence that, in early time windows, the brain extracts and distinguishes not only perceptual but also higher-level information about visually presented stimuli. Our findings confirm that food, like other stimuli with a high psychosocial significance for humans such as faces or words, is recognized and categorized as early as 150 ms post-stimulus onset (Michel, Seeck, & Murray, 2004; Nemrodov, Niemeier, Patel, & Nestor, 2018). After originating at about 50–60 ms from the stimulus onset in the primary visual cortex V1, these responses occur within 150 ms in higher-order areas such as the frontal areas and reflect the so-called P1 component (Fabre-Thorpe, Delorme, Marlot, & Thorpe, 2001).

That higher-level effects may occur early in the timeline of object visual processing found confirmation in recent MEG studies. For instance, Tsourides et al. (2016) provided evidence of a discrimination effect based on edibility in the ventral visual stream within 50 ms from the arrival of information in V1, as early as 85 ms post-stimulus onset stimuli. Likewise, Cichy et al. (2014) reported that in the ventral visual cortex objects were discriminated for naturalness (natural vs. artificial), with a peak at 122 ms post-stimulus onset. Accordingly, the early discrimination reported in our study may reflect a specific instance of the more general categorization mechanism identified by Cichy et al. (2014), constituting the first evidence of a within-category discrimination of food naturalness. Unprocessed foods may resemble natural entities, since no modifications occurred in the structure of such foods they are as they occur in nature. By contrast, processed foods may resemble artifacts, possibly due to the modifications applied by humans on such foods. Together with other pieces of information about the food such as the calorie content, the unprocessed/processed discriminating mechanism contributes to build the representation of food stimuli, and the accumulation of information will eventually lead to make a decision about what to eat (see Rangel, 2013).

The source analysis qualifies these effects further. Differences at the scalp were supported by distinct activations of distributed brain areas in two early time windows (130–171 ms and 187–232 ms), as shown by the source estimation analysis results. On the one hand, wide activations within the occipital cortex were found to be higher in response to processed foods. Greater activation in visual areas has been observed, in response, for instance, to high-calorie foods (Killgore et al., 2003; Simmons, Martin, & Barsalou, 2005; Toepel et al., 2010), as well as to other highly relevant stimuli such as monetary rewards (Small et al., 2005) or emotional faces (Eger, Jedynak, Iwaki, & Skrandies, 2003; Moratti, Keil, & Stolarova, 2004). The difference in occipital activation observed in the present research, in line with previous literature with food stimuli (as in Stingl et al., 2010; Meule et al., 2013; Tsourides et al., 2016), is unlikely to be due to differences in visual complexity of the stimuli.

In our study, different regions of the temporal cortex were found to be more strongly active in response to the two food subcategories along a posterior-to-anterior gradient. Whether this gradient might graft onto the more general discrimination of natural versus man-made objects (Grill-Spector & Weiner, 2014) requires further investigation to be understood fully.

On the other hand, unprocessed foods led to increased activity in the frontal and parietal lobe. More specifically, the left lateral premotor cortex was found greatly activated in response to unprocessed food items. This pattern of activation is consistent with findings on brain correlates of action preparation (Desmurget & Sirigu, 2009; Weinrich, Wise, & Mauritz, 1984). Unprocessed foods might be perceived as requiring some actions in order to be consumed safely, whereas processed foods have already undergone substantial transformation and, as such, are more likely "ready" to be eaten without any risk of infections (Carmody & Wrangham, 2009). This interpretation is in line with previous evidence that unprocessed foods tend to be perceived as more distant from edibility than processed foods that instead are perceived as ready to be consumed (Foroni et al., 2013). Both the inferior frontal and precentral gyri have also been found to represent food words as well as the corresponding action words associated with mouth and tools (Carota, Kriegeskorte, Nili, & Pulvermüller, 2017; see also De Lucia, Clarke & Murray, 2010 for environmental sounds). The results of the source estimation analysis failed to reveal any statistically significant differential activity in the OFC or in any other brain region associated with reward processing (i.e., ventromedial prefrontal cortex, striatum). This might be due to the fact that the participants in our study were satiated and reported a low hunger level, as well as to the nature of the task consisting in a simple food/non-food categorization, compared to the tasks usually used in food-related decision-making protocols that require a more explicit evaluation of the food reward content. It is worth noting that in previous literature, a consistent OFC activation has been observed in response to visually presented food stimuli only in 40% of the studies (for a meta-analysis see Van der Laan et al., 2011). The relevance of controlling for participants' satiety and hunger has received the due attention in recently published methodological guidelines for food-related neuroimaging studies (Smeets et al., 2019). Future food research will have to keep these recommendations into consideration in order to ease data interpretation and to test across-studies reproducibility. In conclusion, the present findings demonstrate that the level of processing is a relevant aspect of food representation, in addition to the more often studied energy content. Our study suggests that food visual recognition takes place as early as 130 ms post-stimulus onset and elicits different responses at the electrode level and in the topographies of the electric field maps generated by distinct and distributed neural sources. This early unprocessed–processed discrimination effect falls within the window of visual object recognition when other salient properties are also detected (Antal et al., 2000; Proverbio et al., 2007; Thorpe et al., 1996). Previous studies showed that the information regarding objects' edibility is coded by the brain at about 85 ms post-stimulus onset (Tsourides et al., 2016), objects' naturalness at about 120 ms (Cichy et al., 2014), and energy level at about 160 ms (Meule et al., 2013; Toepel et al., 2009). We argue that the within-category food unprocessed–processed discrimination is an instance of the broader between-category natural–artifact discrimination.

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CONFLICT OF INTEREST

The authors declare no competing financial interests.

DATA ACCESSIBILITY

The data of the present study can be requested to the corresponding author.

AUTHORS' CONTRIBUTION

CC, UT, RIR conceived the original idea of the present study. CC prepared the stimuli and carried out the EEG recordings, under the supervision of UT. CC, UT performed the statistical analysis, CC, UT, MMM, RIR contributed in interpreting the results. CC, RIR wrote the manuscript, UT, MMM reviewed and finalized the manuscript.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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