The Time-Course of Food Representation in the Human Brain

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ABSTRACT

Humans make decisions about food every day. The visual system provides important information that forms a basis for these food decisions. Although previous research has focussed on visual object and category representations in the brain, it is still unclear how visually presented food is encoded by the brain. Here, we investigate the time-course of food representations in the brain. We used time-resolved multivariate analyses of electroencephalography (EEG) data, obtained from human participants (both sexes), to determine which food features are represented in the brain, and whether focused attention is needed for this. We recorded EEG while participants engaged in one of two tasks. In one task the stimuli were task relevant, whereas in the other task the stimuli were not task relevant. Our findings indicate that the brain can differentiate between food and non-food items from approximately 84 milliseconds after stimulus onset. The neural signal also contained information about food naturalness, the level of transformation, as well as the perceived caloric content. This information was present regardless of whether the food items were task relevant or not. Information about the perceived immediate edibility of the food, however, was only present when the food was task relevant. Furthermore, the recorded brain activity correlated with the behavioural responses in an odd-item-out task. Together, our results contribute to our understanding of how the human brain processes visually presented food.

1. INTRODUCTION

Humans make food choices every day. Our visual system allows us to gather information about distant foods, making visual information an important basis for food choices. There is evidence that food processing through vision and taste rely on overlapping processes, with activation in the same regions (Simmons et al., 2005), and shared information about the taste (Avery et al., 2021), evoked by food that is seen and tasted (cf. Nakamura et al. (2020)). Recent evidence suggests that food could be an important organisational feature in the ventral visual stream, as neural responses in the ventral visual cortex are selective for visual food stimuli (Jain et al., 2023; Khosla et al., 2022). Previous work has shown that information about animacy, category, and exemplars emerges in the brain before 100 ms (Carlson et al., 2013; Cichy et al., 2014; Contini et al., 2017; Grootswagers et al., 2019). However, relatively few studies have focused on the time-course of visually presented food representations.

Several studies have investigated the neural food/non-food distinction in the temporal domain (Stingl et al., 2010; Tsourides et al., 2016). For example, one MEG study showed that information about food vs. non-food emerges from 85 ms after stimulus onset (Tsourides et al., 2016). Fewer studies have investigated whether, and when, other features of food are represented in the brain. Two dimensions that are of particular relevance from an evolutionary perspective are 1) the distinction between natural and prepared food (i.e., food with signs of human intervention), and 2) the energetic value of the food (i.e., calorie content).

The distinction between natural and prepared food may be an important one for modern humans. Even Chimpanzees have been shown to spontaneously prefer cooked food (Warneken & Rosati, 2015; Wobber et al., 2008). Several studies have investigated the neural distinction between natural and prepared foods (Coricelli et al., 2019; Pergola et al., 2017; Vignando et al., 2019). For example, an EEG study showed a difference in visual evoked potentials elicited by images of natural compared to prepared foods as early as 130 ms after stimulus onset (Coricelli et al., 2019). This and other studies suggest that the neural response is modulated by whether food is natural or prepared. However, it is still unclear whether the brain carries information about this distinction, and what the time-course of this information is.

Another important feature of food is the energetic value or caloric content. Several studies have found the brain response to food stimuli is modulated by the caloric content of the stimuli (Killgore et al., 2003; Mengotti et al., 2019). Toepel and colleagues (2009) used EEG to investigate the time-course of activation differences due to the calories of food. Differences in visual evoked potentials associated with viewing high fat compared to low fat foods emerged from 165 ms after viewing the stimulus. Together, the findings are in line with a modulation of the neural response driven by the energetic content of the food. However, it

remains unclear whether and at what time the brain carries information about the energetic content of food.

In addition to features such as naturalness and calorie content, the way the brain processes information about food could depend on perceiver characteristics. For example, one study used multivariate pattern analysis on EEG data to show there was information about the subjective 'tastiness' of the food from approximately 530 ms after stimulus onset (Schubert et al., 2021). It is still unclear whether the brain represents the level of arousal in addition to the valence (palatability) of the food. In addition, it is unclear whether only personal palatability information is encoded, or whether more general food preferences across the population are represented in the brain.

In this study, we used multivariate analysis methods on EEG data to investigate the time-course of the representations of food properties in the brain. In addition, we asked whether focused attention is needed for these representations to emerge.

2. MATERIALS AND METHODS

2.1. Participants

Twenty healthy adults participated in the EEG study. The participants had a mean age of 20.9 years (SD = 3.74, range 18-33 years). Seventeen participants identified as female, two as male and one as non-binary. All participants were right-handed, reported normal or corrected-to-normal vision, and had no history of psychiatric or neurological disorders. The participants were recruited from the University of Sydney and received course credit for their participation. The study was approved by the Human Ethics Committee of the University of Sydney and all participants provided informed consent before participating.

2.2. Experimental design

The stimulus set consisted of 154 food images and 160 non-food object images (Figure 1A). The food images were taken from the Foodcast Research Image Database (Foroni et al., 2013). The subset was chosen to be familiar to Australian participants, and no rotten food items were included. We selected 71 natural food items and 83 transformed (or prepared) food items. The non-food stimuli were from a free image hosting website (PNG Imaging) and were a subset of those used in previous EEG object decoding studies (Grootswagers et al., 2019). The non-food stimulus set consisted of 80 animate and 80 inanimate objects, divided into 8 categories (humans, mammals, birds, insects, plants, clothing, furniture, and tools). Each category had 5 different objects. For example, the 'mammal' category consisted of cow, giraffe, etc. There were four exemplars of each object. Note that the fruit category from this

set was not included because they are foods. The aquatic category was also excluded because of some exemplars might be seen as unprepared foods (e.g., fish or squid).

We used the Psychopy library (Peirce et al., 2019) in Python to run the experiment. The images were presented on a white background and were 256 by 256 pixels. Participants were seated approximately 60 cm from the screen, and the stimuli were approximately 6.25 by 6.25 degrees of visual angle. A central fixation bullseye was presented throughout the experiment, and participants were instructed to remain fixation on the central bullseye. The EEG experiment consisted of two different tasks, a fixation monitoring task and a food categorisation task (Figure 1B and 1C). There were 6 blocks in total, and each block consisted of the fixation monitoring task followed by the food categorisation task. The experiment took approximately 50 minutes to complete. Participants used a button box to respond in both tasks.

2.2.1. Fixation monitoring task (passive viewing)

Figure 1B gives an overview of the fixation monitoring task. During this task, participants viewed streams of images. The images were presented at 6.67 Hz; each stimulus was on the screen for 100 ms, followed by a blank screen for 50 ms. The stimuli consisted of 314 unique images, depicting food (154 images) and non-food objects (160 images). There were 6 blocks in the experiment. Each block consisted of 6 image sequences, and each sequence contained 157 image presentations. This means there were 942 image presentations per block, 3 repeats of the 314 unique images. The order of the stimulus presentations was randomised across two consecutive sequences. Each sequence was approximately 24 seconds, and participants were given the option to have a break after every sequence to minimise fatigue and eye blinks.

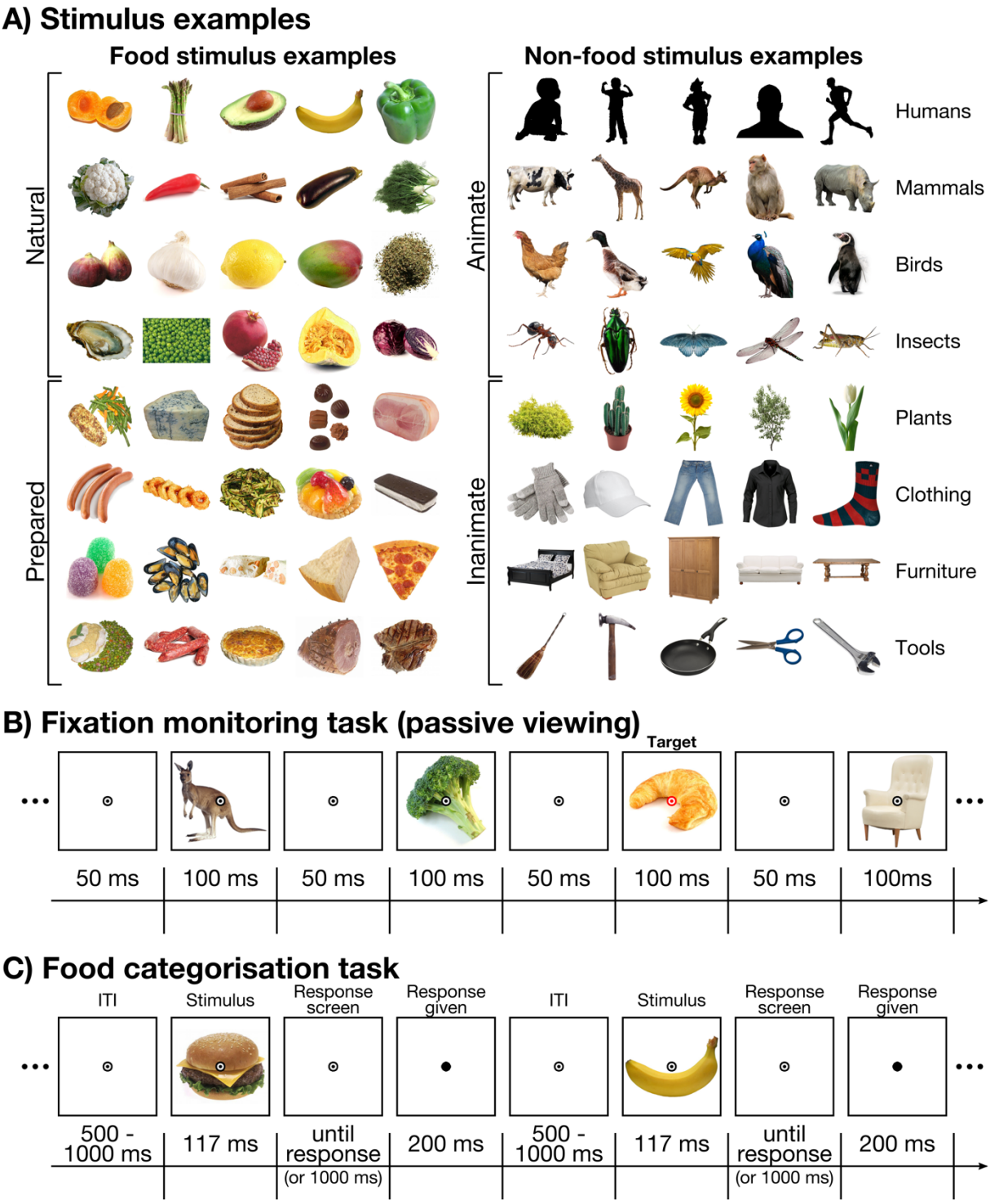


Figure 1. Stimuli and task. A) Shows examples of the stimuli. The left panel shows examples of the 154 food stimuli that were used. Stimuli were selected from the Foodcast Research Image Database (Foroni et al., 2013). The selected stimulus set consisted of 71 natural food images (top) and 83 transformed food images (bottom). The right panel shows examples from the 160 non-food object stimuli. Images were obtained from a free image hosting website (PNG Imaging) and were used in previous work (Grootswagers et al., 2019). The stimulus included 80 animate (top) and 80 inanimate objects (object) from 8 different categories (humans, mammals, birds, insects, plants, clothing, furniture, and tools). Note the stimuli depicting humans (top row) are replaced with silhouettes in this figure to comply with bioRxiv

guidelines. **B)** Shows an overview of the fixation monitoring task, in which the stimuli were not task relevant. Stimuli were presented for 100 ms with an inter-stimulus-interval of 50 ms. Participants pressed a button when the fixation bullseye changed from black to red. The third stimulus on this example (croissant) shows and example of a target. **C)** Shows an overview of the food categorisation task. Participants saw a food stimulus for 117 ms and were asked to indicate whether the depicted food item was natural or prepared. There was a response time-out of 1000 ms. When a response was given, the fixation bullseye turned into a black dot for 200 ms. There was a randomly selected inter-trial-interval ranging between 500 ms and 1000 ms.

The participants monitored the fixation bullseye and pressed a button when the fixation bullseye turned to red instead of black for the duration of a stimulus presentation (100 ms). Participants were instructed to respond as fast and accurately as possible. The purpose of the task was to keep participants engaged and ensure their gaze remained fixated on the centre of the screen. Each sequence had between 2 and 4 targets (fixation colour changes). The targets were presented at random intervals with the following constraints. The first ten and last ten stimulus presentation of the sequence were never targets, and two targets were always at least 15 stimulus presentations apart.

2.2.2. Food categorisation task

Figure 1C provides an overview of the food categorisation task. In this task, participants indicated for each image whether the depicted food was ‘natural’ or ‘prepared’. The stimuli were the same as those used in the fixation monitoring task, but only the food images were used. Each stimulus was presented once per block in a randomised order. Participants completed 6 blocks in total. The food stimulus was presented for 117 ms, and participants had 1000 ms to make a response. If participants responded, the fixation bullseye turned to a filled black dot for 200 ms indicating to the participant that a response was recorded. If no response was made within 1000 ms, feedback was given that the response was too slow, and the experiment automatically moved on to the next trial. There was an inter-trial interval ranging between 500 ms and 1000 ms. Participants were instructed to respond as fast and accurately as possible. They responded by pressing one of two buttons on a button box. The buttons used to indicate whether the food was ‘natural’ or ‘prepared’ switched between each block. This was done to make sure that any differences in the neural signal between natural and prepared foods could not be driven by motor preparation or execution. At the start of each block, instructions were shown detailing the button-response mapping for that block. Participants were given the opportunity to take a break after every 22 trials to avoid fatigue.

2.3. EEG acquisition and pre-processing

The EEG data were recorded with a 128 channel BrainVision ActiChamp system, at a sampling rate of 1000 Hz, referenced online to FCz. The electrodes were placed according to the international 10-20 system (Oostenveld & Praamstra, 2001). We used a minimal EEG pre-processing pipeline, following earlier work (Grootswagers et al., 2021; Robinson et al., 2021). First, we re-referenced to the average of all electrodes. Then we applied a low-pass filter of 100 Hz and a high pass filter of 0.1 Hz, and we down-sampled the data to 250 Hz. Finally, we created epochs locked to each stimulus onset, from -100 ms before stimulus onset to 1200ms after stimulus onset.

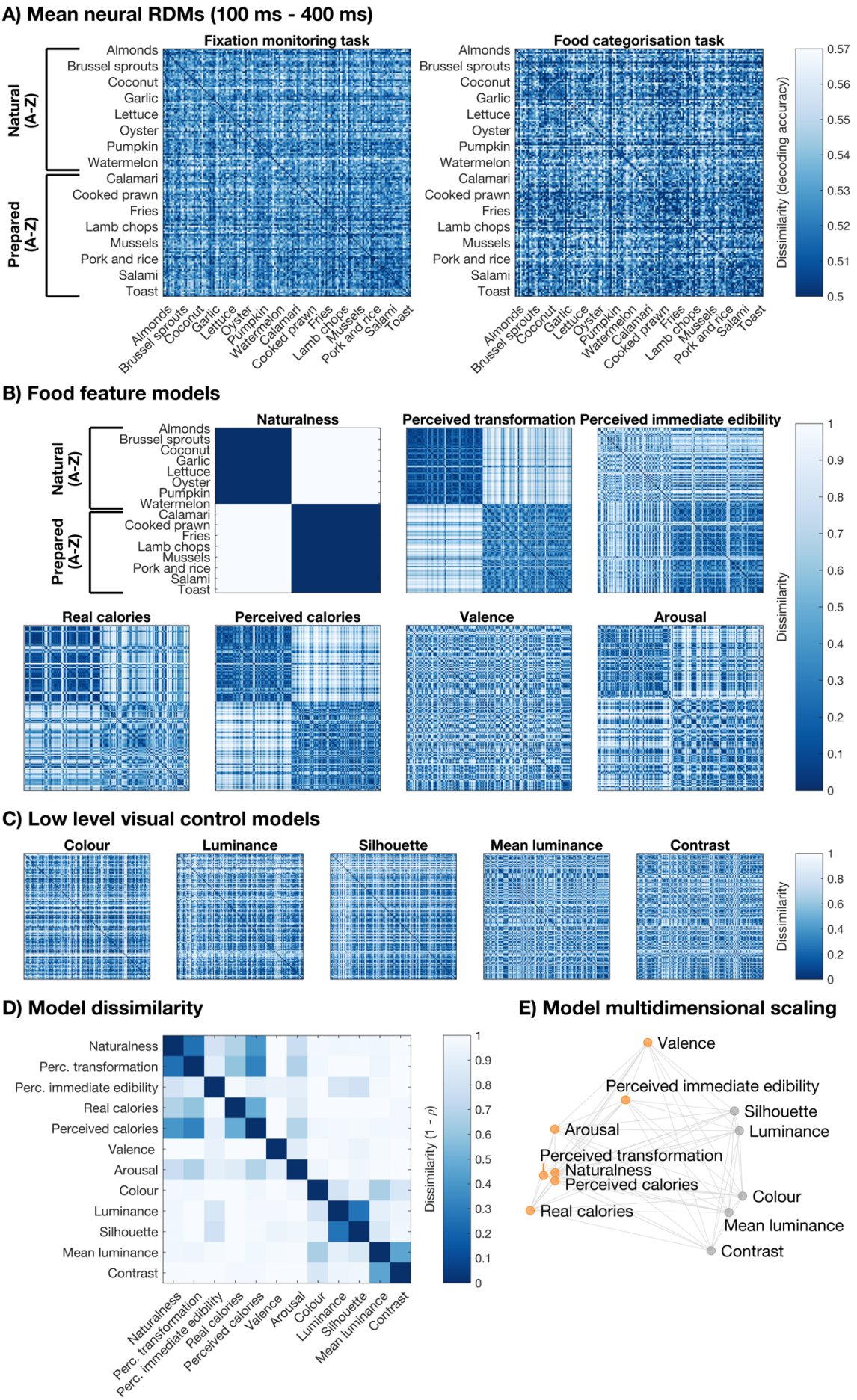
2.4. Decoding analysis

We determined *if* and *when* there was information in the EEG data about 1) whether an object is a food or non-food item, and 2) whether a food is natural or prepared. For these analyses, we used a linear discriminant analysis to distinguish the classes of interest for each timepoint, for each individual participant, using the CoSMoMVPA toolbox for Matlab (Oosterhof et al., 2016). For the EEG data obtained during the fixation monitoring task, we used a leave-one-block-out cross validation, where we iteratively trained on 5 blocks and tested on the left-out block. We used a leave-two-blocks-out cross validation procedure for the data obtained during the food categorisation task. Participants used button presses to indicated whether a food was natural or prepared during this task, which means that motor preparation or execution could contaminate the signal for this task. We left out two blocks with opposite response button mapping as test data, iterating over all 9 possible combinations of two test blocks with opposite button mapping.

To determine the time-course of the representation of edibility, we trained the classifier to distinguish food from non-food objects for each time point. This analysis was done for the fixation monitoring task only because non-food objects were not included in the food categorisation task condition. To determine the time-course of food naturalness representations, we trained the classifier to distinguish between natural and prepared food. We did this for both the fixation monitoring task and the food categorisation task. For the fixation monitoring task, only the food items were included. We balanced the classes of natural and prepared items. Decoding analyses were done separately for each individual participant, and Bayes factors were calculated at the group level.

198 **2.5. Representational similarity analysis**

199 To gain insight into what features of foods are represented in visual processing dynamics, we
200 used Representational similarity analysis (RSA) (Kriegeskorte et al., 2008; Kriegeskorte &
201 Kievit, 2013). RSA Representational Dissimilarity Matrices (RDMs) encode the dissimilarity
202 between two food items. We obtained an RDM based on the EEG data (see figure 2A) for
203 each time-point, individual participant, and for the two different tasks (fixation monitoring and
204 food categorisation). In the fixation monitoring task, we used only the food stimuli to construct
205 the RDMs. Pair-wise decoding was used as a measure of neural dissimilarity, computed using
206 the same decoding methods described above. We made seven models each describing a
207 feature of the foods: naturalness, perceived transformation, perceived immediate edibility, real
208 calories, perceived calories, valence, and arousal (Figure 2B). These models were computed
209 based on data included in FRIDa (Foroni et al., 2013). The naturalness and real calorie models
210 were based on objective values, whereas the other models were based on the subjective
211 behavioural ratings of 73 participants. The naturalness model coded for the dissimilarity in
212 whether the food was natural or prepared. The perceived transformation model coded for the
213 dissimilarity in the level of transformation required, as perceived by the participants. The
214 perceived immediate edibility coded for the dissimilarity in the amount of time and effort that
215 was perceived to be required before the food could be eaten. For example, an apple or
216 cupcake is immediately edible, whereas dried beans or uncooked pasta require time to
217 prepare. The real calorie model was based on the calorie content of 100g of the food. The
218 perceived calorie model was based on subjective behavioural ratings of the caloric content of
219 100g of the food. The valence model was based on how positive or negative the item
220 represented in the image was rated. Finally, the arousal model represents the emotional
221 salience of the items, as rated by the participants.


A) Mean neural RDMs (100 ms - 400 ms)
Fixation monitoring task
Food categorisation task
Natural (A-Z)
Prepared (A-Z)
Almonds
Brussel sprouts
Coconut
Garlic
Lettuce
Oyster
Pumpkin
Watermelon
Calamari
Cooked prawn
Fries
Lamb chops
Mussels
Pork and rice
Salami
Toast
Dissimilarity (decoding accuracy)
0.57
0.56
0.55
0.54
0.53
0.52
0.51
0.5
B) Food feature models
Naturalness
Perceived transformation
Perceived immediate edibility
Real calories
Perceived calories
Valence
Arousal
Dissimilarity
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
C) Low level visual control models
Colour
Luminance
Silhouette
Mean luminance
Contrast
Dissimilarity
1
0.8
0.6
0.4
0.2
0
D) Model dissimilarity
Naturalness
Perc. transformation
Perc. immediate edibility
Real calories
Perceived calories
Valence
Arousal
Colour
Luminance
Silhouette
Mean luminance
Contrast
Dissimilarity (1 - ρ)
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
E) Model multidimensional scaling
Valence
Perceived immediate edibility
Silhouette
Arousal
Luminance
Perceived transformation
Naturalness
Perceived calories
Colour
Real calories
Mean luminance
Contrast

222

Figure 2. Representational similarity analysis overview. A) Shows the representational dissimilarity matrix (RDM) for the EEG data for the fixation monitoring task (left) and the food categorisation task (right), averaged over a 100 ms to 400 ms time-window for visualisation. The RDM is a 154 by 154 matrix and each point codes for the dissimilarity between two food stimuli. The food items are ordered as follows: all natural foods in alphabetical order, followed by all prepared foods in alphabetical order. **B)** Shows the seven food feature model RDMs. All points in the RDMs refer to the same combinations of food items as A. The top row, from left to right, shows the naturalness model, perceived transformation model, and perceived immediate edibility model. The bottom row, from left to right, shows the real calorie model, perceived calorie model, valence model and arousal model. **C)** Shows the five low-level image feature control model RDMs. We used these models control for low-level visual differences between the groups of food stimuli. **D)** Shows the dissimilarity between all models: the seven food feature models and the five low-level image feature control models. The dissimilarity is calculated as 1 – the correlation (Spearman's ρ). **E)** Shows a 2-dimensional projection of all model dissimilarities. The distance between two models approximates their dissimilarity. The configuration was obtained through multi-dimensional scaling. The food feature models are shown in orange and the low-level image feature control models in grey.

For each time-point and individual participant, we correlated the EEG RDM with each of the seven food feature models. To account for low-level visual differences between the stimulus groups, we partialled out five low-level image feature control models from the correlations between the EEG and food models (Figure 2C). This included a silhouette model, a pixel-wise colour model, a pixel-wise luminance model, a mean luminance model and an RMS contrast model (see Moerel and colleagues (2022) for additional information about the models). The silhouette model, pixel-wise colour model, and pixel-wise luminance models are based on vectorised images. The silhouette model used the Jaccard distance between the binary alpha layer of each pair of images as a measure for dissimilarity. The pixel-wise colour model and pixel-wise luminance models were based on the CIELAB colour values and greyscale values respectively, using correlation as a distance measure. The mean luminance model and an RMS contrast model were based on a value calculated across the entire image (Harrison, 2022), using the mean greyscale values of the stimuli and the standard deviation of the greyscale values of the stimuli respectively, and the mean difference as a distance measure. Figure 2D shows the dissimilarity (1-correlation) between the seven food feature models and the five low-level image feature control models, and Figure 2E shows the multidimensional scaling of the model dissimilarities.

To determine if information about whether an object is a food could be driven by low-level visual differences between the stimulus groups, we made EEG RDMs for all stimulus items, food and non-food, presented in the fixation monitoring task. We correlated this to an

edibility model that coded for the dissimilarity in whether an item was a food or non-food object. We also ran a partial correlation, partialling out the 5 low-level image feature control models.

2.6. Investigating the link between brain and behaviour

The analyses described above can provide insight into which features of food stimuli are represented in the brain. To establish a link between the brain's representation and behaviour, we ran an online odd-one-out triplet experiment (Hebart et al., 2020) with new participants. We recruited 114 participants from the University of Sydney to take part in the triplet odd-item-out task. This sample of participants did not participate in the EEG experiment. The participants were healthy adults and received course credit for their participation. The study was approved by the Human Ethics Committee of the University of Sydney and all participants provided informed consent before participating. In this experiment, participants were presented with three food images on the screen and asked to select the odd-one-out, using any criteria. The advantage of the triplet odd-item-out task is that the third food acts as a context for other two foods, allowing us to determine which features are used to make a decision. This allows us to establish a behavioural model of human food discrimination that encompasses multiple features. We used the same 154 food images as in the EEG experiment. Participants completed 150 trials, and the experiment took approximately 35 minutes to complete. We constructed a behavioural similarity model, where similarity was measured as the probability of two foods being chosen together (i.e., if two foods were presented together, what was the probability that the third food was selected as the odd-one-out). We then correlated the behavioural similarity model to the EEG RDM, separately for each individual participant, time-point, and for the two different EEG tasks (fixation monitoring and food categorisation). Note that a subset of the possible combinations of triplets based on 154 items was tested for each participant. Each participant saw a unique combination of triplets, but even across participants it was not possible to test all triplet combinations. This means that a different number of observations contributes towards the dissimilarity score in each cell of the RDM, and 1.54% of cells have no observations. Hebart and colleagues (2020) recently showed that a sample of only 0.14% of possible triplet combinations contained enough information to reliably predict the entire RDM. The cells with no observations were excluded from the correlation analyses.

2.7. Statistical analysis

We used Bayesian statistics (Dienes, 2011; Kass & Raftery, 1995; Morey et al., 2016; Rouder et al., 2009; Wagenmakers, 2007) to assess whether there was evidence for above chance

decoding accuracies or for (partial) correlations different from 0. We used the Bayes Factor R package (Morey & Rouder, 2018) for all statistical analyses. We applied all statistical analyses at the group level.

For the decoding analysis, we used the same analysis for both the fixation monitoring and food categorisation tasks. We applied Bayesian t-tests for each time-point to determine the level of evidence in favour of chance decoding (null hypothesis) or above chance decoding (alternative hypothesis). We used a point null for the null hypothesis and a half-Cauchy prior for the alternative hypothesis to make the test directional (Morey & Rouder, 2011). The prior was centred around chance-level decoding (i.e. $d = 0$) and we used the default prior width of $d = 0.707$ (Jeffreys, 1998; Rouder et al., 2009; Wetzels et al., 2011). We excluded the interval between $d = 0$ and $d = 0.5$ from the prior to exclude small effect sizes, as these have been shown to occur at chance under the null hypothesis (Teichmann et al., 2022). We repeated this Bayesian t-test analysis for each time-point in the epoch.

For the representational similarity analysis, we used a Bayesian t-test for each time-point to test the (partial) correlation against 0. We applied the same Bayesian t-tests for the fixation monitoring task as well as the food categorisation task. We used the same point null as described above, and a full-Cauchy prior for the alternative hypothesis to test for both positive and negative correlations. We used the default prior width of 0.707 and excluded the interval between $d = -0.5$ and $d = 0.5$ from the prior for consistency with the t-test used for the decoding analysis.

Bayes Factors (BFs) above 1 show evidence in favour of the alternative hypothesis (above chance decoding or positive/negative correlation) and BFs below 1 show evidence for the null hypothesis (chance decoding or no correlation). $BF > 3$ or $BF < 1/3$ have been interpreted as weak evidence and $BF > 10$ or $BF < 1/10$ as strong evidence (Schmalz et al., 2020; Wetzels et al., 2011). Here, we use the second consecutive $BF > 10$ to define the onset time of above chance decoding.

3. RESULTS

3.1. Behavioural human food discrimination model

We used RSA to study what features humans use to discriminate food stimuli. We used behavioural responses from an odd-one-out triplet experiment, completed by a different group of participants, to make a behavioural RDM (Figure 3A). Importantly, the feature that was used to make an odd-one-out decision was not constrained, and participants could use any feature they wished to make this decision. To gain insight into the features that contribute to participant's odd-one-out decisions, we correlated the behavioural RDM with the seven food

feature model RDMs (Figure 2B) and the five low-level image feature control model RDMs (Figure 2C). Figure 5B shows the correlations between the behaviour and the food/visual models. All low-level image feature control models had relatively low correlations with the behavioural RDM, suggesting that participants did not often rely on visual differences between stimuli to make their odd-one-out decision. The highest correlations were between the behavioural RDM and perceived transformation, naturalness, and perceived calories. This suggests that participants often rely on one or more of these features to inform their odd-one-out decision. Note, these three food models are correlated (see Figure 2D and 2E), which means it is difficult to distinguish between these features in terms of the driver behind behavioural odd-one-out decisions.

3.2. The decoding of food and naturalness

To determine the time-course of the representation of visually presented food items in the brain, we decoded food vs. non-food object items for the fixation monitoring task. Participants passively viewed sequences of food and non-food object images at 6.67 Hz. Figure 4A shows the food decoding accuracy. There was information in the EEG signal about whether an object was food, starting around approximately 84 ms after stimulus onset with peak food decoding at approximately 228 ms. These results show that after approximately 84 ms, the brain encodes the distinction between food and non-food objects.

To determine whether this edibility distinction (i.e., food versus non-food objects) could be driven by low-level visual differences between the food and non-food objects, we correlated EEG RDMs with an edibility model, partialling out five low-level visual control models (Figure 4B). We found evidence for a full correlation between the EEG and edibility model from 116 ms onwards. When partialling out the low-level visual control models, we found evidence for a partial correlation between the EEG and edibility model from 132 ms onwards. From approximately 100 to 150 ms, there was a lower correlation between the EEG and edibility model when visual information was partialled out compared to the full correlation. This means that in this time window the edibility information could be partly driven by visual differences between food and non-food stimuli. However, there is some information about whether an object is edible, that is independent from the modelled visual differences between stimuli, from 132 ms onwards.

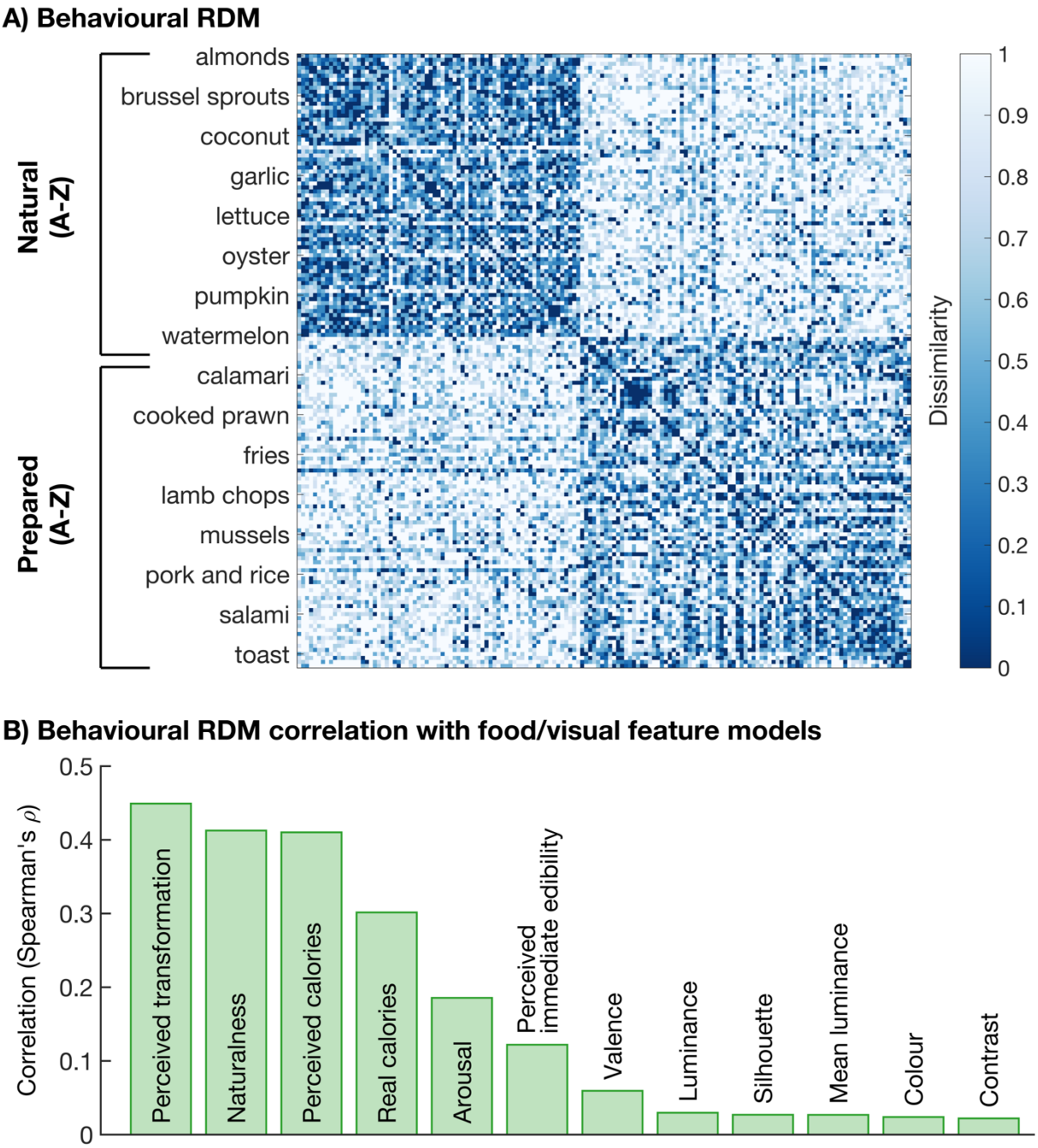


Figure 3. Behavioural human food discrimination model. A) Shows the behavioural RDM, based on the odd-one-out triplet task. Each point in the 154 by 154 RDM represents the dissimilarity between two food stimuli. The food items are ordered as follows: all natural foods in alphabetical order, followed by all prepared foods in alphabetical order. **B)** Shows the correlations between the behavioural RDM and the food/visual feature model RDMs. We included seven food feature models (see Figure 2B) and five low-level image feature control models (see Figure 2C).

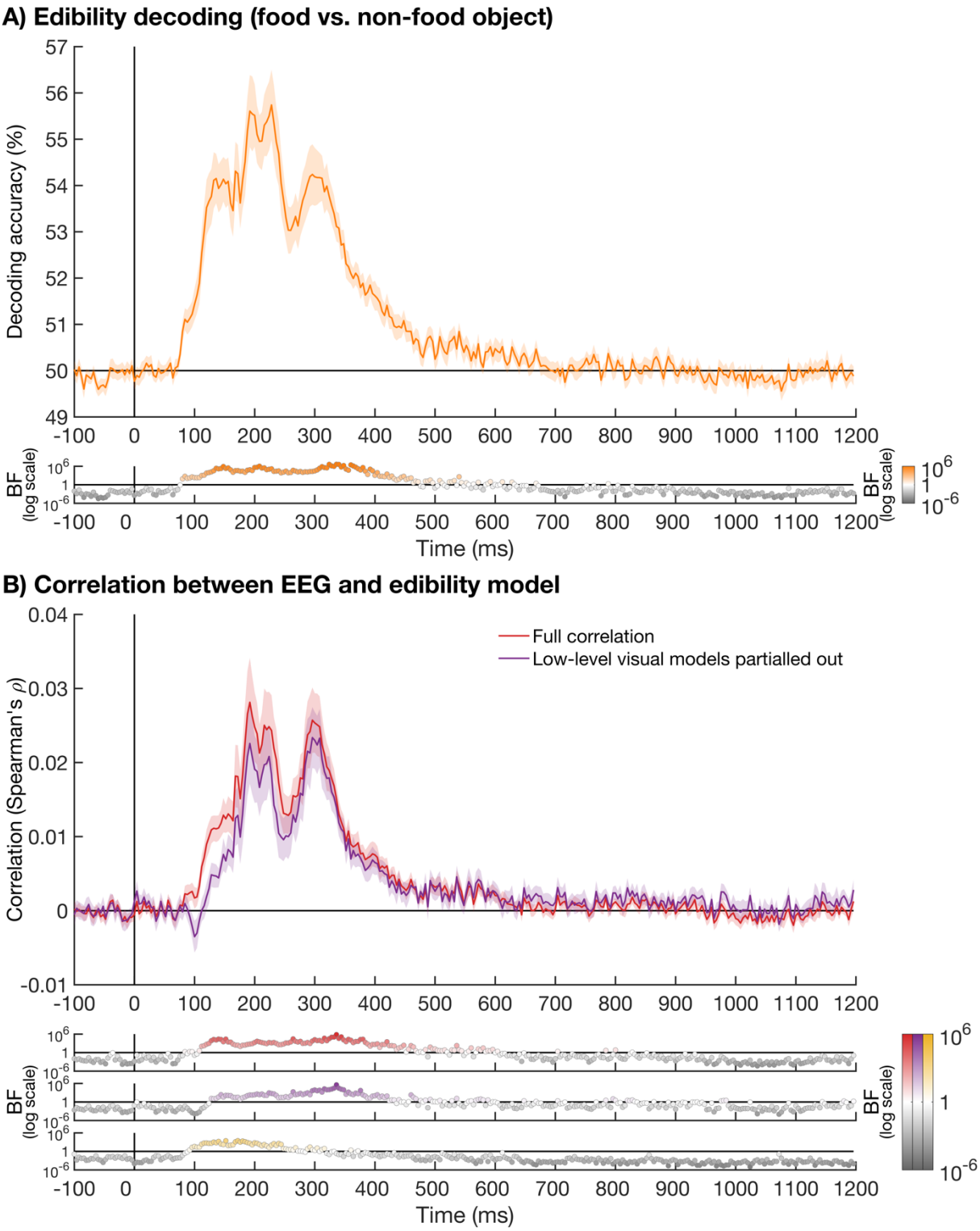


Figure 4. The time-course of food representation. The shaded area around the plot lines shows the standard error of the mean. The Bayes factors (BFs) are shown below the plots on a logarithmic scale. BFs > 1, plotted in the corresponding line colour, show evidence for above chance decoding and BFs < 1, plotted in grey, show evidence for chance decoding. White circles show insufficient evidence (BF close to 1). **A)** Shows the decoding accuracy of food vs. non-food object decoding over time. Theoretical chance is at 50% decoding accuracy. **B)** shows the correlation between the EEG RDMs and the edibility model over time. The red line shows the full correlation, and the purple line shows the partial correlation with the low-level

visual control models partialled out. The BFs are shown below the plot with those for the full correlation plotted in red (top panel) and those for the partial correlation plotted in purple (middle panel). The bottom panel shows the BFs for the difference between the full and partial correlation (yellow). This is based on a one-tailed test of full correlation > partial correlation.

To gain further insight into whether the naturalness distinction between foods is represented in the brain, we decoded natural vs. prepared foods for both the food categorisation and fixation monitoring tasks. For the food categorisation task, participants actively had to think about whether a food was natural or prepared. While in the fixation monitoring task, the food stimuli were not task relevant. The decoding accuracies are shown in Figure 5. For the food categorisation task, the naturalness of the food items could be decoded approximately 104 ms after stimulus onset, with peak decoding around 436 ms. For the fixation monitoring task, the naturalness of food could be decoded approximately 100 ms after stimulus onset, with peak decoding observed around 236 ms. These results show that food naturalness is represented in the brain, from a similar time, regardless of whether this distinction is task relevant. However, the coding of naturalness was sustained for longer when the participant had to make a decision about the naturalness of the food.

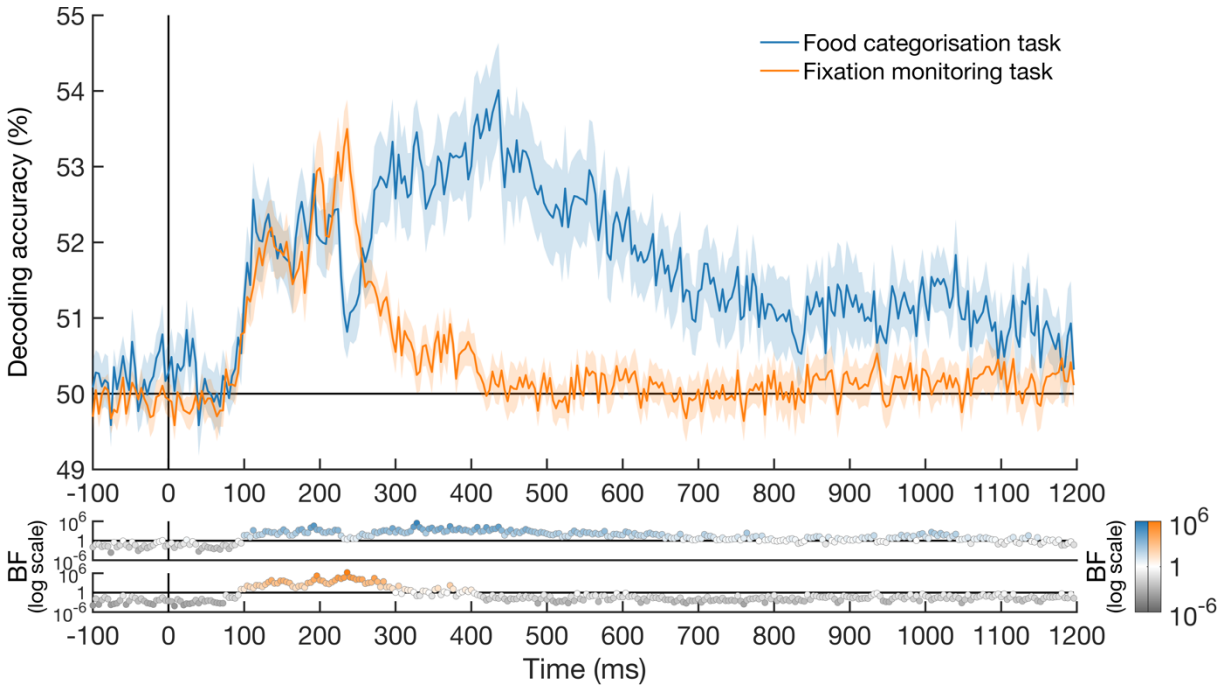


Figure 5. **The time-course of naturalness representation in food items.** The plot lines show the decoding accuracy for natural vs. prepared decoding for the food categorisation task (blue) and the fixation monitoring task (orange). Plotting conventions are the same as in Figure 4. The shaded area around the plot lines indicates the standard error of the mean, and 50% decoding accuracy is theoretical chance. Bayes factors are shown on a logarithmic scale below the plot. BFs > 1, indicating evidence for above chance decoding, are shown in the

corresponding plot colour: blue for the food categorisation task (top) and orange for the fixation monitoring task (bottom). BFs < 1, indicating evidence for chance decoding, are shown in grey.

Taken together, the decoding results show that whether an object is a food is represented in the brain from 80-90 ms after stimulus onset. In addition, the naturalness of a food item is represented from approximately 100-120 ms after stimulus onset. Interestingly, both types of information are represented when the food stimulus is not task relevant. However, it is still unclear whether additional features of food are represented in the brain. In the subsequent analyses, we used RSA to address this question.

3.3. Representation of food properties

We used RSA to determine which dimensions of food were represented in the EEG signal at each time-point. We correlated the EEG RDMs for the fixation monitoring and food categorisation tasks to seven different food models: naturalness, perceived transformation, perceived immediate edibility, calories, perceived calories, valence, and arousal. To minimise the potential contribution of low-level visual differences between the stimuli to these correlations, we partialled out five low-level visual models from the correlations; silhouette, luminance, colour, mean luminance, and RMS contrast (see methods). Figure 6 shows the partial correlation between the food models and the EEG data from the food categorisation task, controlling for the low-level visual models. There was evidence for a partial correlation (BF > 10) between the EEG and naturalness and perceived transformation, starting around 172 ms and 208 ms, and peaking around 444 ms and 432 ms, respectively. There was also evidence for a partial correlation between the EEG and the perceived immediate edibility model. This information emerged around 640 ms after stimulus onset, which is later compared to the onset of naturalness and perceived transformation information. Interestingly, there was evidence for no correlation with the *real* calorie content for most of the time-course except for a small window around 528 ms – 548 ms. However, there was evidence for a correlation with the *perceived* calories of the foods. Evidence for the correlation with the perceived calories emerged approximately 324 ms after stimulus onset, and the partial correlation peaked at 420ms. There was evidence for no partial correlation between the EEG and either valence or arousal. Note that the valence and arousal models were based on ratings from a different cohort of participants. This means these models might not have been a good fit between these groups. We explore this point further in the discussion.

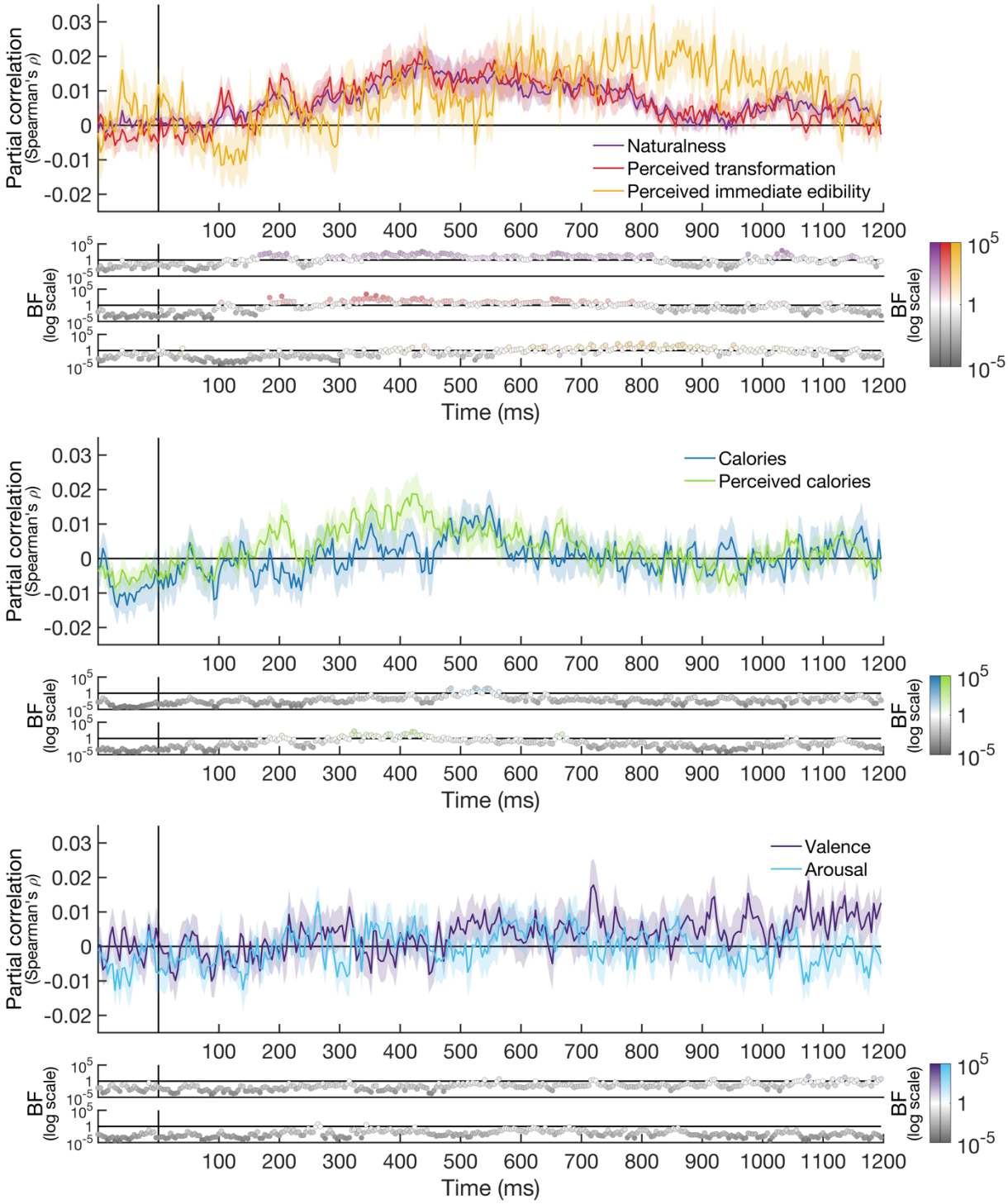


Figure 6. Partial correlations between the food feature models and the *food categorisation task* EEG. The five low-level visual models were partialled out. Plotting conventions are the same for all three panels. The top panel shows the partial EEG correlations with the naturalness model (purple), perceived transformation model (red), and perceived immediate edibility model (yellow). The shaded areas around the plot lines show the standard error of the mean. The Bayes Factors are shown below the plot on a logarithmic scale. BFs > 1 are shown in the corresponding plot colour: purple for the naturalness model (top), red for the perceived transformation model (middle), and yellow for the perceived immediate edibility model (bottom). They indicate evidence for a partial correlation. BFs < 1

are shown in grey and indicate evidence for chance decoding. The middle panel shows the partial correlations between the EEG and the real calories model (blue) and perceived calories model (green). The Bayes Factors are shown below for the real calories model (top) and perceived calories model (bottom). The bottom panel shows the partial EEG correlation with the valence model (purple) and the arousal model (light blue). The corresponding Bayes factors are plotted below for the valence model (top) and the arousal model (bottom).

The data show that the naturalness, perceived transformation, and perceived calories can explain part of the variance in the EEG data. However, it is unclear whether these findings are driven by the task, as participants were asked to report whether the food was natural or prepared, making the naturalness and perceived transformation dimensions task relevant. To determine whether the findings hold when the foods are not task relevant (and presented at a fast rate), we correlated the EEG for the fixation monitoring task with the food models, again partialling out low-level visual models (Figure 7). Overall, the pattern of results is similar to the active food categorisation results. There was a correlation between the EEG and 1) the naturalness model and 2) the perceived transformation model from approximately 132 ms and 120 ms after stimulus onset respectively, both peaking at 232 ms. Note this is slightly earlier compared to the food categorisation task. This difference between tasks likely is driven by differences in power, as there were 3 times more trials in the fixation monitoring task compared to the food categorisation task. Unlike the results for the food categorisation task, there was evidence for no partial correlation between the EEG and perceived immediate edibility for most of the time-course. As in the food categorisation results, the fixation monitoring results showed evidence for no partial correlation between the EEG data and the *real* calorie content, but there was evidence for a partial correlation between the EEG and the *perceived* calorie model. Evidence for the latter emerged approximately 136 ms after stimulus onset. Again, this is slightly earlier compared to food categorisation task, likely due to differences in statistical power between tasks. Finally, the valence model showed no evidence for a partial correlation with EEG for most time-points, with weak evidence in favour of a partial correlation (BF > 3) between 332 ms and 368 ms. There was evidence for no partial correlation between the EEG data and the arousal model. Taken together the results show that the naturalness, perceived transformation, and perceived calorie models explain part of the EEG variance from approximately 100 ms after stimulus onset, whereas the real calories, valence and arousal models have little to no explanatory power. This pattern of results holds regardless of whether the stimuli are task relevant, and when stimulus are presented at a rapid presentation rate (6.67 Hz). There was a late correlation between the EEG and perceived immediate edibility model, but this was only observed when the food was task relevant.

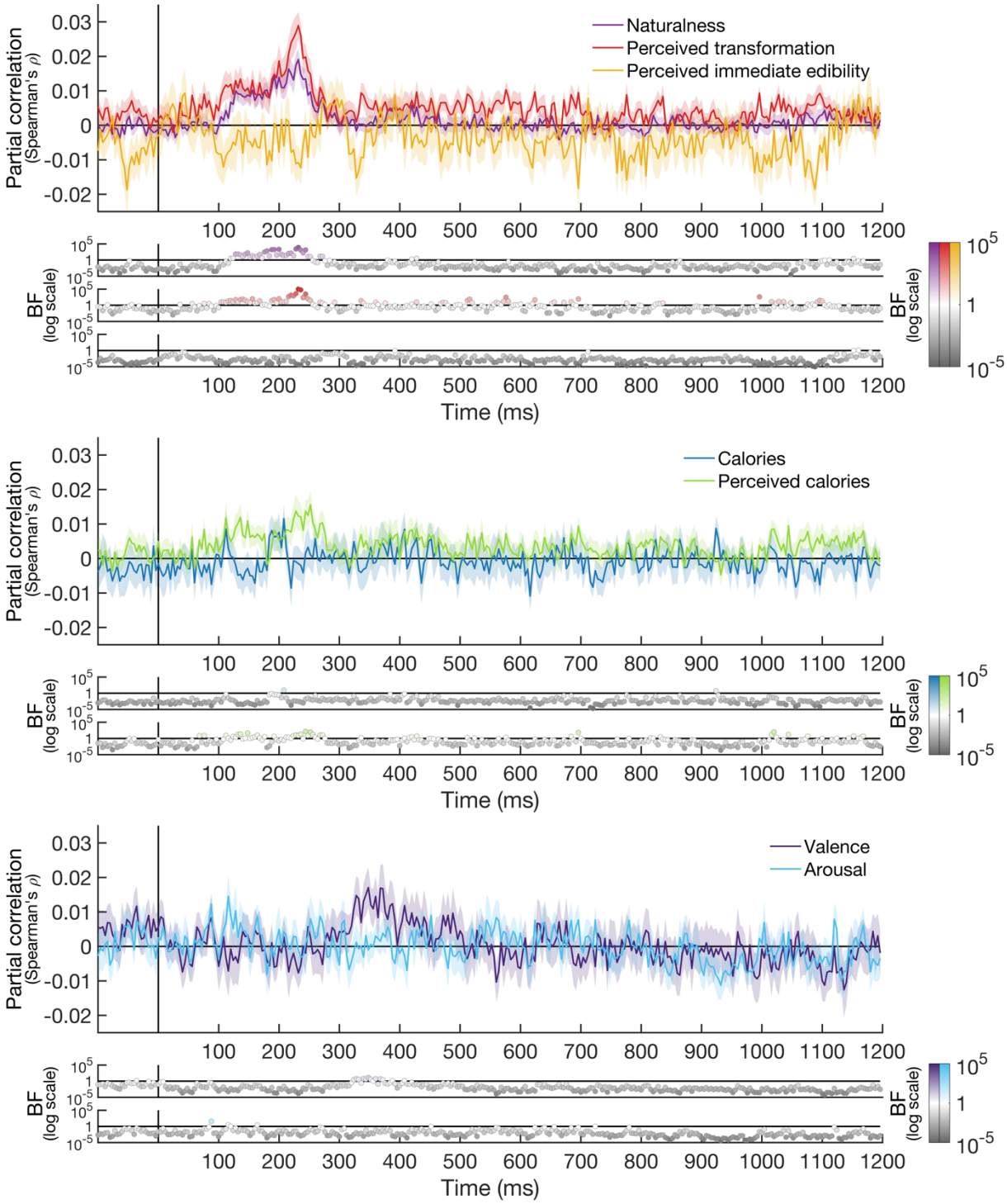


Figure 7. Partial correlations between the food feature models and the *fixation monitoring task* EEG. All plotting conventions are the same as in Figure 6.

3.4. The link between the neural representation of food features and behaviour

The results above elucidate the emerging representation of visually presented food stimuli. To establish a link between the neural representations and behaviour, we correlated the EEG with the behavioural RDM from the triplet data. Figure 8 shows the time-course of the correlation between the EEG for the two tasks and behaviour. There was a correlation between the EEG for the food categorisation task, where participants indicated whether a food was natural or prepared, and the behavioural RDM from approximately 168 ms onwards. Interestingly, there was also a correlation between the EEG data for the fixation monitoring task and the behavioural RDM, even though the food was not task relevant in the EEG task. This correlation emerged around 132 ms after stimulus onset, with a clear peak at 228 ms after stimulus onset. Together, this pattern of results suggests that the features that guide behavioural decisions are represented in the neural signal from approximately 100 ms onwards, regardless of whether or not attention is directed towards the food item.

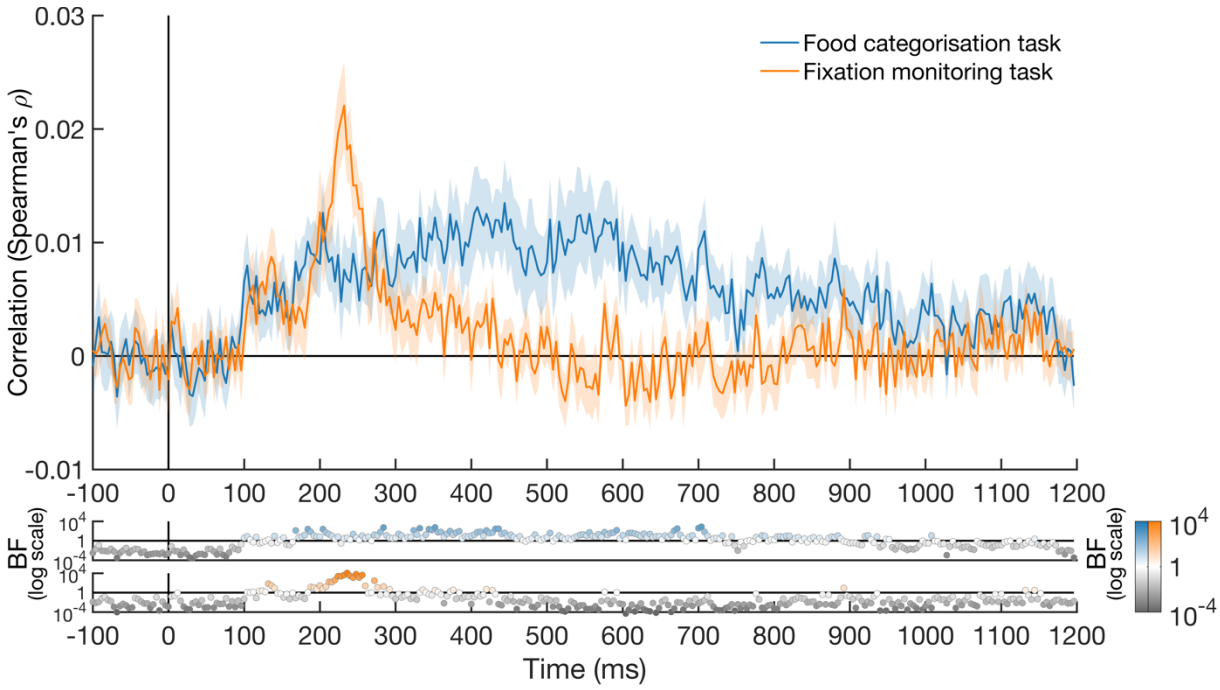


Figure 8. The correlation between the behavioural model RDM and the EEG for the two different tasks. The correlation with the EEG for the food categorisation task is shown in blue and the correlation with the EEG for the fixation monitoring (passive viewing) task is shown in orange. The shaded areas around the plot lines show the standard error of the mean. Bayes factors are shown below the plot. BFs > 1, are shown in blue for the food categorisation task (top) and in orange for the fixation monitoring task (bottom). BFs < 1 are shown in grey.

4. DISCUSSION

In this study, we used time-resolved multivariate analyses to explore the brain processing dynamics of visual food stimuli and asked whether the food item must be task relevant for the brain to represent food stimuli and features (e.g., perceived calories). Results indicate that the brain can distinguish between food and non-food items as early as 84 milliseconds after presentation. Additionally, the neural signal contained information about food naturalness, the level of transformation, and perceived caloric content, regardless of whether the food stimulus was task relevant, whereas perceived immediate edibility was only represented when the food was task relevant. In addition, the recorded brain activity corelated with the behavioural responses of a different group of participants in an odd-item-out task.

The finding that the brain represents edibility information is in line with previous work using fMRI (Avery et al., 2021; Chen et al., 2016; Jain et al., 2023; Khosla et al., 2022; Killgore et al., 2003; Rothemund et al., 2007; Simmons et al., 2005) and MEG (Stingl et al., 2010; Tsourides et al., 2016). For example, Tsourides and colleagues (2016) used multivariate methods on MEG data to show evidence for food vs. non-food information from 85 ms after stimulus onset. We found a remarkably similar onset time at 84 ms. In comparison to previous work, this study 1) actively cued attention away from the stimulus, and 2) presented images at a faster rate, therefore adding further evidence that the brain rapidly, and potentially automatically, makes this distinction. Notably, the onset time of edibility information occurs at a similar time as information about the object, high-level category and animacy (Carlson et al., 2013; Cichy et al., 2014; Contini et al., 2017; Grootswagers et al., 2019).

In addition to representing edibility information, our results show that the brain represents whether food is natural or prepared. This distinction emerged approximately 100-120 ms after stimulus onset, which is later than edibility, and was observed even when controlling for low-level visual information. This finding is consistent with previous EEG work that found differences in amplitude in response to natural compared to prepared foods (Coricelli et al., 2019; Pergola et al., 2017). However, previous work cannot establish whether there is information about naturalness in the brain. Our work builds on previous findings by showing that the brain represents information about food naturalness, regardless of whether the food was task relevant or not. Finally, this information was observed even when the stimuli were presented at a fast rate (6.67 Hz). These findings are consistent with rapid processing by the brain of naturalness information in visually presented food and suggest that the level of transformation is an important dimension along which the brain organises food representations.

In addition to representing the naturalness of food, our results show that the brain represents the energetic/caloric content of food. We observed partial correlations between the EEG and perceived calories, emerging around 136 ms after stimulus onset for the fixation monitoring task. This finding is in line with previous work from fMRI (Killgore et al., 2003; Mengotti et al., 2019) and EEG (Toepel et al., 2009), and suggests that this information could be represented automatically. Our study adds to previous work by showing that the brain represents information about the energetic/caloric content of the food. Interestingly, the EEG did not show reliable evidence for a correlation with the *real* caloric content of the food, except for a small window around 480-530 ms in the stimulus categorisation task. As the perceived calorie model is not based on the participants from the EEG task, it is therefore not personal biases in calorie perception, but rather generalisable ideas about energetic value of foods that are represented in the neural signal.

We also found evidence for information about the perceived immediate edibility of the food in the food categorisation task, although this information emerged much later compared to naturalness information. In addition, immediate edibility information was not found for the fixation monitoring task, where the food was not task relevant. These findings suggest that the coding of the perceived edibility of the food is not automatic and is only present when attention is oriented towards the food item. However, note that although the food is task relevant in the food categorisation task, the 'perceived immediate edibility' dimension itself is not relevant for the task, as participants are asked to rate whether the food is natural or prepared. The naturalness and perceived immediate edibility dimensions are not strongly correlated ($r = 0.19$), suggesting that attending to an unrelated feature of a food item is sufficient for the coding of perceived immediate edibility to occur.

Finally, our results showed that the brain did not reliably represent either valence or arousal. This finding does not seem consistent with that from Schubert and colleagues (2021), who found that information about the subjective tastiness (valence) could be decoded from 530-740 ms onwards, depending on the task. There are a few possible explanations for this apparent difference. First of all, the behavioural valence and arousal ratings in our task were based on a different cohort of participants, whereas this was not the case for the study by Schubert and colleagues (2021). It is possible that these subjective ratings did not transfer across participants. A larger range of food stimuli, including low valence / high arousal foods such as rotten foods, might tap into universal representations of valence and arousal. Alternatively, the lack of this information could also be driven by the internal state of the participant. Participants in the study by Schubert and colleagues (2021) were asked to fast for 4 hours before the study, whereas no specific instructions about fasting were given in this study. It is possible that temporary states, such as hunger, as well as longer-term differences, such as diet and body mass index, can mediate the coding of different food features. Future work can further investigate the degree of universality and individuality of the representation of food features in the brain.

We have shown that the brain rapidly represents various features of food, such as edibility, naturalness, and caloric content. To directly test whether this information is used by the brain to guide behaviour, we correlated the EEG with a behavioural RDM, based on a triple odd-item-out task done by a different group of participants. Our results showed that there was a correlation between brain and behaviour from 132-168 ms onwards. This means that the EEG signal from that time and later could predict the behavioural response of a different group of participants. This correlation was found for both EEG tasks, suggesting that the information about foods is used to guide decisions about the food. Interestingly, the features that were used most by participants to make an odd-one-out decision were naturalness/perceived transformation and perceived calories. These are also the features that are represented in the neural signal. In addition, because the EEG data was obtained from a different group of participants compared to the behavioural data, this suggesting a degree of universality in the features that guide food decisions. This adds further evidence to the importance of naturalness and energetic content in the perception of food.

While it is difficult to directly compare the coding of food naturalness information between the two different tasks, as the number of available trials differs, visual inspection shows a clear pattern. There is information about whether a food is natural or prepared between approximately 100 and 300 ms after stimulus onset, regardless of the task. However, after approximately 400 ms, this information is only represented when the food is task relevant.

This suggests that the early stage of food stimulus processing in the brain could be automatised and therefore unaffected by attention. However, note that the fixation monitoring task was not difficult, which means additional cognitive resources may have been available to participants to process features of the presented food. Future research could use a more difficult task to provide further evidence for the automaticity of the processing of food features. The extended representation of food naturalness when the observer must make a naturalness judgment could reflect the active representation of the relevant feature in short term memory and/or the decision the participant makes about this stimulus. Alternatively, there could have been masking due to the fast nature of the fixation monitoring task (Robinson et al., 2019). The prolonged coding of the attended stimulus is in line with previous attention work that showed initial representation of attended and unattended features, with extended representation of the attended feature only (Goddard et al., 2022; Grootswagers et al., 2021; Moerel et al., 2021; Moerel, Grootswagers, Robinson, Shatek, et al., 2022).

The findings from this study elucidate the time-course with which different food dimensions are represented in the neural signal. Whether an object is edible, along with information about the naturalness and perceived caloric content of the food are represented in a fast and seemingly automatic way in the brain. This suggests that these features are key organising principles in the representational structure of foods.

5. DATA AND CODE AVAILABILITY

The analysis code, figures, and an example dataset can be found via the Open Science Framework: https://osf.io/pwc4k. The full dataset will be made publicly available when the manuscript is accepted for publication.

6. ACKNOWLEDGMENTS

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