Electrophysiological evidence for enhanced representation of food stimuli in working memory

Short title: enhanced food representation in working memory

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Abstract

Studies from our laboratory have shown that, relative to neutral objects, food-related objects kept in working memory (WM) are particularly effective in guiding attention to food stimuli (Higgs et al. 2012). Here, we used electrophysiological measurements to investigate the neural representation of food vs. non-food items in WM. Subjects were presented with a cue (food or non-food item) to either attend to or hold in WM. Subsequently, they had to search for a target, while the target and distractor were each flanked by a picture of a food or non-food item. Behavioural data showed that a food cue held in WM modulated the deployment of visual attention to a search target more than a non-food cue, even though the cue was irrelevant for target selection. Electrophysiological measures of attention, memory and retention of memory (the P3, LPP and SPCN components) were larger when food was kept in WM, compared to non-food items. No such effect was observed in a priming task, when the initial cue was merely identified. Overall, our electrophysiological data are consistent with the suggestion that food stimuli are particularly strongly represented in the WM system.

Highlights

- Food-related objects kept in working memory are particularly effective in guiding attention to food stimuli
- Electrophysiological measures of attention and memory were larger for food versus non food cues
- Food cues are better maintained in working memory than non-food cues, perhaps because of their rewarding properties

Keywords: Attention, working memory, food and non-food cues, long-latency ERPs

1. Introduction

In our current obesogenic environment food cues are found all around us; from shop displays and television adverts, to pictures of food and eating in magazines. Though the abundance of food cues is not in itself problematic, heightened attention to food cues has been shown to enhance motivation to consume foods (Fedoroff et al. 1997; Loxton et al. 2011) and to predict weight gain (Calitri et al. 2010; Yokum et al. 2011), with attentiveness to food cues being particularly marked in obese children and adults (Braet and Crombez 2003; Castellanos et al. 2009; Nijs and Franken 2012). However, despite its potential importance, we lack detailed understanding of the mechanisms that determine heightened attention to food. The present study represents an attempt to do this using evoked response data.

Previously, we have reported that food directs attention in a top-down manner, via its representation in working memory (WM). We found that, in lean subjects, deliberately holding food items in WM is particularly effective in guiding attentional selection when food stimuli are re-presented in a display - with WM-based guidance of attention from food being stronger than the guidance from neutral stimuli (Higgs et al. 2012; Rutters et al. 2013). In these experiments, participants were presented with a food or non-food (neutral) cue to either attend to or hold in WM, and subsequently they had to search for a shape target (cf. (Soto et al. 2005)). The cue could re-appear in the search display either alongside the search target (valid trials) or a distractor (invalid trials). In addition, there were neutral trials, in which the cue did not re-appear. Reaction times were strongly affected by the re-appearance of a food cue, but only when the cues were held in WM rather than merely being attended to, as shown in the priming condition, designed to match the visual sequence used in the WM condition.

The results from our behavioural studies indicate that a food cue in WM exerted a strong effect on search, when compared with neutral cues, and this was not driven by the initial appearance of the cue alone (in the priming condition) (Soto et al. 2005; Soto and Humphreys 2007; Soto et al. 2008; Higgs et al. 2012; Rutters et al. 2013). These data suggest that attentional biases towards food cues can be

mediated by holding food-related information in WM, which in turn guides attention to food-related items in the environment (Higgs et al. 2012).

Here we assessed how the representation of food items in WM modulates attentional bias to food, using electroencephalography (EEG) to examine the time course of stimulus coding in memory and attention. Several studies have investigated the electrophysiological correlates of heightened attentiveness to motivational stimuli, including food cues (Leland and Pineda 2006; Nijs et al. 2008; Stockburger et al. 2008; Babiloni et al. 2009; Nijs et al. 2009; Stockburger et al. 2009; Toepel et al. 2009; Stingl et al. 2010; Svaldi et al. 2010). Only two studies have observed early stage Event Related Potential (ERP) differences between food and non-food items (Stockburger et al. 2008; Stingl et al. 2010), while the majority reported differences in long-latency ERPs (Stockburger et al. 2009; De Pascalis et al. 2010; Eimer and Kiss 2010; Stingl et al. 2010; Eckstein 2011; Yu et al. 2011). Long-latency ERPs are generally thought to represent high-level processes reflecting decision making, memory, reward, motivation, and emotion (Stockburger et al. 2009; De Pascalis et al. 2010; Eimer and Kiss 2010; Stingl et al. 2010; Eckstein 2011; Yu et al. 2011). The three most often studied long-latency ERPs are P300 (P3), the Late Positive Potential (LPP) and the Sustained Posterior Contralateral Negativity (SPCN).

The P3 component is a postive peak that emerges at circa 300 ms after stimulus onset, and is located all over the scalp, with maximal amplitudes in the parietal scalp area (Picton 1992). This component is the first of the so-called endogeneous ERPs that is larger when processing emotional or motivationally relevant stimuli and typically taken to reflect attentional, mnemonic and evaluative processing of stimuli (Friedman and Johnson 2000; Stockburger et al. 2009; De Pascalis et al. 2010; Eckstein 2011; Yu et al. 2011). The LPP component follows the P3 component and is defined as the late positive ERP deflection that occurs 500 ms post stimulus, over the centro-parietal regions (Schupp et al. 2006). This component is thought to represent conscious stimulus recognition, the focussing of attention on a stimulus, and elaborated stimulus analysis, and it is larger for motivationally relevant stimuli than neutral stimuli. The LPP component is also thought to reflect

memory updating, memory load and stimulus maintenance in WM (Picton 1992; Friedman and Johnson 2000; Schupp et al. 2000; Citron 2012; Littel et al. 2012). The SPCN amplitude, which is also called the Contralateral Delay Activity (CDA) (Vogel and Machizawa 2004), is calculated by subtracting ipsilateral activity form contralateral activity relative to the target after about 500 ms post stimulus (Vogel and Machizawa 2004; Eimer and Kiss 2010; Eckstein 2011). The SPCN is often referred to as a long-latency marker for the retention of visual short-term WM. It is larger for more complex patterns and emotionally laden objects, and it returns to baseline sooner for the shorter retention intervals (Holmes et al. 2009; Perron et al. 2009).

Up until now, ERP studies examining the differences between food and non-food stimuli have shown increased P3 and LPP amplitudes for food compared to non-food cues, while no studies have investigated the SPCN amplitude (Leland and Pineda 2006; Nijs et al. 2008; Nijs et al. 2009; Stockburger et al. 2009; Toepel et al. 2009; Nijs et al. 2010a; Svaldi et al. 2010). These findings suggest increased attentional, mnemonic and evaluative processing of food stimuli, as well as increased memory updating, memory load and stimulus maintenance in WM of food stimuli. However, these earlier ERP studies have used several different paradigms to compare food versus non food items, ranging from simple tasks in which subjects only have to look at the presented pictures, to Posner, Stroop, and one-back tasks in which subjects have to attend to and memorize stimuli (Leland and Pineda 2006; Nijs et al. 2008; Nijs et al. 2009; Stockburger et al. 2009; Toepel et al. 2009; Nijs et al. 2010a; Svaldi et al. 2010). In these paradigms it is difficult to identify exactly which cognitive process, of the many potentially involved, is modulated by food. For example, under passive viewing conditions participants may represent the items in WM, and so any effects could reflect the status of the items in WM.

In the present experiment, we will examine long-latency ERPs in the WM-based attentional guidance paradigm previously employed (Higgs et al. 2012). This paradigm is useful because it enables us to assess whether the long-latency ERPs modulated by food are affected by factors such as memory or merely attending to the picture. The WM-based guidance paradigm has been examined once before in

an ERP study, but there was no examination of different cue types (Kumar et al. 2009). In the present study, for the first time, we directly compare food and non-food cues and examine the modulatory effects of food on late acting ERP components, to provide us insight into the electrophysiological correlates of food-related memory coding and attention.

2. Materials and Methods

2.1 Participants

Sixteen students (8 females and 8 males) from the School of Psychology of the University of Birmingham took part in this experiment for either course credits or cash. Their mean age was 23 years (range 19-38 years) and their mean body mass index (BMI) was 24.8 kg/m^2 (range 18.0 – 34.6 kg/m^2), with 50% of the subjects being overweight. All participants had normal to corrected-to-normal-vision. Written informed consent was obtained from all participants. The study was approved by the Ethics Committee of the University of Birmingham, and conformed to the Declaration of Helsinki.

2.2 Tasks

There were two tasks, the priming and working memory tasks, in which we varied the instructions regarding the initial cue presented on each trial. In the priming task, participants were asked to attend to the cue but not to hold it in memory. On a small proportion of trials (20%), the priming cue disappeared and was replaced by a different image. On these priming probe trials participants were instructed not to carry out the search task that normally followed the initial cue. This ensured that participants attended to the cue. In the WM task participants were asked to hold the cue in memory across the trial, for a subsequent memory test on a minority of occasions (again 20% of the trials; see **Figure 1a**). On these memory probe trials, the search display that followed the initial cue was followed by a visual memory probe for 3000ms, which could correspond to the object being held in WM or to another object. Participants made a same or different judgement as to whether the cue and the memory item were the same. The priming and WM tasks were completed in a counterbalanced order. The priming task consisted of 1945 trials, taking about 120 minutes, and the WM task consisted of 1500 trials, and took 106 minutes to complete. The trials were divided into smaller blocks of about 150 trials, after which the subject had a few minutes rest. Each trial started with presentation of the cue for 500ms. The cue was either a picture of a food item, a car, or a stationery item, and 10 different pictures per category were used during both the priming and WM tasks. All pictures were presented in black and white, sized 480 x 480 pixels, and appeared in the middle of the screen with a black background. The cue was followed by a 200 to 1000ms blank interval with a fixation cross. After the interval, a search screen was presented with a target (circle) and a distractor (square) randomly to the

left or right of fixation for 800ms. Participants had to press 'c' if the circle appeared on the left and 'm' if it appeared on the right, with the maximum response time set at 1200ms. The target and the distractor were each flanked by a picture of a food item, or non-food item (a car or stationery item). The search screen was followed by a 400ms blank interval with a fixation cross, and the inter-trial interval was 600ms.

There were three conditions in which the relations between the initial cue and the search display were varied: 1) on valid trials, the target in the search display was flanked by an image that was the same as the cue and the distractor was flanked by an image from one of the other cue categories, 2) on invalid trials, the distractor was flanked by an image that was the same as the cue and the target was flanked by an image from one of the other cue categories, 3) on neutral trials both the target and distractor were flanked by images from categories different from the cue. For example, in the neutral food trial the cue would be a food item and in the search display but the target and the distractor would be flanked by a stationery item or car picture (see **Figure 1b** for an example of the WM task, representing valid, neutral, and invalid trials for food cues). The conditions occurred randomly with equal probability. Trials with incorrect responses to the search task, catch trials, and the memory task, as well as reaction times (RTs) that were +/- 3 standard deviations from the mean, were removed. In both the priming and WM task, the accuracy for the search task was high; an average of 93% correct. In the priming task, responses on catch trials were withheld as instructed; an average of 92% correct, and in the WM task, responses to the memory task were correct in 87% of all cases. There was no evidence of a speed–accuracy trade off.

2.3 Apparatus

Stimuli were presented using E-Prime (Version 2.0– Psychology Software Tools) on a Pentium IV computer with an ATI RAGE PRO 128-MB graphics card, displayed on a SyncMaster 753s colour monitor (SAMSUNG, Seoul, Korea). The monitor resolution was 1024 x 768 pixels and the frame rate was fixed at 85hz.

2.4 Procedure

Participants consumed their regular breakfast half before the start of the study and the other half during the larger 15 minute break. Aspects of appetite were assessed using 100 mm visual analog scales (VAS) with questions about feelings of hunger, satiety, thirst, and desire to eat. Opposing extremes of each feeling were described at either end of the 100-mm horizontal line, and subjects marked the line to indicate how they felt at that moment. Completion of the VAS questionnaire took our experienced subjects about 1 minute. During the protocol, appetite profiles were assessed twice: before and after performing both tasks. The mean feelings of hunger were pre 13.6±13 and post 40.8±29 ($p<0.05$), for satiety pre 62.4±22 and post 38.4±30 ($p<0.05$), for thirst 31.8±22 and post 47.8±22 ($p<0.05$) and for desire to eat pre 14.5±14 and 44.6±29 ($p<0.05$). However, the task order was counterbalanced, which makes it unlikely that changes in motivational state influenced the outcome. Participants completed the priming and working memory (WM) tasks in counterbalanced order, with an option of a 15-minute break between tasks. Before leaving, participants had their height (cm) and weight (kg) measured.

2.5 Electroencephalogram data processing

Electroencephalogram (EEG) recordings for each participant were taken continuously with Ag/AgCl electrodes from 128 scalp electrode locations. The electrodes were placed according to the 10-5 electrode system (Oostenveld and Praamstra 2001) using a nylon electrode cap. A unipolar electrode placed at the infra-orbital area of the left eye monitored vertical eye movements, and a bipolar electrode placed at the outer canthus of the left and right eyes monitored horizontal eye movements. Additional electrodes were used for references and ground. EEG and electro-oculogram signals were amplified (BioSemi ActiveTwo, Amsterdam, the Netherlands) and sampled at 512 Hz. The continuous EEG recordings were off-line referenced to the average of the left and right mastoids and band pass filtered between 0.5 and 30 Hz. Continuous EEG signals were segmented into epochs from 200 ms before search task onset to 900 ms after search task onset for each of the conditions for each subject. The 200 ms prior to the onset of the search task was used as a baseline, and the EEG signals reported have been calculated relative to this baseline activity. Epochs were rejected if the voltage in horizontal eye electrodes exceeded ±60 and ±100 μV in any other electrodes. The EEG data of one participant was discarded because of excessive horizontal eye-movement. Since our focus was to understand the electrophysiological correlates of identifying or holding a cue in WM on its

subsequent coding, we focussed on the long-latency ERPs P3, LPP, and SPCN components occurring after the onset of the search display. The maximum positive deflections in the time windows of 250-450 ms and 460-660 ms were defined as the P3 and LPP respectively, both showing a posterior distribution. The negative deflection around 700-850 ms post-stimulus at posterior sites, contralateral to the evoking stimulus, was defined as the SPCN. The SPCN was computed by subtracting ipsilateral activity form contralateral activity relative to the target.

Further analyses were restricted to regions that showed the highest activity for the particular component of interest. The electrode with the highest activity was identified through visual inspection of the current source density (CSD) map of the grand average waveform. Electrical activity on the four electrodes surrounding the electrode with the highest activity of the particular component was then averaged for each time-point in the epoch interval, to generate a region-specific analysis. The same electrode combinations were then chosen on the contralateral side of the identified region for the particular component. The following electrodes were taken as representing left and right hemispheric activity for the P3 and LPP components: P1, PPO1h, CPP1h, CPP3h, PPO3h and P2, PPO2h, CPP2h, CPP4h, PPO4h. The SPCN component was analysed at the pooled five posterior and lateral occipital electrodes: PPO5h/PPO6h, PO5h/PO6h, PO3h/PO4h, O1/O2, and PO7/PO8 based on the SPCN CSD map where the source of the SPCN activity was observed across the conditions.

2.6 Statistical analyses

Statistical analyses were performed with SPSS version 20.0 (SPSS Inc., Chicago, IL). Continuous data were presented as means ± standard deviation (SD) or standard error of the mean (SEM). Firstly, using repeated-measures ANOVAs, we analysed interactions and differences in reaction times (RTs) (ms) for tasks (WM, priming), trials (valid, neutral, invalid) and cues (food vs. non-food items). Secondly, we assessed the food advantage scores (%RT for [Non-food minus food]/Non-food) for the priming and WM tasks and compared them using paired t-tests. Thirdly, again using repeated-measures ANOVAs we analysed interactions and differences in all three ERP components (mean amplitude) for tasks (WM, priming), hemisphere (left, right), trials (valid, neutral, invalid) and cue (food vs. non-food items). Finally, we used repeated-measures ANOVAs to analyse possible

interaction effects for weight status (BMI > 25 kg/m^2) or hunger scores (median split change in hunger score) and tasks (WM, priming), trials (valid, neutral, invalid) and cue (food vs. non-food items) for all three ERP components.

3. Results

3.1 Reaction times

Mean reaction times (in milliseconds) to the target next to the food or non-food cues for Valid, Invalid, and Neutral trials, for both the Priming and the Working Memory tasks, are presented in **figure 2**. We carried out a 2 X 3 X 2 repeated-measures ANOVA with the factors being task (priming vs. WM task), validity (valid, invalid, neutral trials), and cue (food vs. non-food items). Firstly, we observed several main effects; RTs were slower in the WM task than the priming task ($F(1, 14) = 10.44$; $p < 0.006$, $\eta p^2 = 0.4$), consistent with the greater cognitive load during the WM task (see Soto et al., 2005 (Soto et al. 2005)). There was a main effect of validity ($F(2, 28) = 60.9$; $p < 0.000$, $\eta p^2 = 0.8$), whereby RTs were faster for the valid trials than the neutral and invalid trials, and RTs for the neutral trials were faster than the invalid trials (all $p < 0.05$). There was also a main effect of cue ($F(1, 14) = 5.6$; $p < 0.03$, $\eta p^2 = 0.3$); RTs following the food cues were faster than RTs following the non-food cues.

The three-way interaction between task, validity, and cue ($F(2, 28) = 1.96$; $p = 0.16$ $\eta p^2 = 0.1$), and the two-way interaction between task and cue were not significant ($F(1, 14) = 1.3$; $p = 0.27$ $\eta p^2 = 0.8$). We did observe a significant two-way interaction between task and validity ($F(2, 28) = 21.5$; $p < 0.001$ $\eta p^2 = 0.6$); RTs were faster for valid trials compared to invalid trials ($p < 0.001$), and to neutral trials ($p<0.001$) in the WM task. We observed a similar pattern in the priming task, however the effect was smaller, and only the difference between valid and neutral trials was reliable ($p < 0.05$). Additionally, we observed a significant two-way interaction between validity and cue ($F(2, 28) = 47.8$; $p < 0.001$ $\eta p^2 = 0.8$); RTs were faster following food cues compared to non-food cues in the valid trials ($p<0.001$), but not in the invalid ($p=0.7$) or neutral trials ($p=0.9$). Though there were trends for interactions of cue and task (WM vs. priming), these were not reliable, possibly because the relatively long cue-search display interval allowed all cue types to be consolidated in WM.

However, given our prior results and the a priori prediction, we assessed the food advantage scores (%RT for [Non-food minus food]/Non-food) for the priming and WM tasks. This food advantage

score provides an index of the effectiveness of the food cues in guiding attention. We observed a larger food advantage in the WM task compared to the priming task in the valid trials (3.9±1.6 vs. 2.4±1.6 %, P<0.002), while no significant differences were observed in the neutral (0.6±1.6 vs. 1.0±2.1%, P=0.61) and invalid (-2.0±2.2 vs. -1.9±3.0%, P=0.89) trials. Our results suggest that, compared to the priming condition, RTs were faster following food cues than non-food cues when they re-occurred and matched the flanked image in the WM task.

3.2 Electroencephalography data

To evaluate the long-latency ERPs responses to holding food or non-food information in WM vs. merely attending to these stimuli, we compared the effect of cue type, validity and tasks on the mean amplitudes of the P3, LPP and SPCN components (**Table 1**). First, we carried out a 2 x 2 x 3 x 2 repeated-measures ANOVA with the factors being task (priming, WM), hemisphere (left, right), validity (valid, neutral and invalid trials), and cue (food, non-food) for the P3 component (mean amplitude between 250 to 450 ms). We observed a reliable main effect of validity ($F_{2,28} = 16.9$, $P = 0.001$ $\eta p^2 = 0.6$); the P3 component was larger in the neutral trials compared to the valid and invalid trials. Furthermore, we observed an interaction between task and cue ($F_{1,14} = 4.4$, $P < 0.04$ $\eta p^2 = 0.3$); the P3 component was larger in response to the food compared to the non-food cue in the WM task ($P < 0.03$), while it was not different from the non-food cue in the priming task ($P = 0.67$) (**Figure 3**). There were no main effects on the P3 component of task, hemisphere or cue type (food vs. non-food cues) and there were no additional interaction effects (P>0.1).

Second, we carried out 2 x 2 x 3 x 2 repeated-measures ANOVA with the factors being task (priming, WM), hemisphere (left, right), validity (valid, neutral and invalid trials), and cue (food, non-food) for the LPP component (mean amplitude between 460-660 ms). We observed a reliable interaction between task and cue ($F_{1,14} = 6.7$, $P < 0.03$ $\eta p^2 = 0.3$); the LPP component was larger in response to the food compared to the non-food cue in the WM task (P<0.01), while there was no reliable effect in the priming task ($P = 0.45$) (**Figures 3 & 4**). There were no main effects on the LPP

component for the effects of task, validity, hemisphere or cue type (food vs. non-food cues) and there were no additional interaction effects (P>0.1).

Third, we carried out 2 x 3 x 2 repeated-measures ANOVA with the factors being task (priming, WM), validity (valid, neutral, invalid), and cue (food, non-food) for the SPCN component (mean amplitude between 700 to 850 ms). We observed an effect of validity ($F_{1.14} = 9.46$, $P < 0.001$ $\eta p^2 = 0.4$); the SPCN component was smaller on neutral trials than on the valid and invalid trials. Additionally, we observed a two-way significant interaction between task and validity ($F_{1.14} = 11.4$, $P = 0.001$ $\eta p^2 = 0.4$); the SPCN component was smaller on neutral trials than on the valid and invalid trials in the WM task (P<0.001); no such effect was observed in the priming task (P=0.28). Finally, we observed a two-way significant interaction between task and cue ($F_{1.14} = 4.56$, $P = 0.05$ $\eta p^2 = 0.3$); there was an overall effect of cue in the WM task, the SPCN component was larger in response to the food compared to the non-food cue in the WM task ($P < 0.001$), while there was no reliable effect in the priming task ($P = 0.19$) (**Figure 5**). There were no main effects on the SPCN component for the effect of task or cue type (food vs. non-food cues) and no additional interaction effects (P>0.1).

Finally, we carried out a 2 x 3 x 2 x 2 repeated-measures ANOVA for the P3 and LPP components as well as a 2 x 3 x 2 repeated-measures ANOVA for the SPCN components with weight status (BMI > 25 kg/m^2) and hunger scores (median split change in hunger score) as between subject factors. Overall, we observed no interaction effects of weight status (P>0.1) or hunger scores (P>0.1) for the P3, LPP or SPCN component.

4. Discussion

The aim of our current study was to assess the electrophysiological correlates of food-related memory coding in memory and attention. Our behavioural data replicate earlier reported findings (Higgs et al. 2012; Rutters et al. 2013); a food cue held in WM modulated the deployment of visual attention to a search target more than non-food cues. This led to a larger food advantage on valid trials in the WM condition compared with the priming condition, while effects on neutral and invalid trials did not differ for food relative to non-food stimuli in the WM and priming conditions. In contrast, there were no behavioural effects of cue type when food or non-food stimuli had to be identified but not held in WM, in the priming task (Higgs et al. 2012; Rutters et al. 2013). These findings support our hypothesis that the processing of food-related information in WM is particularly effective for deploying attention to food stimuli, even when there are no differential bottom-up signals favouring food items.

To elucidate the mechanisms that underlie WM-based guidance of attention by food items, we studied differences in long-latency ERPs for food and non-food cues being held in WM or merely being attended to. We discuss only the ERP results that are relevant to our hypothesis, thus omitting our findings regarding validity as well as validity and task interactions, which have been previously been discussed (Kumar et al. 2009). Our main finding was the interaction between task and cue, which was present in all three components of interest: the P3, the LPP and the SPCN. All three components were larger when food items were held in WM compared to non-food items and no such effect was observed in the priming task. The three ERP components have been associated with different underlying processes: the P3 with attention, mnemonic and evaluative processing (Friedman and Johnson 2000; Stockburger et al. 2009; De Pascalis et al. 2010; Eckstein 2011; Yu et al. 2011) the LPP with memory (Picton 1992; Friedman and Johnson 2000; Schupp et al. 2000; Citron 2012; Littel et al. 2012) and the SPCN with the retention of information in visual short-term WM (Eimer and Kiss 2010; Eckstein 2011). Overall, the long-latency ERP components seem to reflect stronger representation of food in WM, implicating food cues are held in the forefront of WM more easily, perhaps because of their having intrinsic rewarding properties.

In previous studies using food versus non-food attention tasks, it is difficult to know exactly which processes are differentially activated by the cues; attention and/or memory. Using our paradigm enabled us to assess both processes separately. Previous studies showed similar differences in P3 and LPP components when they used tasks placing demands on memory, including one-back matching, counting task, oddball detection, Stroop and Posner cueing (Leland and Pineda 2006; Babiloni et al. 2009; Nijs et al. 2009; Nijs et al. 2010a; Nijs et al. 2010b; Stingl et al. 2010). In comparison to these previous studies, our study goes further in linking the effects specifically to the registration of food items held in WM, especially as previous studies did not investigate the SPCN component. Overall, our current findings suggest that the strong representation of food items in WM contributes to food items capturing attention. In contrast to our behavioral findings, we did not observe food versus non-food differences in the ERP components when the WM stimulus aligned with the search target (Higgs et al. 2012). This suggest that the differences in ERPs are only related to keeping food in WM and not specifically to the item in WM reappearing next to the target.

While weight status and hunger status might influence the representation of food in WM, we tested whether there was an effect on whether subjects were thinking about food/non-food and retaining the items in WM or just watching the items by testing for interactions in all three ERPs. We did not observe any interactions involving weight or hunger status. Earlier studies, in which subjects only had to attend to pictures, did show differences in the P3 and LPP components between subjects who were lean or obese as well as hungry or fed subjects (Nijs et al. 2008; Stockburger et al. 2008; Stockburger et al. 2009; Svaldi et al. 2010; Blechert et al. 2012). The absence of weight or hunger status differences might reflect the different paradigms used, the small subject group or the group being quite homogenous (i.e. BMI ranged from 18.0 – 34.6 kg/m^2), compared to more extreme weight groups <25 and >35 kg/m^2 used in other studies. Also due to the length of EEG testing, it was difficult to control appetite and keep it constant. For future studies it will be important to examine specific effects of weight status and hunger status on responding in the WM task.

5. Conclusions

In conclusion, our electrophysiological data are consistent with the suggestion that food stimuli are particularly strongly represented in the WM system.

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Author contributions

Regarding author contribution: F.R and S.K conducted the experiment, analysed the data and wrote the manuscript. S.H. and G.H conceived and designed the study and reviewed and edited the manuscript. F.R. is the guarantor of this work and, as such, had full access to all the data in the study and takes responsibility for the integrity of the data and the accuracy of the data analysis.

Figure Legends

Figure 1a: Illustration of the priming and working memory tasks. Subjects were presented with a cue (food or non-food item) for 500ms to either attend to or hold in working memory. Subsequently, they had to search for a target (for 800ms), while the target and distractor were each flanked by a picture of a food or non-food item. On a small proportion of priming trials (20%), the priming cue disappeared and was replaced by a different image. On these priming probe trials participants were instructed not to carry out the search task that normally followed the initial cue. This ensured that participants attended to the cue. In the working memory task participants were asked to hold the cue in memory across the trial, for a subsequent memory test on a minority of occasions (again 20% of the trials).

Figure 1b: Illustration of trials in the working memory. task, representing food valid, food neutral, and food invalid trials. On valid trials, the target in the search display was flanked by an image that was the same as the cue and the distractor was flanked by an image from one of the other cue categories, while on invalid trials, the distractor was flanked by an image that was the same as the cue and the target was flanked by an image from one of the other cue categories. Finally, on neutral trials, both the target and distractor were flanked by images from categories different from the cue.

Figure 2: Mean reaction times (RTs) (in ms) to the target next to the food or non-food cues for Valid, Invalid, and Neutral trials, for the priming and working memory tasks. Values are means ± SEM

Figure 3: current source density map of the voltage distributions in the 250-450 ms period after search onset, along with the grand-averaged waveforms from the pooled electrodes taken for the P3 analysis from the left and right hemispheres. The shaded area around the grand averaged waveforms shows the standard deviation. There was a reliable difference in P3 activity between the food and non-food cue averaged over valid, invalid and neutral trials for the working memory condition across the 250-450 ms time window.

Figure 4: current source density map of the voltage distributions in the 460-660 ms period after search onset. The chosen electrodes for the LPP analysis were same as the electrodes for the P3 analysis (shown in figure 3). There was a reliable difference in LPP activity following the food and non-food cue averaged over valid, invalid and neutral trials for the working memory condition across the 460-660 ms time window.

Figure 5: current source density map of the voltage distributions in the 700-850 ms period after search onset, along with the grand-averaged waveforms from the pooled electrodes taken for the SPCN analysis. The shaded area around the grand averaged waveforms shows the standard deviation. There was a reliable difference in SPCN activity between the food and non-food cues averaged over valid, invalid and neutral trials for the working memory condition across the 700-850 ms time window.

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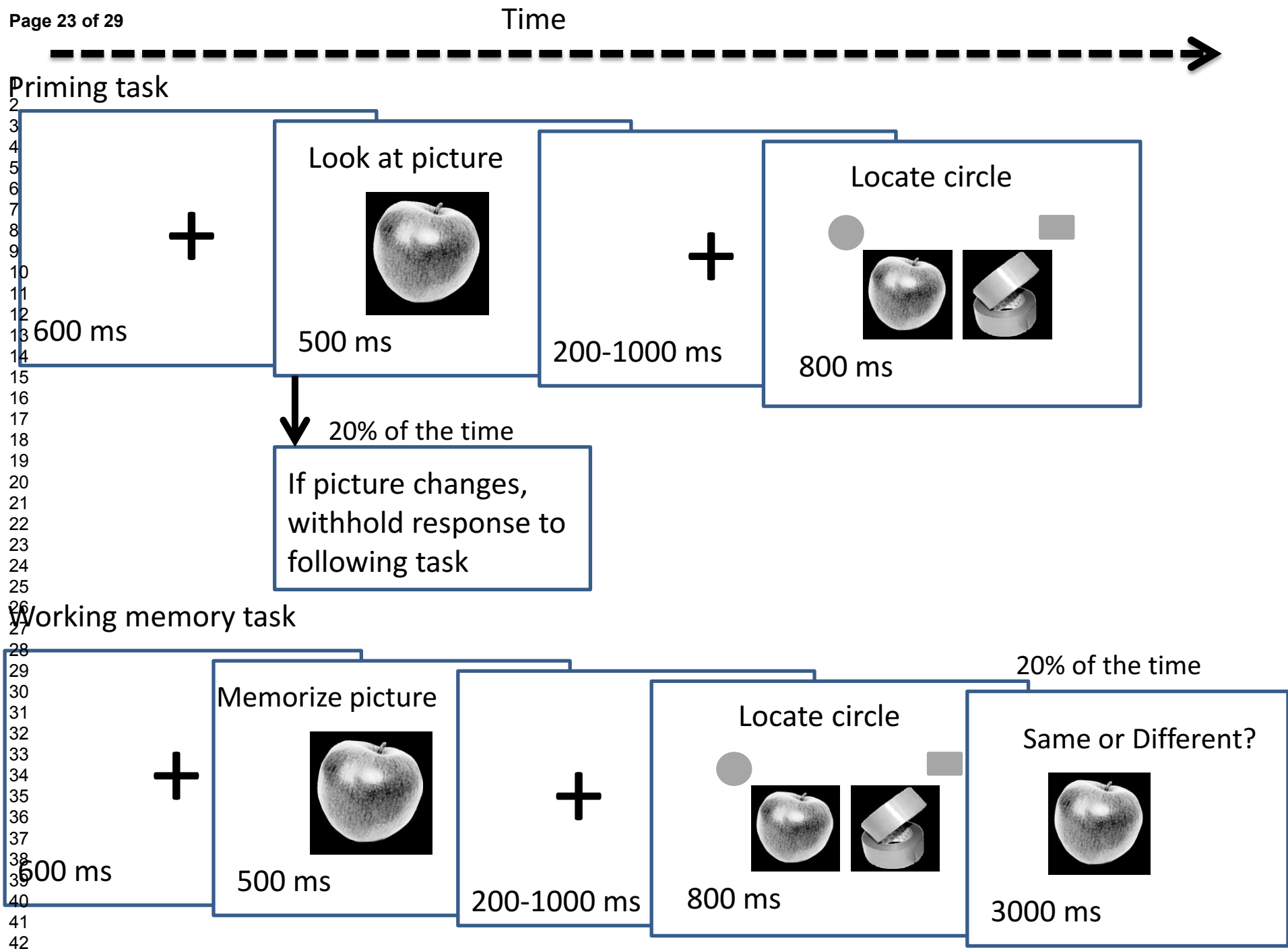
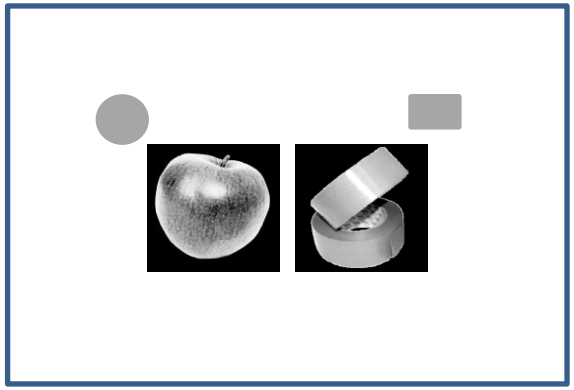
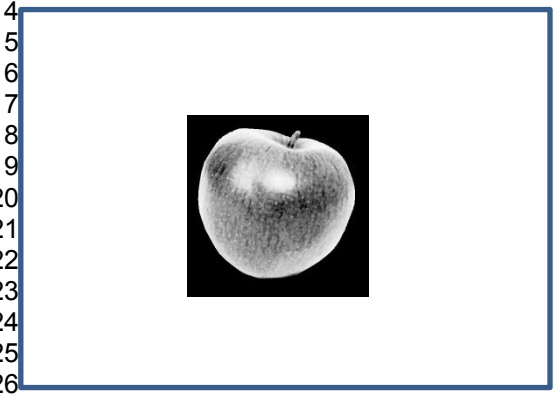

Time
Priming task
600 ms
Look at picture
500 ms
200-1000 ms
Locate circle
800 ms
20% of the time
If picture changes, withhold response to following task
Working memory task
600 ms
Memorize picture
500 ms
200-1000 ms
Locate circle
800 ms
20% of the time
Same or Different?
3000 ms

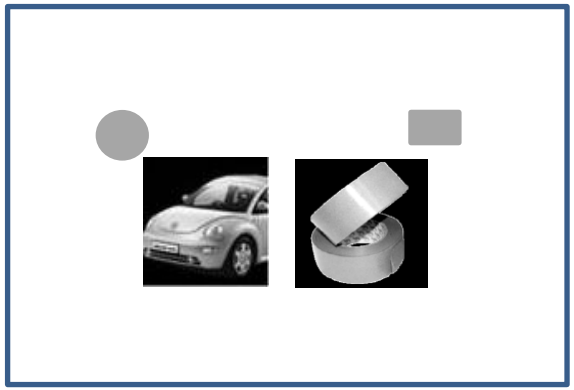
Valid Trial



Cue

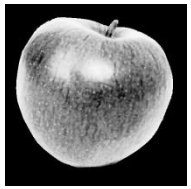


Neutral Trial

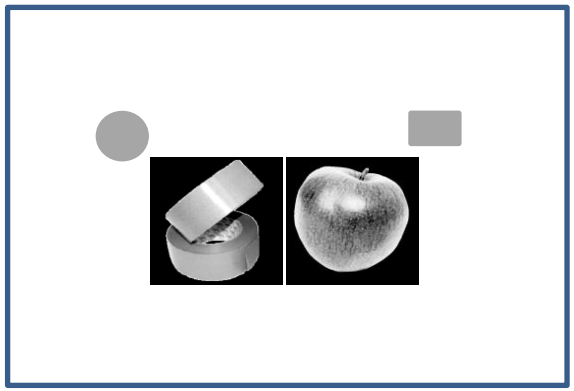


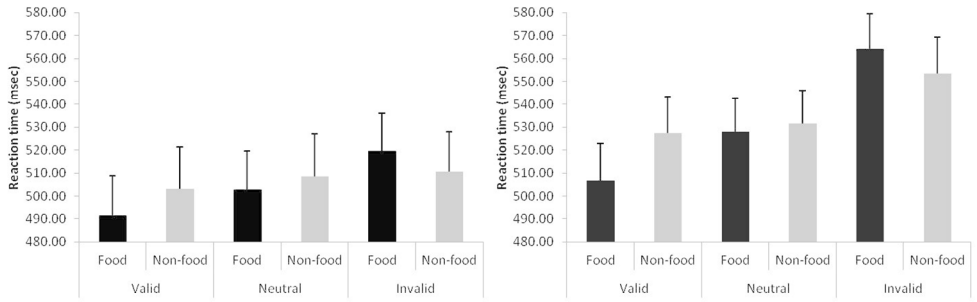
Memory test

Same or different?



Invalid Trial





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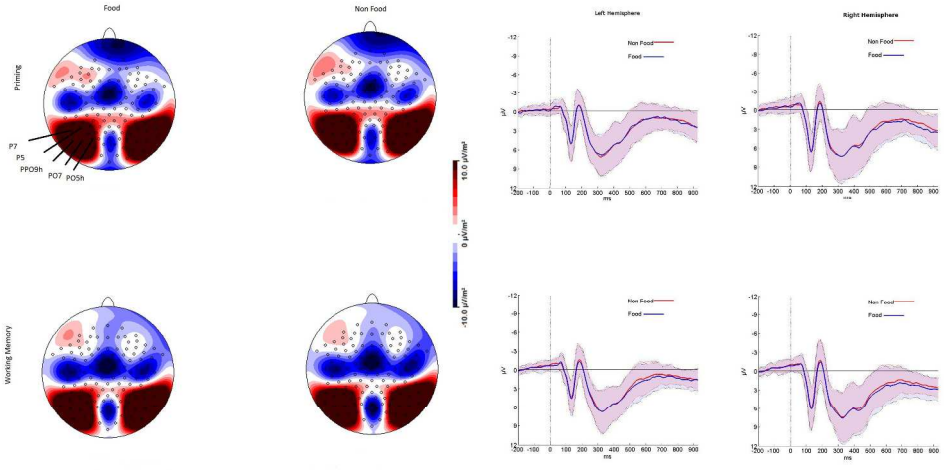

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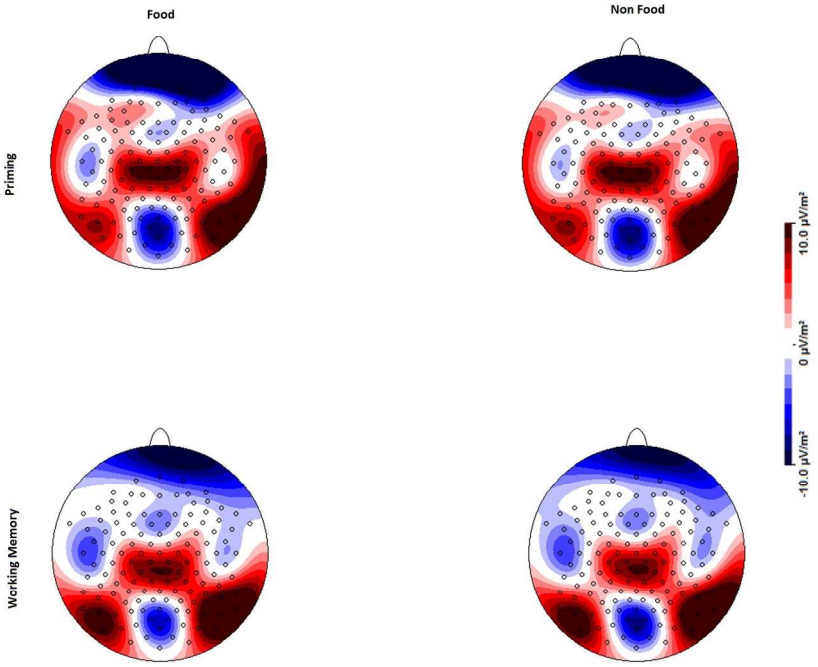

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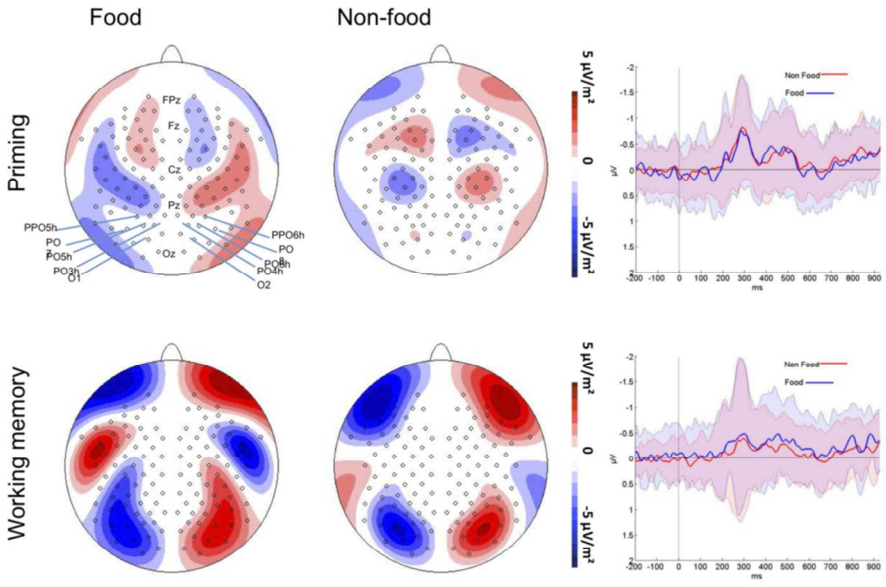
Food
Non-food
Priming
Working memory
FPz
Fz
Cz
Pz
Oz
PPO5h
PO
PO5h
PO3h
O1
PPO6h
PO
PO8h
PO4h
O2
5 µV/m²
0
-5 µV/m²
Non Food
Food
µV
ms

Table 1: the mean amplitudes (μV) of the P3 (left and right hemisphere), LPP (left and right hemisphere) and SPCN components to the target next to the food or non-food cues for Valid, Invalid, and Neutral trials, for the Priming and Working Memory tasks

Task	**Trials**	**P3 left hemisphere**	**P3 right hemisphere**	**LPP left hemisphere**	**LPP right hemisphere**	**SPCN**
Priming	Valid food	5.6 ± 2	6.1 ± 4	1.6 ± 2	2.3 ± 3	-0.2 ± 0.4
	Valid non-food	5.7 ± 3	6.1 ± 4	1.5 ± 3	2.1 ± 3	-0.4 ± 0.4
	Neutral food	6.1 ± 3	6.7 ± 4	1.8 ± 3	2.6 ± 3	-0.1 ± 0.3
	Neutral non-food	6.1 ± 3	6.5 ± 4	1.7 ± 3	2.3 ± 3	-0.2 ± 0.3
	Invalid food	5.6 ± 3	6.3 ± 4	1.5 ± 2	2.5 ± 3	-0.2 ± 0.6
	Invalid non-food	5.8 ± 3	6.0 ± 3	1.8 ± 3	2.3 ± 3	-0.2 ± 0.3
Working memory	Valid food	5.3 ± 2	6.1 ± 3	1.9 ± 3	2.8 ± 3	-0.4 ± 0.5
	Valid non-food	5.2 ± 2	5.9 ± 3	1.4 ± 3	2.4 ± 3	-0.1 ± 0.4
	Neutral food	6.1 ± 3	6.9 ± 4	1.7 ± 3	2.7 ± 3	0.1 ± 0.4
	Neutral non-food	6.3 ± 2	7.1 ± 4	1.9 ± 3	3.2 ± 3	0.1 ± 0.3
	Invalid food	5.7 ± 2	6.6 ± 4	2.4 ± 3	3.6 ± 4	-0.5 ± 0.5
	Invalid non-food	5.3 ± 2	6.1 ± 3	1.8 ± 3	2.9 ± 3	-0.5 ± 0.5