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Rutters, F, Kumar, S, Higgs, S and Humphreys, G (2014) Electrophysiological evidence for enhanced representation of food stimuli in working memory. *Experimental Brain Research*, 233 (2). pp. 519-528.

doi: 10.1007/s00221-014-4132-5

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Electrophysiological evidence for enhanced representation of food stimuli in working memory

Short title: enhanced food representation in working memory

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Conflict of interest: none of the authors disclose any conflict of interest

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Abstract

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5 30 Studies from our laboratory have shown that, relative to neutral objects, food-related objects kept in
6
7 working memory (WM) are particularly effective in guiding attention to food stimuli (Higgs et al.
8
9 2012). Here, we used electrophysiological measurements to investigate the neural representation of
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11 food vs. non-food items in WM. Subjects were presented with a cue (food or non-food item) to either
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13 attend to or hold in WM. Subsequently, they had to search for a target, while the target and distractor
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15 35 were each flanked by a picture of a food or non-food item. Behavioural data showed that a food cue
16
17 held in WM modulated the deployment of visual attention to a search target more than a non-food
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19 cue, even though the cue was irrelevant for target selection. Electrophysiological measures of
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21 attention, memory and retention of memory (the P3, LPP and SPCN components) were larger when
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23 food was kept in WM, compared to non-food items. No such effect was observed in a priming task,
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25 40 when the initial cue was merely identified. Overall, our electrophysiological data are consistent with
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27 the suggestion that food stimuli are particularly strongly represented in the WM system.
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Highlights

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- Food-related objects kept in working memory are particularly effective in guiding attention to
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37 food stimuli
 - Electrophysiological measures of attention and memory were larger for food versus non food
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39 cues
 - Food cues are better maintained in working memory than non-food cues, perhaps because of
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46 50 their rewarding properties
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50 **Keywords:** Attention, working memory, food and non-food cues, long-latency ERPs
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1. Introduction

55 In our current obesogenic environment food cues are found all around us; from shop displays and
6 television adverts, to pictures of food and eating in magazines. Though the abundance of food cues is
7 not in itself problematic, heightened attention to food cues has been shown to enhance motivation to
8 consume foods (Fedoroff et al. 1997; Loxton et al. 2011) and to predict weight gain (Calitri et al.
9 2010; Yokum et al. 2011), with attentiveness to food cues being particularly marked in obese children
10 and adults (Braet and Crombez 2003; Castellanos et al. 2009; Nijs and Franken 2012). However,
11 despite its potential importance, we lack detailed understanding of the mechanisms that determine
12 heightened attention to food. The present study represents an attempt to do this using evoked response
13 data.
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65 Previously, we have reported that food directs attention in a top-down manner, via its representation
66 in working memory (WM). We found that, in lean subjects, deliberately holding food items in WM is
67 particularly effective in guiding attentional selection when food stimuli are re-presented in a display -
68 with WM-based guidance of attention from food being stronger than the guidance from neutral stimuli
69 (Higgs et al. 2012; Rutters et al. 2013). In these experiments, participants were presented with a food
70 or non-food (neutral) cue to either attend to or hold in WM, and subsequently they had to search for a
71 shape target (cf. (Soto et al. 2005)). The cue could re-appear in the search display either alongside
72 the search target (valid trials) or a distractor (invalid trials). In addition, there were neutral trials, in
73 which the cue did not re-appear. Reaction times were strongly affected by the re-appearance of a food
74 cue, but only when the cues were held in WM rather than merely being attended to, as shown in the
75 priming condition, designed to match the visual sequence used in the WM condition.

76 The results from our behavioural studies indicate that a food cue in WM exerted a strong effect on
77 search, when compared with neutral cues, and this was not driven by the initial appearance of the cue
78 alone (in the priming condition) (Soto et al. 2005; Soto and Humphreys 2007; Soto et al. 2008; Higgs
79 et al. 2012; Rutters et al. 2013). These data suggest that attentional biases towards food cues can be
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3 mediated by holding food-related information in WM, which in turn guides attention to food-related
4 items in the environment (Higgs et al. 2012).
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9 Here we assessed how the representation of food items in WM modulates attentional bias to food,
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11 85 using electroencephalography (EEG) to examine the time course of stimulus coding in memory and
12 attention. Several studies have investigated the electrophysiological correlates of heightened
13 attentiveness to motivational stimuli, including food cues (Leland and Pineda 2006; Nijs et al. 2008;
14 Stockburger et al. 2008; Babiloni et al. 2009; Nijs et al. 2009; Stockburger et al. 2009; Toepel et al.
15 2009; Stingl et al. 2010; Svaldi et al. 2010). Only two studies have observed early stage Event Related
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21 90 Potential (ERP) differences between food and non-food items (Stockburger et al. 2008; Stingl et al.
22 2010), while the majority reported differences in long-latency ERPs (Stockburger et al. 2009; De
23 Pascalis et al. 2010; Eimer and Kiss 2010; Stingl et al. 2010; Eckstein 2011; Yu et al. 2011). Long-
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27 latency ERPs are generally thought to represent high-level processes reflecting decision making,
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31 95 memory, reward, motivation, and emotion (Stockburger et al. 2009; De Pascalis et al. 2010; Eimer
32 and Kiss 2010; Stingl et al. 2010; Eckstein 2011; Yu et al. 2011). The three most often studied long-
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The P3 component is a positive 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 endogenous 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

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3 memory updating, memory load and stimulus maintenance in WM (Picton 1992; Friedman and
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5 110 Johnson 2000; Schupp et al. 2000; Citron 2012; Littel et al. 2012). The SPCN amplitude, which is
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7 also called the Contralateral Delay Activity (CDA) (Vogel and Machizawa 2004), is calculated by
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9 subtracting ipsilateral activity from contralateral activity relative to the target after about 500 ms post
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11 stimulus (Vogel and Machizawa 2004; Eimer and Kiss 2010; Eckstein 2011). The SPCN is often
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13 referred to as a long-latency marker for the retention of visual short-term WM. It is larger for more
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15 115 complex patterns and emotionally laden objects, and it returns to baseline sooner for the shorter
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17 retention intervals (Holmes et al. 2009; Perron et al. 2009).
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21 Up until now, ERP studies examining the differences between food and non-food stimuli have shown
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23 increased P3 and LPP amplitudes for food compared to non-food cues, while no studies have
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25 120 investigated the SPCN amplitude (Leland and Pineda 2006; Nijs et al. 2008; Nijs et al. 2009;
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27 Stockburger et al. 2009; Toepel et al. 2009; Nijs et al. 2010a; Svaldi et al. 2010). These findings
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29 suggest increased attentional, mnemonic and evaluative processing of food stimuli, as well as
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31 increased memory updating, memory load and stimulus maintenance in WM of food stimuli.
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34 However, these earlier ERP studies have used several different paradigms to compare food versus non
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36 125 food items, ranging from simple tasks in which subjects only have to look at the presented pictures, to
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38 Posner, Stroop, and one-back tasks in which subjects have to attend to and memorize stimuli (Leland
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40 and Pineda 2006; Nijs et al. 2008; Nijs et al. 2009; Stockburger et al. 2009; Toepel et al. 2009; Nijs et
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42 al. 2010a; Svaldi et al. 2010). In these paradigms it is difficult to identify exactly which cognitive
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44 process, of the many potentially involved, is modulated by food. For example, under passive viewing
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46 130 conditions participants may represent the items in WM, and so any effects could reflect the status of
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48 the items in WM.
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52 In the present experiment, we will examine long-latency ERPs in the WM-based attentional guidance
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54 paradigm previously employed (Higgs et al. 2012). This paradigm is useful because it enables us to
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56 135 assess whether the long-latency ERPs modulated by food are affected by factors such as memory or
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58 merely attending to the picture. The WM-based guidance paradigm has been examined once before in
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3 an ERP study, but there was no examination of different cue types (Kumar et al. 2009). In the present
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5 study, for the first time, we directly compare food and non-food cues and examine the modulatory
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7 effects of food on late acting ERP components, to provide us insight into the electrophysiological
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9 140 correlates of food-related memory coding and attention.
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2. Materials and Methods

2.1 Participants

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7 Sixteen students (8 females and 8 males) from the School of Psychology of the University of
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9 145 Birmingham took part in this experiment for either course credits or cash. Their mean age was 23
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11 years (range 19-38 years) and their mean body mass index (BMI) was 24.8 kg/m² (range 18.0 – 34.6
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13 kg/m²), with 50% of the subjects being overweight. All participants had normal to corrected-to-
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15 normal-vision. Written informed consent was obtained from all participants. The study was approved
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17 by the Ethics Committee of the University of Birmingham, and conformed to the Declaration of
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19 150 Helsinki.

2.2 Tasks

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25 There were two tasks, the priming and working memory tasks, in which we varied the instructions
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27 regarding the initial cue presented on each trial. In the priming task, participants were asked to attend
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29 155 to the cue but not to hold it in memory. On a small proportion of trials (20%), the priming cue
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31 disappeared and was replaced by a different image. On these priming probe trials participants were
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33 instructed not to carry out the search task that normally followed the initial cue. This ensured that
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35 participants attended to the cue. In the WM task participants were asked to hold the cue in memory
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37 across the trial, for a subsequent memory test on a minority of occasions (again 20% of the trials; see
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39 160 **Figure 1a**). On these memory probe trials, the search display that followed the initial cue was
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41 followed by a visual memory probe for 3000ms, which could correspond to the object being held in
42
43 WM or to another object. Participants made a same or different judgement as to whether the cue and
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45 the memory item were the same. The priming and WM tasks were completed in a counterbalanced
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47 165 order. The priming task consisted of 1945 trials, taking about 120 minutes, and the WM task consisted
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49 of 1500 trials, and took 106 minutes to complete. The trials were divided into smaller blocks of about
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51 150 trials, after which the subject had a few minutes rest. Each trial started with presentation of the
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53 cue for 500ms. The cue was either a picture of a food item, a car, or a stationery item, and 10 different
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55 pictures per category were used during both the priming and WM tasks. All pictures were presented in
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57 170 black and white, sized 480 x 480 pixels, and appeared in the middle of the screen with a black
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59 background. The cue was followed by a 200 to 1000ms blank interval with a fixation cross. After the
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61 interval, a search screen was presented with a target (circle) and a distractor (square) randomly to the

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3 left or right of fixation for 800ms. Participants had to press 'c' if the circle appeared on the left and
4 'm' if it appeared on the right, with the maximum response time set at 1200ms. The target and the
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175 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
180 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,
185 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,
190 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
195 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

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3 200 Participants consumed their regular breakfast half before the start of the study and the other half
4 during the larger 15 minute break. Aspects of appetite were assessed using 100 mm visual analog
5 scales (VAS) with questions about feelings of hunger, satiety, thirst, and desire to eat. Opposing
6 extremes of each feeling were described at either end of the 100-mm horizontal line, and subjects
7 marked the line to indicate how they felt at that moment. Completion of the VAS questionnaire took
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12 205 our experienced subjects about 1 minute. During the protocol, appetite profiles were assessed twice:
13 before and after performing both tasks. The mean feelings of hunger were pre 13.6 ± 13 and post
14 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
15 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
16 was counterbalanced, which makes it unlikely that changes in motivational state influenced the
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21 210 outcome. Participants completed the priming and working memory (WM) tasks in counterbalanced
22 order, with an option of a 15-minute break between tasks. Before leaving, participants had their height
23 (cm) and weight (kg) measured.
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29 2.5 Electroencephalogram data processing

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31 215 Electroencephalogram (EEG) recordings for each participant were taken continuously with Ag/AgCl
32 electrodes from 128 scalp electrode locations. The electrodes were placed according to the 10-5
33 electrode system (Oostenveld and Praamstra 2001) using a nylon electrode cap. A unipolar electrode
34 placed at the infra-orbital area of the left eye monitored vertical eye movements, and a bipolar
35 electrode placed at the outer canthus of the left and right eyes monitored horizontal eye movements.
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40 220 Additional electrodes were used for references and ground. EEG and electro-oculogram signals were
41 amplified (BioSemi ActiveTwo, Amsterdam, the Netherlands) and sampled at 512 Hz. The
42 continuous EEG recordings were off-line referenced to the average of the left and right mastoids and
43 band pass filtered between 0.5 and 30 Hz. Continuous EEG signals were segmented into epochs from
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49 225 subject. The 200 ms prior to the onset of the search task was used as a baseline, and the EEG signals
50 reported have been calculated relative to this baseline activity. Epochs were rejected if the voltage in
51 horizontal eye electrodes exceeded ± 60 and ± 100 μV in any other electrodes. The EEG data of one
52 participant was discarded because of excessive horizontal eye-movement. Since our focus was to
53 understand the electrophysiological correlates of identifying or holding a cue in WM on its
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3 230 subsequent coding, we focussed on the long-latency ERPs P3, LPP, and SPCN components occurring
4 after the onset of the search display. The maximum positive deflections in the time windows of 250-
5 450 ms and 460-660 ms were defined as the P3 and LPP respectively, both showing a posterior
6 distribution. The negative deflection around 700-850 ms post-stimulus at posterior sites, contralateral
7 to the evoking stimulus, was defined as the SPCN. The SPCN was computed by subtracting ipsilateral
8 activity from contralateral activity relative to the target.
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16 Further analyses were restricted to regions that showed the highest activity for the particular
17 component of interest. The electrode with the highest activity was identified through visual inspection
18 of the current source density (CSD) map of the grand average waveform. Electrical activity on the
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21 240 four electrodes surrounding the electrode with the highest activity of the particular component was
22 then averaged for each time-point in the epoch interval, to generate a region-specific analysis. The
23 same electrode combinations were then chosen on the contralateral side of the identified region for the
24 particular component. The following electrodes were taken as representing left and right hemispheric
25 activity for the P3 and LPP components: P1, PPO1h, CPP1h, CPP3h, PPO3h and P2, PPO2h, CPP2h,
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30 245 CPP4h, PPO4h. The SPCN component was analysed at the pooled five posterior and lateral occipital
31 electrodes: PPO5h/PPO6h, PO5h/PO6h, PO3h/PO4h, O1/O2, and PO7/PO8 based on the SPCN CSD
32 map where the source of the SPCN activity was observed across the conditions.
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38 2.6 Statistical analyses

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40 250 Statistical analyses were performed with SPSS version 20.0 (SPSS Inc., Chicago, IL). Continuous
41 data were presented as means \pm standard deviation (SD) or standard error of the mean (SEM). Firstly,
42 using repeated-measures ANOVAs, we analysed interactions and differences in reaction times (RTs)
43 (ms) for tasks (WM, priming), trials (valid, neutral, invalid) and cues (food vs. non-food items).
44 Secondly, we assessed the food advantage scores (%RT for [Non-food minus food]/Non-food) for the
45 priming and WM tasks and compared them using paired t-tests. Thirdly, again using repeated-
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50 255 measures ANOVAs we analysed interactions and differences in all three ERP components (mean
51 amplitude) for tasks (WM, priming), hemisphere (left, right), trials (valid, neutral, invalid) and cue
52 (food vs. non-food items). Finally, we used repeated-measures ANOVAs to analyse possible
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interaction effects for weight status (BMI > 25 kg/m²) 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

265 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 ($F(1, 14) = 10.44$; $p < 0.006$, $\eta^2 = 0.4$), 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 ($F(2, 28) = 60.9$; $p < 0.000$, $\eta^2 = 0.8$), 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 ($F(1, 14) = 5.6$; $p < 0.03$, $\eta^2 = 0.3$); RTs following the food cues were faster than RTs following the non-food cues.

The three-way interaction between task, validity, and cue ($F(2, 28) = 1.96$; $p = 0.16$, $\eta^2 = 0.1$), and the two-way interaction between task and cue were not significant ($F(1, 14) = 1.3$; $p = 0.27$, $\eta^2 = 0.8$). We did observe a significant two-way interaction between task and validity ($F(2, 28) = 21.5$; $p < 0.001$, $\eta^2 = 0.6$); 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 ($F(2, 28) = 47.8$; $p < 0.001$, $\eta^2 = 0.8$); 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.

290 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

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3 score provides an index of the effectiveness of the food cues in guiding attention. We observed a
4 larger food advantage in the WM task compared to the priming task in the valid trials (3.9 ± 1.6 vs.
5 2.4 ± 1.6 %, $P < 0.002$), while no significant differences were observed in the neutral (0.6 ± 1.6 vs.
6 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,
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9 295 compared to the priming condition, RTs were faster following food cues than non-food cues when
10 they re-occurred and matched the flanked image in the WM task.
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18 3.2 Electroencephalography data

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20 300 To evaluate the long-latency ERPs responses to holding food or non-food information in WM vs.
21 merely attending to these stimuli, we compared the effect of cue type, validity and tasks on the mean
22 amplitudes of the P3, LPP and SPCN components (**Table 1**). First, we carried out a $2 \times 2 \times 3 \times 2$
23 repeated-measures ANOVA with the factors being task (priming, WM), hemisphere (left, right),
24 validity (valid, neutral and invalid trials), and cue (food, non-food) for the P3 component (mean
25 amplitude between 250 to 450 ms). We observed a reliable main effect of validity ($F_{2,28} = 16.9$, $P =$
26 0.001 $\eta^2 = 0.6$); the P3 component was larger in the neutral trials compared to the valid and invalid
27 trials. Furthermore, we observed an interaction between task and cue ($F_{1,14} = 4.4$, $P < 0.04$ $\eta^2 = 0.3$);
28 the P3 component was larger in response to the food compared to the non-food cue in the WM task (P
29 < 0.03), while it was not different from the non-food cue in the priming task ($P = 0.67$) (**Figure 3**).
30 305 There were no main effects on the P3 component of task, hemisphere or cue type (food vs. non-food
31 cues) and there were no additional interaction effects ($P > 0.1$).
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46 Second, we carried out $2 \times 2 \times 3 \times 2$ repeated-measures ANOVA with the factors being task
47 (priming, WM), hemisphere (left, right), validity (valid, neutral and invalid trials), and cue (food, non-
48 food) for the LPP component (mean amplitude between 460-660 ms). We observed a reliable
49 interaction between task and cue ($F_{1,14} = 6.7$, $P < 0.03$ $\eta^2 = 0.3$); the LPP component was larger in
50 315 response to the food compared to the non-food cue in the WM task ($P < 0.01$), while there was no
51 reliable effect in the priming task ($P = 0.45$) (**Figures 3 & 4**). There were no main effects on the LPP
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3 component for the effects of task, validity, hemisphere or cue type (food vs. non-food cues) and there
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5 320 were no additional interaction effects ($P > 0.1$).

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9 Third, we carried out $2 \times 3 \times 2$ repeated-measures ANOVA with the factors being task
10 (priming, WM), validity (valid, neutral, invalid), and cue (food, non-food) for the SPCN component
11 (mean amplitude between 700 to 850 ms). We observed an effect of validity ($F_{1,14} = 9.46$, $P < 0.001$
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13 325 $\eta^2 = 0.4$); the SPCN component was smaller on neutral trials than on the valid and invalid trials.
14
15 Additionally, we observed a two-way significant interaction between task and validity ($F_{1,14} = 11.4$, P
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17 $= 0.001$ $\eta^2 = 0.4$); the SPCN component was smaller on neutral trials than on the valid and invalid
18
19 trials in the WM task ($P < 0.001$); no such effect was observed in the priming task ($P = 0.28$). Finally,
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21 we observed a two-way significant interaction between task and cue ($F_{1,14} = 4.56$, $P = 0.05$ $\eta^2 = 0.3$);
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23 330 there was an overall effect of cue in the WM task, the SPCN component was larger in response to the
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25 food compared to the non-food cue in the WM task ($P < 0.001$), while there was no reliable effect in
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27 the priming task ($P = 0.19$) (**Figure 5**). There were no main effects on the SPCN component for the
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29 effect of task or cue type (food vs. non-food cues) and no additional interaction effects ($P > 0.1$).

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35 335 Finally, we carried out a $2 \times 3 \times 2 \times 2$ repeated-measures ANOVA for the P3 and LPP
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37 components as well as a $2 \times 3 \times 2$ repeated-measures ANOVA for the SPCN components with weight
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39 status ($BMI > 25 \text{ kg/m}^2$) and hunger scores (median split change in hunger score) as between subject
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41 factors. Overall, we observed no interaction effects of weight status ($P > 0.1$) or hunger scores ($P > 0.1$)
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43 for the P3, LPP or SPCN component.
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3 340 **4. Discussion**

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5 The aim of our current study was to assess the electrophysiological correlates of food-related memory
6 coding in memory and attention. Our behavioural data replicate earlier reported findings (Higgs et al.
7 2012; Rutters et al. 2013); a food cue held in WM modulated the deployment of visual attention to a
8 search target more than non-food cues. This led to a larger food advantage on valid trials in the WM
9 condition compared with the priming condition, while effects on neutral and invalid trials did not
10 differ for food relative to non-food stimuli in the WM and priming conditions. In contrast, there were
11 no behavioural effects of cue type when food or non-food stimuli had to be identified but not held in
12 WM, in the priming task (Higgs et al. 2012; Rutters et al. 2013). These findings support our
13 hypothesis that the processing of food-related information in WM is particularly effective for
14 deploying attention to food stimuli, even when there are no differential bottom-up signals favouring
15 food items.
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29 To elucidate the mechanisms that underlie WM-based guidance of attention by food items, we studied
30 differences in long-latency ERPs for food and non-food cues being held in WM or merely being
31 attended to. We discuss only the ERP results that are relevant to our hypothesis, thus omitting our
32 findings regarding validity as well as validity and task interactions, which have been previously been
33 discussed (Kumar et al. 2009). Our main finding was the interaction between task and cue, which was
34 present in all three components of interest: the P3, the LPP and the SPCN. All three components were
35 larger when food items were held in WM compared to non-food items and no such effect was
36 observed in the priming task. The three ERP components have been associated with different
37 underlying processes: the P3 with attention, mnemonic and evaluative processing (Friedman and
38 Johnson 2000; Stockburger et al. 2009; De Pascalis et al. 2010; Eckstein 2011; Yu et al. 2011) the
39 LPP with memory (Picton 1992; Friedman and Johnson 2000; Schupp et al. 2000; Citron 2012; Littell
40 et al. 2012) and the SPCN with the retention of information in visual short-term WM (Eimer and Kiss
41 2010; Eckstein 2011). Overall, the long-latency ERP components seem to reflect stronger
42 representation of food in WM, implicating food cues are held in the forefront of WM more easily,
43 perhaps because of their having intrinsic rewarding properties.
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7 370 In previous studies using food versus non-food attention tasks, it is difficult to know exactly which
8 processes are differentially activated by the cues; attention and/or memory. Using our paradigm
9 enabled us to assess both processes separately. Previous studies showed similar differences in P3 and
10 LPP components when they used tasks placing demands on memory, including one-back matching,
11 counting task, oddball detection, Stroop and Posner cueing (Leland and Pineda 2006; Babiloni et al.
12 2009; Nijs et al. 2009; Nijs et al. 2010a; Nijs et al. 2010b; Stingl et al. 2010). In comparison to these
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16 375 previous studies, our study goes further in linking the effects specifically to the registration of food
17 items held in WM, especially as previous studies did not investigate the SPCN component. Overall,
18 our current findings suggest that the strong representation of food items in WM contributes to food
19 items capturing attention. In contrast to our behavioral findings, we did not observe food versus non-
20 food differences in the ERP components when the WM stimulus aligned with the search target
21 (Higgs et al. 2012). This suggest that the differences in ERPs are only related to keeping food in WM
22 and not specifically to the item in WM reappearing next to the target.
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33 While weight status and hunger status might influence the representation of food in WM, we tested
34 whether there was an effect on whether subjects were thinking about food/non-food and retaining the
35 items in WM or just watching the items by testing for interactions in all three ERPs. We did not
36
37 385 observe any interactions involving weight or hunger status. Earlier studies, in which subjects only had
38 to attend to pictures, did show differences in the P3 and LPP components between subjects who were
39 lean or obese as well as hungry or fed subjects (Nijs et al. 2008; Stockburger et al. 2008; Stockburger
40 et al. 2009; Svaldi et al. 2010; Blechert et al. 2012). The absence of weight or hunger status
41 differences might reflect the different paradigms used, the small subject group or the group being
42 quite homogenous (i.e. BMI ranged from 18.0 – 34.6 kg/m²), compared to more extreme weight
43 groups <25 and >35 kg/m² used in other studies. Also due to the length of EEG testing, it was difficult
44 to control appetite and keep it constant. For future studies it will be important to examine specific
45 effects of weight status and hunger status on responding in the WM task.
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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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Acknowledgements

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5 This work was supported by grants from the Biotechnology and Biological Research Council, the
6
7 Economic and Social Research Council, the European Union (FP7), and the Medical Research
8
9 405 Council, UK.

Author contributions

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14 Regarding author contribution: F.R and S.K conducted the experiment, analysed the data and wrote
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16 the manuscript. S.H. and G.H conceived and designed the study and reviewed and edited the
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18 410 manuscript. F.R. is the guarantor of this work and, as such, had full access to all the data in the study
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20 and takes responsibility for the integrity of the data and the accuracy of the data analysis.
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Figure Legends

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5 **Figure 1a:** Illustration of the priming and working memory tasks. Subjects were presented with a cue
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7 415 (food or non-food item) for 500ms to either attend to or hold in working memory. Subsequently, they
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9 had to search for a target (for 800ms), while the target and distractor were each flanked by a picture of
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11 a food or non-food item. On a small proportion of priming trials (20%), the priming cue disappeared
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13 and was replaced by a different image. On these priming probe trials participants were instructed not
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15 to carry out the search task that normally followed the initial cue. This ensured that participants
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17 420 attended to the cue. In the working memory task participants were asked to hold the cue in memory
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19 across the trial, for a subsequent memory test on a minority of occasions (again 20% of the trials).
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23 **Figure 1b:** Illustration of trials in the working memory task, representing food valid, food neutral,
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25 and food invalid trials. On valid trials, the target in the search display was flanked by an image that
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27 425 was the same as the cue and the distractor was flanked by an image from one of the other cue
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29 categories, while on invalid trials, the distractor was flanked by an image that was the same as the cue
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31 and the target was flanked by an image from one of the other cue categories. Finally, on neutral trials,
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33 both the target and distractor were flanked by images from categories different from the cue.
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37 430 **Figure 2:** Mean reaction times (RTs) (in ms) to the target next to the food or non-food cues for Valid,
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39 Invalid, and Neutral trials, for the priming and working memory tasks. Values are means \pm SEM
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43 **Figure 3:** current source density map of the voltage distributions in the 250-450 ms period after
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45 search onset, along with the grand-averaged waveforms from the pooled electrodes taken for the P3
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47 435 analysis from the left and right hemispheres. The shaded area around the grand averaged waveforms
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49 shows the standard deviation. There was a reliable difference in P3 activity between the food and non-
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51 food cue averaged over valid, invalid and neutral trials for the working memory condition across the
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53 250-450 ms time window.
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3 440 **Figure 4:** current source density map of the voltage distributions in the 460-660 ms period after
4 search onset. The chosen electrodes for the LPP analysis were same as the electrodes for the P3
5 analysis (shown in figure 3). There was a reliable difference in LPP activity following the food and
6 non-food cue averaged over valid, invalid and neutral trials for the working memory condition across
7 the 460-660 ms time window.
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15 **Figure 5:** current source density map of the voltage distributions in the 700-850 ms period after
16 search onset, along with the grand-averaged waveforms from the pooled electrodes taken for the
17 SPCN analysis. The shaded area around the grand averaged waveforms shows the standard deviation.
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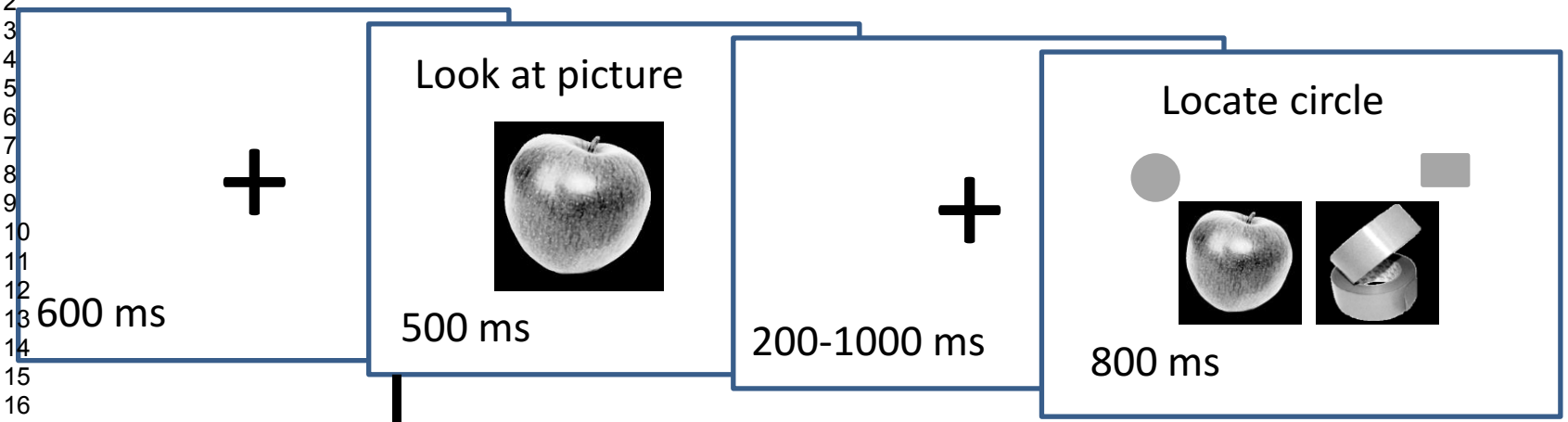
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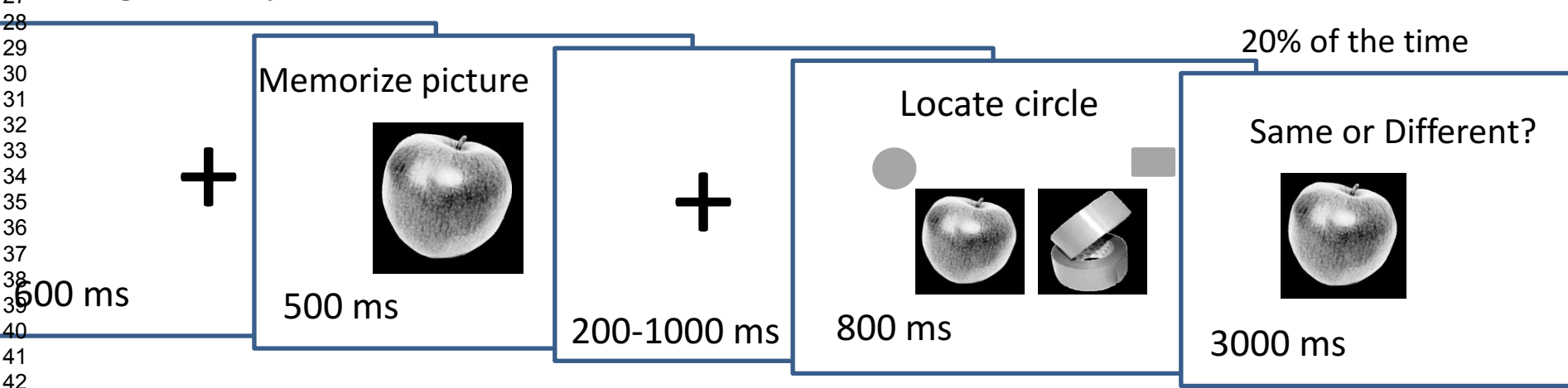
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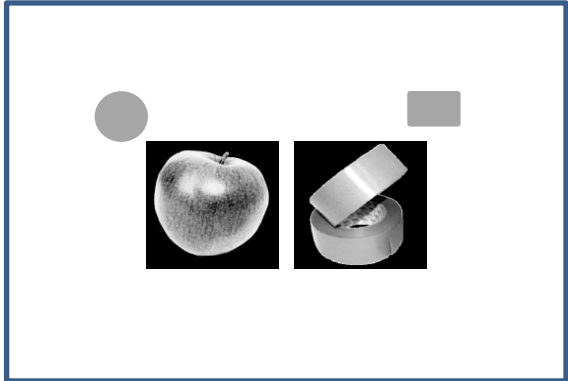
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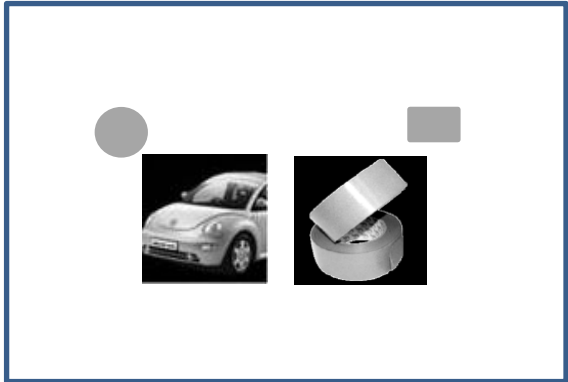
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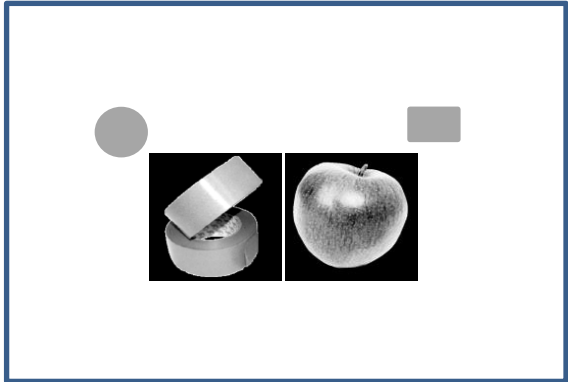
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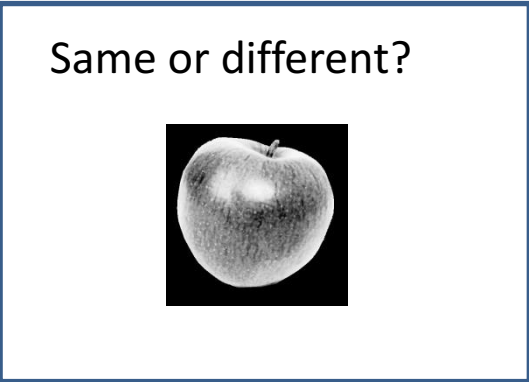
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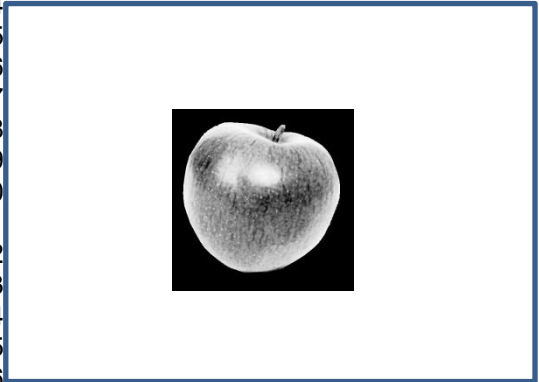
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Memory test

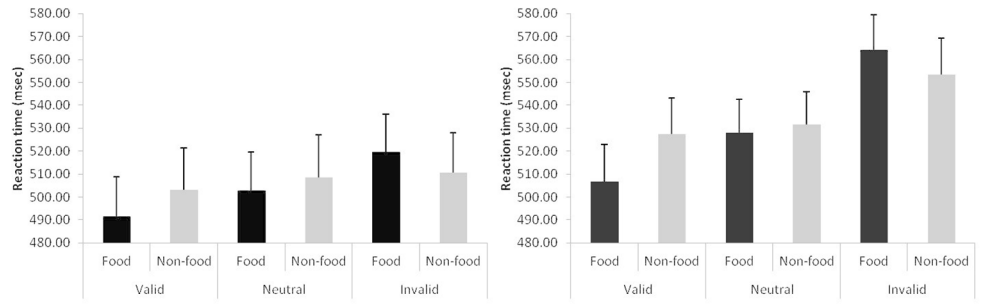


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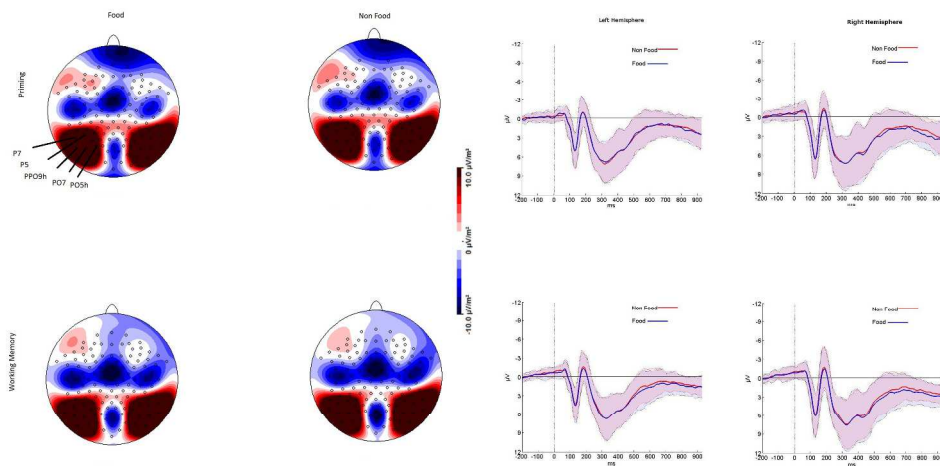
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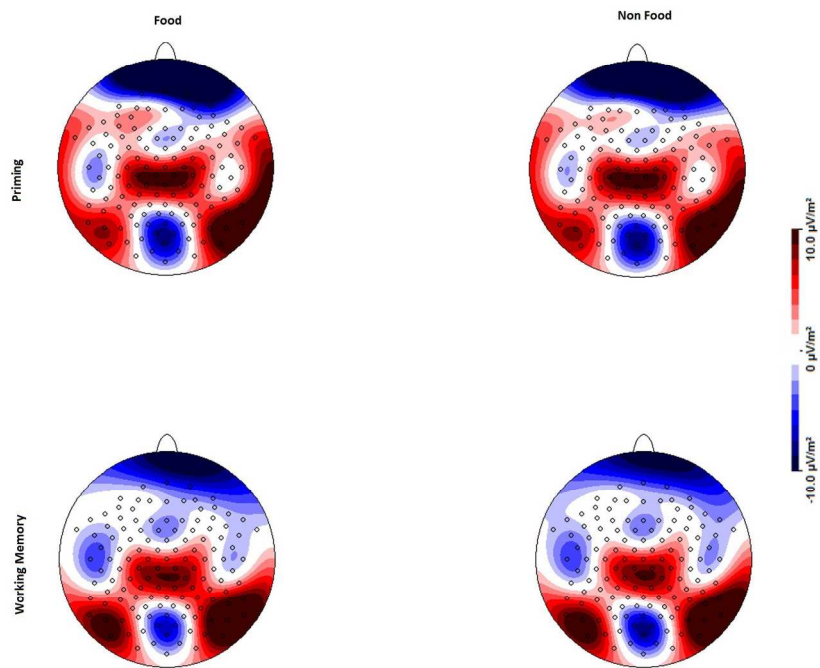
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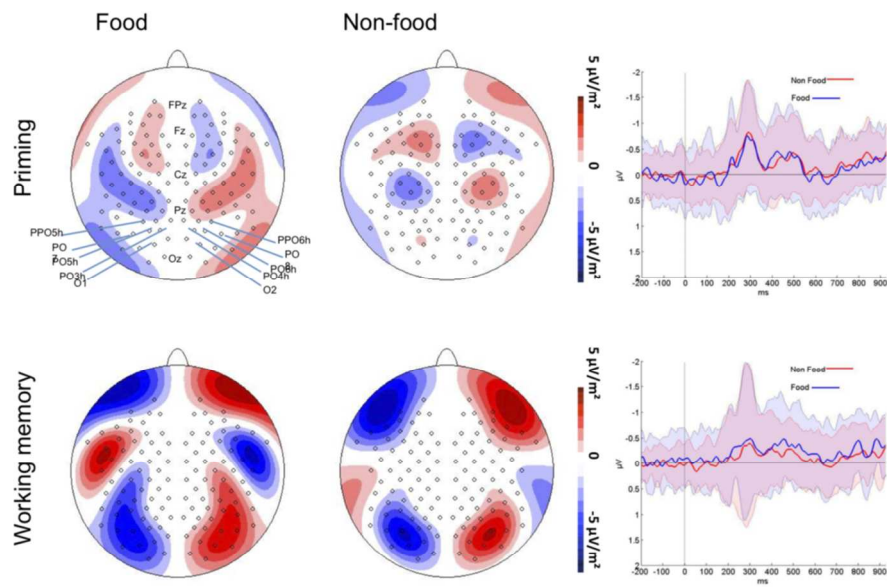


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Table 1: the mean amplitudes (μV) of the P3 (left and right hemisphere), LPP (left and right hemisphere) and SPCN components to the target next to the food or non-food cues for Valid, Invalid, and Neutral trials, for the Priming and Working Memory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

Task	Trials	P3 left hemisphere	P3 right hemisphere	LPP left hemisphere	LPP right hemisphere	SPCN
<i>Priming</i>	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
<i>Working memory</i>	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