

Deprivation Selectively Modulates Brain Potentials to Food Pictures

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Event-related brain potentials (ERPs) were used to examine whether the processing of food pictures is selectively modulated by changes in the motivational state of the observer. Sixteen healthy male volunteers were tested twice 1 week apart, either after 24 hr of food deprivation or after normal food intake. ERPs were measured while participants viewed appetitive food pictures as well as standard emotional and neutral control pictures. Results show that the ERPs to food pictures in a hungry, rather than satiated, state were associated with enlarged positive potentials over posterior sensor sites in a time window of 170–310 ms poststimulus. Minimum-norm analysis suggests the enhanced processing of food cues primarily in occipito-temporo-parietal regions. In contrast, processing of standard emotional and neutral pictures was not modulated by food deprivation. Considered from the perspective of motivated attention, the selective change of food cue processing may reflect a state-dependent change in stimulus salience.

Keywords: human eating behavior, food deprivation, motivation, visual attention, ERPs

In natural environments, selective attention effects are often regulated by motivational states (Derryberry & Tucker, 1994). Attention can be captured according to the inherent motivational significance of external cues, or it can vary by the organism's current need state. The former route of attention direction has been extensively studied in the past decade, comparing motivationally significant cues with neutral stimuli (Bradley et al., 2003; Lang, Bradley, & Cuthbert, 1997; Öhman, Flykt, & Lundqvist, 2000; Schupp, Junghöfer, Weike, & Hamm, 2003; Vuilleumier, 2005). In contrast, much less is known about the latter route: the impact of dynamically shifting internal motivational states. When related to current motivational needs, stimuli may reflexively capture attentional resources to facilitate efficient responding (Lang et al., 1997). Food deprivation provides a model system to explore the neural mechanisms of state-dependent shifts in the perception of need-related food stimuli.

An attention bias for food cues in hungry state has already been suggested in behavioral research. By studying food words in the

modified Stroop paradigm, it has been shown that food deprivation delayed the naming of the color of food words (Channon & Hayward, 1990; Lavy & van den Hout, 1993; but see reservations in meta-analyses, Dobson & Dozois, 2004). Similarly, research with the dot probe paradigm revealed that the attention capture of food words was enhanced in a hungry state but not a satiated state (Mogg, Bradley, Hyare, & Lee, 1998; Placanica, Faunce, & Soames Job, 2002). A differential processing for food pictures in a hungry state in comparison with that in a satiated state has also been demonstrated by psychophysiological measures (e.g., Drobles et al., 2001; Mauler, Hamm, Weike, & Tuschen-Caffier, 2006). More direct evidence that hunger increases selective attention to food stimuli has been obtained using neuroimaging measures. A functional magnetic resonance imaging (fMRI) study revealed that viewing food pictures in a hungry state enhanced the activity in visual-associative brain regions as well as in the amygdala, a structure known to be involved in the detection of motivational and emotional significant stimuli (LaBar et al., 2001; Sabatinelli, Bradley, Fitzsimmons, & Lang, 2005). An important extension of these findings is to determine the temporal dynamics of deprivation-induced effects on food cue processing.

This study explores whether hunger already modulates the perceptual processing of food cues by using event-related brain potentials. To reveal the obligatory nature of deprivation effects, participants passively viewed the stimuli. Because selective-attention studies observed changes in stimulus perception primarily under conditions of high perceptual load (cf. Luck, Woodman, & Vogel, 2000), pictures were presented as a rapid serial stream. A further aim of this study was to determine the specificity of state-dependent variation in motivational sig-

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nificance. The use of nonfood appetitive as well as aversive pictures allowed us to test whether deprivation specifically modulates the processing of food cues. Deprivation may influence cortical reactions to appetitive stimuli in general (food and pleasant) or to emotional stimuli regardless of hedonic valence (pleasant and unpleasant).

Method

Participants

Sixteen healthy right-handed male volunteers (mean age: 24.3 years, $SD = 4.8$) from the University of Greifswald participated in this study. Women were excluded for the chosen two-session design because of possible confounds due to the menstrual cycle. The mean body mass index was 23.1 ($SD = 2.2$). Participants received 15 € upon participation in both experimental sessions.

Stimulus Materials

Thirty-two appetizing food pictures depicting principle meals and desserts were taken from commercially available cookbooks. Nonfood control pictures ($N = 96$) were selected from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2005), including pleasant, neutral, and unpleasant contents. The stimuli were presented as a continuous stream without a perceivable interstimulus gap, with each picture shown for 333 ms. Pictures were presented in random order, assuring that the categories were equally often preceded by each other category. To increase signal-to-noise ratio, we repeated the set 10 times.¹

Procedure

Participants first attended a screening session, in which they were informed about the requirements for implementing the food deprivation condition and the normal eating condition. Questions from the Diagnostisches Interview bei Psychischen Störungen (Diagnostical Interview for Mental Disorders; Margraf, Schneider, & Ehlers, 1991) were administered, and eating habits were assessed by standardized eating scales (Inventar zum Essverhalten und Gewichtsproblemen; Diehl & Staufienbiehl, 1994; including German adaptations from the Three-Factor Eating Questionnaire (TFEQ), Stunkard & Messick, 1985). Participants with eating disorders, food allergies, vegetarian diet, or other patterns of selective eating were excluded. Further exclusion criteria were current use of medication, psychiatric or neurological illness, and diabetes mellitus. Written informed consent approved by the Review Board of the University of Greifswald was provided by the participants.

Each participant was tested on 2 days, 1 week apart, either in a food-deprived state or a satiated state. The order of these experimental sessions was counterbalanced. Testing always occurred after lunch time to control for variations in circadian rhythm. Before the food deprivation session, participants were asked to refrain from eating anything and drinking sweetened beverages for 24 hr. Instructions for the satiated session required participants to follow their normal eating habits and to have a regular lunch. Before both testing sessions, participants were requested to record their food and fluid intake and to abstain from drinking alcohol. Participants were informed that they

would have to give a urine sample prior to each session and were thus encouraged to disclose any food that they had eaten (used as a bogus pipeline; cf. Drobles et al., 2001). All participants (except 1 who was excluded from the final sample) reported that they had complied with these requirements.

On each session, participants rated their subjective feeling of hunger and appetite. For the EEG measurement, participants were instructed to passively view the picture stream. Afterward, pictures had to be evaluated on a 9-point Likert scale on the dimensions of valence and arousal (cf. Bradley & Lang, 1994).

Data Collection, Reduction, and Analysis

Subjective Ratings

Hunger and appetite ratings were separately analyzed by using *t* tests that compared hungry versus satiated states. Picture ratings were analyzed for valence and arousal with analyses of variance (ANOVAs) with repeated measurement on the factors of *State* (hungry and satiated) and *Picture Category* (food, pleasant, neutral, and unpleasant).

Event-Related Brain Potentials (ERPs)

Electrophysiological data were collected from the scalp by means of a 129-lead geodesic sensor net (Electrical Geodesics, Inc. [EGI], Eugene, OR). The EEG was recorded continuously with a sampling rate of 250 Hz, with the vertex sensor as reference electrode, and was filtered online from .01 to 100 Hz by using Netstation acquisition software and EGI amplifiers. Impedances were kept below 30 kΩ, as is recommended for this type of amplifier by EGI guidelines. Off-line analyses were performed using ElectroMagnetic EncephaloGraphy Software (EMEGS) (Junghöfer & Peyk, 2004), including low-pass filtering at 30 Hz, artifact detection, sensor interpolation, baseline correction, and conversion to an average reference (Junghöfer, Elbert, Tucker, & Rockstroh, 2000). Separate averages were calculated for food and nonfood control pictures in the two sessions for each sensor and participant.

To uncover effects of motivational state on picture processing, a first stream of analysis was based on single-sensor waveform analyses. In these analyses, ANOVAs containing the within-subjects factors of *State* (hungry and satiated) and *Category* (food, pleasant, neutral, and unpleasant) were calculated for each time point after picture onset separately for each individual sensor. To guard against chance findings, we considered significant effects meaningful only when the effects were observed for at least six continuous data points (24 ms) and two neighboring sensors (cf. Sabbagh & Taylor, 2000). Results revealed a significant interaction of *State* and *Category* in the time window from 170 to 310 ms poststimulus over posterior sensor sites. These effects were mirrored over centrofrontal sites, that is, with opposite polarity.

In a second stream of analysis, these effects were explored by conventional ANOVA analyses on the basis of mean activity in selected sensor clusters and time windows. For brevity, only

¹ Previous studies already showed that the processing of emotional stimuli does not vary as a function of stimulus novelty (cf. Schupp et al., 2006).

posterior sensor regions are reported. Mean amplitudes from representative posterior sensor clusters, identified by both visual inspection and waveform analyses, were averaged for three time intervals ranging from 170 to 210 ms, from 220 to 260 ms, and from 270 to 310 ms.² Data were entered into a four-factorial ANOVA including the within-subjects factors *Time* (three intervals: 170–210, 220–260, and 270–310), *State* (hungry and satiated), *Picture Category* (food, pleasant, neutral, and unpleasant), and *Laterality* (left and right).

Additional control analyses concerning potential carryover effects in the rapid serial presentation paradigm indicated that the deprivation effects were not modulated as a function of the valence of the preceding picture: *State* × *Preceding Picture Category*, $F(2, 30) = 1.8$, *ns*.

L2 minimum-norm analysis. L2 minimum-norm (MN) solutions were calculated to provide neural-source estimations for the differential processing of food stimuli as a function of motivational state. Calculations were based on a spherical four-shell isotropic volume conductor head model with 3 (radial, azimuthal, and polar direction) × 197 evenly and spherically distributed dipoles as a source model. A source shell radius of 6 cm was chosen as a trade-off between depth sensitivity and spatial resolution (Hauk, 2004).

Replication of selective emotion processing. To replicate previous findings of selective emotion processing, and to explore unspecific effects of food deprivation on emotion processing, we scored the early posterior negativity (EPN) in bilateral temporo-occipital clusters in a time window from 200 to 300 ms (cf. Schupp et al., 2007). Data were entered into an ANOVA, including *State*, *Valence* (pleasant, neutral, and unpleasant), and *Laterality*.

Results

Behavioral Data

Hunger and Appetite

As was expected, subjective feelings of hunger and appetite were increased in deprived states in comparison with satiated states, $t(1, 15) = 17.9$ and 13.4 , $p < .001$, respectively (see Table 1).

Table 1
Subjective Ratings of Hunger and Appetite and Picture Evaluation on Dimensions of Valence and Arousal for Food and Nonfood Control Picture

Variable	Satiated	Hungry
Hunger ^a	2.85 (1.09)	8.00 (0.68)*
Appetite ^b	1.44 (1.81)	8.41 (1.62)*
Valence ^c		
Food	6.36 (1.10)	7.53 (0.90)*
Pleasant	7.18 (0.87)	7.20 (0.91)
Neutral	5.43 (0.78)	5.47 (0.62)
Unpleasant	2.92 (0.61)	2.93 (0.87)
Arousal ^d		
Food	2.75 (1.50)	4.39 (1.78)*
Pleasant	4.96 (1.74)	4.86 (1.57)
Neutral	2.47 (1.25)	2.35 (0.92)
Unpleasant	5.68 (1.45)	5.54 (1.36)

Note. Standard deviations are in parentheses.

^a Score range from 1 to 9, with higher scores indicating stronger feelings of hunger. ^b Score range from 0 to 10, with higher scores indicating stronger feelings of appetite. ^c Score range from 1 (very unpleasant) to 9 (very pleasant). ^d Score range from 1 (very calm) to 9 (very exciting).

* Significant difference between satiated and hungry state, $p < .01$.

Picture Evaluation

When food-deprived, participants rated the food pictures as significantly more pleasant, $t(15) = 5.0$, $p < .001$, and arousing, $t(15) = 4.0$, $p = .001$, in comparison with the satiated state. Specificity of deprivation effects for food stimuli was indicated by significant interactions of *State* × *Picture Category* for valence and arousal ratings, $F_s(3, 45) > 10.8$, $p < .001$. Valence and arousal ratings of the nonfood emotional control pictures were not influenced by deprivation, *State*: $F_s(1, 15) < 1$; *State* × *Picture Category*: $F_s(2, 30) < 1$.

As in previous research, ratings of pleasant, neutral, and unpleasant control pictures significantly varied in valence, $F(2, 30) = 161.7$, $p < .001$. Furthermore, pleasant and unpleasant pictures were evaluated as more arousing than were neutral stimuli, $F(2, 30) = 74.6$, $p < .001$ (see Table 1).

ERP Data

As is illustrated in Figures 1A and 1B, the ERPs to food pictures in a hungry, rather than a satiated, state were associated with enlarged positive potentials over posterior sensor sites in a time window from 170 to 310 ms poststimulus. This deprivation effect was specifically observed for the processing of food cues. There were no significant differences in the processing of nonfood control pictures between the hungry state and the satiated state (cf. Figure 1C). Statistical analyses supported these observations. A significant interaction of *State* and *Picture Category*, $F(3, 45) = 4.2$, $p < .05$, was obtained, which was followed up by separate analyses of food and nonfood control pictures.

Food Cues

Food cues elicited an increased posterior positivity in a hungry state in comparison with a satiated state, $F(1, 15) = 4.6$, $p < .05$. The interaction of *Time* × *State* was not significant, $F(2, 30) < 1$. For exploratory purposes, the time intervals were analyzed separately. As is illustrated in Figures 1B and 1C, the effect of food deprivation appeared most pronounced in the first and last time intervals, $F_s(1, 15) = 5.3$ and 7.3 , $p < .05$, respectively, while it attenuated in the second interval, $F(1, 15) = 1.6$, *ns*. While laterality effects are suggested in Figure 1, neither the main effect of *Laterality*, $F(1, 15) < 1$, nor higher-order interactions of *State* × *Laterality*, $F(1, 15) = 2.0$, *ns*, or *State* × *Laterality* × *Time*, $F(1, 15) < 1$, were significant.

Nonfood Control Pictures

The processing of the nonfood control pictures was not influenced by deprivation for pleasant, neutral, and unpleasant pictures, $F_s(1, 15) < 1.9$, *ns*, respectively. No higher-order interactions, including *State* × *Time*, reached significance, $F_s < 1$.

² As the topographical focus of the difference varied over time, the clusters for the three intervals were adjusted (EGI sensor numbers of the first cluster: 31, 32, 37, 38, 43, 48, 51, 52, 53, 54, 59, 60, 61, 66, 67, 72 [left]; 77, 78, 79, 80, 81, 85, 86, 87, 88, 92, 93, 94, 98, 99, 105, 106 [right]; second cluster: 32, 38, 43, 52, 53, 54, 61 [left]; 79, 80, 81, 87, 88, 93, 94 [right]; third cluster: 7, 31, 32, 37, 38, 43, 48, 52, 53, 54, 60, 61, 67 [left]; 78, 79, 80, 81, 86, 87, 88, 93, 94, 99, 105, 106, 107 [right]).

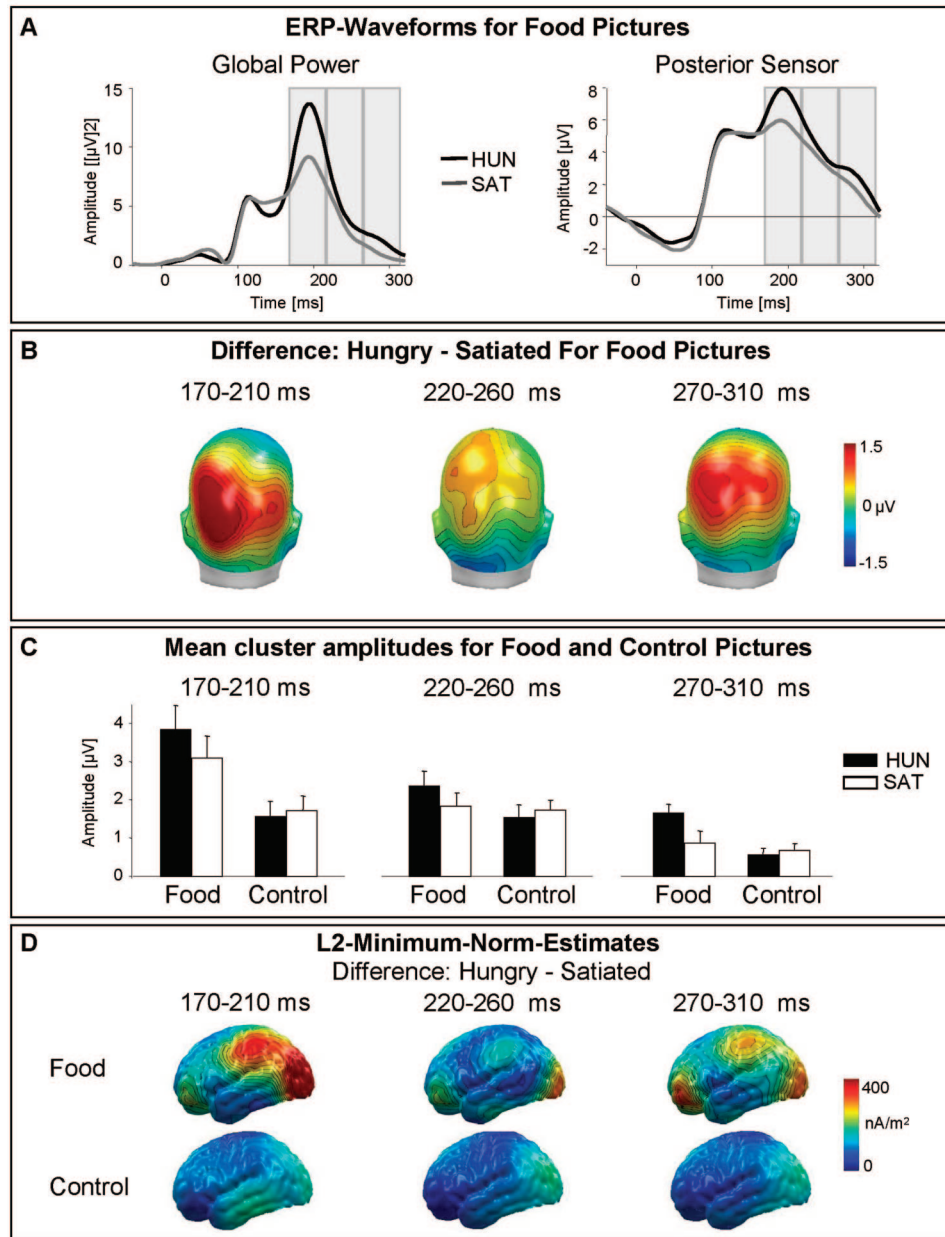


Figure 1. (A) Event-related brain potential (ERP) waveforms for food pictures in hungry (HUN) and satiated (SAT) states. The left side illustrates the global field power (i.e., the mean of the squared potentials across all electrodes) serving as a global measure of scalp potentials. The right side shows the waveform of a representative posterior sensor (#66). (B) Scalp potential maps show the topography of the difference between hungry and satiated states for food-cue processing in three time intervals from 170 to 310 ms. Illustrated is the back view of a model head. Voltages were interpolated to the scalp surface with spherical splines. (C) Mean amplitudes of selected posterior sensor clusters (averages across left and right), showing differences between hungry (HUN) and satiated (SAT) states for food and nonfood control pictures, averaged across pleasant, neutral, and unpleasant picture contents. (D) L2 minimum-norm estimates of the deprivation effects for food and nonfood control pictures for the three time intervals.

L2 MN Analysis

As is shown in Figure 1D, the difference in processing food cues in a deprived state in comparison with a satiated state was primarily modeled by sources over occipito-temporo-parietal

regions. Moreover, L2 MN solutions indicated secondary sources over frontal regions, suggesting that the polarity reversal of the deprivation effect over anterior sites may not solely reflect polarity reversal but, at least in part, engagement of

anterior brain regions. In contrast, L2 MN solutions for nonfood control pictures showed no systematic differences as a function of the food deprivation.

Replication of Selective Emotion Processing: Early Posterior Negativity

Previous studies consistently observed that emotional rather than neutral picture processing is associated with an increased early posterior negative (EPN) potential, most pronounced between 200 and 300 ms poststimulus (Schupp et al., 2007). To pursue these findings, we explored whether the EPN component is affected by food deprivation. By replicating previous findings, we observed a significant main effect of *Valence*, $F(2, 30) = 63.9, p = .001$. Pleasant and unpleasant pictures elicited a more pronounced posterior negativity in comparison with neutral pictures, $F_s(1, 15) = 102.2$ and $71.4, p < .001$, respectively. Furthermore, this analysis indicated neither a differential influence of the motivational state on emotional picture processing, $State \times Valence, F(2, 30) < 1$, nor a significant main effect of *State*, $F(1, 15) = 3.0, p = .11$.

Discussion

This study explores whether the perceptual processing of food pictures is modulated by the current motivational state. In support of this hypothesis, we observed a significant deprivation effect over posterior sensor clusters contrasting the processing of food cues in hungry and satiated states. The results revealed that deprivation effects were limited to food cues and did not extend to the processing of nonfood appetitive or aversive stimuli. The novel finding of this study is that internal motivational factors already modulate the perception of food stimuli around 170 ms poststimulus. Such a state-dependent increase in the salience of food cues may be an important mechanism to efficiently organize food-related behaviors (LaBar et al., 2001; Lang et al., 1997; Öhman et al., 2000).

A number of recent Positron Emission Tomography (PET)- and fMRI studies suggest that food deprivation and food stimulus processing affect the activity in limbic structures (amygdala, orbitofrontal gyrus, and insular cortex) as well as the extrastriate visual cortex (Cheng, Meltzoff, & Decety, 2007; Killgore et al., 2003; LaBar et al., 2001; Morris & Dolan, 2001; Simmons, Martin, & Barsalou, 2005; Porubská, Veit, Preissl, Fritsche, & Birbaumer, 2006; Uher, Treasure, Heining, Brammer, & Campbell, 2006). Most relevant to this study, LaBar et al. (2001) observed that food deprivation enhanced the activity in higher-order visual-associative regions and the amygdala when processing food pictures, considered to reflect the enhancement of visual attention to the need-related cues. The finding that hunger increased visual attention to food cues was followed up by this study, emphasizing the temporal dynamics of these effects. Confirming the selective processing of food pictures, ERPs revealed enhanced posterior positive deflections for food pictures in a hungry versus a satiated state, developing already around 170 ms and lasting for approximately 150 ms. Enhancing the spatial resolution of surface-recorded brain potentials by L2 MN source calculations, deprivation effects on food processing were associated with primary activations in posterior perceptual representation networks. In addition, secondary activations were suggested over anterior brain

regions. However, spatial resolution is insufficient to determine whether this finding relates to orbitofrontal activations, which were observed when comparing food-cue processing in hungry and satiated states and food stimuli varying in their incentive value (Arana et al., 2003; Critchley & Rolls, 1996; Gottfried, O'Doherty, & Dolan, 2003; Morris & Dolan, 2001; O'Doherty et al., 2000). Furthermore, deprivation effects appeared more pronounced over left-hemispheric regions. Recent fMRI studies observed that the activation of the amygdala in the context of food-cue processing is more pronounced in the left amygdala (LaBar et al., 2001; Morris & Dolan, 2001). Considering the hypothesis that perceptual processing at the cortical level is regulated by activity in subcortical limbic structures (cf. Vuilleumier, 2005), one may speculate whether lateralized ERP findings reflect effective connectivity of cortico-subcortical structures. Overall, consistent with the hypothesis of the state-dependent motivational regulation of selective attention, the present findings demonstrate that hunger modulates the processing of food cues early in the visual processing stream.

An important feature of the present design was to include emotionally significant control materials to determine the specificity of food-deprivation effects (Drobes et al., 2001; Lüthy et al., 2003; Mauler et al., 2006). Consistent with previous research, deprivation specifically affected subjective evaluation of food pictures. With regard to enhanced positive potentials for food cues over posterior regions, deprivation had no effect on appetitive, neutral, or aversive control materials. Furthermore, the finding that the emotion-sensitive EPN component did not vary as a function of hunger state also suggests that food deprivation did not elicit general arousal effects (cf. Hull, 1943). Thus, regarding the processing of emotional control pictures, no evidence was observed for the interaction of the two routes of motivational influence, that is, the inherent significance of the stimulus and the current motivational state. The present findings are furthermore consistent with research demonstrating that food deprivation specifically enhanced the reinforcing value of food cues and approach tendencies toward food cues (Epstein & LeDey, 2006; Seibt, Häfner, & Deutsch, 2007). All told, this study obtained evidence that food-deprivation effects are specific to the processing of food cues.

While the latency of the deprivation effect was similar as in previous studies that examined emotionally significant cues or explicit feature-based selective attention, the effects appear different with regard to their topographical attributes (cf. Codispoti, Ferrari, Junghöfer, & Schupp, 2006; Junghöfer, Bradley, Elbert, & Lang, 2001). Specifically, the difference potential associated with stimulus significance is characterized by a broadly distributed negativity over occipitotemporal areas and a positive difference over central sites. In comparison, the deprivation effect observed here revealed small negative deflections over inferior occipital areas and a predominant positive difference over parieto-occipital sites (see Figure 1B). While the present data do not allow us to know whether these differences reflect a reversal in polarity or reveal a shift in topography, several aspects may contribute to these differences. Food stimuli may elicit activity in distinct higher-order visual-associative regions, as has been reported for faces, human bodies, tools, and locations (reviewed by Malach, Levy, & Hasson, 2002). Thus, in comparison with the topography of selective visual attention effects associated with emotion and target processing, differences in scalp potential fields associated with need-related changes in food processing may reflect differ-

ences in the engagement of food-selective visual-associative brain regions, differences in dipole orientation, or both. Interestingly, L2 MN source analysis revealed increased activation over posterior perceptual and anterior regions for the cue-specific deprivation effect, concurring with neural source analysis reported for emotional and target stimulus processing (cf. Codispoti et al., 2006; Junghöfer et al., 2001, 2006). Thus, while the data are consistent with the notion of a state-dependent regulation of perception and visual attention, more research is needed to demonstrate that both the state-dependent motivational and the emotional regulation of visual attention are based on similar neural mechanisms.

Some limitations with regard to this study need to be considered. Compliance with the instruction was measured by means of self-report and a “bogus pipeline” urine sample (cf. Drobles et al., 2001). However, subjective ratings of hunger pronouncedly increased (Drobles et al., 2001; Leland & Pineda, 2006; Mogg et al., 1998), and as in previous research (Lüthy et al., 2003; Mauler et al., 2006), food stimuli were judged more pleasant and more arousing after deprivation than in a satiated state. Thus, while no physiological data were obtained as a manipulation check, subjective report suggests that participants complied with the eating protocol. Furthermore, only men were examined. As recent studies have shown gender differences in the context of food deprivation (Stoessel, Cox, Cook, & Weller, 2007; Uher et al., 2006), the selective processing of food cues in a hungry state needs to be further explored in women.

In conclusion, this study provides evidence for the notion that hunger modifies the perceptual processing of food cues. Food-deprivation effects were specific to food stimuli and did not affect the perceptual processing of pleasant, neutral, and unpleasant natural scenes taken from the IAPS library. Considered from the perspective of motivated attention (Lang et al., 1997), the state-dependent increase in the salience of food-related visual cues may foster behaviors needed to restore energy levels.

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