Neurosci Bull June 1, 2015, 31(3): 317–330. http://www.neurosci.cn
DOI: 10.1007/s12264-014-1520-6

·Original Article·

Event-related potential signatures of perceived and imagined emotional and food real-life photos

Fernando Marmolejo-Ramos[1], Kim Hellemans[2], Amy Comeau[2], Adam Heenan[3], Andrew Faulkner[2], Alfonso Abizaid[2], Amedeo D'Angiulli[2, 4]

[1]*Department of Psychology, Stockholm University, Stockholm, Sweden*

[2]*Department of Neuroscience, Carleton University, Ottawa, Ontario, Canada*

[3]*Department of Psychology, Queens University, Kingston, Ontario, Canada*

[4]*Institute of Interdisciplinary Studies, Carleton University, Ottawa, Ontario, Canada*

Corresponding author: Amedeo D'Angiulli. E-mail: amedeo.dangiulli@carleton.ca

ABSTRACT

Although food and affective pictures share similar emotional and motivational characteristics, the relationship between the neuronal responses to these stimuli is unclear. Particularly, it is not known whether perceiving and imagining food and affective stimuli elicit similar event-related potential (ERP) patterns. In this study, two ERP correlates, the early posterior negativity (EPN) and the late positive potential (LPP) for perceived and imagined emotional and food photographs were investigated. Thirteen healthy volunteers were exposed to a set of food photos, as well as unpleasant, pleasant, and neutral photos from the International Affective Picture System. In each trial, participants were first asked to view a photo (perception condition), and then to create a visual mental image of it and to rate its vividness (imagery condition). The results showed that during perception, brain regions corresponding to sensorimotor and parietal motivational (defensive and appetitive) systems were activated to different extents, producing a graded pattern of EPN and LPP responses specific to the photo content – more prominent for unpleasant than pleasant and food content. Also, an EPN signature occurred in both conditions for unpleasant content, suggesting that, compared to food or pleasant content, unpleasant content may be attended to more intensely during perception and may be represented more distinctly during imagery. Finally, compared to LLP activation during perception, as well as imagery and perception of all other content, LPP activation was significantly reduced during imagery of unpleasant photos, suggesting inhibition of unwanted memories. Results are framed within a neurocognitive working model of embodied emotions.

Keywords: food; emotion; perception; mental imagery; ERP; EPN; LPP; vividness; International Affective Picture System; embodiment

INTRODUCTION

Attentive engagement with real-life photographs is thought to be determined by the emotional salience of the stimuli, the consequent activation of the brain's appetitive and defensive motivation systems, and phenomenological as well as behavioral correlates[1]. Regardless of the system recruited, brain activation is strongest for highly arousing photos, both pleasant (e.g. erotic) and unpleasant (e.g. mutilation), indicating greater attention to and encoding of strong emotional stimuli[2]. The more emotionally arousing and motivationally salient the photo, the stronger the activation – typically, in the centro-parietal and occipital midline areas[3], and the response amplitudes are correlated with the self-reported vividness of the visual experience[4]. Neuroimaging and behavioral evidence also shows that in normal-weight individuals, food-related stimuli markedly increase cortical and limbic activation compared to neutral stimuli[5, 6]. Also, motivation for food is associated with the activation of some of the same limbic structures, such as the amygdala and anterior cingulate gyrus, which are also typically associated with emotional processing and reward[7].

While food pictures may have emotional characteristics and motivational activation similar to emotional stimuli, the relationship between the neuronal responses to food photos (whether seen or imagined) and those to emotional (pleasant or unpleasant) photos has not been thoroughly investigated. In particular, what is not clearly understood is the nature of motivation related to food and eating and how it interacts with cognitive components such as perception and mental imagery, which are considerably modulated by motivation. For example, it is not known whether being in front of a specific food with a high incentive value (e.g. chocolate cake) elicits a drive that is perceived (or imagined) as negative and that requires fulfilment (e.g. eating the cake), or whether the high incentive value of the food elicits a positive motivational state (through perception and imagery) related to the hedonic value of the specific food stimulus. One way to answer these types of questions is by examining brain activation to investigate whether event-related potentials (ERPs) correlate with perceived and imagined emotional photos. In this study, we investigated two specific ERP correlates [the early posterior negativity (EPN), and the late posterior potential (LPP)] of perceived and imagined unpleasant and pleasant emotional photos, and their relations to the perception and imagery of food photos.

Emotions and Sensorimotor and Somatosensory Systems

Research on the processing of emotions has used pleasant, neutral, and unpleasant stimuli. The results indicate that, compared to pleasant and neutral stimuli, unpleasant stimuli take longer to be reliably appraised, likely because they represent a threat[8]. Behavioral studies support this claim; for example, see [9] and [10]. Further evidence indicates that while unpleasant images cause a tendency to move away from the stimulus, pleasant images do not induce a tendency to approach[11]. Thus, it seems that identifying, attending to, and localizing unpleasant stimuli are necessary to avoid threats to well-being (see also [12]). More importantly, these results suggest a link between the processing of unpleasant stimuli and sensorimotor processes, which may reflect the embodiment of emotional states.

Indeed, embodied cognition theories propose that the processing of emotionally-laden stimuli entails the activation of somatosensory and sensorimotor areas[13]. fMRI data support this proposition in that cortical areas such as the superior frontal gyrus and the precuneus are activated during the experience of interoceptive bodily states[14]; the premotor and the supplementary motor cortex (anterior paracentral lobule) are also activated during the viewing of emotionally-laden images[15]. In the specific case of unpleasant images (such as mutilation), the premotor cortex, the left orbitofrontal cortex, and the left and right supplementary motor cortex are also activated[15].

Experimental Stimuli Used in Emotion Research

One of the most widespread stimulus databases used to study the ERP correlates of emotional and motivational processing is the International Affective Picture System (IAPS)[16]. The IAPS photos include contents normed as unpleasant (e.g., threat scenes, mutilation), neutral (e.g., household objects), and pleasant (e.g., erotica, sports scenes). Both pleasant and unpleasant IAPS photos elicit two replicable ERP signatures: the EPN and the LPP[17]. The EPN typically starts becoming evident at ~150 ms following stimulus onset, becoming progressively and maximally negative 300–400 ms after the stimulus[18-21]. Prominent at bilateral temporo-occipital sites[18-22], the EPN seems to originate from the visual cortices and may reflect increased activity in relatively early visual processing that supports the initial encoding of a scene[23]. The LPP is a large positive waveform evident ~500 ms after stimulus onset, maximal at midline parietal sites after ~700–1000 ms[2, 24-26]. It is sustained for as long as the affective stimulus is present, and may not resolve even after stimulus offset[27]. Combined fMRI/ERP data[28, 29] show that the LPP correlates with activation in the lateral occipital, inferotemporal, and parietal visual areas, suggesting that it reflects an enhancement of the representation underlying motivationally and emotionally salient stimuli, similar to the distinct working memory representation of task-relevant stimuli[23].

Despite the modest spatial resolution of EEG techniques, the cortical areas under or very close to the electrodes display characteristic ERP signatures. In addition, inferences from potential topological distributions combined with the EPN and LPP latencies can offer information about cognitive processes. Thus, if LPP signals complex social stimuli with emotional processing as posited by embodied theories[17], this signature should be observed during the processing of unpleasantly-laden images, mainly around the parietal area, since this area harbors the precuneus and the somatosensory cortex. Further, the EPN should be recorded in fronto-central sites at a minimum in two critical temporal windows: (1) 80–200 ms, presumably reflecting bottom-up sensory mechanisms relevant to stimulus salience, and (2) 300–800 ms, presumably reflecting top-down control mechanisms that support the processing of task-relevant stimuli[17] (see 'Experimental Procedure' in the Methods section).

Models of Emotional Processing

The processing of IAPS photos has been mainly explained by underlying processes involving the appetitive motivational system (A-system) and/or the defensive motivational system (D-system). These are two sets of neuronal circuitry that mediate approach and aversion and that are described as the (dual-system) motivational salience network (MSN)[30-32].

Research in emotion and motivation is not clear-cut as to whether these systems share common neuronal mechanisms[33]. However, if emotions and motivations, in tandem, have a direct effect on general affective, cognitive, and associated bodily states, it is tenable that imaging studies report brain areas common to both systems. Some cortical areas that have been reported to activate during emotion and motivation processes are the prefrontal cortex and the parietal lobe. In addition, the anterior cingulate cortex in the limbic lobe has been flagged as an area that plays a key role in both emotion and motivation processing[33-37]. However, more specific areas such as the superior frontal gyrus (SFG; Brodmann's areas 4, 6, and 8), anterior paracentral lobule (supplementary motor area; SMA), primary and secondary somatosensory areas (SI and SII), motor and premotor cortices (M and PM), cuneus (C), and precuneus gyrus (PCG) seem important to the processing of emotions and motivations[35, 38]. The reason why these areas seem relevant is because they coordinate sensory systems (e.g. SFG), control movement (e.g., SMA), manage the reception of sensory and motor stimuli (e.g. SI, SII, M, PM), and deal with visuo-spatial processing and episodic memories (e.g. C and PCG). Although such functions are acknowledged in embodied cognition research[39], some of the brain areas related to those functions have not been studied thoroughly in the emotion research area. Thus, as recently proposed[37], melding research in the embodiment of cognition and research in emotions can be useful in producing comprehensive explanatory models. The main message from brain studies in emotion and motivation is that both seem to be part of a unitary affective system that modulates affective, cognitive, and bodily states.

LeDoux[40] proposes that emotions, motivations, reinforcement, and arousal can be pieced together in what he calls a survival circuit model (SCM). According to the model, survival circuits (innate circuits controlling responses to survival-related stimuli[41]) are activated by innate or learned emotional stimuli encountered during interactions with the environment. This model further argues that sensorimotor and somatosensory systems have evolved to assist the organism's interactions with the environment and facilitate its adaptation to challenging situations. In the SCM, experiences with the environment are registered in memory systems and are given meaning *via* language. That language participates in the processing of emotions is an important characteristic of the SCM model in that language enables the creation of mental models of social situations that entail mental and emotional states (see also [42] for a model of cognition in which language plays a central role). Another key aspect of the SCM model is that it is compatible with the idea that emotions and their somatosensory and sensorimotor correlates can be shaped by sociocultural contexts[43]. For example, approach and aversion behaviours can be tuned to the specific context in which they take place. Thus, there should be evidence of a link between the activation of somatosensory and sensorimotor processes and the activation of an approach and aversion (dual-system) MSN.

Goals and Hypotheses

Based on the characteristics of the models described above, it is reasonable to predict that evidence of a link between the activation of somatosensory and sensorimotor processes and activation of the dual-system MSN may manifest as pleasant and unpleasant photos eliciting two distinct ERP patterns reflecting the different relation of the MSN to sensorimotor processes: (1) a relatively prevalent activation of the appetitive motivation system associated with seeing and imagining pleasant photos; and (2) a relatively prevalent activation of the defensive motivation system associated with seeing and imagining unpleasant photos. Many (but not all) previous studies have found that pleasant and unpleasant IAPS photos prompt similar ERPs when matched for arousal (see review in [44]). A critical difference between the present approach and most studies is that, to disambiguate the relative contribution of the two motivational systems possibly related to embodied sensorimotor processes, we selected photos that are not matched in arousal or valence (as in [45]). This should produce the specific predicted effects for unpleasant or pleasant contents, depending upon how they are rated regarding arousal and valence (reviewed and discussed in [45]).

A related goal of this study was to determine which unpleasant or pleasant ERP responses would be similar to the ERP response to food photos. The latter test would satisfy the two possible alternative hypotheses regarding the relative prominence of affiliation of the neuronal correlates of food content visualization with either one of the two motivation systems associated with sensorimotor activation.

Finally, we hypothesized that some of the ERP patterns would be similar in both perception and imagery; however, we also expected differences in the amplitude of their relative signatures; lower in imagery than in perception. Thus, to compare the distinctiveness of the recollective representations generated in episodic memory in the two subsequent conditions, we predicted that self-rated vividness of imagery would correlate with the ERP gradient observed over content types during perception. Because unpleasant photos seem to elicit the most distinctive underlying memory representations[4, 46], the latter should be experienced and rated as the most vivid. Surprisingly, very few studies have specifically focused on the link between ERP signatures during visual perception of photos and ERP signatures, as well as recollection vividness, during subsequent visual mental imagery of the same episodic content.

METHODS

Participants

Seventeen healthy right-handed undergraduate students (9 females, 20–30 years old) participated in this study. All participants were recruited from an institutional subject pool, and received a course credit for participation. Written consent for participation and anonymous inclusion in aggregate data for publication purposes was given by the participants according to the Declaration of Helsinki[47]. This experiment was approved by the Institutional Research Board (IRB) of Carleton University.

The final dataset consisted of 13 participants (7 females) after excluding data from four (two showed EEG artefacts across all electrodes and two had unacceptably high Beck Depression Inventory[48] or State-Trait Anxiety Inventory[49, 50] scores). Two participants that had EEG data which contained too many artefacts across all electrodes were eliminated from the analysis. In one case, the artefacts were due to unexplained high impedance presumably from an unidentified external source (15%–60% of bad trials in any condition and up to 70% trials in midline electrodes). In the other case, equipment malfunction (intermittent electrical failure in multiple electrodes) resulted in a very small usable number of trials (~20% per condition) in most electrodes. Based on the few salvageable trials, the averages for both participants appeared extremely noisy and distorted. In addition, we decided to discard the entire data rather than introduce confounds in the grand averages as the artefacts could not be successfully modelled or corrected reliably. Two participants with unacceptably high BDI[48] or STAI[49, 50] scores were also excluded, due to ethical concerns and potential confounds resulting from mood and anxiety disorders. The tests were conducted on participants' arrival in the laboratory. Also, no participant reported potential eating disorders during the test administration phase. Following the guidelines of the IRB and due to the sensitive nature of the unpleasant photos, recruitment and testing were stopped once the minimal significant effect size was reached in a preliminary analysis. The estimated effect size is representative of experiments with sample sizes similar to ours (i.e., $t(12) = 2.24$, $P = 0.045$, corresponding to Cohen's d of 1.29, and an effect size (r) of 0.54; for an example see [51]).

Experimental Procedure

Upon arrival, participants completed questionnaires to measure the level of hunger/food craving (General Food Craving Questionnaire - State - G-FCQ-S[52]) and obtain basic demographics. Participants were then fitted with EEG caps connected to data acquisition hardware. Prior to the experimental trials, 10 practice trials with neutral photos were run to ensure that the participants understood the instructions. Then two experimental blocks were performed – one containing 25 neutral and 25 food photos, and one containing 20 neutral, 20 pleasant, and 20 unpleasant photos. This block design and the use of the two sets of intermixed "buffering" neutral images minimize confounds between food and unpleasant/pleasant content[53, 54]. After the experimental blocks, participants were shown 20 emotionally pleasant photos to displace potential negative emotions caused by the unpleasant photos.

Each trial began with a 1-s display of a blank white screen, followed by a screen containing only a horizontally and vertically centered "×", also for 1 s. A stimulus image was then displayed for 3 s, followed by another blank white screen for 1 s. For the next 3 s, participants were asked to form a mental image of the stimulus just viewed, and rate its vividness from 1 to 5 (1, no image; 5, very vivid) (Fig. 1). To avoid the confounding effects of uncontrolled mind-wandering, we asked the participants to focus on a specific structured imagery task that reliably engages specific imagery behavioral mechanisms[55, 56].

In this experiment, concurrent ERPs were recorded when the participants first viewed IAPS[16] photos of food, unpleasant, pleasant, or neutral content (perception condition) in each trial and then created a visual mental image. The vividness of the photo, i.e. clarity and detail (imagery condition), was also rated. Visual mental imagery was included as a way of distinguishing top-down processes (i.e. activation of centro-posterior dorsal and ventral visual cortical pathways in the absence of retinal input) involved in the high-level visual processing of photos[57, 58].

Presentation was conducted under normal room light

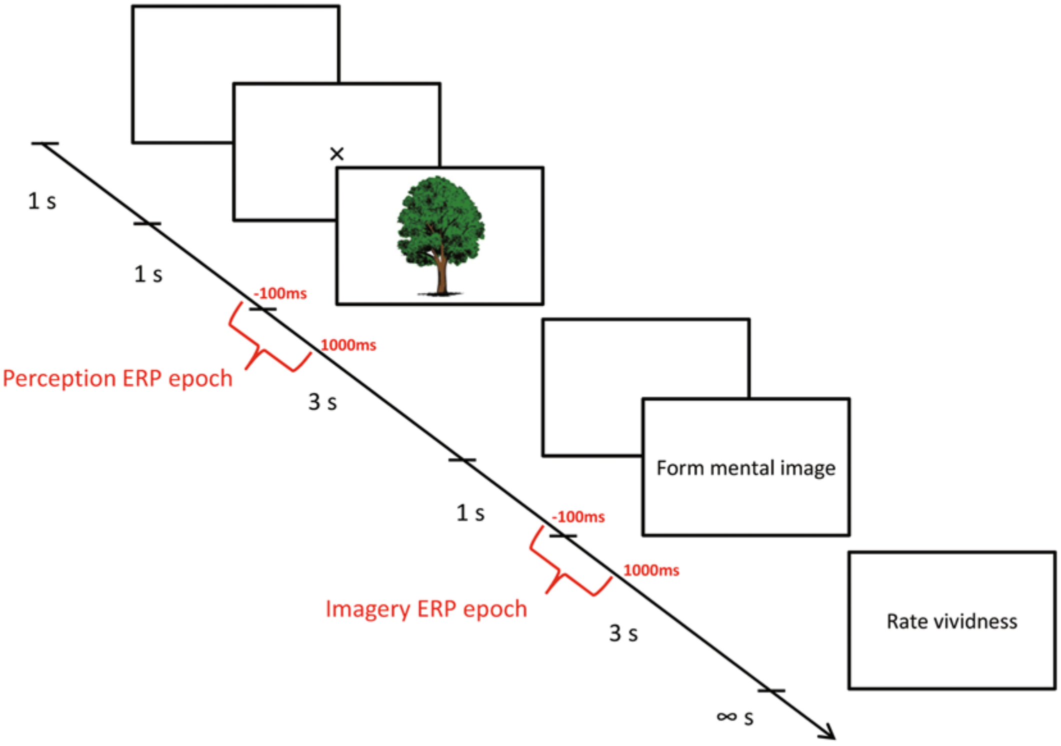

Fig. 1. **The procedure and sequence used in each experimental trial. The red segments correspond to the pre- and post-stimulus intervals (−100 to 1000 ms) with EEG epochs for ERP analysis.**

and with monitor display settings (luminance, brightness, and contrast) set at medium. No afterimages were reported.

Stimuli

Photos were selected from the IAPS. Pleasant, unpleasant, and neutral images were selected based on normative IAPS valence scores, with categories containing images rated in the top 20%, bottom 20%, and middle 20%, respectively. These types of unpleasant and pleasant photos have been previously used in affective processing studies[2, 26, 30, 59]. However, for food images, only those within the top 50% of valence scores, i.e., images expected to elicit robust appetitive responses, were included based on previous extensive pilot studies[54, 55] showing that this sub-category elicits distinctly different rating behaviors (related to both viewing and imagery) from the other categories of emotional pictures[60]. In addition, our previous studies showed that erotic content may introduce several complex confounds, so photos of a sexual nature were excluded. The characteristics of the selected stimuli are summarized in Figure 2A.

EEG Data Acquisition

EEG data were collected with the gel-free 32-channel Neuroscan Quik-Cap electrode placement system, which corresponds to the international 10-20 system. Data were recorded using SynAmps 2 amplifiers and Neuroscan SCAN 4.4 software. All electrode sites were referred to the tip of the nose. Electrooculograms were recorded from electrodes placed on the outer canthus of each eye, and above and below the left eye. During recording, impedance was kept at <5 KΩ.

ERP Processing

Prior to analysis, the EEG data were low-pass filtered (30 Hz, causal filter), and eye movements were modelled *via*

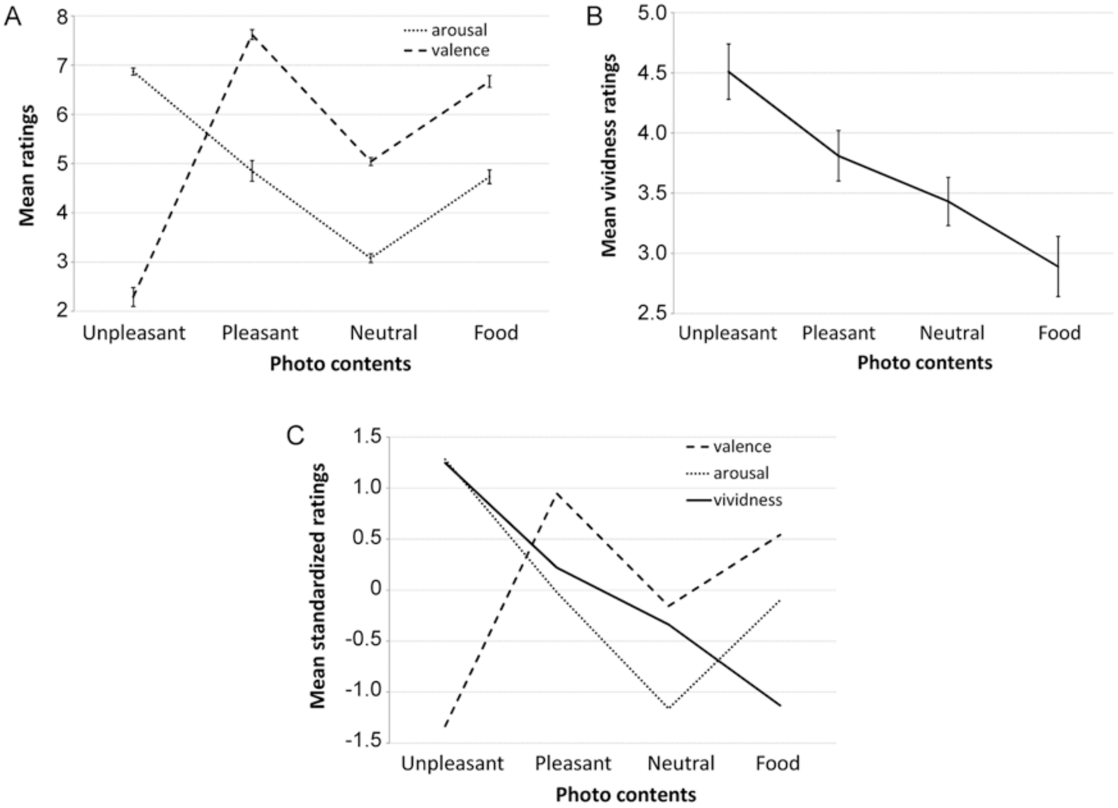

Fig. 2. Mean ratings of the IAPS photos selected as experimental stimuli. Mean arousal and valence ratings extracted from the IAPS (A), mean imagery vividness ratings given by participants (B) and mean standardized arousal, valence and vividness ratings (C). Error bars represent ±SEM.

a regression-based ocular artefact reduction algorithm[61]. Epochs were set between -100 ms pre-stimulus and 1000 ms post-stimulus, with baseline correction taken from -100 to 0 s. Offline averaging and peak analysis were performed using the amplitudes recorded over 4 midline electrodes (FZ, CZ, PZ, and OZ). Peak amplitudes of interest were time-locked to the time-intervals ~200–500 ms and ~500–950 ms, defining the EPN and LLP waveform complexes, respectively. Because preliminary exploratory analyses across the entire sweeps of waveform data revealed an identical pattern of results, for parsimony and clarity we report here the simpler, more focused analyses. To rule out averaging artefacts, we first confirmed that averaged ERPs in each participant reflected the morphological patterns of the group grand averages, and confirmed the reliability of the results by comparing grand averages with averages across all trials by condition (i.e., assuming independence of observations collapsed across all observations irrespective of participants) and showed no significant differences.

Data Analysis

Given that no block order effects for the design and no covariate effects of craving levels reported in the questionnaire were found in preliminary analyses (food craving ratings varied little across participants and explained <1% of the variation in the EEG data and their inclusion did not change the outcome of the analysis), those variables were dropped from further analysis. Also, no reliable effects of sex distribution were found to warrant further analysis. Thus, the analysis included a 2×4×4 repeated-measures ANOVA with the factors Condition (perception *vs* imagery) × Content type (pleasant, unpleasant, neutral, and food) × Electrode (FZ, CZ, PZ, OZ). Based on omnibus tests, we computed focused multiple pairwise contrasts, with Greenhouse-Geisser adjustment for within-participant effects, to calculate the mean standardized difference (in μV) needed at each electrode location for the neuronal activation patterns to differ significantly (such differences can be directly interpreted as effect sizes in the same meaningful metric[62]). Contrasts between mean amplitudes were made across the entire epoch, not just the EPN and LPP windows of interest. For ease of interpretation, the standardized mean difference valid for all the simultaneous multiple comparisons between types of content is shown in Figure 3.

RESULTS

ANOVA analysis (encompassing the entire epoch) revealed main effects of Electrode [$F(3, 36) = 33.19$, $P < 0.0001$] and Condition [$F(1, 12) = 4.17$, $P < 0.05$]. Significant interactions were found between Condition and Electrode [$F(3, 36) = 3.11$, $P < 0.05$], and between Content type and Electrode [$F(9, 108) = 3.80$, $P < 0.001$]. No other significant interactions were found.

In the grand averaged ERPs for the perception condition, the EPN was evident in both posterior and anterior electrodes followed by the LLP in centro-parietal electrodes (Fig. 3, left). This pattern was more evident in the perception of unpleasant photos than food photos. The perception of food photos showed an activation pattern intermediate between unpleasant and neutral/pleasant photos, which in turn showed a similar pattern of activation. The *post-hoc* Greenhouse-Geisser-adjusted simple contrasts of EPN and LPP amplitudes collapsed across Condition and Electrode indicated that, over centroparietal electrodes, both waveforms evoked by unpleasant photos were significantly greater than those elicited by pleasant, food, and neutral content. For both EPN and LPP waveform contrasts, the relative pairwise standardized mean differences exceeded 2.55 μV at CZ, 2.65 μV at OZ, 3.44 μV at FZ, and 3.78 μV at PZ [$t_{\text{contrast}}(12) > 7.06$, $P < 0.0001$]. Particularly, at FZ, the EPN amplitudes evoked by unpleasant content were again significantly greater than those evoked by all other types of content. In addition, at PZ, the LPPs for unpleasant and food photos significantly differed from one another at 450 ms. From 450 ms on, the LPPs of both unpleasant and food photos were significantly different from those of neutral and pleasant photos.

As to the grand averaged ERPs for the imagery condition, different patterns of activation for unpleasant *versus* food photos were evident (Fig. 3, right). For the unpleasant photo imagery, we recorded an early large EPN deflection first ~200–300 ms in the anterior electrodes (central midline) and then in the posterior electrodes (parietal midline and occipital midline). This was followed by a gradually increasing and then sustained LPP-like peak at ~600–700 ms. For food imagery, we found only a very late, positive waveform of modest amplitude from 650–700 ms onward, which was similar across all anterior and posterior electrodes. The large EPN effect for the unpleasant photos

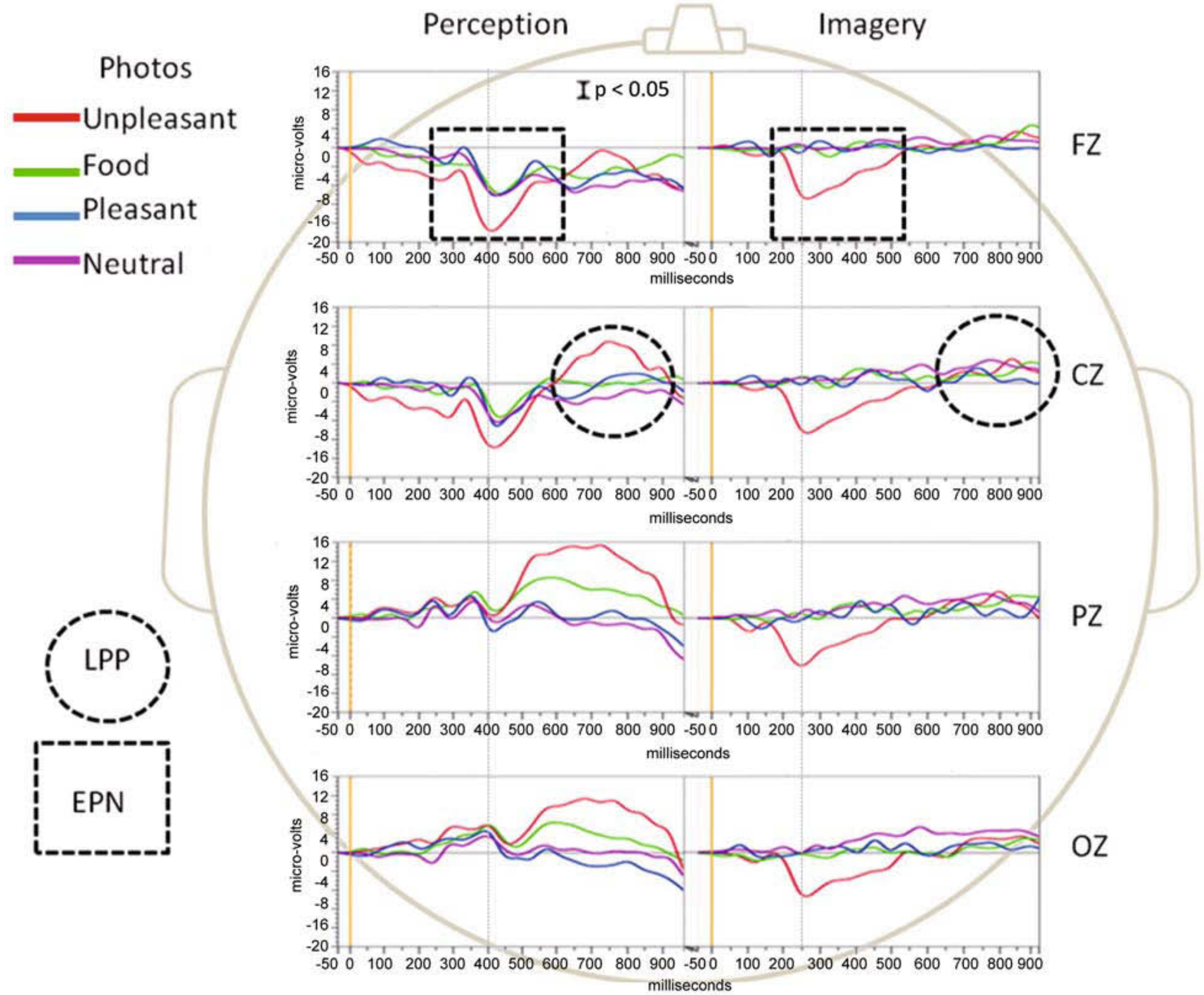

Fig. 3. Neuronal activation patterns at the midline locations averaged across participants for the 1000 ms following image presentation and 1000 ms after mental image formation. Pairwise standardized mean differences for peaks corresponding to the EPN and LPP waveforms are indicated. Due to graphical constraints and lack of relevant effects, the millisecond x-axis only shows the perception and imagery ERP intervals between -50 ms (prestimulus) and 950 ms (poststimulus).

began in the centro-parietal electrodes at ~170 ms and then in the frontal (200 ms) and occipital electrodes at 220 ms. The maximum negativity occurred at 250 ms for all midline electrodes, with a largest average negativity of ~−10 to −11 μV. For both EPN and LPP waveform imagery contrasts, the relative pairwise standardized mean differences exceeded 1.93 μV at OZ, 2.15 μV at PZ, 2.24 μV at CZ, and 2.01 μV at FZ [$t_{\text{contrast}}(12) = 3.54$, P <0.01]. Like the case of perception, the pleasant and neutral imagery EPNs did not differ significantly, and did not differ from the food imagery EPN. In contrast, the unpleasant imagery not only showed the largest EPN deflection but also the lowest LPP activation. In addition, during the LPP time interval, the LPP gradient was almost inverse to that found for perception, with the LPP for pleasant imagery showing the fastest and highest amplitude increase over all other types of imagery between 500 and 800 ms. The LPP for unpleasant imagery was subsequently followed by a progressive late (non-significant) amplitude increase in the LLP for food imagery from 800 to 1000 ms; by this late interval, both unpleasant and food imagery showed similarly higher LPPs than those for neutral and unpleasant imagery, which did not differ from baseline.

The EPNs for unpleasant imagery had a similar shape but longer duration and higher amplitude than those for unpleasant perception. However, the LPP for unpleasant imagery was markedly reduced compared to unpleasant perception. This pattern was reversed for all other types of content, with smaller EPNs during perception and no clear or minimally detectable EPNs during imagery, and the opposite pattern for LPPs.

In addition, paired sample *t*-tests (adjusted for multiple comparisons with the Bonferroni-Simes procedure[63]) confirmed that the vividness ratings were higher for unpleasant imagery than for any other imagery type [$t(12) = 3.34$, $P < 0.01$]. The vividness ratings of pleasant and neutral imagery did not differ [$t(12) = 1.80$, $P = 0.08$], but they were higher than those of food imagery [$t(12) = 3.40$, $P < 0.01$].

The mean standardized ratings of each photo item, comprising vividness rated by participants and the normed values for valence and arousal are shown in Fig. 2C. It is clear that there were no strong correlations between levels across the different measures for each of the means corresponding to the ERP patterns. This was supported by a by-item analysis which showed no significant relationships within the selected corpus of stimuli between mean perception and imagery ERP amplitudes and vividness ratings, for both EPN and LPP, *vs* arousal and valence values [for all ten correlations median $r(19) = 0.23$, or $r(24) = 0.19$, all $P > 0.30$]. These results confirm that the pattern of ERP and vividness relationships found did not have any direct and systematic counterpart in the distribution of the effects of the photos themselves; hence, it is implausible that arousal and valence values can, by themselves, explain the observed ERP patterns.

DISCUSSION

In this study, we found different patterns of ERP responses to different content types within each of the perception and imagery conditions, and between perception and imagery conditions.

In order to interpret the findings in terms of current theories, we propose a modified version of the 'shared circuits' model in which specific cognitive systems are necessary for processing of information. Specifically, we adopt a neurocognitive model that accounts for the processing of visual[42] and linguistic information[64-66] and that highlights the use of inference memory and simulation systems as essential to any cognitive process. More importantly, this model predicts that sensorimotor systems are required during dynamic interactions between vision and language, and recent behavioral[67] and imaging[68] evidence supports these predictions. Figure 4 illustrates this neurocognitive model as adapted for the processing of emotionally-laden stimuli (NeCoPES).

Our model predicts that key cognitive processes work together for the processing of emotionally-laden stimuli. In the NeCoPES model, memory systems in the hippocampus and related areas retain information about perceived events that have occurred and that are no longer present. Inferences are logical judgments based on the available evidence, previous memory records, and prior conclusions. Imaging studies suggest that the prefrontal cortex not only deals with emotions and motivations, but also performs inference processes[69]. Finally, simulations are dynamic mental models of actions, perceptions, and future events[70] and it is very likely that the mirror neuron system[38, 71] plays a part in this process.

In the perception condition, we recorded higher EPN and LPP activation for unpleasant photos, followed by food and then by pleasant and neutral photos. In the imagery condition, again EPN activation was higher for unpleasant than for all other content types, which themselves elicited similar responses. However, the LPP activation during imagery was lowest for unpleasant and neutral photos and highest for food and pleasant ones. These differences may be interpreted as partial support for the NeCoPES model. On one hand, unpleasant photos may activate a pattern of response predominantly (although not exclusively) linked with the defensive motivational system. On the other hand, both pleasant and food photos may predominantly activate a fronto-parietal response linked with the appetitive motivational system. The topography and time-course of the ERP patterns are consistent with the NeCoPES interpretation. During perception, the EPN first appeared at the frontal and occipital midline electrodes followed by the LPP in centro-parietal electrodes. During imagery, both EPNs and LPPs first appeared as more posterior (occipito-parietal) and earlier than perception yet with a similar

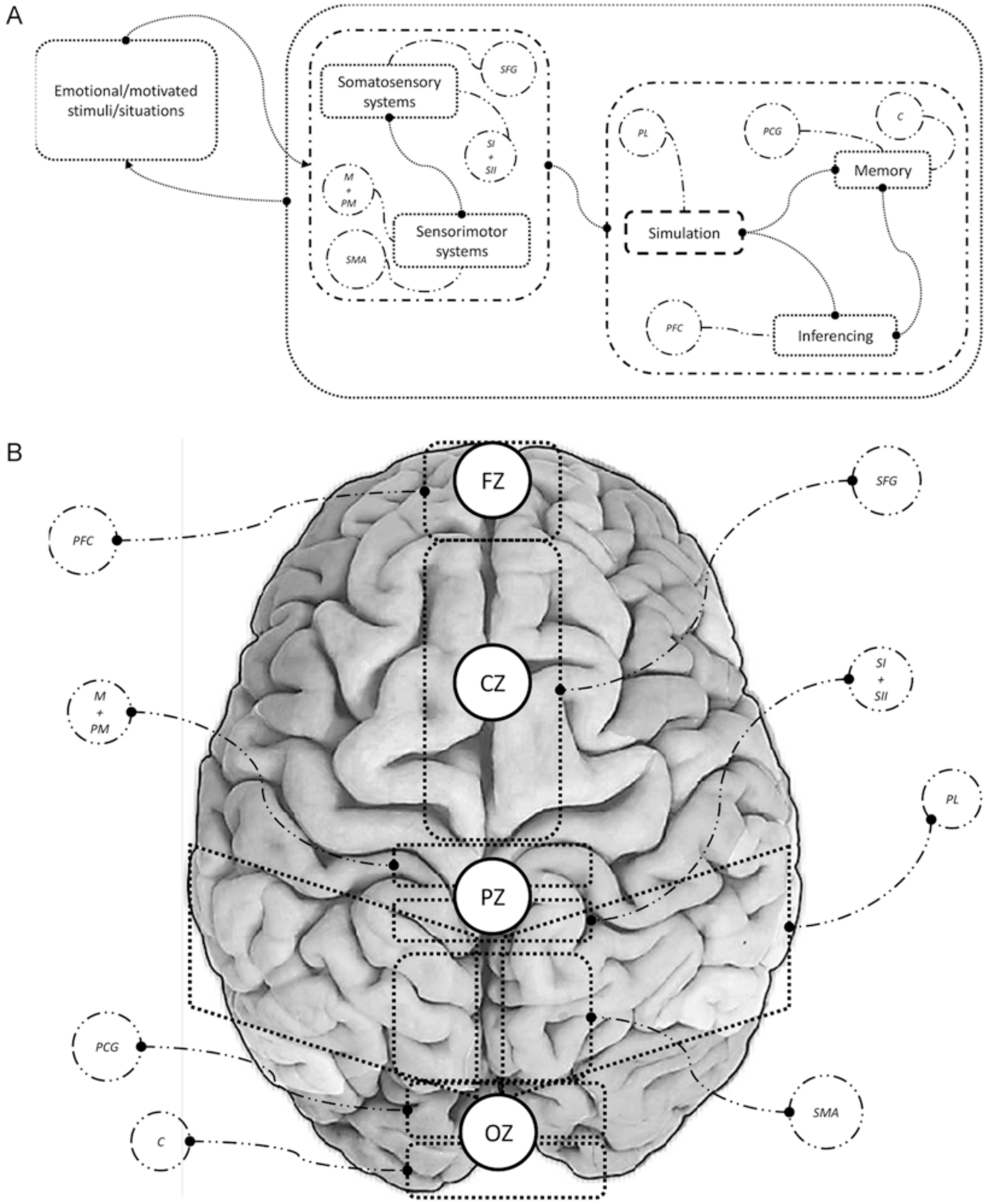

Fig. 4. A neurocognitive model for the processing of emotionally-laden stimuli, NeCoPES (A) and localization of areas of interest (B). The NeCoPES model focuses on superior midline neocortical areas and relies on high-order cognitive processes. The four midline electrodes used during the ERP sessions are also shown. PFC, prefrontal cortex; PL, parietal lobe; SFG, superior frontal gyrus; SMA, supplementary motor area (anterior paracentral lobe); SI + SII, primary and secondary somatosensory areas; M + PM, motor and premotor areas; C, cuneus; and PCG, precuneus.

temporal delay between them.

Comparison of EPN signatures between imagery and perception showed remarkable morphological similarities for unpleasant content. If the EPN reflects relatively early visual processing that supports the initial perceptual encoding of a scene[23], it is reasonable to conclude that the EPN correlates of perception may be reinstated during imagery, suggesting top-down processes similar to those involved in perceptual encoding and episodic memory. Consistent with reports that unpleasant content enhances perception[4] and memory accuracy[46, 74], our EPN and vividness findings suggest that unpleasant content may be recollected more distinctly and in more detail than food or pleasant content.

It is important to note that even if some of the same centers involved in mind-wandering (i.e., default networks) are shared by mental imagery, the effects of mind-wandering can occur over several seconds. Our imagery data relate to the first 950 ms of processing and showed differential patterns according to the type of picture imagined. This is unlikely to be explained by sustained mind-wandering, which would be revealed over a much longer time span and would not be expected to vary selectively as a function of the imagery task manipulation, but rather by fluctuations of task-unrelated thoughts[75].

Our EPN results add a novel insight to the literature. Emotion-enhancement during the perception of unpleasant photos reveals properties that seem to be shared when forming and using visual mental images of the same content. Accordingly, vividness may be best understood as an overarching binding feature deriving from higher-order top-down processes such as metacognition[76] or episodic memory[77] that are conjointly modulated by visual pathways and inputs from the arousal and limbic systems[78-80]. Although the neurobehavioral[57] and phenomenal relationships[56] between perception and imagery have long been established in the context of cognitive processes, until now empirical confirmation in relation to emotional processes has been relatively scarce and indirect. In terms of the NeCoPES model, such results lend support to the close relationship between memory, inferencing, and simulation neurocognitive systems. That is, emotionally-laden memory traces seem to have an effect on the formation of images *via* simulation processes (Fig. 4A).

Another finding of our study, however, highlights divergence rather than convergence between perception and imagery in relation to emotion. We found that the extent of LPP activation was significantly lower during unpleasant imagery than with other content and declined to minimum levels compared to unpleasant perception. Consequently, these findings invite an interpretation opposite to that of LPP in the role of enhancement. That is, following the initiation of recall of unpleasant mental images, LPP could be linked to suppression and inhibition of the emotional reaction stirred by the meaning of the representations reactivated in memory[81]. Therefore, it is possible that during unpleasant imagery the LPP may reflect a function that is different from the enhancement of stimulus processing served during perception and imagery of both pleasant and food content. Indeed, this is supported by evidence from Moser and colleagues[82], who demonstrated that processes involved in purposeful emotion regulation, such as mental imagery, can modulate LPP amplitude, which becomes less positive with instructions to intentionally block emotional responses to unpleasant photos. If, as the NeCoPES model assumes, memory and inferencing neurocognitive systems interact to feed the simulation processes, then further research is needed to establish how the simulation of negatively-laden imagery is attenuated. This is a future topic that could be conceptualized in terms of the NeCoPES model as these systems are explicitly considered in the processing of emotional stimuli.

The present findings indicate that both frontal and posterior-parietal electrodes corresponding to defensive and appetitive motivational systems are recruited during perception and imagery of photos. Critically, however, the magnitude of the activation in these systems differs with respect to content: defensive activation appears to be more prominent for unpleasant content, whereas the appetitive system is more prominent for pleasant and food content. Moreover, unpleasant content is attended to more intensely during perception, and is represented in memory more distinctly during imagery, than food or pleasant content. Thus, the early neuronal correlates of perception are reinstated during imagery, suggesting similar top-down processes involved in both the perceptual encoding and subsequent episodic memory of the experienced unpleasant content. By contrast, the late neuronal activation associated with semantic elaboration of the content was significantly reduced compared to other content types during the imagery task, which may be due to suppression and inhibition rather than a form of enhancement.

These findings may also help better understand the neuronal substrates of eating disorders that are characterized either by the inability to control food cravings, e.g., binge eating disorder, or disorders such as posttraumatic stress disorder that are associated with traumatic experiences and are also co-morbid with obesity. The NeCoPES model could be used as a test-bed for food-related studies. This area of research is only now emerging (e.g. [83, 84]) and the NeCoPES model may offer some initial neurocognitive insights.

ACKNOWLEDGEMENTS

We thank Yeh Wei-Hsien for help with data collection. This work was supported by funds from Carleton University (Faculty of Science), the Social Science and Humanities Research Council of Canada, and the Canadian Institute for Health Research. We also thank Robyn Groves and Rosie Gronthos for proofreading the manuscript.

Received date: 2014-08-14; Accepted date: 2014-12-12

REFERENCES

[1] Bradley M, Lang P. Emotion and motivation. In: Cacioppo J, Tassinary L, Berntson G (Eds.) Handbook of Psychophysiology (2nd Edition). New York: Cambridge University Press, 2006: 581–607.

[2] Cuthbert B, Schupp H, Bradley M, Birbaumer N, Lang P. Brain potentials in affective picture processing: covariation with autonomic arousal and affective report. Biol Psychol 2000, 52: 95–111.

[3] Nijs I, Franken I, Muris P. Food cue-elicited brain potentials in obese and healthy-weight individuals. Eat Behav 2008, 9: 462–470.

[4] Todd R, Talmi D, Schmitz T, Susskind J, Anderson A. Psychophysical and neural evidence for emotion-enhanced perceptual vividness. J Neurosci 2012, 32: 11201–11212.

[5] Killgore W, Young A, Femia L, Bogorodzki P, Rogowska J, Yurgelun-Todd D. Cortical and limbic activation during viewing of high-versus low-calorie foods. Neuroimage 2003, 19: 1381−1394.

[6] Wang G, Volkow N, Telang F, Jayne M, Ma J, Rao M, *et al.* Exposure to appetitive food stimuli markedly activates the human brain. Neuroimage 2004, 21: 1790−1797.

[7] Kavanagh D, Andrade J, May J. Beating the urge: Implications of research into substance-related desires. Addict Behav 2004, 29: 1359–1372.

[8] Flykt A, Dan ES, Scherer KR. Using a probe detection task to assess the timing of intrinsic pleasantness appraisals. Swiss J Psychol 2009, 68: 161–171.

[9] Ikeda H, Watanabe K. Anger and happiness are linked differently to the explicit detection of biological motion. Perception 2009, 38: 1002–1011.

[10] Stins JF, Beek PJ. Effects of affective picture viewing on postural control. BMC Neurosci 2007, 8: 83.

[11] Stins JF, Beek PJ. Organization of voluntary stepping in response to emotion-inducing pictures. Gait Posture 2011, 34: 164–168.

[12] Bradley MM. Natural selective attention: orienting and emotion. Psychophysiology 2009, 46: 1–11.

[13] Niedenthal PM, Winkielman P, Mondillon L, Vermeulen N. Embodied emotion concepts. J Pers Soc Psychol 2009, 96: 1120–1136.

[14] Terasawa Y, Fukushima H, Umeda S. How does interoceptive awareness interact with the subjective experience of emotion? An fMRI Study. Hum Brain Mapp 2013, 34: 598–612.

[15] Henderson LA, Stathis A, James C, Brown R, McDonald S, Macefield VG. Real-time imaging of cortical areas involved in the generation of increases in skin sympathetic nerve activity when viewing emotionally charged images. Neuroimage 2012, 62: 30–40.

[16] Lang P, Bradley M, Cuthbert B. International affective picture system (IAPS): Instruction manual and affective ratings. The Center for Research in Psychophysiology, University of Florida, 1999.

[17] Ibañez A, Melloni M, Huepe D, Helgiu E, Rivera-Rei A, Canales-Johnson A, *et al.* What event-related potentials (ERPs) bring to social neuroscience? Soc Neurosci 2012, 7: 632–649.

[18] Schupp H, Cuthbert B, Bradley M, Cacioppo J, Ito T, Lang P. Affective picture processing: the late positive potential is modulated by motivational relevance. Psychophysiology 2003, 37: 257–261.

[19] Schupp H, Markus J, Weike A, Hamm A. Emotional facilitation of sensory processing in the visual cortex. Psychol Sci 2003, 14: 7–13.

[20] Schupp H, Junghöfer M, Weike A, Hamm A. The selective processing of briefly presented affective pictures: An ERP analysis. Psychophysiology 2004, 41: 441–449.

[21] Schupp H, Öhman A, Junghöfer M, Weike A, Stockburger J, Hamm A. The facilitated processing of threatening faces: an ERP analysis. Emotion 2004, 4: 189–200.

[22] Junghöfer M, Sabatinelli D, Bradley M, Schupp H, Elbert T, Lang P. Flee-ting images: rapid affect discrimination in the visual cortex. Neuroreport 2006, 17: 225–229.

[23] Schupp H, Flaisch T, Stockburger J, Junghofer M. Emotion and attention: event-related brain potential studies. Prog Brain Res 2006, 156: 31–51.

[24] Foti D, Hajcak G, Dien J. Differentiating neural responses to emotional pictures: Evidence from temporal-spatial PCA. Psychophysiology 2009, 46: 521–530.

[25] Hajcak G, Nieuwenhuis S. Reappraisal modulates the electrocortical response to unpleasant pictures. Cog Affect Behav Neurosc 2006, 6: 291–297.

[26] Keil A, Bradley M, Hauk O, Rockstroh B, Elbert T, Lang P. Large-scale neural correlates of affective picture processing. Psychophysiology 2002, 39: 641–649.

[27] Hajcak G, Olvet D. The persistence of attention to emotion: brain potentials during and after picture presentation. Emotion 2008, 8: 250–255.

[28] Sabatinelli D, Bradley M, Lang P, Costa V, Versace F. Pleasure rather than salience activates human nucleus accumbens and medial prefrontal cortex. J Neurophysiol 2007, 98: 1374–1379.

[29] Sabatinelli D, Lang P, Keil A, Bradley M. Emotional perception: correlation of functional MRI and event-related potentials. Cereb Cortex 2007, 17: 1085–1091

[30] Lang P, Bradley M, Cuthbert B. Emotion, motivation, and anxiety: brain mechanisms and psychophysiology. Biol Psychiatry 1998, 44: 1248–1263.

[31] Bradley M, Sabatinelli D, Lang P, Fitzsimmons J, King W, Desai P. Activation of the visual cortex in motivated attention. Behav Neurosci 2003, 117: 369–380.

[32] Purves D, Brannon E, Cabeza R, Huettel S, LaBar K, Platt M, *et al.* Principles of Cognitive Neuroscience. Sunderland, Massachusetts: Sinauer, 2008.

[33] Chiew KS, Braver TS. Positive affect versus reward: emotional and motivational influences on cognitive control. Front Psychol 2011, 2: 279.

[34] Damasio AR. Descartes' Error: Emotion, Reason, and the Human Brain. New York: Grosset/Putnam, 1994.

[35] Damasio AR, Carvalho GB. The nature of feelings: evolutionary and neurobiological origins. Nat Rev 2013, 14: 143–152.

[36] Lewis MD. Bridging emotion theory and neurobiology through dynamic systems modelling. Behav Brain Sci 2005, 28: 169–245.

[37] Price TF, Peterson CK, Harmon-Jones E. The emotive neuroscience of embodiment. Motiv Emot 2012, 36: 27–37.

[38] Keysers C, Gazzola V. Integrating simulation and theory of mind: from self to social cognition. Trends Cogn Sci 2007, 11: 194–196.

[39] Meteyard L, Rodríguez S, Bahrami B, Vigliocco G. Coming of age: A review of embodiment and the neuroscience of semantics. Cortex 2012, 48: 788–804.

[40] LeDoux J. Rethinking the emotional brain. Neuron 2012, 73: 653–676.

[41] LeDoux J. Comment: what's basic about the brain mechanisms of emotion? Emot Rev 2014, 6: 318–320.

[42] Mishra R, Marmolejo-Ramos F. On the mental representations originating during the interaction between language and vision. Cogn Process 2010, 11: 295–305.

[43] Mesquita B, Boiger M. Emotions in context: a sociodynamic model of emotions. Emot Rev 2014, 6: 298–302.

[44] Bradley M, Lang PJ. The International Affective Picture System (IAPS) in the study of emotion and attention. In: JA Coan, JJB Allen (Eds.). Handbook of Emotion Elicitation and Assessment. Oxford University Press, 2007: 29–46.

[45] Lavoie M, O'Connor K. Effect of emotional valence on episodic memory stages as indexed by event-related potentials. World J Neurosci 2013, 3: 250–262.

[46] Kensinger E, Addis D, Atapattu R. Amygdala activity at encoding corresponds with memory vividness and with memory for select episodic details. Neuropsychologia 2011, 49: 663–673.

[47] World Medical Association. Ethical principles for medical research involving human subjects. World Medical Association, 2013.

[48] Beck A, Steer R, Brown G. Manual for Beck Depression Inventory II (BDI-II). San Antonio, TX: Psychology Corporation, 1996.

[49] Spielberger C, Gorsuch R, Lushene R. Manual for the State-Trait Anxiety Inventory. Palo Alto, CA: Consulting Psychologists Press, 1970.

[50] Spielberger C, Gorsuch R, Lushene R. Manual for the state-trait anxiety scale. Consulting Psychologists, 1983.

[51] Norberg J, Wiens S. Effects of attention manipulations on motivated attention to feared and nonfeared negative distracters in spider fear. BMC Neurosci 2013, 14: 139.

[52] Cepeda-Benito A, Gleaves D, Williams T, Erath S. The development and valid-ation of the state and trait food cravings questionnaires. Behav Ther 2000, 31: 151–173.

[53] Comeau A, Yeh WH, Abizaid A, Hellemans K, D'Angiulli A. Chopped Arms & Big Macs: ERP correlates of viewing and imagining aversive and food photos. Nat Preced 2010, doi:10.1038/npre.2010.4576.1.

[54] Delplanque S, N'Diaye K, Scherer KR, Grandjean D. Spatial frequencies or emotional effects? A systematic measure of spatial frequencies for IAPS pictures by a discrete wavelet analysis. J Neurosci Methods 2007, 165: 144–150.

[55] D'Angiulli A, Reeves A. Generating mental images: Latency and vividness are inversely related. Mem Cognit 2002, 30: 1179–1188.

[56] D'Angiulli A, Reeves A. The relationship between self-reported vividness and latency during mental size scaling of everyday items: Phenomenological evidence of different types of imagery. Am J Psychol 2007, 120: 521–551.

[57] Kosslyn S. Image and Brain: The Resolution of the Imagery Debate. MIT Press, Cambridge, MA, 1994.

[58] Kosslyn SM, Ganis G, Thompson WL. Mental imagery and the human brain. In: Jing Q, Rosenzweig MR, D'Ydewalle

G, Zhang H, Chen HC, Zhang K (Eds.). Progress in Psychological Science Around the World Vol. 1 Neural, Cognitive and Developmental Issues. London: Psychology Press, 2006: 195–209.

[59] Sabatinelli D, Bradley M, Fitzsimmons J, Lang P. Parallel amygdala and inferotemporal activation reflect emotional intensity and fear relevance. Neuroimage 2005, 24: 1265–1270.

[60] Faulkner A, Hellemans K, Abizaid A, D'Angiulli A. The neurophysiology of craving and drug-related cues: Evidence from event-related potentials. In: Honeycutt JM, Sawyer CR, Keaton S (Eds.). The Influence of Communication in Physiology and Health Status. New York: NY Peter Lang Publishing Inc, 2014: 189–206.

[61] Semlitsch H, Anderer P, Schuster P, Presslich O. A solution for reliable and valid reduction of ocular artifacts applied to the P300 ERP. Psychophysiology 1986, 23: 695–703.

[62] Shadish WR, Haddock CK. Combining estimates of effect size. In: Cooper H, Hedges LV (Eds.). The Handbook of Research Synthesis. New York: Russell Sage Foundation, 1994: 261–281.

[63] Simes R. An improved Bonferroni procedure for multiple tests of significance. Biometrika 1986, 73: 751–754

[64] Cevasco J, Marmolejo-Ramos F. The importance of studying the role of prosody in the comprehension of spontaneous spoken discourse. Rev Latinoam Psicol 2013, 45: 21–33.

[65] Marmolejo-Ramos F. Nuevos avances en el estudio científico de la comprensión de textos. Univer Psych 2007, 6: 331–343.

[66] Marmolejo-Ramos F, Cevasco J. Text comprehension as a problem solving situation. Univer Psych 2014, 13: 725–743.

[67] Iossifova R, Marmolejo-Ramos F. When the body is time: spatial and temporal deixis in children with visual impairments and sighted children. Res Dev Disabil 2013, 34: 2173–2184.

[68] Griffiths G, West R, D'Angiulli A. Cognitive modeling of event-related potentials. Proceedings of the 33th Cognitive Science Society Annual Meeting, 2011.

[69] Barbey AK, Patterson R. Architecture of explanatory inference in the human prefrontal cortex. Front Psychol 2011, 2: 162.

[70] Hesslow G. Conscious thought as simulation of behavior and perception. Trends Cogn Sci 2002, 6: 242–247.

[71] Heyes C. Where do mirror neurons come from? Neurosci Biobehav Rev 2010, 34: 575–583.

[72] Molenberghs P, Cunnington R, Mattingley J. Brain regions with mirror properties: A meta-analysis of 125 human fMRI studies. Neurosci Biobehav Rev 2012, 36: 341–349.

[73] Iacoboni M, Woods RP, Brass M, Bekkering H, Mazziotta JC, Rizzolatti G. Cortical mechanisms of human imitation. Science 1999, 286: 2526–2528.

[74] Kensinger E. Negative emotion enhances memory accuracy: Behavioral and neuroimaging evidence. Curr Dir Psychol Sci 2007, 16: 213–218

[75] Barron L, Riby LM, Greer J, Smallwood J. Absorbed in thought: The impact of mind-wandering on the processing of relevant and irrelevant events. Psychol Sci 2011, 22: 596–601.

[76] Pearson J, Rademaker R, Tong F. Evaluating the mind's eye: the metacognition of visual imagery. Psychol Sci 2011, 22: 1535–1542.

[77] D'Angiulli A, Runge M, Faulkner A, Zakizadeh J, Chan A, Morcos S. Vividness of visual imagery and incidental recall of verbal cues, when phenomenological availability reflects long-term memory accessibility. Front Psychol 2013, 4: 1.

[78] Anderson A, Yamaguchi Y, Grabski W, Lacka D. Emotional memories are not all created equal: Evidence for selective memory enhancement. Learn Mem 2006, 13: 711–718.

[79] Kensinger E, Garoff-Eaton R, Schacter D. How negative emotion enhances the visual specificity of a memory. J Cogn Neurosci 2007, 19: 1872–1887.

[80] Kensinger E, Garoff-Eaton R, Schacter D. Effects of emotion on memory specificity: Memory trade-offs elicited by negative visually arousing stimuli. J Mem Lang 2007, 56: 575–591.

[81] Brown SBRE, van Steenbergen H, Band GPH, de Rover M, Nieuwenhuis S. Functional significance of the emotion-related late positive potential. Front Hum Neurosci 2012, 6: 33.

[82] Moser JS, Hajcak G, Bukay E, Simons RF. Intentional modulation of emotional responding to unpleasant pictures: An ERP study. Psychophysiology 2006, 43: 292–296.

[83] Gerdes ABM, Wieser MJ, Bublatzky F, Kusay A, Plichta, MM, Alpers GW. Emotional sounds modulate early neural processing of emotional pictures. Front Psychol 2013, 4: 741.

[84] Razumiejczyk E, Macbeth G, Leibovich de Figueroa N. Interferencia entre el procesamiento de estímulos gustativos y estímulos visuales lingüísticos incompletos en la memoria operativa. Rev Latinoam Psicol 2013, 45: 231–239.