Mental imagery of emotions: Electrophysiological evidence

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ABSTRACT

Affective stimuli such as emotional words, scenes or facial expressions elicit well-investigated emotional responses. For instance, two distinct event-related brain potentials (ERPs) have been reported in response to emotional facial expressions, the early posterior negativity (EPN), associated with enhanced attention and perception of affective stimuli, and a later centro-parietal positivity (LPP) that is taken to reflect evaluations of the intrinsic relevance of emotional stimuli. However, other rich sources of emotions that have as yet received little attention are internal mental events such as thoughts, memories and imagination. Here we investigated mental imagery of emotional facial expressions and its time course using ERPs. Participants viewed neutral familiar and unfamiliar faces, and were subsequently asked to imagine the faces with an emotional or neutral expression. Imagery was compared to visually perceiving the same faces with the different expressions. Early ERP modulations during imagery resemble the effects frequently reported for perceived emotional facial expressions, suggesting that common early processes are associated with emotion perception and imagination. A later posterior positivity was also found in the imagery condition, but with a different distribution than for perception. These findings underscore the similarity of the brain's responses to internally generated and external sources of emotions.

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Introduction

Emotions are our everyday companions, and internal mental events such as thoughts, memories and imagination are rich sources of emotion, whether we remember bad experiences, imagine happy events we wish to take place, or vividly imagine the smiling face of a close but absent friend. However, even though such internally generated emotion events may trigger strong affective responses, emotion research has thus far mostly focused on effects of external stimuli such as visually presented emotionally arousing scenes, objects or faces displaying emotional expressions. Thus, little is known about affective brain responses to internally generated emotions. This holds particularly for the time course of these responses. In the present study we used electrophysiological measures of brain activity to investigate how the brain responds to internally generated emotional stimuli. Specifically, we tracked the temporal unfolding of affective responses triggered by mental imagery of facial expressions with event-related brain potentials (ERPs).

Mental imagery can be described as the ability to reactivate modality-specific mental representations from memory and to manipulate these representations without concurrent sensory stimulation or overt motor activity (Kosslyn, 1980; for a review see Kosslyn et al., 2001; Ganis and Schendan, 2011). This reactivation is often associated with the subjective experience of perceiving or acting within one's

mental world (Schendan and Ganis, 2012), and indeed, imagery is assumed to share to a great extent the processes underlying perception. For instance, research on single cell recordings in the human brain has demonstrated stimulus-type selective firing rates of neurons in the medial temporal lobe, with similar patterns of selectivity during perception and imagery, suggesting a common neural substrate for the processing of external visual information and visual recall (Kreiman et al., 2000). This conclusion is supported by other studies using functional magnetic resonance imaging (fMRI). O'Craven and Kanwisher (2000) found that the fusiform face area (FFA), a face-sensitive cortical region, and the parahippocampal place area (PPA), a region which is predominantly involved in the processing of visual scenes, show similar sensitivity patterns during mental imagery. That is, when faces are imagined FFA activation increases, whereas PPA shows stronger activation when visual scenes are imagined, analogously to activation patterns often observed for the perception of faces and scenes (Kanwisher et al., 1997; Epstein and Kanwisher, 1998).

Concerning emotion, a few studies suggest that imagery of emotional contents can induce affective responses in the form of, for instance, activations of the autonomic nervous system and several brain structures known to play a role in emotion processing (e.g., amygdala). Thus, Lang et al. (1993) observed an increase of heart and breathing rate and skin conductance not only when participants viewed pictures of threatening objects but also when the objects were mentally visualized. In a study using positron emission tomography (PET) mental images of aversive pictures activated the anterior insula, a major cortical structure receiving input from the autonomic nervous system (Kosslyn et al., 1996). Additionally, Kim et al. (2007) observed activations of the

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amygdala and several other brain areas when participants imagined affective compared to neutral facial expressions of unfamiliar persons. The authors concluded that the brain areas involved in the perception of facial expressions are also active during imagery, with the amygdala playing a central role. Together, these findings support the idea that mental imagery involves activations of neural structures and associated functional mechanisms that are also recruited during perception, and that emotion related cortical structures and the autonomic system are involved when emotional contents are imagined (e.g., Kosslyn et al., 2009).

In contrast to the well-established evidence on overlapping cortical regions and shared neural selectivity patterns in visual perception and imagery, little is known about the time course of mental imagery in general, and the time course of emotional imagery is yet to be established. Since imagery is a top-down triggered process in the absence of external stimulation, its time course may differ significantly from perception, even though the same brain structures may be involved.

Until now, ERP research on imagery has focused on emotionally neutral stimuli, such as letters (e.g. Farah, 1985, 1988; Qui et al., 2007), words (West and Holcomb, 2000), objects or faces with neutral expression (e.g. Ganis and Schendan, 2008; Wu et al., 2012). For example, Farah (1985, 1988) compared the perception of objects with and without additional instruction to imagine the same objects and reported facilitated perception, suggesting an interaction of perception and imagery at some common locus of activity. Recently, Schendan and Ganis (2012) used a matching task to reveal top-down cortical mechanisms for mental simulation of faces and objects. The authors concluded that top-down processes of mental imagery sustain an imagistic representation that mimics perception sufficiently to prime subsequent perception.

To summarize, ample evidence suggests that perception and imagery are governed by similar underlying mechanisms, and that imagery of emotional events leads to activations of the autonomic nervous system and brain regions associated with emotion processing. Yet, even though the same regions are involved in perception and imagery, these processes may differ significantly in their time course. Specifically, it is unclear whether internally generated emotion events or, as tested here, imaginations of facial expressions, are associated with comparable involuntary and fast affective responses as reported for emotional stimuli such as objects and scenes, including visually presented faces displaying emotional expressions (see below).

In the present study, we directly compared the perception of faces displaying happy, angry or neutral expressions with imagining the expressions of the same faces in the absence of external stimulation. In the ERP, the early posterior negativity (EPN), a relative negative deflection at posterior electrode sites around 200 to 300 ms, has been associated with automatic attention to and enhanced perception of affective stimuli, including facial expressions (e.g., Schacht and Sommer, 2009; Schupp et al., 2003, 2004a,b; Kissler et al., 2007) or emotionally arousing pictures (e.g. Junghöfer et al., 2001). It has been shown that this component is influenced by the arousal induced by emotional contents. That is, highly arousing pictures containing, for instance, mutilations or erotic scenes elicit a more pronounced EPN than less arousing pictures (Junghöfer et al., 2001; Schupp et al., 2004b). Furthermore, Schupp et al. (2006b) reported that the amplitude strength did not vary as a function of stimulus repetition. The authors concluded that the near absence of habituation during perception of emotional stimuli suggests a high degree of automaticity of the EPN.

A recent study by Löw et al. (2013) systematically investigated the influence of several factors such as picture content (presence of people or not), picture type (figure-ground or scenes) and arousal (emotionally arousing or neutral) on the EPN. All factors modulated the EPN, with the greatest enhancement for figure-ground compositions compared to scenes. Therefore, the authors suggest that this component can be described as reflecting natural selective attention. On a more general level, perceptual processing and encoding can be assumed to be guided

at least in part by underlying motivational systems of avoidance and approach (Schupp et al., 2006a,b; Pourtois et al., 2013). If imagining facial expressions includes comparable early reflexive affective responses as perceiving these stimuli, including enhanced attention levels facilitating perception-related processes, EPN effects with a similar time course and scalp distribution should be found for perception and imagery. Other perception related components that have been associated with the processing of faces and their emotional expressions are the P1 and N170 component (Bentin et al., 1996; Eimer, 2000). The N170 is an index of structural encoding and seems to be insensitive to familiarity and facial expressions (Eimer and Holmes, 2002; Herrmann et al., 2002).

Furthermore, at a later point in time, the perception of emotional stimuli and facial expressions is associated with a relative positivity at central sites at about 400 to 600 ms, the late positive potential (LPP; e.g., Cuthbert et al., 2000; Schupp et al., 2006a,b). Several findings suggest that the LPP is sensitive to manipulations of attention, and the component may reflect operations of a capacity-limited system (Schupp et al., 2006a,b). Furthermore, It has been suggested that the LPP reflects stimulus representations in working memory (Donchin and Coles, 1988) as well as a gateway to conscious recognition (Luck et al, 2000; Kranczioch et al., 2003). More generally, this component is taken to reflect sustained aspects of evaluating the intrinsic relevance of emotional stimuli. Because similar late evaluative and attentive processes should be associated with perceived and imagined facial expressions, we expected comparable LPP modulations during perception and imagery.

Previous studies on mental imagery have mostly used highly salient and well-known stimuli that are stored in long-term memory, such as words, letters, common objects or faces of celebrities. Thus, in addition to our main research question, we were interested in whether emotional mental imagery differs between well-known faces that are stored in and can be retrieved from long-term memory and unfamiliar faces that have not been seen before, and for which imagery of emotional expressions cannot simply be achieved by long-term memory retrieval. Concerning visual perception, the relation between identification/familiarity and emotion is a matter of ongoing debate (e.g., Bruce and Young, 1986; Haxby et al., 2000; Tranel et al., 1988; Young et al., 1993), ERP (Bobes et al., 2000) and fMRI studies (Phillips et al., 1998).

The influence of face familiarity on the EPN in face perception has yet to be established. However, there are hints on the interplay of familiarity and the late positivity. Studies focusing on familiarity have found increases in the late positivity at posterior electrode sites (Eimer, 2000; Voss and Paller, 2006; Yovel and Paller, 2004). In addition, enhanced amplitudes have also been found, when faces were high in social relevance (e.g. romantic partner, family members; famous persons with negative or positive biography; Abdel Rahman, 2011; Guerra et al, 2012; Bublatzky et al., 2014; Tiedt et al., 2014).

Methods

Participants

Twenty-four participants (15 female; mean age = 24.58 years, range 19–34) with normal or corrected-to-normal vision took part in the experiment for monetary compensation or for course credits. Informed consent was obtained from all participants before the experiment started. The study was approved by the institutions' ethical review committee.

Materials

We selected colored photographs of 20 familiar and 20 unfamiliar individual faces. Each individual face was presented with an angry, happy and neutral expression. All photographs were frontal headshots, scaled to 3.5 × 3.5 cm at a viewing distance of about 90 cm. Faces were

overlaid with a gray oval mask leaving only the faces visible without hair and neck parts. Unfamiliar faces were taken from the FACES Database (Ebner et al., 2010).

Faces of well-known actors, athletes and politicians known through their wide media presence were selected from the internet (see Appendix A). A rating with eight participants who did not take part in the main experiment was conducted. Participants rated the familiarity (1: unfamiliar, 2: familiar), valence and arousal of the expressions of all faces online. Valence and arousal ratings ranged from negative (−2) to positive (2) on a five-point-scale that was analog to the Self-Assessment Manikin (Bradley and Lang, 1994). Mean ratings for the faces were as follows: valence for a) angry faces: −1.87, b) happy faces: 1.92, c) neutral faces: 0.56; arousal for a) angry faces: 1.67, b) happy faces: 1.72, c) neutral faces: −1.59; familiarity for familiar faces: 1.87, unfamiliar faces: 1.24.

The unfamiliar face stimuli were adjusted by several measures (saturation, contrast, graining etc.) so they would appear as "real" images of unfamiliar faces, rather than faces from a controlled and highly homogeneous dataset.

Procedure

A trial (see Fig. 1) started with the presentation of a cue face that always displayed a neutral expression for 800 ms. After the subsequent presentation of a fixation cross for 500 ms, either a photograph of the same person with an angry, happy or the same neutral expression or an empty frame was presented for maximally 3 s. Participants were instructed to classify the expression as fast and accurately as possible using one of three buttons (angry, happy, neutral) when the second face was presented, and to imagine the cue face with an angry, happy or neutral expression when the empty frame was presented.. The type of expression to be imagined was indicated by the color of the frame. Participants classified which expression they had imagined or whether imagination had failed using one of four buttons (angry, happy, neutral, imagery failed). In the perception condition the faces were also presented with a frame in the corresponding color in order to keep physical appearances between stimuli as similar as possible. Task conditions

(perception or imagery) were randomized. Between trials a fixation cross was presented for 1100 ms. Participants were not familiarized with the face stimuli before the experiment.

The English translations of the instructions for the two tasks were as follows: a) perception condition "If you see a face, please decide via button press which emotion is expressed by the face (negative, neutral, positive). Thereby, it is very important that you concentrate on the face!", b) imagery condition "If you see the colored frame without a face, please imagine the before presented face in one of the 3 emotions — depending on the frame color. Please indicate via button press which emotion you have imagined. Thereby, it is very important that you truly imagine the face!". Practice trials with a face not used in the actual experiment were included. After the participant had understood the procedure fully, the experiment started.

The assignment of frame colors to facial expressions was counterbalanced across participants. Furthermore, secondary colors (RGBs: green — 84 255 60; orange — 255 165 0; violet — 224 102 255; turquoise — 0 194 255) were chosen to avoid a priori associations between colors and emotions that may be particularly strong for primary colors (e.g., red associated with angry). Participants learned the specific assignment of colors before the experiment. A fourth empty frame indicated a no-go trial implemented as control condition. Thus, participants had to refrain from imagining a facial expression and press the "imagery failed" button.

The assignment of classifications (happy, angry, neutral and imagery failed/no-go) to response buttons and the assignment of color to emotion condition were counterbalanced across participants. All faces in the three emotion conditions were presented four times in the perception and imagined four times in the imagery condition. In addition, 240 no-go trials were presented, leading to 1200 trials in total (80 trials per expression and familiarity). The experiment had a duration of about 2.5 h.

EEG data recording and analysis

The EEG was recorded with a BrainVision Recorder (Brain Products). 62 Ag/AgCl electrodes were used and placed in accordance to the
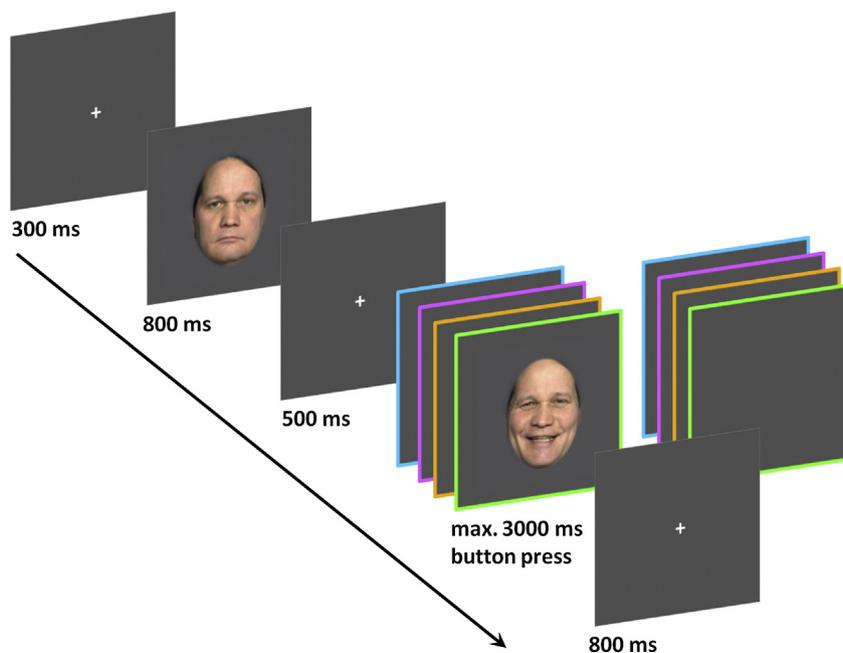

Fig. 1. Example trial. Please note that the two different frame colors are considered as examples for different emotion conditions, not for different tasks. The same colors were used in both the perception and the imagery task and referred to one of the three facial expressions (angry, happy, neutral) or a control trial balanced over participants.

extended 10–20 system. The EEG was referenced to the left mastoid and recorded with a sampling rate of 500 Hz. Both electrooculograms, the horizontal and vertical were measured with electrodes that were externally attached beneath and above the left eye and to the left and right canthi of both eyes. The electrode impedance was kept lower than 5 kΩ. After the experiment a short calibration procedure was applied to obtain prototypical eye movements from every participant. These were later used to correct for eye movement artifacts.

Offline, using BrainVision Analyzer 2 (Brain Products), the raw EEG was re-referenced to average reference. Afterwards data were low-pass filtered at 30 Hz. To remove eye movement artifacts, a spatiotemporal dipole modeling procedure using BESA (Berg and Scherg, 1991) was applied. The remaining artifacts (amplitudes over $\pm 200\,\mu V$, changing more than 50 μV between samples or more than 200 μV within single epochs, or containing baseline drifts) were eliminated with a semiautomatic artifact rejection method. Per task, the following mean amount of trials was included in the analysis: perception: 441.2/480; imagery: 408.8/480; no-go: 211/240. Error- and artifact-free EEG data were segmented into epochs of 2.4 s with a 100 ms pre-stimulus baseline. Epochs started at the onset of the second face stimulus or the empty colored frame, respectively.

Mean reaction times and ERP amplitudes were assessed with repeated-measures analysis of variance (ANOVA) with factors *Task* (perception, imagery), *Familiarity* (familiar, unfamiliar) and *Emotion* (angry, happy, neutral). EEG analyses focused on the EPN (electrode sites: PO3, PO4, PO7, PO8, PO9, PO10) and LPP (electrode sites: Pz, Cz, C1, C2, CP1, CP2) in the typical time windows of 200 to 300 ms and 400 to 600 ms, respectively. Huynh–Feldt corrections (Huynh and Feldt, 1976) were applied when appropriate. Post-hoc tests were Bonferroni corrected. To be able to report on potential hemispheric differences ERP analysis included the additional factor *Laterality* (left, right). We had no a priori assumptions on laterality effects.

In addition, to control for possible effects of facial mimicry (participants may tend to unconsciously mimic the facial expression they are imagining or perceiving), we recorded the electromyogram (EMG) for the corrugator supercilii and zygomaticus major muscles, using Ag/AgCl electrodes (Fridlund and Cacioppo, 1986). Impedances were kept below 15 kΩ. Data were sampled at a rate of 500 Hz. In postprocessing data were first filtered using a 30 Hz low-pass filter, then rectified and smoothed with a time constant of 30 ms and finally eye movement artifacts were removed with an automated ocular correction routine (Gratton et al., 1983).

Effects on the average EMG activity were tested with ANOVAs in the perception and imagery task with factors *Emotion* (angry, happy, neutral) and *Familiarity* (familiar, unfamiliar). Statistical analysis was realized with IBM SPSS Statistics Version 19.

Results

Behavioral results

Participants were faster in the perception task than in the imagery task, $F(1,23) = 26.45$; $p < .000$, $\eta^2 = .535$ (1.059 ms vs. 1.307 ms). Furthermore, reactions (RTs) for familiar faces were faster than for unfamiliar faces, $F(1,23) = 5.51$; $p < .05$, $\eta^2 = .193$ (1.173 ms vs. 1.193 ms). In addition, a main effect of *Emotion*, $F(2,46) = 7.48$; $p < .01$, $\eta^2 = .245$ (neutral: 1.123 ms vs. angry: 1.234 ms vs. happy: 1.194 ms) and interactions of *Task* and *Emotion*, $F(2,46) = 10.73$; $p < .001$, $\eta^2 = .318$, and *Familiarity* and *Emotion*, $F(2,46) = 4.60$; $p < .05$, $\eta^2 = .167$, with a statistical trend of *Emotion* for familiar faces, $F(1,23) = 4.16$; $p = .053$, $\eta^2 = .153$ and no significant effect of *Emotion* for unfamiliar faces, $F(1,23) = 2.81$; $p > .1$, $\eta^2 = .110$ were observed. Lastly, a three-way interaction of all factors, $F(2,46) = 5.04$; $p < .05$, $\eta^2 = .180$ was found.

Separate analyses for perception revealed no significant RT effects. However, for imagery, familiar faces were imagined faster than unfamiliar faces, $F(1,23) = 5.80$; $p < .05$, $\eta^2 = .201$ (1.291 ms vs. 1.324 ms).
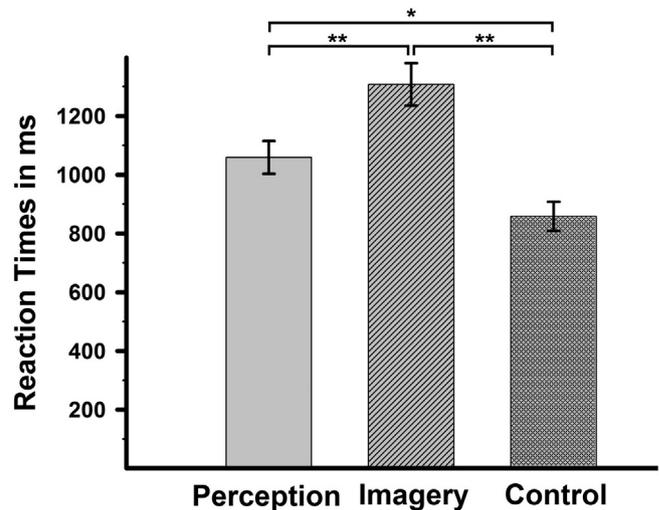

Fig. 2. Mean reaction times (in ms) in the perception, imagery and control condition.

Furthermore, we observed a significant effect of *Emotion*, $F(2,46) = 13.17$; $p < .001$, $\eta^2 = .364$ (neutral: 1.211 ms vs. angry: 1.376 ms vs. happy: 1.337 ms) and an interaction of *Familiarity* and *Emotion*, $F(2,46) = 6.52$; $p < .01$, $\eta^2 = .221$, with a stronger effect of *Emotion* for unfamiliar, $F(2,46) = 18.961$; $p < .001$, $\eta^2 = .452$ than for familiar faces, $F(2,46) = 5.95$; $p < .01$, $\eta^2 = .205$.

When comparing reaction times for perception, imagery and no-go trials in an overall analysis, a main effect was observed, $F(2,46) = 29.24$; $p < .001$, $\eta^2 = .560$ with faster reaction times for no-go trials relative to perception, $F(1,23) = 12.05$; $p < .01$, $\eta^2 = .344$ and imagery, $F(1,23) = 42.83$; $p < .001$, $\eta^2 = .651$ as well as faster reaction times for perception relative to imagery, $F(1,23) = 26.45$; $p < .001$, $\eta^2 = .535$, see Fig. 2 for presentation of mean reaction times.

Error rates were analyzed separately with a 2 (Familiarity: familiar, unfamiliar) × 3 (Emotion: angry, happy, neutral) ANOVA, as they were conceptually different for perception and imagery[1]. For perception no significant differences were found. For imagery, we observed an effect of *Familiarity* with familiar faces being more often correctly imagined relative to unfamiliar faces, $F(1,23) = 4.77$; $p < .05$, $\eta^2 = .172$ (6.7% vs. 8%). In addition, we found an interaction of *Familiarity* and *Emotion*, $F(2,46) = 6.26$; $p < .05$, $\eta^2 = .214$, driven by a marginally significant effect of *Emotion* for unfamiliar faces, $F(2,46) = 3.23$; $p = .07$, $\eta^2 = .123$. No significant effect of *Emotion* for familiar faces was found, $F(2,46) = 2.15$; $p > .1$, $\eta^2 = .086$.

ERP results

EPN (200–300 ms)

ERPs and scalp distributions for perception and imagery of familiar and unfamiliar faces are presented in Fig. 3. In the EPN time window of 200 to 300 ms we found a main effect of *Emotion*, $F(2,46) = 13.34$; $p < .001$, $\eta^2 = .377$ with angry and happy facial expressions eliciting more negative amplitudes than neutral expressions, respectively (angry: $F(1,23) = 13.58$; $p = .001$, $\eta^2 = .382$; happy: $F(1,23) = 22.85$; $p < .001$, $\eta^2 = .498$). Happy and angry expressions did not differ

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[1] Responses for imagined facial expressions were counted as correct when participants imagined the facial expression that was determined by the frame color and pushed the respective button. Accordingly, trials for which participants imagined a deviating expression and therefore pushed the "wrong" button were counted as incorrect.
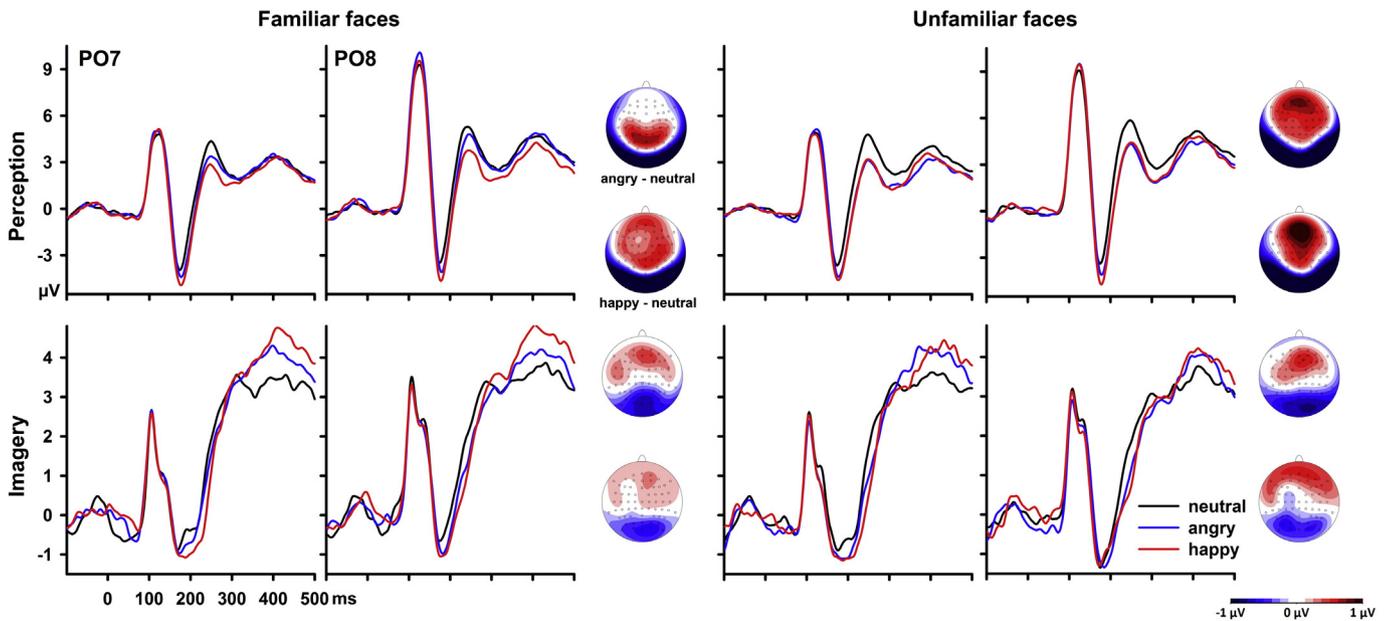
Fig. 3. EPN. Grand average event-related brain potentials associated with the processing of affective facial expressions during perception and imagery for familiar (left) and unfamiliar faces (right) at electrodes PO7 and PO8. Scalp distributions of the differences between angry and neutral and happy and neutral facial expressions are depicted for perceived and imagined familiar and unfamiliar faces between 200 and 300 ms, respectively.

significantly, $F(1,23) = .97$; $p > .1$, $\eta^2 = .042$. A marginally significant main effect of *Task* was found with a generally more negative amplitude for imagined relative to perceived facial expressions, $F(1,23) = 4.18$; $p = .053$, $\eta^2 = .160$. No main effect of *Familiarity* was found, $F(1,23) = 1.59$; $p > .1$, $\eta^2 = .067$. Additionally, the analysis yielded interactions of *Task* and *Emotion*, $F(2,46) = 3.41$; $p < .01$, $\eta^2 = .134$, of *Task* and *Familiarity*, $F(1,23) = 8.42$; $p < .01$, $\eta^2 = .277$, and a three way interaction of *Task*, *Familiarity* and *Emotion*, $F(2,46) = 3.74$; $p < .01$, $\eta^2 = .145$, that were followed up by separate analyses of the perception and imagery task.

For the perception task, a main effect of *Emotion* was found, $F(2,46) = 12.98$; $p < .001$, $\eta^2 = .361$ with angry as well as happy expressions eliciting stronger negative amplitudes compared to neutral expressions (angry: $F(1,23) = 12.25$; $p < .01$, $\eta^2 = .348$; happy: $F(1,23) = 22.86$; $p < .001$, $\eta^2 = .498$). Mean amplitudes did not differ between emotion conditions, $F(1,23) = 1.32$; $p > .1$, $\eta^2 = .054$. Furthermore, *Familiarity* and *Emotion* interacted, $F(2,46) = 4.66$; $p < .05$, $\eta^2 = .168$. For both, familiar and unfamiliar faces an effect of *Emotion* was present, but stronger for unfamiliar faces (unfamiliar: $F(2,46) = 18.63$; $p < .001$, $\eta^2 = .447$; familiar: $F(2,46) = 7.10$; $p < .01$, $\eta^2 = .236$).

Separate analyses for imagery yielded a similar main effect of *Emotion*, $F(2,46) = 5.17$; $p < .05$, $\eta^2 = .190$ with angry and happy facial expressions eliciting more negative amplitudes compared to neutral facial expressions (angry: $F(1,23) = 5.83$; $p < .05$, $\eta^2 = .209$; happy: $F(1,23) = 7.91$; $p = .01$, $\eta^2 = .256$). Mean amplitudes did not differ between the angry and happy condition, $F(1,23) = 1.40$; $p > .1$, $\eta^2 = .006$. Furthermore, a main effect of *Familiarity* with a more negative amplitude for unfamiliar relative to familiar faces was observed, $F(1,23) = 9.75$; $p < .01$, $\eta^2 = .307$. No interaction of *Familiarity* and *Emotion* was observed. No main effects of Laterality or interactions with this factor were observed.

LPP (400–600 ms)

In the LPP component between 400 and 600 ms we found a main effect of *Emotion*, $F(2,46) = 11.05$; $p < .001$, $\eta^2 = .334$ with angry and happy expressions eliciting more positive amplitudes than neutral expressions (angry: $F(1,23) = 11.86$; $p = .01$, $\eta^2 = .350$; happy:

$F(1,23) = 18.96$; $p < .001$, $\eta^2 = .452$). Angry and happy expressions did not differ, $F(1,23) = .13$; $p > .1$, $\eta^2 = .006$. Furthermore, there was a main effect of *Task* with more positive amplitudes for perceived compared to imagined expressions, $F(1,23) = 69.96$; $p < .001$, $\eta^2 = .761$, and a main effect of *Familiarity* with more positive amplitudes for familiar relative to unfamiliar faces, $F(1,23) = 7.82$; $p < .05$, $\eta^2 = .262$. In addition, the analyses yielded interactions of *Task* and *Familiarity*, $F(1,23) = 6.68$; $p < .05$, $\eta^2 = .233$ and *Task* and *Emotion*, $F(2,46) = 20.95$; $p < .001$, $\eta^2 = .488$, followed up by separate analyses of the two tasks.

For perception we found an effect of *Emotion*, $F(1,46) = 25.34$; $p < .001$, $\eta^2 = .524$ with a more positive amplitude for angry and happy compared to neutral expressions (angry: $F(1,46) = 25.77$; $p < .001$, $\eta^2 = .528$; happy: $F(1,46) = 39.01$; $p < .001$, $\eta^2 = .629$). Angry and happy conditions did not differ, $F(1,46) = .01$; $p > .1$, $\eta^2 = .000$. Additionally, an effect of *Familiarity* was observed with more positive amplitudes for familiar than unfamiliar faces, $F(1,23) = 11.54$; $p < .01$, $\eta^2 = .334$.

In contrast to our predictions, the analysis for imagery yielded no significant effects in the LPP region of interest. The emotion effects found in the LPP time window between 400 and 600 ms showed a more posterior maximum than the centro-parietal maximum typically reported (and found here) for the LPP in response to visually presented facial expressions (see Fig. 4). An analysis using an adjusted region based on visual inspection of the emotion induced positivity (P3, Pz, P4, PO3, POz, PO4) yielded a significant main effect of *Emotion*, $F(2,46) = 5.38$; $p < .01$, $\eta^2 = .196$ with happy facial expressions eliciting a more positive amplitude than neutral and angry expressions (happy vs. neutral: $F(1,23) = 9.14$; $p < .01$, $\eta^2 = .284$; happy vs. angry: $F(1,23) = 7.99$; $p = .01$, $\eta^2 = .266$). Amplitudes for angry and neutral expressions did not differ significantly, $F(1,23) = 0.68$; $p > .1$, $\eta^2 = .030$. No other effects reached significance.

EMG results

Appendix B shows statistical values for the overall-analysis of both tasks. Main and interaction effects in the imagery and perception
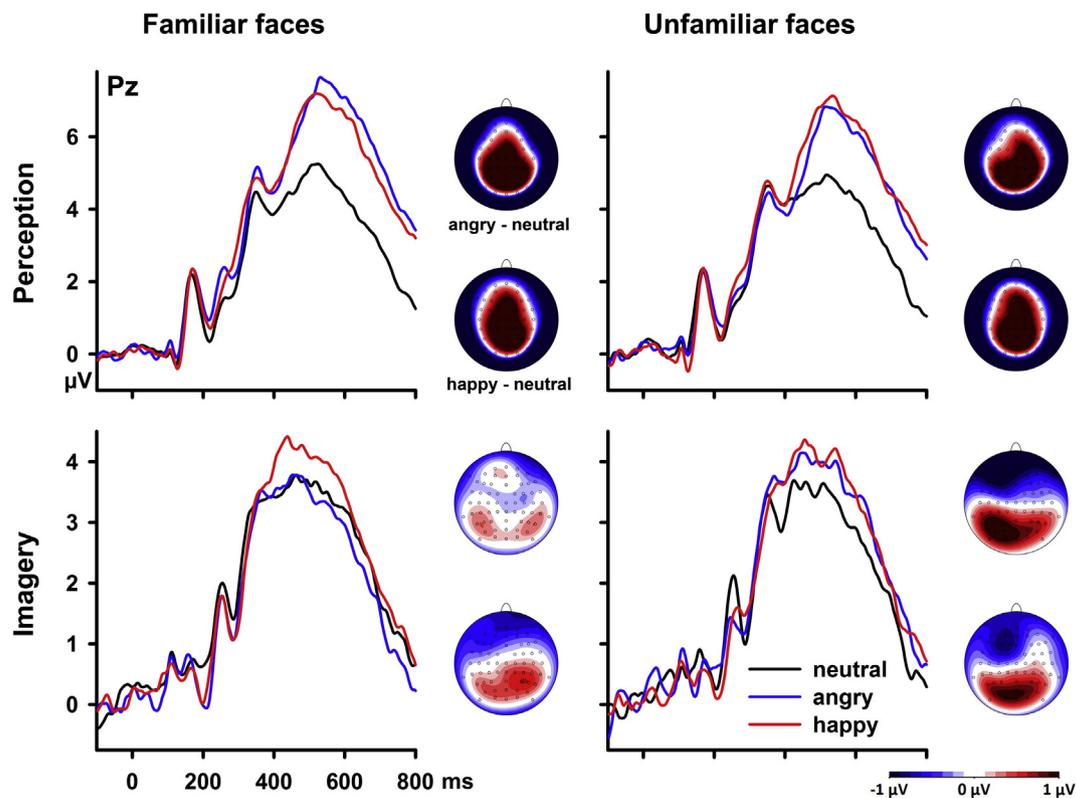
Fig. 4. LPP. Grand average event-related brain potentials associated with affective facial expressions during perception and imagery of familiar (left) and unfamiliar faces (right) at electrode Pz. Scalp distributions of the differences between angry and neutral and happy and neutral facial expressions are depicted for perceived and imagined familiar and unfamiliar faces between 400 and 600 ms, respectively.

condition separately for all time-windows for the corrugator supercilii are presented in Appendix C. Fig. 5 shows a histogram of corrugator activity in the perception and imagery condition, respectively.

For corrugator activity, the ANOVA in eight consecutive 100-ms segments revealed effects of *Emotion* starting at 400 ms continuing until 800 ms. Post-hoc analyses indicated that the corrugator activity in response to happy faces was diminished relative to angry and neutral faces in all segments between 400 and 800 ms. In the last two time-windows, 600–700 ms and 700–800 ms, we found a significant interaction effect of *Emotion* and *Familiarity* that again was driven by a diminished corrugator activity for happy faces, both familiar and unfamiliar. However, the effect was stronger for familiar faces.

In order to find out if the corrugator activity was specific to the imagery condition we additionally analyzed it for perception trials. Here, we found the same diminished activity for happy faces as for imagery. However, the effect started already after 100 ms.

For the zygomaticus we were not able to obtain clear and decisive data, probably due to the high variability of the morphology of this muscle (Pessa et al., 1998). Thus, we did not analyze zygomaticus activity.

Discussion

In the present study we investigated brain responses to internally generated images of emotional facial expressions that were assumed to be associated with emotional responses similar to those triggered by external events. Specifically, we recorded ERPs with their good temporal resolution to elucidate the time course and electrophysiological correlates of mental imagery of emotions, directly comparing this emotion generation task with the processing of visually

perceived angry, happy or neutral facial expressions. For the perception condition we found an EPN and a later LPP modulation, replicating previous reports (e.g. Bayer and Schacht, 2014; Schupp et al., 2004a,b; Holmes et al., 2009). Crucially, an early posterior negativity and a subsequent later positive potential at posterior sites in the same time windows were also found in the imagery condition. This suggests that the brain responds in a similar way – and with comparable speed – to externally and internally generated emotional events. Specifically, the EPN is assumed to reflect increased levels of attention and enhanced perception of emotional relative to neutral stimuli. Accordingly, the EPN response observed in the imagery task – albeit not as strong as in the perception task – can be taken to reflect similar attentional and perceptual mechanisms: imagining emotions is thus associated with enhanced attention and augmented processing at the level of (simulated) perception. This finding is in line with other reports using imaging techniques that demonstrated that emotion-related cortical structures and the autonomic system are involved when emotional contents are imagined (Kosslyn et al., 1996; Kim et al., 2007).

Later on, the intrinsic value of the perceived or imagined stimulus is processed, reflected in LPP modulations in both tasks. However, here, a marked difference in the distribution of the effects was found, with a typical centro-parietal maximum for perceived and a more posterior maximum for imagined expressions. The latter modulation was found mainly for happy, rather than angry expressions. How can we account for the more pronounced posterior distribution of the emotion effects in the imagery condition? Even though this difference was not predicted, we assume that the positive modulations in the LPP time window reflect internal evaluations not only in the perception but also in the imagery task. However, during mental imagery, additional perception-related sub-processes might
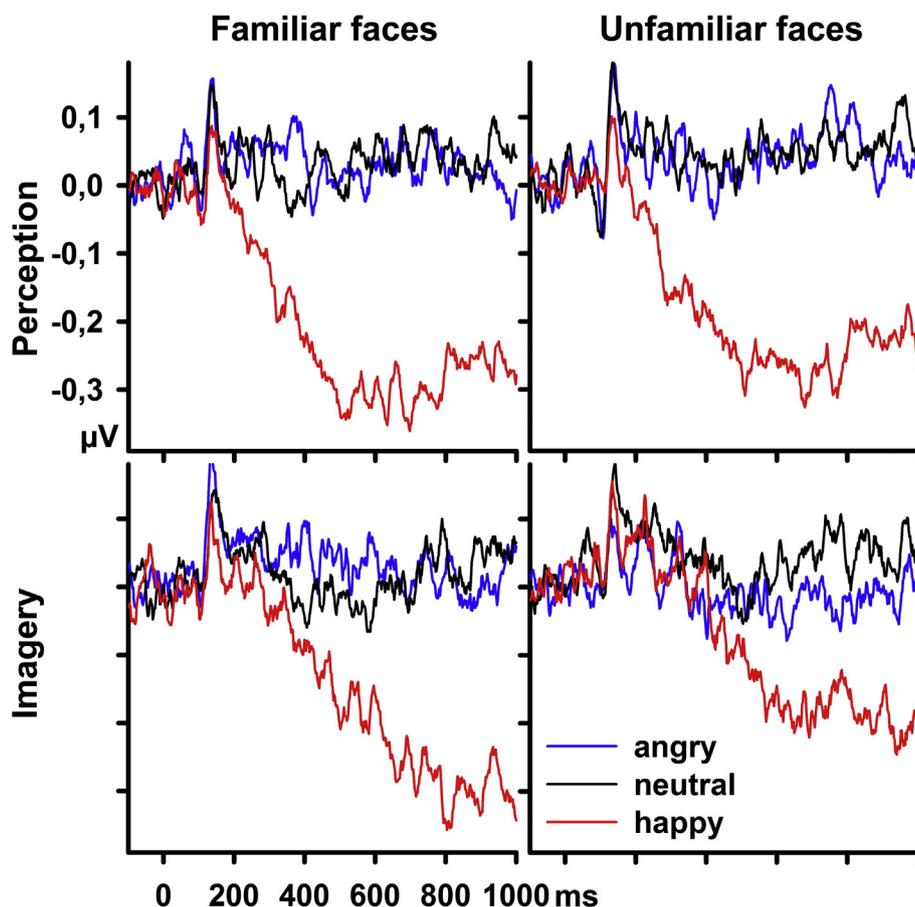
Fig. 5. Corrugator activity for neutral, negative and positive familiar and unfamiliar faces in the perception and imagery condition.

come into play. Specifically, while the evaluation during the perception of facial expressions is based on available visual information that has been processed before, it might not include any further perceptual processes. In contrast, during imagery, perceptual simulations might still be going on even if the EPN results suggest very early effects of emotion in the imagery condition. Furthermore, no perceptual input is available for verification of the evaluative processes. Thus, it is conceivable that perceptual simulation is still ongoing or is needed as a feedback for internal evaluations of the imagined expressions. Such internal comparisons should result in a more intense recruitment of posterior brain regions associated with visual perception. In line with these assumptions, the effect was found primarily for happy facial expressions that were also described by most (20 out of 24) participants as easier to imagine than angry or neutral expressions. Participants might have maintained the mental images of happy faces longer or easier than those of angry faces. However, other theoretical accounts are conceivable, and more research is needed to better understand the determinants of LPP modulations during mental imagery of emotions.

With respect to the EMG that was recorded as a control for facial mimicry effects we found reduced corrugator activity when participants imagined happy faces (see Fig. 5). Whereas the activation levels associated with the negative and neutral conditions are around zero, diminished activity can be seen in response to happy faces. This observation clearly speaks against mimicking of angry and neutral expressions during imagery. Comparable effects have consistently been reported in EMG research (Larsen et al., 2003; Achaibou et al., 2007; Künecke et al., 2014) and may be interpreted in terms of reduced mental effort needed to imagine happy faces,

which would be in line to the above mentioned description of the participants that happy faces were easier to imagine. Interestingly, we also found the diminished corrugator activity in response to perceived happy faces. These results nicely complement the ERP effects, suggesting that participants genuinely have been imagining the facial expressions and that cognitive processes during perception and imagery are similar even in other aspects such as corrugator activity.

In the present study we included familiar and unfamiliar faces to investigate possible effects of familiarity on mental imagery. Thus, while imagery of facial expressions can be based on stored information, the smiling or angry expressions of unfamiliar faces must be imagined without information from long-term memory. However, while a behavioral facilitation effect was found for imagery — with faster and more accurate processing of familiar relative to unfamiliar faces, interestingly neither early nor late ERP effects were significantly influenced by this factor. Therefore, we conclude that the time course of emotional mental imagery of facial expressions is independent of whether the face is stored in long-term memory. This new finding adds to the body of knowledge on the mechanisms of mental imagery that thus far has been investigated with highly salient stimuli.

Interestingly, for perceived faces we did find an influence of familiarity. Familiar faces independent of facial expressions elicited an enhanced amplitude of the late posterior positivity, a finding that fits nicely with other recent studies comparing familiar and unfamiliar faces (Abdel Rahman, 2011; Eimer, 2000; Voss and Paller, 2006; Yovel and Paller, 2004). However, familiarity did not interact with earlier processes in perception, here reflected by the EPN. This also is in line with a

recent study (Suess et al., 2015) that found an early posterior negativity in response to familiar as well as unfamiliar faces. Therefore, face familiarity seems to not influence early automatic processes reflected in the EPN in the perception of faces.

One issue when investigating the time course of mental imagery using ERPs is to precisely determine the beginning of the imagery process. In our study, one may argue that participants started to imagine the expressions directly after the neutral cue face was presented. However, one argument speaks against this idea. Participants had no information about which expression should be imagined because this information was given with the (empty) frame presented after the cue face (cf. Fig. 1), and a specific facial expression was to be imagined in only about 13% of all trials. Thus, given the high chance of preparing the wrong response, early imagery before the response cue is unlikely. Furthermore, the comparison of mean RTs in the control and imagery condition (see Fig. 2) demonstrates that participants followed our instructions, and this should presumably also be the case for other aspects of the instructions. Taking these aspects together, we are confident that our timing estimates in the ERPs are valid.

One potential problem related to our experimental design might be that the cue face was always a face with neutral expression. Therefore, it is not entirely clear whether the imagination of a neutral face is qualitatively different from the imagination of emotional faces. The fast succession of the neutral cue and an imagined neutral target face may have contributed to the behavioral advantage of neutral compared to emotional faces. However, as already mentioned, this is not in line with the participant's subjective experience that happy faces were easier to imagine than neutral and angry faces. In previous studies investigating mental imagery of faces with ERPs, other cues than neutral faces were applied to trigger mental imagery. For instance, in the study by Ganis and Schendan (2008) the name of the face that was to be imagined was presented as a cue. Wu et al. (2012) implemented an auditory cue (using only two distinct faces). In the fMRI study by Kim et al. (2007) the different emotion conditions were presented in a block-wise manner. However, with our design we would not have been able to implement any of these variants. As we also included unfamiliar faces presenting the name or an auditory cue was not possible. Furthermore, presenting emotion conditions in blocks could have induced early spurious condition differences before cue presentation. However, in future research, in addition to neutral affective cues could be presented.

Moreover, one might argue that the observed modulations in the mental imagery condition reflect effects of explicit visual attention, rather than emotional mental imagery. Generally, as discussed in the introduction, there is evidence for an intimate relation of attention and emotion (e.g., Pourtois et al., 2013; Vuilleumier, 2005) during visual perception, and different sources can guide attention (exogenous, endogenous or emotional) and facilitate sensory processing. With respect to "emotional attention" the amygdala plays a crucial role in providing top-down signals on perceptual processing (e.g., Amaral et al., 2003; Lang and Davis, 2006; Vuilleumier, 2005) via direct connections to early visual areas in both the striate and extrastriate cortex. Furthermore, the frontal cortex may play a special role during emotional perception (Barrett and Bar, 2009). Such feedback connections may be responsible for the perceptual enhancement of emotionally relevant stimuli. Crucially, the same processes and/or neural mechanisms may be involved in emotional mental imagery. It has been shown that the imagery of aversive pictures (Kosslyn et al., 1996) or affective faces (Kim et al., 2007) is associated with activation of the amygdala and as other brain areas involved in the perception of these stimuli.

In the present study, participants were cued by an empty colored frame to imagine the before presented face with a specific facial expression, indicated by the frame color. Even though identical colored frames were presented in the perception condition to keep the conditions as similar as possible, differences in attention allocation between the two tasks are likely. However, our main focus on differences between emotion conditions within the tasks is not confounded. Except for attentional modulations due to emotional factors attention should not differ between emotion conditions within the imagery (and perception) task. In addition, when comparing imagery and no-go trials (processing an empty colored frame in the control condition) we find an early modulation of a perception related ERP component that has a topographical distribution that resembles the N170, a component that is associated with the encoding of faces (see Appendix D.1 for a figure and statistical analysis). However, our effect has a later onset than the N170, at about 200 ms. The observation of differences between the (perceptually identical) control and imagery condition suggests that participants comply with the instructions. Furthermore, the time course with an onset at about 200 ms directly following the N170 peak suggests that mental imagery can be related to visual perception. Pronounced earlier differences in the P1 and N170 were observed between the imagery and perception conditions (cf. Appendix D.1). However, because we did not find any differences between imagery and the control condition in these time windows, these P1 and N170 effects are most likely due to physical differences in visual stimulation (face present vs. absent) and were therefore not further analyzed.

We conclude that internally generated emotional events, as the imagery of a happy or angry face, induce comparable early reflexive cortical responses as the direct confrontation with happy or angry faces. Subsequent evaluative processes have a similar time course but differ in topographical distributions for perception and imagery which can be accounted for with additional perception (simulation) related processes necessary during imagery. These findings underscore the similarity of the brain's responses to external and internal sources of emotions. Electrophysiological investigations of mental imagery have thus far focused exclusively on neutral materials such as faces, objects, letters or words, whereas emotional aspects have been neglected. Therefore, little is known about the time course and electrophysiological correlates of imagining emotions. Our study provides first insights on these issues and closes the gap between electrophysiological emotion and imagery research. Crucially, at a more general level, internally generated sources of emotion can strongly influence our feelings and behavior. Therefore, they deserve more empirical attention than they have received thus far.

Appendix A

Alphabetical list with all names of the familiar faces/persons presented in the experiment.

Alec Baldwin	Oliver Kahn
Boris Becker	Daniela Katzenberger
David Beckham	Renate Künast
Dieter Bohlen	Angela Merkel
Nicolas Cage	Jack Nicholson
Tom Cruise	Queen Elizabeth II.
Leonardo Di Caprio	Nicolas Sarkozy
Mel Gibson	Arnold Schwarzenegger
Clint Eastwood	Til Schweiger
Samuel Jackson	Sebastian Schweinsteiger

Appendix B

Table B.1
p-Values and effect sizes for overall ANOVA with task (perception and imagery) as factor for all time-windows between 0 and 800 ms for the corrugator supercilii.

	0–100		100–200		200–300		300–400		400–500		500–600		600–700		700–800	
	p	η^2	p	η^2	p	η^2	p	η^2	p	η^2	p	η^2	p	η^2	p	η^2
Task (T)	–	–	–	–	.014	.244	.006	.294	.039	.180	–	–	–	–	–	–
Emotion (E)	–	–	.025	.159	.000	.384	.000	.381	.000	.429	.001	.366	.000	.388	.000	.383
Familiarity (F)	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
T × E	–	–	–	–	.016	.197	.000	.351	.001	.296	.008	.232	–	–	–	–
T × F	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
E × F	–	–	–	–	–	–	.018	.170	.013	.180	.043	.153	–	–	–	–
T × E × F	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

Only significant effects are reported.

Appendix C

Table C.1
p-Values and effect sizes for main and interaction effects in the imagery and perception condition for all time-windows between 0 and 800 ms for the corrugator supercilii.

		0–100		100–200		200–300		300–400		400–500		500–600		600–700		700–800	
		p	η^2	p	η^2	p	η^2	p	η^2	p	η^2	p	η^2	p	η^2	p	η^2
Imagery	Emotion (E)	584	024	284	056	232	065	136	092	008	**247**	003	**274**	000	**353**	000	**341**
	Familiarity (F)	495	021	761	004	539	017	244	061	861	001	927	000	238	063	111	111
	E × F	524	027	149	083	191	075	098	100	062	089	099	107	038	**138**	013	**191**
Perception	Emotion	494	029	013	**174**	000	**413**	000	**440**	000	**426**	001	**354**	001	**341**	001	**322**
	Familiarity	801	003	301	046	893	001	697	007	629	010	136	094	527	018	222	064
	E × F	798	009	894	004	605	018	219	064	333	047	741	009	666	017	598	022

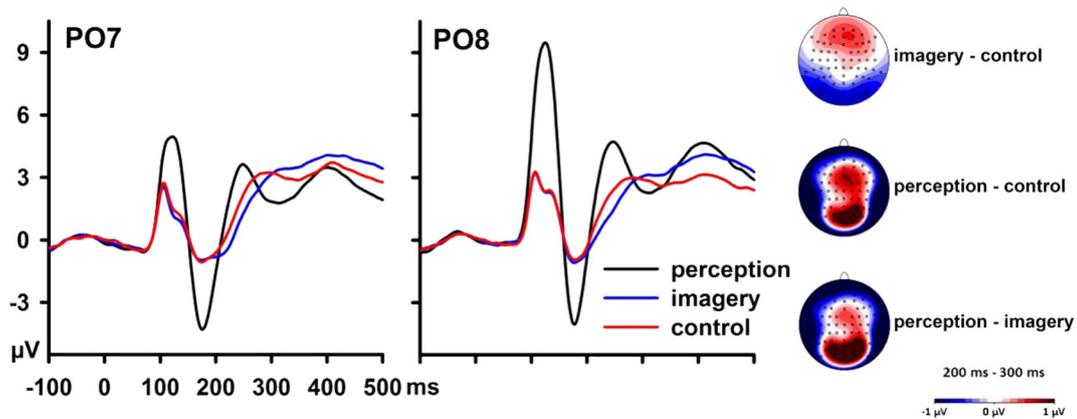Significant effect sizes are in bold.

Appendix D

Fig. D.1. Grand average event-related brain potentials for the three tasks perception, imagery and control at electrodes PO7 and PO8. Scalp distributions of the differences between imagery and control, perception and control, and perception and imagery between 200 and 300 ms are depicted, respectively.

Post-hoc analyses comparing the three tasks between 200 and 300 ms for electrodes PO3, PO4, PO7, PO8, PO9, and PO10 lead to the following results:

For imagery vs. control we found a main effect of *Task*, $F(1,23) = 9.57$; $p < .01$, $\eta^2 = .303$, with a more negative amplitude for imagery than control trials. The topographical distribution resembles the distribution of the N170 component. Perception did not differ significantly from control in this time window, $F(1,23) = 0.61$; $p > .1$, $\eta^2 = .026$ or from imagery, $F(1,23) = 3.73$; $p = .066$, $\eta^2 = .145$.
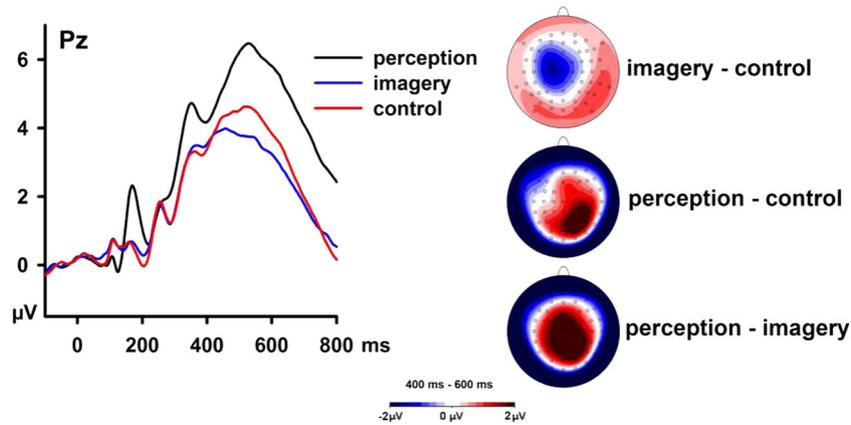
Fig. D.2. Grand average event-related brain potentials for the three tasks perception, imagery and control at electrode Pz. Scalp distributions of the differences between imagery and control, perception and control, and perception and imagery between 400 and 600 ms are depicted, respectively.

Post-hoc analyses comparing the three tasks between 400 and 600 ms for electrodes P3, Pz, P4, PO3, POz, and PO4 lead to the following results: For imagery vs. control we found no effect of *Task*, $F(1,23) = 0.13; p > .1, \eta^2 = .001$. As already described in the main statistics perception differed significantly from imagery, $F(1,23) = 16.65; p < .001, \eta^2 = .431$, and from control, $F(1,23) = 12.44; p < .01, \eta^2 = .351$.

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