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Stimulus novelty and emotion perception: the near absence of habituation in the visual cortex

Harald T. Schupp[a], Jessica Stockburger[a], Maurizio Codispoti[d], Markus Junghöfer[b], Almut I. Weike[c] and Alfons O. Hamm[c]

[a]Department of Psychology, University of Konstanz, Konstanz, [b]Institute for Biomagnetism and Biosignalanalysis, Münster University Hospital, Münster, [c]Department of Psychology, University of Greifswald, Greifswald, Germany and [d]Department of Psychology, University of Bologna, Bologna, Italy

Correspondence and requests for reprints to Dr Harald T. Schupp, Institute of Psychology, University of Konstanz, PO Box D36, 78457 Konstanz, Germany
Tel: +49 7531 882504; fax: +49 7531 882971; e-mail: Harald.Schupp@uni-konstanz.de

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In rapid serial visual presentation of pictures, an early event-related brain potential component shows enlarged negativity over occipital regions for emotional pictures compared with neutral pictures. The present study examined whether the processing of emotional target pictures varies as a function of stimulus repetition. Accordingly, pictures of erotica, neutral contents, and mutilations were repeatedly presented (90 times) while the electroencephalogram was recorded with a 129 dense sensor array. As in previous studies, emotional pictures were associated with a larger posterior negativity than neutral pictures. Furthermore, differential emotion processing did not vary as a function of stimulus repetition and was similarly expressed across blocks of picture presentation. These findings suggest the near absence of habituation in differential emotion processing during perceptual processing. *NeuroReport* 17:365–369 © 2006 Lippincott Williams & Wilkins.

Keywords: attention, emotion, event-related brain potential, habituation

Introduction

Growing evidence from electroencephalographic and neuroimaging research demonstrates the preferential processing of emotional stimuli. Functional magnetic resonance imaging (fMRI) revealed increased blood oxygen level-dependent signal in the extrastriate, occipito-parietal, and inferior temporal cortex when viewing emotionally arousing pictures compared to neutral pictures [1–3]. Furthermore, a recent study determined that increased activity to emotional stimuli in the lateral inferior occipital and inferior temporal visual cortex is observed when the stimulus materials are shown at rapid presentation rates [4]. These results concur with recent event-related brain potential (ERP) studies detailing the temporal dynamics of differential emotion processing. When pictures are presented at rapid rates, a difference in processing pleasant and unpleasant, compared to neutral pictures, is shown by a larger early posterior negativity (EPN) developing around 150 ms after stimulus onset and lasting until about 300 ms. Estimating the generator sources of the differential ERP activity suggested that emotional stimuli receive enhanced processing in occipito-temporo-parietal regions, particularly pronounced for right hemispheric regions [5,6]. Interestingly, paying explicit selective attention to specific stimulus features (e.g. color, orientation, or shape) and higher-order categories (animal vs. non-animal) is reflected by differential ERP activity with similar topography and latency [7,8]. Accordingly, enlarged EPN amplitudes of emotional stimuli have been considered from the perspective of ‘natural selective attention’ proposing that attention and perception are in part directed by underlying motivational systems of avoidance and approach [9]. Currently, however, it is not determined to what extent the early differential perceptual processing of emotional pictures depends on stimulus novelty.

The repeated presentation of sensory stimuli prompts habituation, that is, decrement across several response systems, considered to reflect a basic learning mechanism [10]. By studying habituation in the processing of emotional cues, recent studies reveal that several output responses (e.g. skin conductance responses, heart rate, and corrugator muscle activity) depend to a great extent on stimulus novelty [11–13], when these cues are not associated with behavioral consequences. Furthermore, fMRI studies also reported habituation in emotional stimulus processing with repeated stimulus presentation in selected limbic cortical and subcortical regions [14–17]. Several studies observed a rather rapid habituation of amygdala activations with repeated presentation of emotional facial expressions. In addition, the cingulate cortex, hippocampus, and dorsolateral prefrontal cortex also showed habituation effects. These findings contrast with observations that habituation was less pronounced in the visual cortex when aversive and neutral pictures were repeated a few times [17]. Thus, habituation effects may differ for the various neural structures implicated in stimulus evaluation and response organization. Here, we pursue this hypothesis focusing on the differential emotion processing indicated by the EPN, which appeared as the first reliable ERP component discriminating the processing of emotional from neutral scenes.

In the present study, dense sensor ERPs were measured while participants passively viewed pleasant pictures depicting erotic scenes, unpleasant images showing mutilated bodies, and neutral control images. The picture set was repeated 90 times in order to explore the effects of stimulus repetition on differential emotion processing indexed by the EPN component. In contrast to responses associated with motor preparation, it was assumed that differential emotion processing at the level of perception and evaluation is mandatory and not sensitive to stimulus repetition.

Materials and methods

Participants

Participants were eight introductory psychology students from the University of Greifswald (four women; 20–34 years, mean age 24.0 years). They received course credits toward their research requirements.

Stimulus materials and procedure

Stimulus materials included 10 images of erotic couples, 20 neutral pictures showing humans in neutral contexts, and 10 pictures depicting scenes of mutilations drawn from the International Affective Picture System [18]. As the EPN amplitude is differentiating between emotionally arousing and neutral contents, the number of stimuli was equated for the arousal rather than the valence dimension. An unpublished follow-up study replicated the results reported here, equating the number of pictures for the valence dimension. Erotic, neutral, and mutilation pictures were presented in a perceptually random order as a continuous stream without perceivable interstimulus interval for 330 ms [4,6]. The picture set was repeated 90 times in different orders, amounting to a total of 3600 picture presentations.

Apparatus and data analysis

Electrophysiological data were collected from the scalp using a 129-channel system (EGI; Electrical Geodesics, Inc., Eugene, Oregon, USA). Scalp impedance for each sensor was kept below 30 kΩ, as recommended by EGI systems guidelines. The electroencephalogram was collected continuously in the 0.1–100 Hz frequency range, with a sampling rate of 250 Hz. Continuous electroencephalogram data were low-pass filtered at 35 Hz before stimulus synchronized epochs were extracted from 48 ms before until 330 ms after picture onset. A statistical approach was applied for artifact correction, including the transformation of the ERP data to an average reference [19].

Separate ERPs were calculated as a function of picture valence and picture repetition. To achieve an acceptable signal/noise ratio, ERPs were averaged over five repetitions of each picture set, resulting in 18 blocks of stimulus exposure. A two-step procedure was used to analyze the modulation of the ERP waveform as a function of affect and stimulus exposure. First, repeated measures analyses of variance (ANOVAs), including the factors Affect (erotic, neutral, mutilation pictures) and Stimulus Exposure (18 blocks), were calculated for each time point after picture onset separately for each individual sensor in order to identify the temporal and spatial characteristics of affective ERP modulation. These waveform analyses were conducted using a significance criterion of $P < 0.01$. In order to avoid false positives, significant effects were only considered meaningful when the effects were observed for at least eight continuous data points (32 ms) and two neighboring sensors, revealing significant affective modulation. Second, to provide a more conventional ERP analysis, the EPN amplitude was scored as mean activity over a time interval from 200 to 300 ms in anterior and posterior sensor clusters on the basis of outcome of the waveform analyses. The temporo-occipital cluster comprised the following EGI sensors of the net: 56, 63, 64, 65, 66, 69, 70, 71, 74, 75 (left hemisphere) and 83, 84, 85, 89, 90, 91, 95, 96, 100, 108 (right hemisphere). The fronto-central cluster comprised the following sensors of the net: 7, 12, 13, 21, 29, 30, 31, 35, 36, 37, (left hemisphere) and 5, 105, 106, 107, 111, 112, 113, 117, 118, 119 (right hemisphere). Separate repeated measures ANOVAs including the factors Affect (erotica, neutral, mutilation pictures), Stimulus Exposure (18 blocks), and Laterality (left vs. right) were conducted for temporo-occipital and fronto-central sensor clusters. For effects involving repeated measures, the Greenhouse Geisser procedure was used to correct for violations of sphericity.

Results

To determine the interaction of stimulus exposure and affect, a first analysis calculated repeated measures ANOVAs for each sensor and time point separately. Of primary interest, no significant interaction between the factors Affect and Stimulus Exposure was obtained by single sensor waveform analysis. By replicating previous findings, a highly significant main effect of Affect was, however, revealed over temporo-occipital and fronto-central sites beginning around 160 ms poststimulus and being most pronounced in the 200–300 ms time window. These results are illustrated in Fig. 1c for the time region of interest (160–312 ms), summarized in 32 ms bins for illustrative purposes only. In these analyses, a P-level of <0.05, 0.01, and 0.001 corresponds to a main effect of Affect $F(2,14)=3.7$, 6.5, and 11.8, respectively.

To further detail the differential processing of emotion as a function of picture repetition, conventional repeated measures ANOVAs were calculated for the mean ERP amplitudes across the left and right occipito-temporal sensor clusters. Neither the main effect Stimulus Exposure nor an interaction involving Stimulus Exposure approached significance, $F<1$, NS. As expected, selective emotion processing was readily apparent at occipito-temporal sensor clusters, Affect $F(2,14)=25.8$, $P<0.0001$. Furthermore, affective modulation was more pronounced over the right hemisphere, Affect × Laterality $F(2,14)=8.7$, $P<0.05$. Accordingly, separate post-hoc tests were conducted for left and right temporo-occipital sensor clusters. Specifically, erotic images were associated with a more pronounced posterior negativity than neutral images over the left and right temporo-occipital clusters, $F(1,7)>25.2$, $P<0.01$. Similarly, pictures of mutilations evoked increased EPN amplitudes compared with neutral images over the left and right

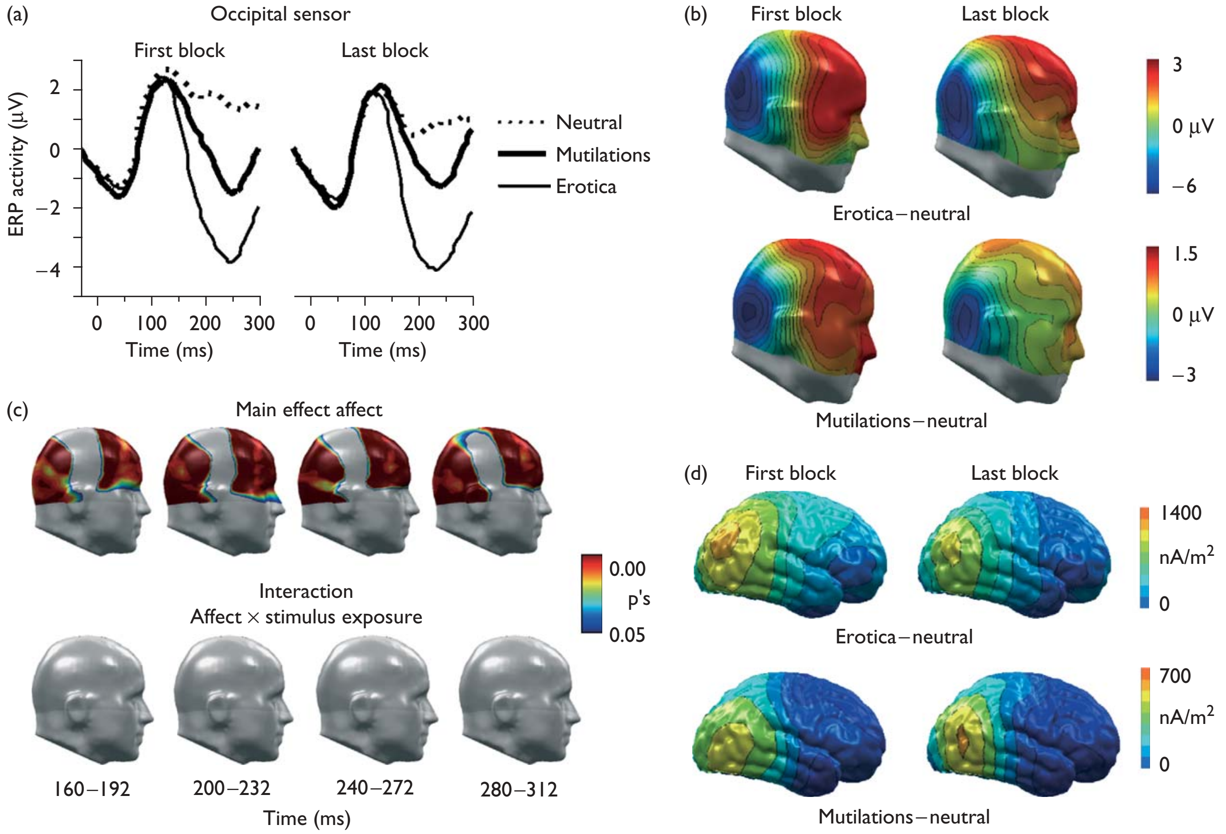

Fig. 1 Effects of emotion and stimulus repetition. (a) Grand-averaged event-related brain potential waveforms for a selected right occipital sensor (#90) as a function of affect and first and last block of picture viewing. (b) Difference scalp potential maps (emotional−neutral) for first and last block of picture presentation separately. (c) Illustration of the statistical effects observed in repeated measure ANOVAs calculated for each sensor and time point shown for the time window of interest (160–312 ms). (d) Calculation of the L2-Minimum-Norm estimate for the scalp potential difference (emotional−neutral) separately for first and last block of picture presentation. All maps display a right-side view.

posterior clusters, $F(1,7) > 16.0$, $P < 0.01$. Furthermore, as in previous studies, erotic images elicited more pronounced EPN amplitudes than mutilations over both hemispheres, $F(1,7) > 19.8$, $P < 0.01$. As shown in Fig. 2, a polarity reversal of the EPN effect was observed over fronto-central sites. The statistical effects observed at frontal sites mirrored the findings obtained for the temporo-occipital regions.

Furthermore, as illustrated in Fig. 1a and b, the differential processing of emotional compared with neutral stimuli was similarly pronounced when directly comparing the first and last block of picture viewing, Affect $F(2,14) = 34.7$, $P < 0.0001$; again, no interaction of Affect × Stimulus Exposure was observed ($F(2,14) = 1.1$, NS). Additionally, L2-Minimum-Norm solutions were calculated to provide neural source estimations for the differential processing of emotional cues without the necessity of a priori assumptions regarding the location and/or number of current sources. The calculation of the L2-Minimum-Norm was based on a spherical four-shell isotropic volume conductor head model with 3 (radial, azimuthal, and polar direction) × 197 evenly and spherically distributed dipoles as a source model. A source shell radius of 6 cm was chosen as a trade-off between depth sensitivity and spatial resolution [20]. As shown in Fig. 1d, differential processing of erotica and mutilation contents was modeled by sources over occipito-temporo-parietal regions, similarly pronounced for the first and last block of picture viewing.

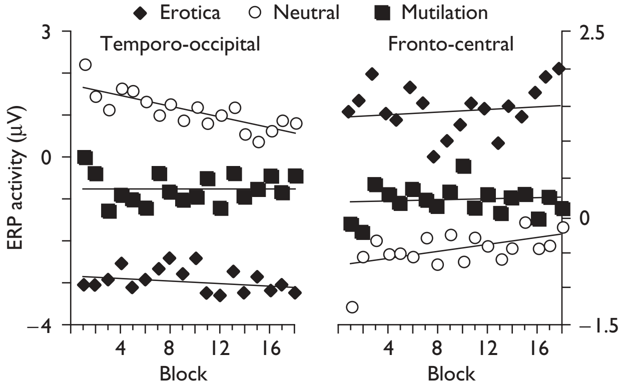

Fig. 2 Mean event-related brain potential activity for right temporo-occipital (left panel) and fronto-central (right panel) sensor clusters as a function of affect and stimulus exposure.

Discussion

The present data replicated previous findings demonstrating enlarged negativity over occipital regions for emotional compared with neutral pictures, particularly pronounced for erotic stimuli [5,6]. Building upon this replication, the primary goal of the present study was to explore to what extent the differential processing of emotional cues is dependent on stimulus novelty. Within the context of the present study, results appeared rather clear: repeated stimulus presentation did not abolish the differential processing of emotional compared with neutral cues as indexed by the early occipital negativity. These findings suggest that the detection of emotionally significant stimuli in the environment is an obligatory task of perception, evincing little evidence for habituation as a function of passive stimulus experience.

In contrast, response output indices of emotional orienting typically show rapid habituation [11–13]. In these studies, autonomic responses like skin conductance and heart rate as well as facial somatic responses over the corrugator muscle region were selectively engaged when stimuli were novel, but became rapidly habituated after a few stimulus repetitions. A functional analysis of the different facets of affective responses has been suggested to meaningfully explain differences in habituation [13]. Specifically, heart rate is considered to facilitate processes of sensory intake, whereas skin conductance has been associated with preparation for action. With repeated stimulus presentation, neither preparation for action nor continued sensory intake is necessary, and thus, these responses diminish. Each new stimulus, however, needs to be analyzed up to the level of recognition before it can be categorized as previously presented. Thus, facilitated processing of emotional cues during perceptual encoding appeared to be an obligatory process that did not diminish with stimulus repetition.

The perceptual processing in the cortex is suggested to be regulated by subcortical structures involved in appetitive or defensive responding [2,3,21,22]. Recent fMRI studies suggest rather rapid habituation of processing of emotional cues in limbic and paralimbic structures [14–17], which appears inconsistent with the present ERP findings revealing the near absence of habituation of differential emotion processing. A number of critical issues and findings, however, need to be considered. First, it is questionable whether the temporal resolution of fMRI is appropriate to assess the fleeting stage of processing indexed by the EPN. Second, a recent study observed that patients with amygdala lesions did not show enhanced activity to fearful faces in the fusiform and occipital gyrus, which was observed in a group of healthy controls [23]. Third, as observed in a classical conditioning fMRI study, habituation may vary for the various anatomical subregions of the amygdala that perform distinct functions [24]. Fourth, recent studies revealed sizeable blood oxygen level-dependent activations in the amygdala for highly arousing emotional materials used in the present study [2,3], and it remains to be determined in future studies whether the amygdala reveals rapid habituation to these emotionally evocative stimuli. Thus, more research is needed to evaluate the hypothesis that the preferential processing of emotional stimuli in the extended visual cortex is secondary to appraisal of significance in the amygdala. Alternatively, as discussed in associative learning, limbic structures such as the amygdala might modulate the associative strength of cortical stimulus representation of emotionally significant stimuli [25].

Conclusion

Emotional stimuli receive preferential processing during perceptual encoding presumed to reflect a state of 'natural selective attention' regulated by underlying motivational systems of avoidance and approach. Here, we observed that the early differential processing of emotional compared with neutral stimuli as indexed by the EPN does not depend on stimulus novelty. These findings suggest that detecting emotionally significant stimuli in the environment might be an obligatory task of the organism, apparently not habituating as a function of repeated passive exposure.

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