

## Research Article

# EMOTIONAL FACILITATION OF SENSORY PROCESSING IN THE VISUAL CORTEX

Harald T. Schupp,<sup>1</sup> Markus Junghöfer,<sup>2</sup> Almut I. Weike,<sup>1</sup> and Alfons O. Hamm<sup>1</sup>

<sup>1</sup>University of Greifswald, Greifswald, Germany, and <sup>2</sup>University of Konstanz, Konstanz, Germany

**Abstract**—A key function of emotion is the preparation for action. However, organization of successful behavioral strategies depends on efficient stimulus encoding. The present study tested the hypothesis that perceptual encoding in the visual cortex is modulated by the emotional significance of visual stimuli. Event-related brain potentials were measured while subjects viewed pleasant, neutral, and unpleasant pictures. Early selective encoding of pleasant and unpleasant images was associated with a posterior negativity, indicating primary sources of activation in the visual cortex. The study also replicated previous findings in that affective cues also elicited enlarged late positive potentials, indexing increased stimulus relevance at higher-order stages of stimulus processing. These results support the hypothesis that sensory encoding of affective stimuli is facilitated implicitly by natural selective attention. Thus, the affect system not only modulates motor output (i.e., favoring approach or avoidance dispositions), but already operates at an early level of sensory encoding.

Although emotional expressions, bodily changes, and reported feelings vary idiosyncratically according to dispositional (e.g., temperament) and situational factors, many theorists claim that the emotional or affect system has evolved from a motivational basis that has a much simpler two-factor organization (Cacioppo, Gardner, & Berntson, 1999; Lang, 1995; Lang, Bradley, & Cuthbert, 1990, 1997). Because motivated behavior is both energetic and goal directed, numerous researchers have proposed that the emotional-motivational system can be subdivided into an aversive and an appetitive system. Activation of one of the two systems defines the valence of an emotion. Arousal is viewed as reflecting variations in the activation of either or both systems (see Lang, 1995). According to this view, emotions can be functionally considered to be action dispositions preparing the organism for either avoidance- or approach-related behaviors, interrupting ongoing behavior and mental processes (e.g., Frijda, 1986; Lang et al., 1997). In this emotional priming model (Lang, 1995), it is assumed that affective engagement of either the appetitive or the aversive motivational system primes associations, representations, and action programs linked to the engaged motivational system. Thus, when the aversive motivational system is activated, defensive and protective behaviors are facilitated in order for the organism to withdraw from the aversive stimulation as quickly as possible. Activation of the appetitive system primes approach behaviors to pleasant stimuli.

The startle response has proven to be a convenient defensive reflex for testing the emotional priming hypothesis. It has been demonstrated both in animals (Davis, 1997) and in humans (Hamm, Greenwald, Bradley, & Lang, 1993) that the startle response to an acoustic probe

stimulus is facilitated (i.e., augmented or potentiated) during fear conditioning. The startle response is also potentiated during viewing of unpleasant pictures and inhibited during viewing of pleasant pictures (for reviews, see Bradley, 2000; Lang et al., 1997). This affective modulation of the startle reflex is enhanced with increasing intensity of the emotional stimuli (Cuthbert, Bradley, & Lang, 1996).

However, in order to prepare an appropriate behavioral output, the organism has to discriminate hostile from hospitable stimuli. Affective cues signal important events that guide attentional processes. In other words, the organization of successful behavioral strategies depends on efficient extraction of critical information in the environment (Öhman, Flykt, & Lundqvist, 2000). Accordingly, emotional modulation might not only be evident in the behavioral output system but may also facilitate the sensory encoding of affective cues. It is well established that perceptual encoding of visual stimuli can be modified not only by voluntarily directed visual attention, but also by reflexive attention that is captured by the visual cue (Hopfinger & Mangun, 1998). In a similar vein, emotionally significant stimuli might also reflexively capture the organism's attention and facilitate the processing of these cues.

This hypothesis was recently supported by a series of studies measuring regional cerebral blood flow during processing of emotionally laden visual stimuli. Using positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) measures, these studies demonstrated that viewing of pleasant and unpleasant pictures elicited increased regional blood flow in the occipital cortex (Brodmann areas 18 and 19) relative to viewing of neutral materials (Lane, Reiman, Ahern, & Schwartz, 1997; Lang et al., 1998). Moreover, patients with specific phobias showed increased activity in the visual associative cortex while viewing fear-relevant films (Fredrikson et al., 1993). Although these brain-imaging methods provide a good spatial resolution of *in vivo* human brain functions, they do not reveal the time course of the affective visual sensory processing. Therefore, it is unclear whether affective tuning of visual associative cortices appears only at later stages of stimulus analysis (i.e., when capacity-limited controlled processing modes are engaged), or whether the early sensory analysis of affective cues is already selectively facilitated. The measurement of event-related brain potentials (ERPs) is most suitable for elucidating the time course of the cortical responses during the encoding of affective pictures.

Previous ERP studies showed that pleasant and unpleasant images elicited larger late positive potentials in the P300 time region than neutral cues (e.g., Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000; Schupp, Cuthbert, et al., 2000). Augmented P300 responses are a hallmark finding in cognitive psychology when subjects explicitly attend to certain stimuli while ignoring others (Johnson, 1988). Thus, the greater cortical positivity evoked by pictures with emotional content might reflect the increased attentional engagement evoked by these cues. However, the P300 is considered to index postsensory (higher-order) stages of stimulus evaluation. Because of methodological limitations (i.e., limited numbers of sensors and reference-dependent char-

Address correspondence to Harald T. Schupp, Department of Biological and Clinical Psychology, Institute of Psychology, University of Greifswald, Franz-Mehring-Str. 47, 17487 Greifswald, Germany; e-mail: schupp@uni-greifswald.de.

acterization of field potentials<sup>1</sup>), these studies were limited in their ability to reveal early selective stimulus processing in the visual cortex. Therefore, the present study investigated electrocortical activity during processing of emotional pictures using multichannel ERP recordings (129 sensors) that provide an improved spatial resolution and a reference-independent characterization of the brain potentials. It was expected that emotionally significant cues would selectively facilitate stimulus processing at an early stage of visual encoding.

## METHOD

### Participants

Participants were 20 (12 female) introductory psychology students from the University of Greifswald, Greifswald, Germany. They received course credits toward their research requirements.

### Stimulus Materials and Procedure

Twenty pleasant (erotic couples, babies, family scenes), 20 neutral (neutral people, household objects), and 20 unpleasant (mutilations, violence) pictures were selected from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 1999). These images had simple figure-ground distinctions and were similar in content to the pictures used in previous fMRI and EEG (electroencephalogram) studies. Because of possible confounds with specific stimulus features of the neutral household items (e.g., reduced perceptual complexity), we report here analyses in which only colored pictures of humans were included in the neutral category.

The pictures were displayed for 1.5 s each and presented in sequences of 6 pictures (cf. Cacioppo, Crites, Berntson, & Coles, 1993). On each trial, a warning dot preceded picture onset to ensure that the subject was fixating on the center of the screen. After picture offset, the subject was asked to categorize the picture as either pleasant, neutral, or unpleasant using a three-way response button. The intertrial interval (ITI; including overt response) was 3 s. The subject initiated each sequence of 6 pictures by a button press, and a total of 40 such sequences were presented. Thus, each picture was viewed four times in the total of 240 picture presentations. Pleasant, neutral, and unpleasant pictures were presented in a random order with the exception that no more than 2 pictures of the same valence were allowed in each sequence. All 60 different exemplars were presented before the series was presented again (in a different order). The order of picture presentation was different for each subject. One sequence of 6 pictures served as a practice trial.

1. In general, electrical field potentials are recorded as voltage difference between two locations on the scalp. However, there is no consistent zero potential for all electrical generators. In particular, common reference sites used in earlier studies (e.g., linked ears) are electrically active and may vary with every time sample. Therefore, choice of reference can result in distorted representations of the "true" field potentials, and the appearance of the field potentials depends on the reference site. One way to achieve the goal of reference-independent characterizations of the field potentials is to calculate the average reference potential (Tucker, Liotti, Potts, Russell, & Posner, 1994). This method is based on the physical rule that the surface integral of the field potentials equals zero. However, the accuracy of this method depends on the accurate assessment of the surface integral, and therefore a large number of sensors (more than 64) must be evenly spaced over the scalp surface (Tucker et al., 1994).

### Apparatus and Data Analysis

Electrophysiological data were collected from the scalp using a 129-channel system (Electrical Geodesics, Inc., Eugene, Oregon). Scalp impedance for each sensor was kept below 30 k $\Omega$ . The EEG was collected continuously in the 0.1- to 100-Hz frequency range with a sampling rate of 250 Hz. Continuous EEG data were low-pass filtered at 35 Hz before stimulus-synchronized epochs were extracted from 124 ms before until 776 ms after picture onset. Single-trial epochs were corrected for vertical and horizontal eye movements (Miller, Gratton, & Yee, 1988). A statistical approach described in Junghöfer, Elbert, Tucker, and Rockstroh (2000), including the transformation of the ERP data to an average reference, was applied for artifact correction.

A two-step procedure was used to analyze the affective modulation of the ERP waveform. First, repeated measures analyses of variance (ANOVAs) including the factor affect (pleasant, neutral, unpleasant) 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  $p < .01$ . In order to avoid false positives, we considered significant effects meaningful only when the effects were observed for at least eight continuous data points (32 ms) and two neighboring sensors revealed significant affective modulation. Furthermore, post hoc comparisons among the three valence categories were conducted to supplement the overall ANOVAs. The outcome of these waveform analyses suggested two effects of affective modulation, that is, an early posterior negativity and a late centro-parietal positive potential.

In the second step, the outcome of these waveform analyses was used as the basis for collapsing information according to the spatial focus and temporal characteristics of the affective modulation. Regions of interest were defined, and the average of the selected sensors was calculated for each of these regions. Similarly, the mean activity in critical time windows was obtained. This information was analyzed by repeated measures ANOVAs in order to provide a more standard ERP analysis and enable a brief presentation of results.

#### *Early posterior negativity*

An early affective modulation appeared with the negative slope of the P100 and was maximally pronounced at 312 ms after picture onset. This modulation was observed in bilateral clusters of increased temporo-occipital negativity and corresponding centro-medial positivity for affective compared with neutral cues. No other regions, such as anterior sites, revealed a significant modulation as a function of affect. Accordingly, the early affective modulation was captured by calculating the mean activity over a 40-ms time interval centered at the peak of differentiation at 312 ms for left and right temporo-occipital and centro-medial<sup>2</sup> sensor clusters. Conventional repeated measures ANOVAs included the factors affect (pleasant, neutral, unpleasant), site (temporo-occipital, centro-medial), and laterality (left, right).

2. The temporo-occipital cluster comprised the following sensors of the net: 56, 63, 64, 65, 66, 69, 70, 71, 74, and 75 in the left hemisphere, and 83, 84, 85, 89, 90, 91, 95, 96, 100, and 108 in the right hemisphere. The centro-medial cluster comprised the following sensors of the net: 7, 13, 30, 31, 32, 36, 37, and 38 in the left hemisphere, and 81, 88, 105, 106, 107, 111, 112, and 113 in the right hemisphere.

### Late centro-parietal positive potential

The second affective modulation was maximally pronounced in the time window from 416 to 456 ms. During this window, enlarged late positive potentials (LPPs) were observed for affective relative to neutral pictures over the centro-parietal sensors. Although other sensor sites revealed corresponding enlarged negative potentials for affective materials, these effects were not meaningful according to our criteria for significant effects. Accordingly, an ANOVA including the factors affect and laterality was calculated for the LPP collapsed over centro-parietal sensors.<sup>3</sup>

## RESULTS

### Early Posterior Negativity

As illustrated in Figure 1, there was evidence for an affective modulation of the ERP waveform preceding the LPP. Overall, the ERP waveform presented a positive polarity over posterior sensors and a negative polarity over anterior sites. However, the encoding of affective pictures resulted in a pronounced relative negative shift in the ERP waveform over left- and right-hemisphere temporo-occipital clusters of sensors, as illustrated in Figure 1 by the waveforms for representative left- and right-hemisphere temporo-occipital sensors (70 and 90). Furthermore, a corresponding positive shift was observed at clusters of sensors over left and right centro-medial sites, again illustrated in Figure 1 by two representative left- and right-hemisphere sensors (7 and 107). Figure 2 highlights this affective differentiation in temporo-occipital negativity at sensors 70 and 90 by showing the difference waveforms obtained by subtracting the waveforms elicited by neutral pictures from the waveforms evoked during viewing of affective images. The temporal information displayed in Figures 1 and 2 indicates that the increased temporo-occipital negativity for pleasant and unpleasant pictures emerged with the negative slope of the P100 and was maximally pronounced around 300 ms after stimulus onset.

Supplementing the temporal information, Figure 3 illustrates the spatial topography of the scalp field potentials represented as the mean activity of a 40-ms time window centered at the peak of affective differentiation (312 ms). Again, these maps are based on the differences between affective and neutral ERPs, thus illustrating the affective modulation. These field potential maps reveal two bilateral sources of augmented temporo-occipital negativity for affective compared with neutral images, with a polarity reversal over anterior sites. Moreover, a current source density analysis further increased spatial resolution. This technique emphasizes focal over global (widespread and blurred) sources of activation (electrical generators). The outcome of this analysis supports the notion of bilateral activation of occipital brain areas. In addition, there was evidence for the activation of parietal areas, mainly in the right hemisphere (cf. Junghöfer, Bradley, Elbert, & Lang, 2001).

Statistical analyses supported the significance of this affective ERP modulation. Compared with neutral images, pleasant and unpleasant images elicited significantly larger negativity over temporo-occipital sites,  $F_s(1, 19) > 33$ ,  $p_s < .0001$ , and stronger positivity over centro-medial sites,  $F_s(1, 19) > 20$ ,  $p_s < .0001$ , thus resulting in a significant

affect-by-site interaction in the overall analysis,  $F(2, 38) = 31.2$ ,  $p < .0001$ . The calculation of simple difference scores demonstrated that 19 of 20 subjects contributed to the effects at temporo-occipital and centro-medial clusters. Furthermore, the comparison between pleasant and unpleasant images was not significant for temporo-occipital or centro-medial sensors,  $F_s(1, 19) < 1$ . Also, affective modulation did not interact with laterality at centro-medial or temporo-occipital sensors,  $F_s(2, 38) < 1$ . As already indicated in the Method section, the analyses of individual sensors and further control analyses revealed no significant affective modulation of the ERPs at anterior or other sites, suggesting that the effects were specific for the temporo-occipital and centro-medial clusters.

Further analyses explored the hypothesis that the posterior negativity increased with the affective engagement prompted by the pictures. It is well established that erotic pictures elicit stronger skin conductance responses (SCRs) and are rated as more arousing than other pleasant materials. In the same vein, pictures of mutilated bodies evoke stronger SCRs and are rated as more arousing than pictures with other unpleasant content (Hamm, Schupp, & Weike, in press). Accordingly, we predicted that the posterior negativity was most pronounced for pictures displaying erotic scenes and mutilations. As shown in Table 1, erotic images and pictures of mutilations indeed elicited a more pronounced relative negative shift over temporo-occipital sites compared with less arousing pictures of the same valence,  $F_s(1, 19) = 20.0$  and  $4.5$ ,  $p < .0001$  and  $p < .05$ , respectively. However, the less arousing pleasant pictures of families and babies and the unpleasant pictures of violence still elicited significantly enhanced posterior negativity compared with neutral images,  $F_s(1, 19) > 19$ ,  $p_s < .0001$ . The relative polarity reversal over centro-medial sites (i.e., positive potentials) also significantly reflected emotional intensity, as indicated by calculating the same contrasts as for the temporo-occipital sites,  $F_s(1, 19) > 8.5$ ,  $p_s < .01$ . These results demonstrate the sensitivity of the temporo-occipital negativity to the intensity of affective stimulation.

### Late Centro-Parietal Positive Potential

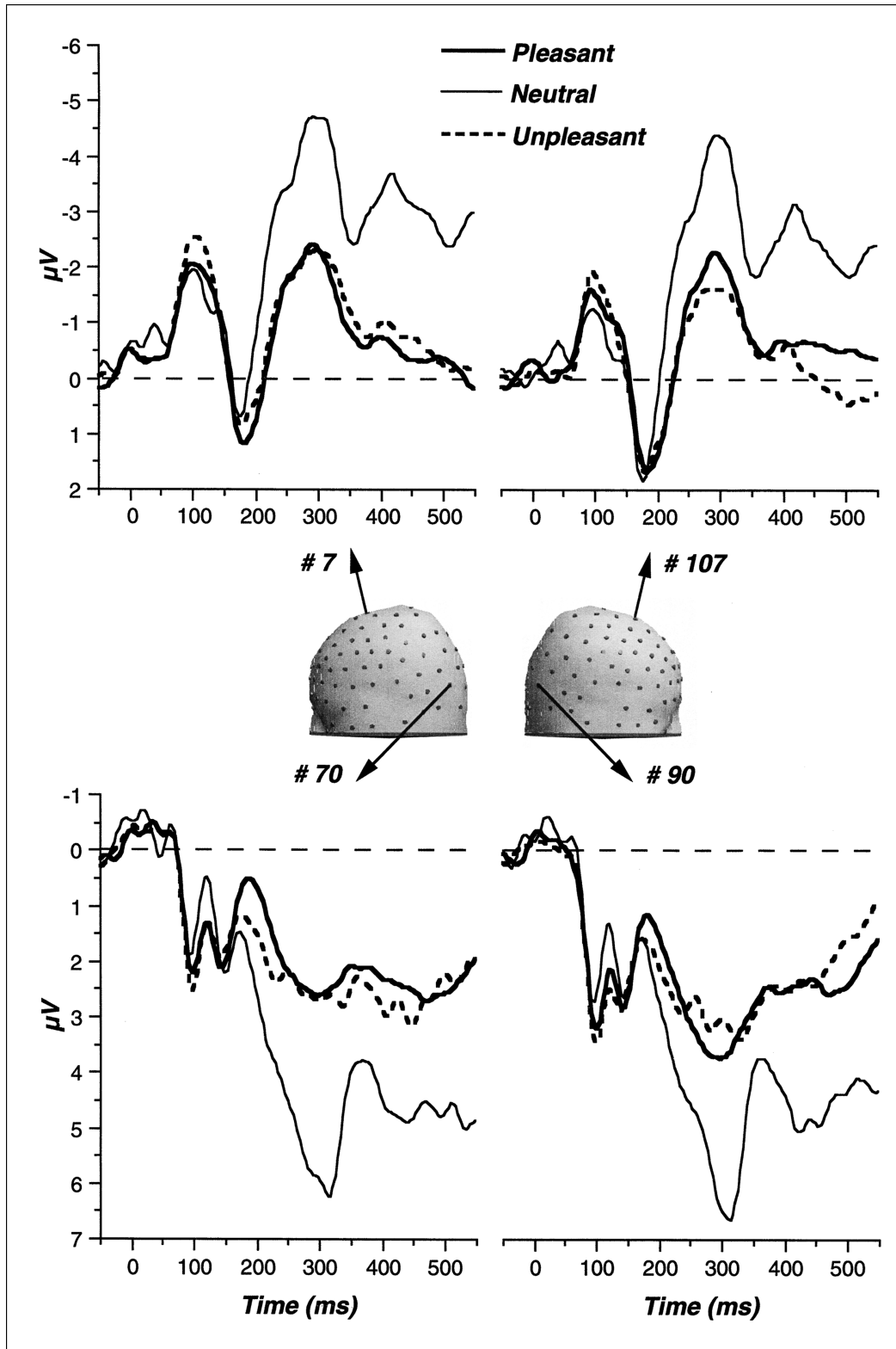
Higher-order aspects of stimulus encoding were assessed by means of the LPP. The results replicated previous findings. The amplitude of the LPP was modulated by the affective categories of the stimuli,  $F(2, 38) = 22.2$ ,  $p_s < .0001$ . Pleasant and unpleasant pictures elicited enlarged LPPs compared with neutral images,  $F_s(1, 19) > 20.5$ ,  $p_s < .0001$ . Furthermore, pleasant and unpleasant pictures elicited comparable LPPs,  $F(1, 19) = 1.6$ , n.s. Thus, these data indicate that higher stages of stimulus processing are modulated by affective cues, implying that affective cues are associated with greater relevance than neutral images.

## DISCUSSION

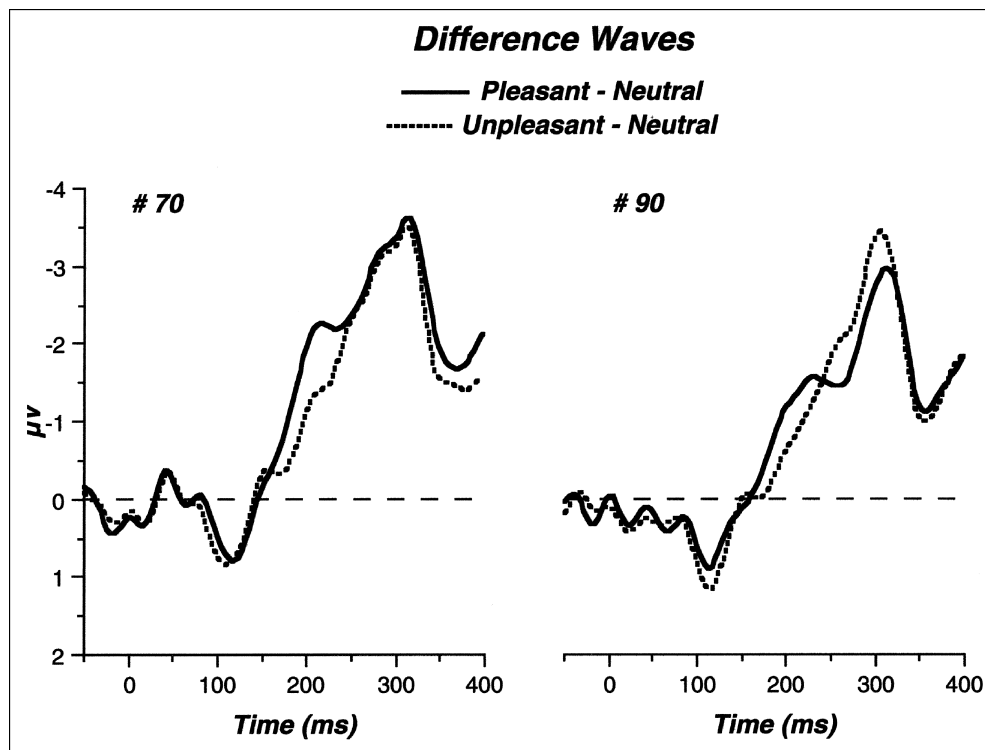
In the present study, we explored the hypothesis that the emotional content of visual cues facilitates the sensory encoding of these stimuli. The results supported this hypothesis. Affective pictures elicited an endogenous negative shift over temporo-occipital sites that started with the negative slope of the P100 and reached its peak around 300 ms. The spatial focus of this early emotion discrimination indicates primary sources of activation in the visual system. Furthermore, posterior negativity increased with the arousal level of the emotional pictures. Thus, it appears that facilitated stimulus encoding of affective visual

3. The centro-parietal cluster comprised the following sensors of the net: 7, 13, 31, 32, 38, 43, 53, 54, and 61 in the left hemisphere, and 79, 80, 81, 87, 88, 94, 106, 107, and 113 in the right hemisphere.

Emotional Facilitation in the Visual Cortex



**Fig. 1.** Grand-averaged event-related potential (ERP) waveforms while viewing pleasant, neutral, and unpleasant pictures. The bottom graphs show the posterior negativity elicited by pleasant and unpleasant images over two representative temporo-occipital sites, one in the left hemisphere (70) and one in the right hemisphere (90). The top graphs show the polarity reversal of the affective modulation over two representative centro-medial sensors (7 and 107).



**Fig. 2.** Illustration of the enlarged temporo-occipital negativity elicited by affective pictures. Difference waveforms for temporo-occipital sensors 70 and 90 were obtained by subtracting waveforms elicited by pictures with neutral content from waveforms elicited by pictures with affective (pleasant and unpleasant) content.

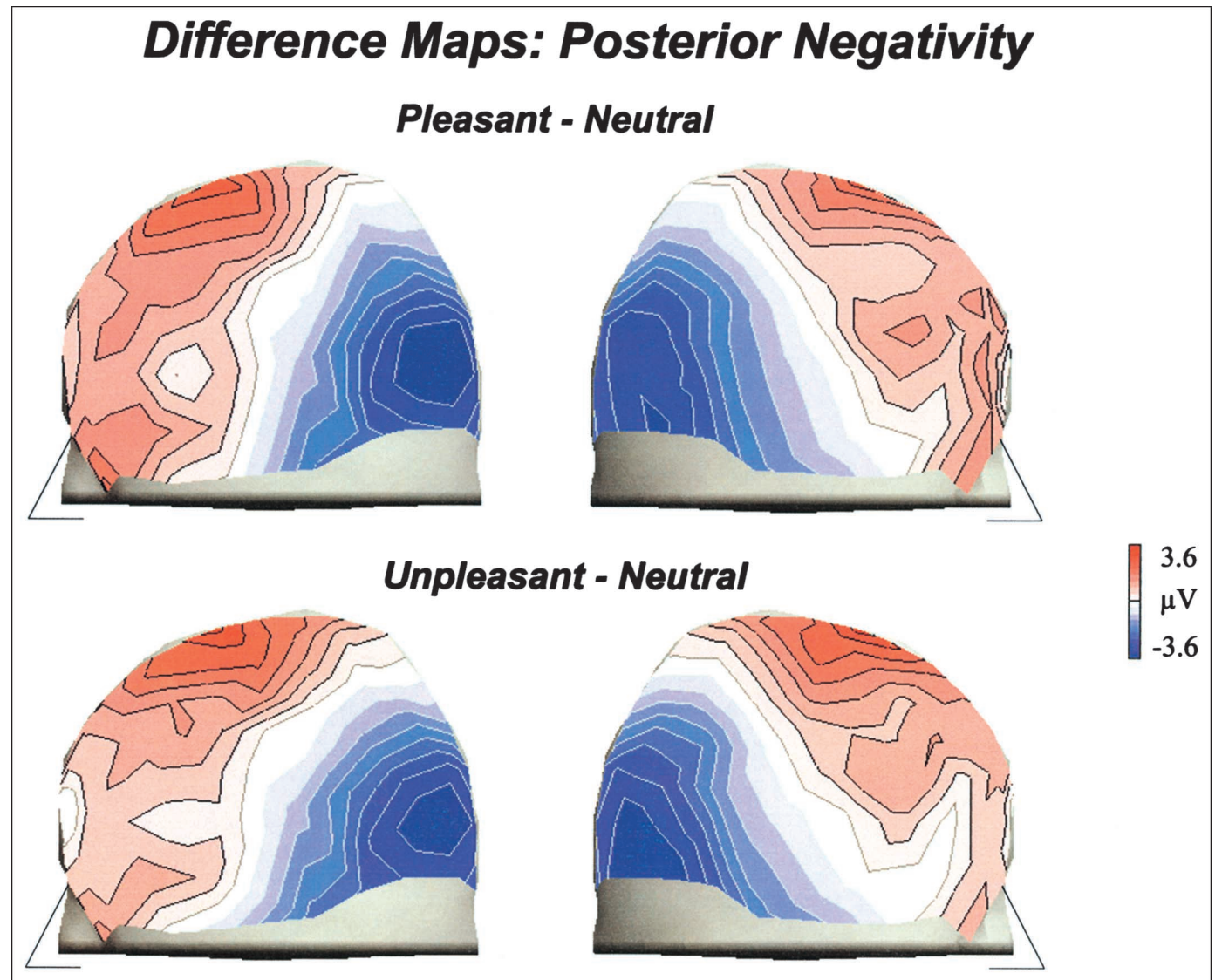
cues varies as a function of affective engagement elicited by the cues. Following this early facilitated sensory processing of affective cues, higher stages of stimulus processing (i.e., stages when rather capacity-limited controlled processing modes are engaged) are also modulated by affective valence. That is, as found previously (Cuthbert et al., 2000; Schupp, Cuthbert, et al., 2000), the amplitudes of the centro-parietal LPP were augmented for affective images relative to neutral pictures. In cognitive tasks, the LPP is increased for stimuli that are task-relevant (Johnson, 1988). Thus, these findings suggest that affective cues may intrinsically have a higher relevance than neutral materials.

The emotional guidance of attentional resources seemed to be similarly pronounced for pleasant and unpleasant stimuli. Both the posterior negativity and the LPP were remarkably similar for pleasant and unpleasant stimuli. From a functional perspective, these observations might not be surprising: Both pleasant and unpleasant pictures activate their corresponding motivational system of approach or avoidance. Facilitated stimulus encoding of salient affective cues seems to be important for implementing successful behavioral strategies irrespective of the affective direction. Accordingly, both ERP measures are silent with regard to the affective valence of the stimuli, but rather reflect the intensity of affective engagement of either of the motivational systems.

It is instructive to relate the affective discrimination of the ERPs to the modulation of the ERPs by cognitive events. It has been consistently demonstrated that attending selectively to the location of a visual stimulus results in increased amplitudes of the P1 and N1 components of the ERP over lateral occipital regions (Mangun & Hillyard, 1991). Although this selective attention to stimulus location op-

erates already at 70 to 90 ms after stimulus onset, selective attention to certain stimulus features such as color, orientation, or shape is associated with a temporo-occipital negativity, developing around 150 to 200 ms and lasting for approximately 100 ms (Näätänen, 1992; Smid, Jakob, & Heinze, 1999). These results were obtained in studies focused on the effects of voluntary attentional orienting, that is, the purposeful allocation of attention by a willing subject (Yantis, 1996). The similarities to the ERP modulation obtained in the present experiment, in both time course and brain topography, are noteworthy. In the current experiment, however, the pictures were presented in a random order, and no selective task was associated with the picture viewing.<sup>4</sup> Thus, the observed ERP discrimination is not a result of voluntary attentional orienting, but rather reflects a process of reflexive attention (see Mangun, Jha, Hopfinger, & Handy, 2000). The increased posterior negativity to voluntarily attended targets is considered to reflect a process by which specific stimuli are selected for more elaborated processing (cf. Näätänen, 1992). Similarly, the increased posterior nega-

4. The finding of facilitated processing of affective compared with neutral cues is unlikely to be due to the evaluation task or to anticipation of the stimulus. A recent study (Junghöfer et al., 2001) also found an early facilitated processing of affective cues without any explicit task instruction. Furthermore, varying stimulus anticipation explicitly by presenting the affective pictures interspersed in an affective picture sequence of the same or different valence also revealed results similar to those reported in the present study (Schupp, Weike, & Hamm, 2000).



**Fig. 3.** Scalp potential maps revealing the topography of the early affective modulation. These brain maps were derived by interpolating voltages to the scalp surface using spherical splines and back-projection to a model head. Contour lines were spaced every  $0.4 \mu\text{V}$ . Left- and right-side views of the model head are illustrated.

tivity to emotional cues might reflexively select affective stimuli for more elaborate stimulus processing. Furthermore, this process of natural selective capture of attention might involve neural structures that are at least partially separate from those involved in the regulation of explicit voluntary selective attention.

Recent studies have revealed that affective cues activate a number of subcortical structures. For example, aversive cues activate the amygdala, the basal forebrain, and the pulvinar (Morris, Friston, & Dolan, 1997; Morris, Öhman, & Dolan, 1998). Activation of these structures might facilitate selective processing in the visual cortex via direct projections (Emery & Amaral, 2000) or ascending neuromodulatory systems (Derryberry & Tucker, 1991). Moreover, several limbic structures (including the amygdala) also project to the anterior cingulate cortex, which is part of the anterior attentional system organizing explicit selective attention (Posner & Petersen, 1990). These various anatomical

hypotheses might be tested by combining neuroimaging measures (i.e., multichannel ERP and fMRI of the whole brain) to assess the temporal and spatial dynamics of the brain response to affective images.

In summary, the present results support the hypothesis that the sensory encoding of affective stimuli is facilitated by early implicit selective attention. ERP waveforms revealed that the brain systematically differentiated emotionally significant from affectively neutral visual inputs. Early selective encoding effects of pleasant and unpleasant images appeared as posterior negativity, indicating primary sources of activation in the visual cortex. In addition, affective cues had increased stimulus relevance at higher-order stages of stimulus processing, as indexed by augmented LPPs for affective cues. Thus, the affect system not only primes motor output (i.e., favoring approach or avoidance dispositions; see Lang et al., 1997), but already facilitates stimulus encoding at an early level of sensory processing. Reflexive attention

**Table 1.** Peak event-related potential amplitude (in microvolts) for specific pleasant and unpleasant picture categories at temporo-occipital and centro-medial sites

Sensor region	Picture category				
	Pleasant		Neutral	Unpleasant	
	Erotic images	Family and baby pictures	Neutral people	Human violence	Mutilated bodies
Temporo-occipital	+1.2 ( $\Delta$ -3.8)	+2.9 ( $\Delta$ -2.1)	+5.0	+2.7 ( $\Delta$ -2.3)	+1.8 ( $\Delta$ -3.2)
Centro-medial	-0.2 ( $\Delta$ +2.5)	-1.6 ( $\Delta$ +1.1)	-2.7	-1.4 ( $\Delta$ +1.3)	-0.6 ( $\Delta$ +2.1)

*Note.* Results are averaged over left- and right-hemisphere sites. For the pleasant and unpleasant categories, values in parentheses indicate the difference from the neutral category.

to affective cues might also have interesting implications for testing clinical models predicting that selective attention to certain threat-related stimuli is a crucial factor in several anxiety disorders (Mathews & MacLeod, 1994).

**Acknowledgments**—This research was supported by German Research Foundation Grants Schu1074/7-1 to Harald T. Schupp and Ha1593/10-2 to Alfons O. Hamm. We thank Silva Rosolski, Andrea Siegmund, and Jessica Stockburger for their assistance in data collection.

## REFERENCES

- Bradley, M.M. (2000). Emotion and motivation. In J.T. Cacioppo, L.G. Tassinary, & G.G. Berntson (Eds.), *Handbook of psychophysiology* (pp. 602–642). New York: Cambridge University Press.
- Cacioppo, J.T., Crites, S.L., Jr., Berntson, G.G., & Coles, M.G.H. (1993). If attitudes affect how stimuli are processed, should they not affect the event-related brain potential? *Psychological Science*, 4, 108–112.
- Cacioppo, J.T., Gardner, W.L., & Berntson, G.G. (1999). The affect system has parallel and integrative processing components: Form follows function. *Journal of Personality and Social Psychology*, 76, 839–855.
- Cuthbert, B.N., Bradley, M.M., & Lang, P.J. (1996). Probing picture perception: Activation and emotion. *Psychophysiology*, 33, 103–111.
- Cuthbert, B.N., Schupp, H.T., Bradley, M.M., Birbaumer, N., & Lang, P.J. (2000). Brain potentials in affective picture processing: Covariation with autonomic arousal and affective report. *Biological Psychology*, 52, 95–111.
- Davis, M. (1997). Neurobiology of fear responses: The role of the amygdala. *The Journal of Neuropsychiatry and Clinical Neurosciences*, 9, 382–402.
- Derryberry, D., & Tucker, D.M. (1991). The adaptive base of the neural hierarchy: Elementary motivational controls on network function. In R.A. Dienstbier (Ed.), *Nebraska Symposium on Motivation, 1990: Perspectives on motivation* (pp. 289–342). Lincoln: University of Nebraska Press.
- Emery, N.J., & Amaral, D.G. (2000). The role of the amygdala in primate social cognition. In R.D. Lane & L. Nadel (Eds.), *Cognitive neuroscience of emotion* (pp. 156–191). New York: Oxford University Press.
- Fredrikson, M., Wik, G., Greitz, T., Eriksson, L., Stone, E.S., Ericson, K., & Sedvall, G. (1993). Regional cerebral blood flow during experimental phobic fear. *Psychophysiology*, 30, 126–130.
- Frijda, N.H. (1986). *The emotions*. Cambridge, England: Cambridge University Press.
- Hamm, A.O., Greenwald, M.K., Bradley, M.M., & Lang, P.J. (1993). Emotional learning, hedonic change, and the startle probe. *Journal of Abnormal Psychology*, 102, 453–465.
- Hamm, A.O., Schupp, H.T., & Weike, A.I. (in press). Motivational organization of emotions: Autonomic changes, cortical responses, and reflex modulation. In R.J. Davidson, K. Scherer, & H.H. Goldsmith (Eds.), *Handbook of affective sciences*. Oxford, England: Oxford University Press.
- Hopfinger, J.B., & Mangun, G.R. (1998). Reflexive attention modulates processing of visual stimuli in human extrastriate cortex. *Psychological Science*, 9, 441–447.
- Johnson, R.J. (1988). The amplitude of the P300 component of the event-related potential: Review and synthesis. In P.K. Ackles, J.R. Jennings, & M.G.H. Coles (Eds.), *Advances in psychophysiology* (Vol. 3, pp. 69–137). Greenwich, CT: JAI Press.
- Junghöfer, M., Bradley, M.M., Elbert, T.R., & Lang, P.J. (2001). Fleeting images: A new look at early emotion discrimination. *Psychophysiology*, 38, 175–178.
- Junghöfer, M., Elbert, T., Tucker, D.M., & Rockstroh, B. (2000). Statistical control of artifacts in dense array EEG/MEG studies. *Psychophysiology*, 37, 523–532.
- Lane, R.D., Reiman, E.M., Ahern, G.L., & Schwartz, G.E. (1997). Neuroanatomical correlates of happiness, sadness, and disgust. *American Journal of Psychiatry*, 154, 926–933.
- Lang, P.J. (1995). The emotion probe. *American Psychologist*, 50, 372–385.
- Lang, P.J., Bradley, M.M., & Cuthbert, B.N. (1990). Emotion, attention, and the startle reflex. *Psychological Review*, 97, 377–395.
- Lang, P.J., Bradley, M.M., & Cuthbert, B.N. (1997). Motivated attention: Affect, activation, and action. In P.J. Lang, R.F. Simons, & M. Balaban (Eds.), *Attention and orienting: Sensory and motivational processes* (pp. 97–135). Mahwah, NJ: Erlbaum.
- Lang, P.J., Bradley, M.M., & Cuthbert, B.N. (1999). *International Affective Picture System (IAPS): Technical manual and affective ratings*. Gainesville, FL: Center for Research in Psychophysiology.
- Lang, P.J., Bradley, M.M., Fitzsimmons, J.R., Cuthbert, B.N., Scott, J.D., Moulder, B., & Nangia, V. (1998). Emotional arousal and activation of the visual cortex: An fMRI analysis. *Psychophysiology*, 35, 199–210.
- Mangun, G.R., & Hillyard, S.A. (1991). Modulation of sensory-evoked brain potentials provide evidence for changes in perceptual processing during visual-spatial priming. *Journal of Experimental Psychology: Human Perception and Performance*, 17, 1057–1074.
- Mangun, G.R., Jha, A.P., Hopfinger, J.B., & Handy, T.C. (2000). The temporal dynamics and functional architecture of attentional processes in human extrastriate cortex. In M.S. Gazzaniga (Ed.), *The new cognitive neurosciences* (2nd ed., pp. 701–710). Cambridge, MA: MIT Press.
- Mathews, A.M., & MacLeod, C. (1994). Cognitive approaches to emotion and emotional disorders. *Annual Review of Psychology*, 45, 25–50.
- Miller, G.A., Gratton, G., & Yee, C.M. (1988). Generalized implementation of an eye movement correction procedure. *Psychophysiology*, 25, 241–243.
- Morris, J.S., Friston, K.J., & Dolan, R.J. (1997). Neural responses to salient visual stimuli. *Proceedings of the Royal Society of London, Series B, Biological Sciences*, 264, 769–775.
- Morris, J.S., Öhman, A., & Dolan, R.J. (1998). Conscious and unconscious emotional learning in the human amygdala. *Nature*, 393, 467–470.
- Näätänen, R. (1992). *Attention and brain function*. Hillsdale, NJ: Erlbaum.
- Öhman, A., Flykt, A., & Lundqvist, D. (2000). Unconscious emotion: Evolutionary perspectives, psychophysiological data and neuropsychological mechanisms. In R.D. Lane & L. Nadel (Eds.), *Cognitive neuroscience of emotion* (pp. 296–327). New York: Oxford University Press.
- Posner, M.I., & Petersen, S.E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, 13, 25–42.
- Schupp, H.T., Cuthbert, B.N., Bradley, M.M., Cacioppo, J.T., Ito, T., & Lang, P.J. (2000). Affective picture processing: The late positive potential is modulated by motivational relevance. *Psychophysiology*, 37, 257–261.
- Schupp, H.T., Weike, A., & Hamm, A. (2000). Affect and evaluative context: High-density ERP recordings during picture processing [Abstract]. *Psychophysiology*, 37, S88.
- Smid, H.G.O.M., Jakob, A., & Heinze, H.J. (1999). An event-related brain potential study of visual selective attention to conjunctions of color and shape. *Psychophysiology*, 36, 264–279.
- Tucker, D.M., Liotti, M., Potts, G.F., Russell, G.S., & Posner, M.I. (1994). Spatiotemporal analysis of brain electrical fields. *Human Brain Mapping*, 1(2), 134–152.
- Yantis, S. (1996). Attentional capture in vision. In A.F. Kramer, M.G.H. Coles, & G.D. Logan (Eds.), *Converging operations in the study of visual selective attention* (pp. 45–76). Washington, DC: American Psychological Association.

(RECEIVED 4/18/01; REVISION ACCEPTED 8/17/01)