

Recognition Memory for Emotional and Neutral Faces: An Event-Related Potential Study

Mikael Johansson, Axel Mecklinger, and Anne-Cécile Treese

Abstract

■ This study examined emotional influences on the hypothesized event-related potential (ERP) correlates of familiarity and recollection (Experiment 1) and the states of awareness (Experiment 2) accompanying recognition memory for faces differing in facial affect. Participants made gender judgments to positive, negative, and neutral faces at study and were in the test phase instructed to discriminate between studied and nonstudied faces. Whereas old–new discrimination was unaffected by facial expression, negative faces were recollected to a greater extent than both positive and neutral faces as

reflected in the parietal ERP old–new effect and in the proportion of remember judgments. Moreover, emotion-specific modulations were observed in frontally recorded ERPs elicited by correctly rejected new faces that concurred with a more liberal response criterion for emotional as compared to neutral faces. Taken together, the results are consistent with the view that processes promoting recollection are facilitated for negative events and that emotion may affect recognition performance by influencing criterion setting mediated by the prefrontal cortex. ■

INTRODUCTION

Although many of the numerous episodes and events that constitute our experience are rapidly forgotten or remembered poorly, memories for some events tend to be particularly enduring and detailed. An extensive amount of experimental research and studies of autobiographical memories have highlighted the modulatory role of emotion on memory and frequently revealed an advantage for emotionally significant events over more mundane events (see Christianson, 1992, for a review). From an evolutionary perspective, the benefit of emotion on memory may be considered adaptive as it increases the chances that survival-relevant information will be available in the future (Dolan, 2002; Hamann, 2001). Here we focus on how emotion- and memory-related functioning interact in the processing of human faces, a stimulus type of particular relevance for social and emotional behavior.

Data from animal, neuroimaging, lesion, and pharmacological studies converge on the role of the amygdala in the encoding, consolidation, and retrieval of memory for emotionally intense events (see McGaugh & Cahill, 2003, for a review). Neuroimaging studies have demonstrated that amygdalar activity during encoding of emotionally provocative stimuli correlates with subsequent memory performance (e.g., Cahill, Haier, et al., 1996). This has been observed for stimuli of both positive and negative valence (Hamann, Ely, Grafton, & Kilts, 1999),

supporting the idea that amygdalar influences on memory are triggered by the emotional arousal rather than by the valence. Furthermore, patients with bilateral amygdala lesions fail to show the emotion-induced memory enhancement evident in controls (Cahill, Babinsky, Markowitsch, & McGaugh, 1995) and preserved in patients with temporal lobe amnesia (Hamann, Cahill, McGaugh, & Squire, 1997). It has been proposed that the amygdala exerts its influence on memory through the modulation of hippocampal activity and via interaction with prefrontal cortices and additional cortical regions that have been shown to play a significant role in episodic memory (Dolan, 2002; Hamann, 2001; Cahill & McGaugh, 1998; Amaral, Price, Pitkänen, & Carmichael, 1992).

The starting point for the present study is the fact that while an emotion-induced memory enhancement has consistently been observed in studies of recall (e.g., Cahill, Haier, et al., 1996), the results from recognition memory studies have been less consistent and the reason for this discrepancy remains unclear. In accord with the effects on recall performance, several studies have shown that participants' ability to recognize previously studied items may indeed be greater for emotionally negative as compared to neutral items. However, the increased hit rate is often coupled with a parallel increase in the false alarm rate, yielding comparable old–new discrimination performance for emotionally negative and neutral words (Windmann, Sakhavat, & Kutas, 2002; Windmann & Kutas, 2001) or even worse performance for the negative words (Maratos, Allan, & Rugg, 2000; Danion, Kauffmann-Muller, Grange, Zimmermann,

Saarland University, Saarbrücken, Germany

& Greth, 1995; Leiphart, Rosenfeld, & Gabrieli, 1993). Consequently, an examination of response bias measures reveals a more liberal bias for emotionally negative words, a phenomenon that has been referred to as the “emotion-induced recognition bias” (Windmann & Kutas, 2001). At least two explanations have been proposed for this finding. The first is based on the fact that negative words share a stronger inter-item association strength than neutral words. It is argued that this may cause an elevated false alarm rate to new negative words (Maratos et al., 2000) analogously to the false alarms consistently observed for new words semantically related to studied material (e.g., Roediger & McDermott, 1995). Thus, this account does not attribute the effect to the negative valence per se, but rather to the more cohesive semantic category formed by negative as compared to neutral words. In contrast, after having made an effort to equalize the inter-item relatedness for negative and neutral words, Windmann and Kutas (2001) argued that the difference in response bias reflects flexible criterion setting triggered by emotional valence that works to ensure that negative stimuli are not missed or considered irrelevant.

However, Ochsner (2000) reported higher old–new discrimination for negative pictures than for positive and neutral pictures, suggesting an emotion-induced memory enhancement also on recognition memory. As noted by Dougal (2003), the levels of false alarms in this latter study were generally very low, making hits the main source of discrimination differences. An important aspect of Ochsner’s study was that participants were encouraged to report the subjective state of awareness that accompanied each “old” response according to the “remember/know” procedure (Tulving, 1985). Accordingly, participants were instructed to respond “remember” whenever they were able to become consciously aware of some aspect of the previous presentation of the recognized picture and “know” whenever the picture was familiar but failed to bring to mind any details of the picture’s previous occurrence. Interestingly, these judgments showed that negative pictures were remembered to a greater extent than both positive and neutral pictures, suggesting qualitative differences in recognition memory as a function of emotional valence.

One potential explanation for the disparity between the results of recall and recognition studies is that performance on these tasks draws differentially on the two distinct processes held to support memory in dual-process models: “familiarity” and “recollection” (see Yonelinas, 2002, for a review). These models posit that recognition may be based on (a) a feeling of familiarity resulting from a fast assessment of the global similarity between the studied and tested items or (b) recollection resulting from a somewhat slower consciously controlled retrieval of detailed information that binds an item to a specific temporal and spatial study context (cf. remember). While familiarity would suffice for accurate

recognition performance, recall tasks necessitate that a controlled search in memory is initiated that, if successful, enables retrieval of the sought-after episode. Thus, it is conceivable that emotional influences on recollective processes lead to a memory enhancement on tasks such as recall, but may go unnoticed when task performance relies heavily on familiarity-based responding as is the case on recognition memory tasks (cf. Dougal, 2003). Moreover, when a fast assessment of familiarity forms the basis of responding “old” or “new,” emotion may be more apt to influence performance by lowering the response criterion (cf. Windmann & Kutas, 2001) and/or give rise to an elevated false alarm rate to new negative words by virtue of this category being more semantically cohesive than neutral words (cf. Maratos et al., 2000). Thus, a further examination of emotional influences on the contributions of familiarity and recollection to recognition memory may provide important information. In addition, the use of a nonverbal stimulus material may potentially reconcile whether the emotion-induced response bias reflects a general criterion shift triggered by emotional valence or is caused by nonemotional factors (i.e., inter-item association strength).

The present study employed event-related potentials (ERPs) to examine recognition memory for faces differing in facial expression. Faces were chosen for two main reasons. First, they are not associated with the same potential confound of semantic relatedness as words when investigating emotion-specific effects. Second, faces are particularly salient cues in conveying emotional information and it has been proposed that the amygdala shows a considerable specialization in recognizing emotion in facial expressions (Adolphs & Tranel, 2003). The link between the amygdala and face processing is also established by single-cell recordings in the human amygdala revealing neurons that fire relatively selectively to faces (Fried, MacDonald, & Wilson, 1997) and by the fact that bilateral amygdala damage leads to impaired recognition of emotion in facial expression, despite intact identity recognition (e.g., Adolphs, Tranel, Damasio, & Damasio, 1994).

An extensive amount of research has demonstrated that ERPs are sensitive to the processes underlying recognition memory and it has been proposed that different ERP memory effects may be used to dissociate familiarity and recollection (e.g., Curran, 2000; Friedman & Johnson, 2000; Mecklinger, 2000; Rugg, Mark, et al., 1998). In general, correct responses to old items elicit more positive-going ERPs than correctly rejected new items (see Friedman & Johnson, 2000; Rugg & Allan, 2000, for reviews). This so called old–new effect starts approximately 300 msec poststimulus and may last for several hundreds of milliseconds. Within this broad time window, several subcomponents have been identified based on their spatio-temporal characteristics and sensitivity to experimental manipulations. For present purposes, the most important effects are an early

mid-frontal old–new effect (300–500 msec) hypothesized to reflect familiarity and a somewhat later effect (400–800 msec) maximal over (left) parietal regions thought to index recollection. An additional late on-setting and sustained old–new effect is frequently observed over right frontal regions and is considered to reflect postretrieval processes (e.g., Mecklinger, 2000; Rugg & Wilding, 2000).

Previous ERP studies of recognition memory for emotional material have either shown that negative and neutral words elicit comparable old–new effects (Windmann & Kutas, 2001) or that negative words elicit smaller parietal and right frontal old–new effects than neutral words (Maratos et al., 2000). The latter finding may be attributed to the more positive-going ERPs elicited by correctly rejected negative as compared to neutral words. Maratos and colleagues argued that this reflects the tendency to falsely recollect new negative words due to their strong inter-item relatedness. In contrast, Windmann and Kutas observed that both correct and incorrect “old” responses to negative words were associated with an early (300–500 msec) positive-going modulation at mid-frontal electrode sites that they argued reflects prefrontal activity mediating a more relaxed criterion for responding to negative words.

In the present study, participants made gender judgments while encoding unfamiliar faces differing in facial affect (positive, negative, neutral) and were in the test phase instructed to discriminate between previously

studied and nonstudied faces. Capitalizing on the proposed ERP correlates of familiarity and recollection described above, we set out to examine the relative contribution of these processes to recognition memory for the emotional and neutral faces. In addition to examining memory effects and their potential interaction with our manipulation of emotion, we aimed at investigating how emotional arousal and/or valence elicited by a nonverbal stimulus material modulate frontally recorded ERPs as this might shed some light upon the mechanism underlying the emotion-induced recognition bias.

RESULTS

Experiment 1

Behavioral Data

An overview of participants’ recognition memory performance is given in Table 1.

Memory performance. The analysis of variance (ANOVA) performed on the measures of discrimination accuracy (Pr) revealed no significant effect involving the factor of emotion (positive, negative, neutral; $F_s < 1$, ns), suggesting that the facial expressions did not influence participants’ ability to accurately discriminate between old and new faces.

However, the analysis of the response bias measures revealed an interaction between expressiveness (high, low) and emotion [$F(2,30) = 8.34$, $p = .002$]. The sub-

Table 1. Probabilities of Correct Responses to Old and New Items, Reaction Times, and Measures of Old–New Discrimination and Response Bias in Experiment 1

	Item Type				Performance Measure	
	Old		New		Pr	Br
Emotion and Expressiveness	<i>p</i> (“Old” Response)	RT	<i>p</i> (“New” Response)	RT		
Positive						
Overall	.57 (.03)	1039 (44)	.69 (.02)	1032 (43)	.26 (.03)	.43 (.03)
High	.57 (.04)	1025 (44)	.68 (.02)	1060 (45)	.25 (.04)	.44 (.03)
Low	.57 (.03)	1053 (45)	.70 (.02)	1003 (42)	.26 (.03)	.42 (.03)
Negative						
Overall	.60 (.03)	1005 (41)	.67 (.02)	1043 (42)	.26 (.02)	.45 (.03)
High	.63 (.03)	1011 (44)	.63 (.03)	1038 (45)	.26 (.03)	.50 (.04)
Low	.56 (.03)	1000 (39)	.71 (.03)	1048 (42)	.27 (.03)	.40 (.03)
Neutral						
Overall	.56 (.03)	996 (41)	.70 (.02)	1019 (41)	.26 (.02)	.42 (.04)
High	.52 (.03)	1012 (44)	.73 (.03)	1021 (44)	.25 (.03)	.36 (.04)
Low	.60 (.04)	980 (40)	.67 (.03)	1017 (40)	.26 (.02)	.47 (.04)

Standard errors of the means (*SEM*) are given in the parentheses. Reaction times (RTs) are displayed in msec.

subsidiary one-way ANOVAs showed a main effect of emotion for faces rated high on expressiveness [$F(2,30) = 9.17, p = .003$], but not for those rated low [$F(2,30) = 1.82, ns$]. Planned pairwise comparisons showed that emotional faces were associated with a more liberal response bias than neutral faces and further that the two types of emotional facial expressions differed in a negative more-liberal-than-positive pattern. This finding suggests that criterion setting may be influenced by stimuli giving rise to emotional arousal and not only those characterized by negative valence.

Reaction times. The ANOVA on the reaction-time measures gave rise to a significant Expressiveness \times Emotion \times Response (“old,” “new”) interaction [$F(2,30) = 6.83, p = .001$]. Old judgments were faster for emotional faces than for neutral faces rated high on expressiveness. For faces rated low on this dimension, old judgments took longer for positive than for neutral faces.

ERP Data

Grand averages for correct responses to old and new positive, negative, and neutral faces are depicted in Figure 1, together with topographic maps showing the distribution of the old–new effects across the three time

windows used in the analyses. As expected, correctly recognized old faces elicited more positive-going ERPs than correctly rejected new faces, beginning approximately 380 msec poststimulus onset and lasting until the end of the epoch at anterior electrode sites. Importantly, the scalp distribution of these old–new effects appears to differ as a function of time and facial expression. While positive and neutral faces were associated with an old–new difference maximum over mid-frontal regions, negative faces elicited an effect that was largest at posterior electrode sites. The spatio-temporal characteristics of these effects correspond well with the old–new effects associated with familiarity and recollection in previous research (e.g., Nessler & Mecklinger, 2003; Curran, 2000). The outcomes of the statistical evaluation of the ERP memory and emotion effects are described in the following two sections.

ERP memory effects. Table 2 shows the results of the initial ANOVAs performed for each time window. As is evident from these analyses, reliable effects involving emotion and item type (old, new) were present in all three time windows. We begin by describing effects involving item type that did not interact with the factor emotion. The interaction between item type and HEM (left, midline, right) found in the 380–500 msec time

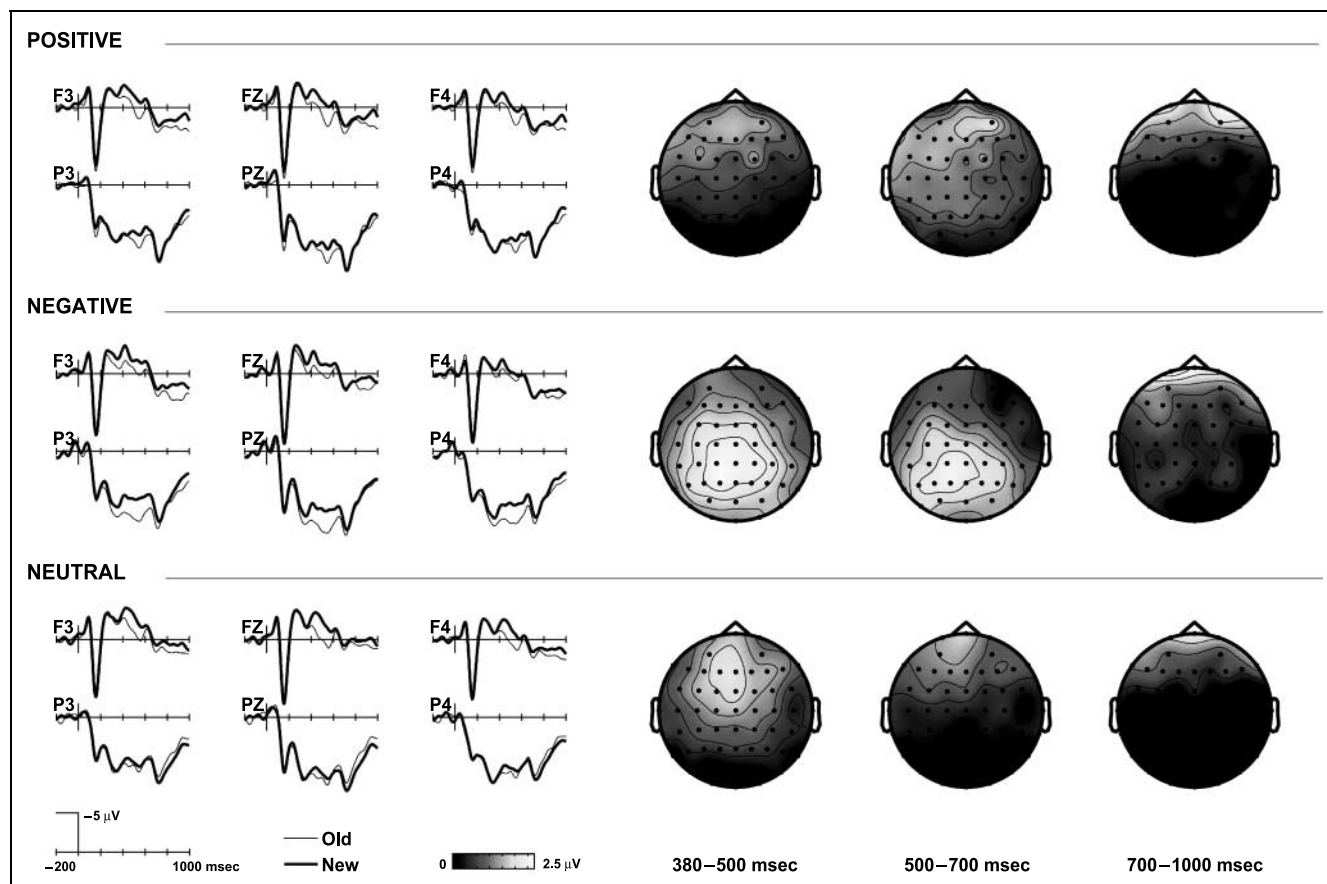


Figure 1. Grand average ERPs elicited by correctly judged old and new items depicted separately for positive, negative, and neutral facial expressions. The topographic maps show the scalp distribution of the old–new effects in the three time windows used in the analyses.

Table 2. ANOVA Results from the Mean Amplitude Analyses

<i>Time Window and Effect</i>	<i>df</i>	<i>F</i>	<i>p</i>
380–500 msec			
EMO	2,30	6.23	.006
TYPE	1,15	11.91	.004
TYPE × AP	1,15	7.63	.015
TYPE × HEM	2,30	6.99	.010
EMO × TYPE × AP	2,30	4.28	.030
500–700 msec			
EMO	2,30	4.71	.021
TYPE	1,15	7.37	.016
EMO × AP	2,30	3.56	.048
EMO × HEM	4,60	3.33	.030
EMO × TYPE × AP	2,30	3.81	.044
700–1000 msec			
EMO	2,30	4.43	.028
TYPE × AP	1,15	13.66	.002
EMO × HEM	4,60	3.60	.020

EMO (positive vs. negative vs. neutral); TYPE (old vs. new); AP (anterior vs. posterior); HEM (left vs. midline vs. right).

window reflects the fact that the overall old–new difference was largest over the midline regions (see Figure 1). Furthermore, the Item type × AP (anterior, posterior) interaction in the late 700–1000 msec time window reflects the pronounced anterior distribution of the old–new effect by the end of the recording epoch. This late old–new difference was restricted to anterior regions [$F(1,15) = 9.90, p = .007$], showed a bilateral distribution [Item type × HEM: $F(2,30) < 1, ns$], and was unaffected by emotion ($F_s = 1.44, ns$). Most important for present purposes were, however, the significant Emotion × Item type × AP interactions found in the 380–500 and the 500–700 msec intervals. The results of the subsidiary analyses are presented in Table 3 (main effects of item type indicate reliable old–new effects) and will be discussed next.

In the early time window (380–500 msec), significant old–new effects were present over anterior regions (midline maximum) for all types of facial expressions. A follow-up analysis of differences measures (i.e., old minus new) showed that the magnitude of the effect did not differ as a function of emotion ($F_s < 1, ns$; see left and middle section of Figure 2). At posterior sites, only negative faces were associated with a significant old–new difference. Turning to the later time window (500–700 msec), the anterior old–new effect remained reliable only for positive faces and a posterior old–new effect was observed exclusively for negative faces.

Topographic analyses were conducted on rescaled difference measures in order to assess whether the scalp distribution of the old–new effect varied as a function of emotional valence. Importantly, the Emotion × AP interaction was significant in the 380–500 msec time window [$F(2,30) = 4.66, p = .022$] and was marginally significant in the 500–700 msec time window [$F(2,30) = 3.63, p = .057$]. As suggested by Figure 1, all facial expressions elicited early old–new effects distributed over anterior regions, whereas only negative faces elicited an additional more posteriorly distributed effect, presumably reflecting different contributions of familiarity and recollection to recognition memory performance.

Emotion-specific effects. We also set out to examine ERP correlates of emotion-specific processing. By focusing on the correctly rejected new faces, we intended to minimize the potentially confounding factor of retrieval success inherent in hit responses. As can be seen in Figure 3, the main differences in the ERPs elicited by positive, negative, and neutral faces are present at the frontal leads. Emotional faces evoked more positive-going ERPs in time windows overlapping with the old–new effects examined above. In addition, negative faces were associated with a larger P2 component (peaking at ~160 msec poststimulus) than positive and neutral faces.

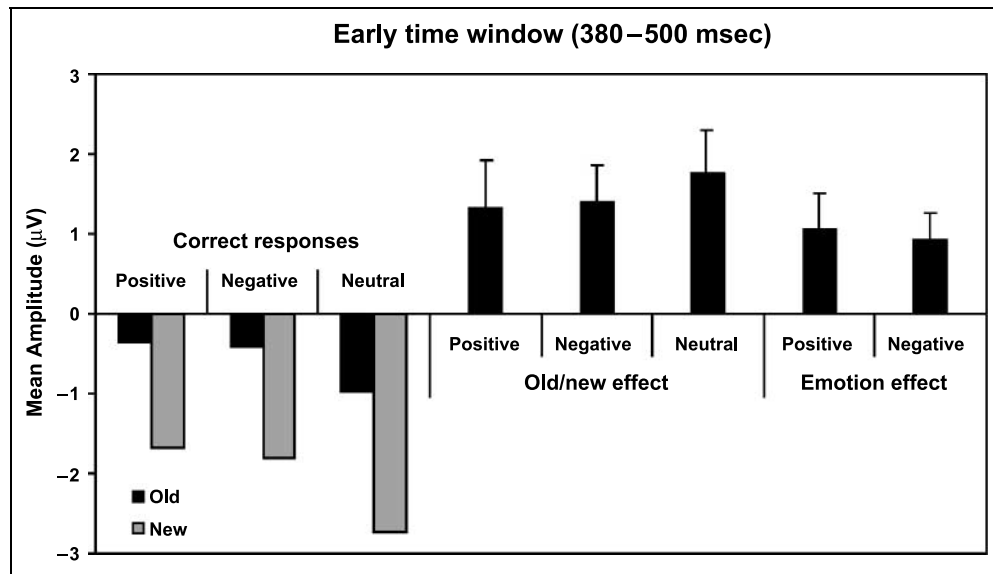
Separate analyses were performed on data in the three time windows used above. There was a main effect of emotion in the 380–500 msec time interval [$F(2,30) = 3.78, p = .042$]. Correctly rejected emotional faces were more positive-going than neutral faces [EMO contrast, i.e., positive/negative vs. neutral: $F(1,15) = 6.41, p = .023$; VAL contrast, i.e., positive vs. negative: $F(1,15) < 1, ns$]. As can be seen in the right panel of Figure 3, the topography of the difference between emotional and neutral faces is highly similar to the

Table 3. Results of the Subsidiary Analyses of the Mean Amplitude Measures Contrasting ERPs Elicited by Correctly Judged Old and New Faces

<i>Time Window and Region</i>	<i>Emotion</i>					
	<i>Positive</i>		<i>Negative</i>		<i>Neutral</i>	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
380–500 msec						
Anterior	4.67	.047	7.52	.015	8.37	.011
Posterior	< 1	<i>ns</i>	20.49	.000	< 1	<i>ns</i>
500–700 msec						
Anterior	5.95	.028	4.24	<i>ns</i>	3.19	<i>ns</i>
Posterior	1.01	<i>ns</i>	15.12	.001	< 1	<i>ns</i>

Significant effects represent reliable old–new effects (main effects of item type). Degrees of freedom are 1,15 for all of the effects. *ns* = not significant.

Figure 2. Mean amplitudes recorded over the midline anterior region in the 380–500 msec time window. The left section shows the mean values for correctly judged old and new faces, the middle section shows the old–new effect (i.e., old minus new), and the right section shows the emotion effect (i.e., positive/negative minus neutral). Error bars represent the standard error of the mean.



mid-frontal old–new effect observed in the same time window. Given the view that this early mid-frontal ERP modulation is related to familiarity, the results suggest that an item may be familiar not only because it has been previously encountered, but also as a function of its emotional arousal. This latter finding is illustrated in more detail in Figure 2, depicting the magnitude of the old–new effect and emotion effect (i.e., new emotional faces minus new neutral) over the midline anterior region. As can be seen, the mid-frontal negativity is attenuated by two apparently additive factors: old–new status and emotional arousal.

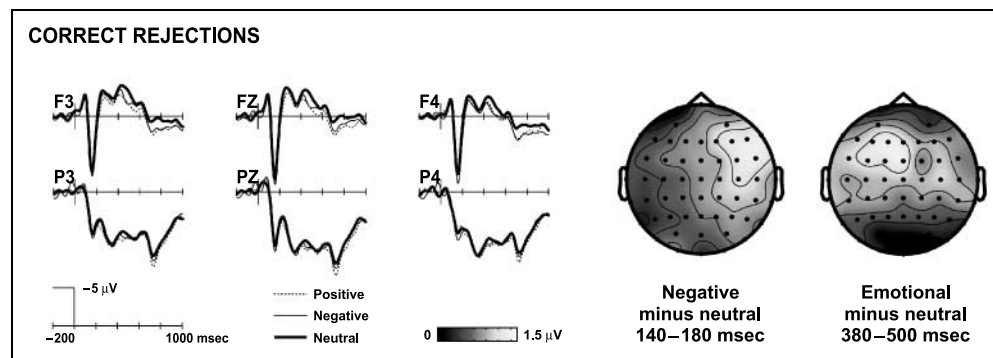
A final analysis was performed to assess the reliability of the larger P2 component to negative faces as is suggested by the ERPs presented in Figure 3. Data in a 140–180 msec time window were subjected to an ANOVA using the factors of emotion and HEM. The main effect of emotion and the interaction with HEM were marginally significant [$F(2,30) = 3.23, p = .079$ and $F(4,60) = 2.56, p = .076$]. Both the EMO and the VAL contrasts were significant when data from the right anterior region were analyzed [EMO contrast: $F(1,15) =$

$5.35, p = .035$; VAL contrast: $F(1,15) = 7.57, p = .015$]. Thus, negative faces evoked a P2 with a right anterior distribution that was of greater magnitude than those evoked by positive and neutral faces. In contrast to the emotion-related difference in the 380–500 msec time window, the P2 was sensitive to negative valence rather than emotional arousal.

Discussion

The ERP results of Experiment 1 suggest that the relative proportions of familiarity and recollection processes in recognition memory for faces are influenced by the facial expression of the to-be-remembered face. Notably, this differential contribution of the processes was observed even though recognition performance did not differ as a function of emotion type and face identity rather than emotional expression was relevant for the task. More specifically, while all faces were associated with an early mid-frontal old–new effect previously linked to familiarity-based recognition judgments,

Figure 3. Grand average ERPs elicited by new correctly rejected positive, negative, and neutral faces. The topographic maps depict the distribution of the differences between negative and neutral faces in the early 140–180 msec time window (left) and between emotional and neutral faces in the 380–500 msec time interval (right).



negative faces were characterized by an additional posterior old–new effect that has been considered to tap recollection-based judgments. The topographic analyses performed on rescaled data confirmed and extended this finding by revealing that the old–new effects elicited by positive/neutral and negative faces were generated by qualitatively different neuronal circuitries (Rugg & Coles, 1995). Thus, our results support the view that stimuli (i.e., faces) of negative valence may be recollected to a higher degree than positive and neutral stimuli despite equal levels of recognition accuracy. To further examine the validity of this interpretation, we conducted a follow-up behavioral study in which we aimed at substantiating the ERP evidence for a differential involvement of familiarity and recollection in recognition memory for faces differing in facial affect. In this experiment, the same facial expressions were used as in Experiment 1 and following each recognition judgment, participants gave an additional remember/know judgment. Based on the results of Experiment 1, we predicted that the proportion of remember judgments would be higher for negative faces than for positive and neutral faces.

Experiment 2

The results are summarized in Table 4 in which the overall rates of “old” responses to old and new faces are presented together with discrimination and response bias measures and the states of awareness accompanying the recognition judgments.

Memory Performance

As in Experiment 1, no effect involving the factor emotion was reliable for the Pr measures ($F_s = 1.98$, ns) and, additionally, an Expressiveness \times Emotion interaction was observed for the Br measures [$F(2,26) = 3.72$, $p = .039$]. The follow-up analyses showed a marginally significant effect of emotion for faces rated

high on expressiveness [$F(2,26) = 2.52$, $p = .10$], but a significant effect for those rated low [$F(2,26) = 3.65$, $p = .040$]. To relate to the results of Experiment 1, we performed pairwise comparisons also for high-expressiveness stimuli. Negative faces were, as expected, associated with a more liberal response bias than positive faces and marginally so in comparison with neutral faces ($p = .078$), but no difference was found between positive and neutral faces (positive: .47; negative: .59; neutral: .48). Positive faces rated low on expressiveness gave rise to a more conservative response bias than neutral (positive: .44; negative: .51; neutral: .56).

The analysis of the RT measures revealed a marginally significant Emotion \times Response interaction [$F(1,13) = 4.36$, $p = .057$], but follow-up comparisons failed to reveal any significant effects.

State of Awareness

Remember judgments. The proportion of remember responses varied as a function of emotion for both correct and incorrect “old” responses [$F(2,26) = 5.47$, $p = .010$; $F(2,26) = 5.18$, $p = .013$]. As predicted, correctly recognized negative faces received more remember responses than positive faces and marginally more than neutral ($p = .10$), suggesting that negative valence increases the likelihood that a correctly recognized item will be remembered. In contrast, false alarms to both positive and negative faces were given more remember responses than neutral. A marginally significant main effect of emotion was revealed when examining the discrimination measures [remember Pr; $F(2,26) = 2.74$, $p = .10$]. As a consequence of the increased number of false remember responses to emotional faces, no difference was observed between negative and neutral faces (.23 and .22), but both were associated with a greater discriminability than positive faces (.15). An effect of emotional arousal on the tendency to respond remember was evident when response bias measures were examined [remember Br; $F(2,26) = 8.49$, $p = .001$]. Participants were reliably more liberal in responding

Table 4. Probabilities of Responding “Old” to Old and New Items, the Accompanying States of Awareness, and Measures of Old–New Discrimination and Response Bias in Experiment 2

Emotion	Item Type								Performance Measure	
	Old				New				Pr	Br
	Overall	R	K	G	Overall	R	K	G		
Positive	.65 (.03)	.32 (.04)	.33 (.03)	.35 (.06)	.30 (.04)	.18 (.05)	.31 (.06)	.51 (.08)	.35 (.04)	.45 (.05)
Negative	.68 (.04)	.45 (.05)	.25 (.03)	.29 (.03)	.39 (.04)	.20 (.05)	.26 (.04)	.54 (.07)	.30 (.03)	.56 (.05)
Neutral	.69 (.04)	.37 (.05)	.26 (.04)	.38 (.06)	.32 (.03)	.09 (.05)	.22 (.06)	.69 (.09)	.38 (.03)	.52 (.06)

Standard errors of the means (*SEM*) are given in the parentheses. R = remember; K = know; G = guess. Cases in which the proportions of remember, know, and guess responses do not add up to 1.0 reflect rounding error.

remember to positive and negative as compared to neutral faces (.08 and .10 vs. .06).

Know judgments. The analysis of the know responses only revealed a main effect of emotion for correct responses [$F(2,26) = 4.05, p = .031$], which was due to a greater proportion of know judgments to positive than to both negative and neutral faces (cf. Ochsner, 2000). However, both discrimination measures (know Pr) and response bias measures (know Br) were uninfluenced by emotion ($F_s < 1.07$).

Discussion

While again no difference existed in old–new discrimination as a function of emotion, participants' subjective ratings suggest that the state of awareness accompanying face recognition was influenced by the type of facial expression. An interesting finding was that emotionally arousing items were more likely to be falsely endorsed as remembered as compared to neutral (see Dewhurst & Parry, 2000, for a similar result using verbal material). According to Rajaram (1996), manipulations that enhance the distinctiveness by which study items are processed tend to increase the number of remember responses. It might be that relative increases of distinctiveness evoked also during retrieval are interpreted as diagnostic for episodic remembering, which may lead to an elevated level of false remember responses for distinctively processed stimuli such as emotionally arousing faces. However, the most important finding of Experiment 2 was that correctly recognized negative faces tended to be remembered and presumably recollected to a greater extent than positive and neutral faces. In addition, the analysis of discrimination measures for remember responses showed a reliable difference between negative and positive faces, a comparison that was not confounded by differences in false remembering. Taken together, these results support the conclusion that negative valence enhances the likelihood of accurate remembering.

GENERAL DISCUSSION

We used behavioral and electrophysiological measures to examine the subprocesses mediating recognition memory for emotional and neutral faces. In two experiments, old–new discrimination performance was unaffected by the manipulation of facial expression. However, the electrophysiological (Experiment 1) and the behavioral (Experiment 2) indices of familiarity and recollection suggested that these processes differed in their contributions to performance as a function of emotional valence. While accurate recognition of positive and neutral faces was predominantly based on a feeling of familiarity, performance for negative faces was to a greater extent based on recollection. This latter

finding confirms the result reported by Ochsner (2000) and extends it by revealing the effect in the electrophysiological correlates of familiarity and recollection and, further, when faces are conveying the emotional information. Moreover, analyses of response bias measures suggest that emotional arousal (Experiment 1) or negative valence (Experiment 2) made participants more inclined to respond “old” when uncertain. This corresponds to the emotion-induced recognition bias reported in previous studies using verbal stimulus materials (e.g., Windmann & Kutas, 2001; Maratos et al., 2000).

Taken as a whole, the findings suggest that emotion may influence memory in at least two ways: by improving the efficacy of the mechanisms supporting recollection and by inducing a more liberal response criterion. As discussed above, emotional arousal typically leads to a memory enhancement on recall, but has a less clearcut impact on the accuracy of recognition memory. We hypothesized that the influence of emotion on memory performance is affected by the extent to which task performance relies on recollection and familiarity. It is conceivable that emotion enhances memory when recollection is the main source for performance (e.g., recall), whereas the enhancement on performance is diminished when familiarity is sufficient for correct performance and old–new discrimination is affected by the tendency to endorse new emotional items as old (e.g., recognition). The present results are in accord with this idea. They show that the parietal old–new effect, indicating recollection-based recognition, is sensitive to emotional valence despite the absence of any enhancement on recognition accuracy.

Most neurocognitive models of memory, although varying in detail, hold the medial temporal region and specifically the hippocampus as crucial for recollection (O'Reilly & Norman, 2002; Shastri, 2002; Eichenbaum, 2000; McClelland, McNaughton, & O'Reilly, 1995; Treves & Rolls, 1994). The hippocampus is considered to be involved in binding together the various attributes constituting an event to permit a later retrieval of a bound representation corresponding to the former episode. Based on animal and human data, it has been proposed that the medial temporal lobe system may be functionally subdivided into an extended hippocampal system (including the hippocampus, the fornix, and the anterior thalamus) supporting recollection and the perirhinal cortex mediating familiarity and recency discrimination (Brown & Aggleton, 2001; Aggleton & Brown, 1999; but see Reed & Squire, 1997). The finding of facilitated recollection for negative faces suggests that the efficacy of the hippocampal binding mechanisms is enhanced for episodes characterized by negative emotional valence. One manner in which this may occur is by direct influence of the amygdala on hippocampal binding and consolidation mechanisms (see Abe, 2001, for an overview). Alternatively, a more indirect way in which

the amygdala may affect subsequent memory is through its extensive reentrant projections to cortical regions involved in sensory processing (e.g., Amaral et al., 1992). Support for such a neuromodulatory role of the amygdala comes from studies showing that amygdalar activity resulting from face perception predicts neural activity in the extrastriate cortex (e.g., Morris et al., 1998). It is conceivable that amygdalar responses to negative faces modulate sensory processing in a way that enhances the perception of more detailed or distinctive information as compared to neutral faces, which eventually will be bound by the hippocampus to retrievable memory representations. Such an account would be consistent with the attention-capturing (Pratto & John, 1991) and perception-enhancing (Anderson & Phelps, 2001) power of emotionally significant events. However, further research is needed to assess the extents to which the aforementioned candidate mechanisms contribute to the facilitated recollection observed for negative faces.

As noted above, it has been suggested that amygdalar influences on memory are predicted by the emotional arousal rather than the emotional valence of a stimulus (Hamann, Ely, et al., 1999). This raises the question why recollection was found enhanced only for negative faces in the present study. One potential explanation is that positive and negative faces were eliciting emotional arousal to different levels. As noted by Anderson, Christoff, et al. (2003), the frequently reported finding of greater activation in the amygdala in response to negative as compared to positive stimuli may be due to the difficulty in reliably matching the two stimulus types with respect to arousal. Nonetheless, it should be noted that we found emotion-specific modulations of the ERPs that were comparable for positive and negative faces. Furthermore, in agreement with the present results, Ochsner (2000) observed greater involvement of recollection for negative as compared to positive stimuli using photos of pleasant, aversive, and neutral objects and scenes. As he put it: “a chocolate sundae might not predict happiness in quite the same way as a snake bite could determine unhappiness” (p. 257). In the present case, seeing a prospective friend in a happy face might not demand as rapid recruitment of immediate preparedness to take action as when encountering a threatening face (cf. Öhman, Flykt, & Lundqvist, 2000). While both faces signal information of high behavioral significance, there is an apparent difference in the proximity of the predictable consequences. Interestingly, Cahill, Prins, Weber, and McGaugh (1994) showed that the administration of a β -adrenergic blocker attenuated the normal memory enhancement found for negative scenes while leaving memory for neutral scenes unaffected. Thus, it is conceivable that an acute release of stress hormones mediated the facilitated recollection for negative faces found in the present study and for negative objects and scenes in the Ochsner study.

By examining correctly rejected new faces, we were able to examine emotion-specific ERP modulations while attenuating the influence of successful memory retrieval. These analyses revealed a very early right-frontally distributed component (i.e., the P2) that was sensitive to negative valence and a later positive-going modulation that was sensitive to emotional arousal (positive and negative). While the functional significance of the P2 effect remains uncertain, we note that the very fast time course and lateralization agree well with single-cell recordings in the right prefrontal cortex showing responses selectively for negative stimuli (faces and scenes) approximately 120–160 msec post-stimulus onset (Kawasaki et al., 2001). In addition, the right hemisphere distribution is in accord with the view that right prefrontal regions are particularly important for withdrawal-related behavior triggered by aversive events and negative emotional states (see Davidson, 2003, for a review).

The later emotion effect observed in the ERPs overlapped spatio-temporally with the mid-frontal old–new effect considered to tap familiarity-based responding. Thus, in this time window (380–500 msec), both the repeated presentation and the emotional arousal gave rise to a positive-going mid-frontal effect. With respect to its spatio-temporal characteristics, this modulation corresponds well with that reported by Windmann and Kutas (2001) and related to the emotion-induced recognition bias (see also Maratos et al., 2000). As argued by these authors, when encountering an emotionally negative stimulus, orbito-frontal regions relax the criterion for evaluating the outcome of memory retrieval in order to ensure that negative stimuli are not missed or considered irrelevant. The drawback of this lowered threshold is that new negative items may be falsely accepted, which may lower recognition accuracy. The finding of a more liberal response bias for both positive and negative faces in the present study coupled with a similar positive-going modulation of the ERPs is in agreement with this interpretation and suggests further that a flexible criterion setting may occur as a function of emotional arousal rather than of negative valence. Because the present study did not use verbal stimuli, the observed effect is difficult to explain by referring to semantic cohesiveness (see McNeely, Dywan, & Segalowitz, 2004, for additional challenges to the semantic cohesiveness explanation). Rather, the present data, together with those of Windmann and Kutas (2001), suggest that changes in criterion setting may be induced by emotionally arousing stimuli irrespective of stimulus formats.

An alternative account for the observed mid-frontal emotion effect is that it reflects the operation of orbito-frontal control processes that act to modulate the subcortical and posterior cortical regions responsive to emotional events (Shimamura, 2000). As facial affect was irrelevant to the present identity recognition task, it is

conceivable that control mechanisms worked to limit processing of the emotional information. The prefrontal cortex is also considered to house more general control functions that ensure that task-relevant processing is maintained and task-irrelevant processing is inhibited (cf. Miller & Cohen, 2001). Speculatively, these control mechanisms may become temporally suppressed for emotionally arousing events, releasing additional resources that enable privileged processing of emotionally arousing stimuli.

The spatio-temporal similarity between the early mid-frontal old–new effect and the emotion effect is interesting and deserves some consideration. While the emotion effect may have a medial prefrontal generator (cf. Windmann & Kutas, 2001), it has been suggested that the memory effect may reflect familiarity-sensitive processing in the perirhinal cortex (Mecklinger, 2000). However, the spatial resolution of EEG and the high interconnectivity between orbito-frontal and anterior medial-temporal lobe regions make it difficult to resolve these potential neuronal sources by means of scalp recordings. Future research using functional magnetic resonance imaging might be better suited to examine the neural generators of the memory- and the emotion-related effects.

In summary, we set out to examine emotional influences on the hypothesized ERP correlates of familiarity and recollection in recognition memory for faces. The main finding was that familiarity was largely unaffected by facial expression, whereas recollection was sensitive to the emotional valence of the face. Specifically, correct recognition of negative faces was characterized by a greater contribution of recollection as reflected in the parietal ERP old–new effect and in the proportion of remember judgments. In addition, emotion-specific modulations were observed in frontally recorded ERPs elicited by correctly rejected new faces that were paralleled by a more liberal response bias. While the former finding is in agreement with the view that processes promoting recollection are facilitated for negative events by amygdalar influences on hippocampal functioning and/or visual cortical activity during encoding, the latter finding suggests that emotion may affect recognition performance by influencing prefrontal cortex structures mediating criterion setting.

METHODS

Experiment 1

Participants

Sixteen healthy undergraduate students (8 women) at Saarland University participated in two sessions on separate days and were paid 5.5 € per hour. All participants had normal or corrected-to-normal vision and were right-handed as determined by self-report. The mean age of the participants was 24 years (range: 19–28).

Stimulus Materials

The employed stimulus materials were developed in a separate rating study in which a larger pool of pictures collected from various databases of pictures of facial affect (e.g., Ekman & Friesen, 1975) were rated on the dimensions of: (a) type of emotion (i.e., anger, happiness, disgust, surprise, sadness, and fear), (b) emotional expressiveness, and (c) picture quality. In a second step, trained experts on the facial action coding system categorized the pictures into positive, negative, and neutral expressions. Based on these ratings, a picture database was formed comprising 204 pictures of unknown faces (50% women) with either a positive (68), negative (68), or a neutral (68) facial expression (see Treese, Brinkmann, & Johansson, 2003, for a more detailed description). All pictures were in grayscale and made homogenous with respect to size, background color (black), luminosity, and contrast. The pictures in each emotional category were divided into four subsets (17 items per emotion and set) that were matched with respect to emotional expressiveness and gender of the face. For each subject, two of these subsets were used as studied items and two as new items in the test phases. The assignment of old–new status was counterbalanced across participants. All pictures were presented at the center of the screen (black background) and subtended 5° of visual angle horizontally and 7° vertically.

Design and Procedure

The experiment consisted of two sessions separated by ~24 to 48 hr. The sessions were identical with the exception that the old–new status of items was changed. In each session, participants took part in two study-test blocks in which 51 faces (17 per emotion type) were studied and 102 faces (34 per emotion type) were presented as test probes.

During each study phase, participants were told to make a gender discrimination for each presented face by pressing one of two response keys with their left or right index fingers. Each study trial began with a 300-msec fixation sign (*) that was followed by a 200-msec blank screen that preceded the onset of the face. The face was presented for 300 msec and was followed by a 1500-msec blank screen during which the response was collected. Immediately after each study phase, participants were given a 30-sec distractor task in which they had to count backward in threes starting with a three-digit number. Thereafter, participants were given instructions for the recognition memory test. They were told to use their left and right index fingers to indicate whether the faces were previously studied (“old”) or not (“new”) and to make these recognition judgments as quickly and as accurately as possible. Each test trial began with a 300-msec fixation sign (*) that was followed by a 200-msec blank screen preceding the onset

of the face. The face was presented for 500 msec and participants were given an additional 3000 msec to respond (blank screen). Mapping between response hand and male/female and old–new judgment was counter-balanced across participants.

Electrophysiological Methods

Electroencephalograms (EEG) were continuously recorded from 61 Ag/AgCl scalp electrodes mounted in an elastic cap and labeled according to the extended 10–20 system (Sharbrough et al., 1990). The EEG from all sites was recorded with reference to the left mastoid electrode, and re-referenced off-line to the average of the left and right mastoids. Vertical and horizontal electrooculograms were recorded with additional electrodes located above and below the right eye and outside the outer canthi of both eyes. All channels were amplified with a band-pass from DC to 100 Hz and A–D converted with 16 bit resolution at a rate of 500 Hz. Interelectrode impedances were kept below 5 k Ω . Further off-line data processing included a digital low-pass filter set to 12 Hz (–3 dB cutoff) to increase the signal-to-noise ratio. The duration of the epochs used for analyses was 1200 msec commencing 200 msec prior to stimulus onset (baseline). Trials including eye movements were corrected using a linear regression approach and trials with recording artifacts were rejected prior to averaging. ERP averages were formed for correct responses to old and new items separately for the three emotional categories. To achieve an acceptable signal-to-noise ratio, averaging was collapsed across the factor of expressiveness resulting in at least 16 artifact-free trials in each condition per participant (mean trials/condition: old-positive = 30; old-negative = 33; old-neutral = 31; new-positive = 37; new-negative = 35; new-neutral = 39).

Data Analyses

Data were analyzed with repeated-measures ANOVAs (alpha level = .05). The Greenhouse–Geisser adjustment for nonsphericity was used where appropriate (Winer, 1971) and the corrected *p* values are reported together with the uncorrected degrees of freedom.

Behavioral data. Measures of old–new discrimination, $Pr [p(\text{hit}) - p(\text{false alarm})]$, and response bias, $Br [p(\text{false alarm})/p(1 - Pr)]$, were calculated separately for positive, negative, and neutral faces (two-high-threshold theory, Snodgrass & Corwin, 1988). The initial ANOVAs conducted on these performance measures employed the factors of emotion (positive vs. negative vs. neutral) and expressiveness (high vs. low). RTs were analyzed in an initial ANOVA employing the factors of emotion, expressiveness, response (“old” vs. “new”), and accuracy (correct vs. incorrect).

ERP data. ERP waveforms were quantified by measuring the mean amplitudes in three consecutive time

windows (380–500, 500–700, and 700–1000 msec). The selection of these time windows was based on previous research and a visual inspection of the waveforms and aimed primarily at tapping the old–new effects related to familiarity and recollection. To avoid a loss of statistical power that is implicated when repeated-measures ANOVAs are used to quantify multichannel and multi-time window data (e.g., Oken & Chiappa, 1986), electrode sites were pooled to six topographical regions: left anterior (F7, F5, F3, FP1, AF3), midline anterior (F1, FZ, F2, FPZ, FC3), right anterior (F8, F6, F4, FP2, AF4), left posterior (P7, P5, P3, PO7, PO3), midline posterior (P1, PZ, P2, CPZ, POZ), and right posterior (P8, P6, P4, PO8, PO4).

Two sets of statistical analyses were performed (a) to examine the effects of emotion on correct recognition memory and (b) to investigate any general (i.e., memory independent) emotion-specific processing during recognition memory. Significant effects are reported only when involving the factors of item type and/or emotion.

For each time window, an initial ANOVA using the factors of emotion, item type (old vs. new), AP (anterior vs. posterior), and HEM (left vs. midline vs. right) was performed. In case of a significant effect involving the factor of item type, planned subsidiary analyses were conducted in order to test whether reliable old–new effects were present for positive, negative, and neutral faces. In a second step, we evaluated whether the magnitude of the old–new effect was influenced by emotion. To this end, difference measures (i.e., old minus new) were calculated for each level of the factor emotion and contrasted over the regions showing reliable old–new effects. We also examined whether the topography of the old–new effect differed as a function of facial expression. To eliminate any confounding effects of differences in magnitude, the difference measures were rescaled by the vector length method (McCarthy & Wood, 1985) and subjected to an ANOVA using the factors of emotion, AP, and HEM for the time windows that showed a reliable interaction between these factors in the mean amplitude analyses.

Emotion-specific effects were investigated by an examination of the ERPs elicited by correctly rejected new faces. Given previous results suggesting a modulatory role of frontal regions in both the processing of emotional stimuli and in memory tasks, analyses were performed on data recorded at the anterior electrode sites, employing the factors of emotion and HEM. Effects involving the factor emotion were investigated with the following contrasts: VAL (positive vs. negative) and EMO (emotional vs. neutral).

Experiment 2

Participants

All participants in Experiment 1 were invited to revisit the lab for a follow-up experimental session approximately 9 months following their first participation.

Fourteen (7 women) were available and agreed to take part and were paid at a rate of 5.5 € per hour. The mean age of the participants was 23 years (range: 19–28).

Stimulus Materials, Design, and Procedure

The methods were identical to Experiment 1, except that Experiment 2 consisted of only one session, no EEG was recorded, and the remember/know procedure was included in the test phase.

Participants were told to report the subjective state of awareness associated with memory for each recognized face. Instructions for these judgments were adopted from Gardiner and Richardson-Klavehn (2000) and participants were encouraged to respond “remember” if they could mentally re-experience the previous presentation of a face, that is, recollect some specific contextual information pertaining to the study episode (e.g., association, thought, feeling, etc.). In contrast, they were instructed to respond “know” for familiar faces that they were sure that they studied, but that lacked the retrieval of any specific details. Because it has been argued that particularly the “know” response category may be affected by “old” judgments based on low-confidence guesses (see Gardiner & Richardson-Klavehn, 2000, for a discussion), participants were given a third response option (“guess”) in order to purify the other response categories. Following each “old” response in the test phase, the text “remember/know/guess” was presented at the center of the screen and participants were given 3000 msec to respond by pressing one of three keys with their right-hand fingers.

Data Analyses

Measures of old–new discrimination (Pr) and response bias (Br) were calculated and analyzed as in Experiment 1. To exclude a potential influence of differences in recognition memory accuracy, estimates of participants’ states of awareness were derived contingent on the initial old–new judgment (i.e., the probability that a recognized face received a remember or know or guess response). These estimates were subjected to separate one-way ANOVAs for correct and incorrect “old” judgments employing the factor of emotion (collapsed across expressiveness). Measures of discrimination (Pr) and response bias (Br) were calculated separately for remember/know/guess responses and analyzed in a similar fashion. To avoid a lowered sensitivity due to missing values, analyses of RTs were collapsed across expressiveness and the outcome of the subsequent remember/know/guess judgment.

Acknowledgments

This research was supported by the German Research Society (grant FOR448). We thank Jörg Merten for valuable assistance

with stimulus material development and three anonymous reviewers for comments on an earlier version of the manuscript.

Reprint requests should be sent to Mikael Johansson, Experimental Neuropsychology Unit, Department of Psychology, Saarland University, Saarbrücken, Germany, or via e-mail: m.johansson@mx.uni-saarland.de.

REFERENCES

- Abe, K. (2001). Modulation of hippocampal long-term potentiation by the amygdala: A synaptic mechanism linking emotion and memory. *Japanese Journal of Pharmacology*, *86*, 18–22.
- Adolphs, R., & Tranel, D. (2003). Amygdala damage impairs emotion recognition from scenes only when they contain facial expressions. *Neuropsychologia*, *41*, 1281–1289.
- Adolphs, R., Tranel, D., Damasio, H., & Damasio, A. (1994). Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. *Nature*, *372*, 669–672.
- Aggleton, J. P., & Brown, M. W. (1999). Episodic memory, amnesia, and the hippocampal-anterior thalamic axis. *Behavioral and Brain Sciences*, *22*, 425–444.
- Amaral, D. G., Price, J. L., Pitkänen, A., & Carmichael, S. T. (1992). Anatomical organization of the primate amygdaloid complex. In J. P. Aggleton (Ed.), *The Amygdala: Neurobiological aspects of emotion, memory, and mental dysfunction* (pp. 1–67). New York: Wiley-Liss.
- Anderson, A. K., Christoff, K., Stappen, I., Panitz, D., Ghahremani, D. G., Glover, G., Gabrieli, J. D., & Sobel, N. (2003). Dissociated neural representations of intensity and valence in human olfaction. *Nature Neuroscience*, *6*, 196–202.
- Anderson, A. K., & Phelps, E. A. (2001). Lesions of the human amygdala impair enhanced perception of emotionally salient events. *Nature*, *411*, 305–309.
- Brown, M. W., & Aggleton, J. P. (2001). Recognition memory: What are the roles of the perirhinal cortex and hippocampus? *Nature Reviews Neuroscience*, *2*, 51–61.
- Cahill, L., Babinsky, R., Markowitsch, H. J., & McGaugh, J. L. (1995). The amygdala and emotional memory. *Nature*, *377*, 295–296.
- Cahill, L., Haier, R. J., Fallon, J., Alkire, M. T., Tang, C., Keator, D., Wu, J., & McGaugh, J. L. (1996). Amygdala activity at encoding correlated with long-term, free recall of emotional information. *Proceedings of the National Academy of Sciences, U.S.A.*, *93*, 8016–8021.
- Cahill, L., & McGaugh, J. L. (1998). Mechanisms of emotional arousal and lasting declarative memory. *Trends in Neurosciences*, *21*, 294–299.
- Cahill, L., Prins, B., Weber, M., & McGaugh, J. L. (1994). Beta-adrenergic activation and memory for emotional events. *Nature*, *371*, 702–704.
- Christianson, S.-A. (Ed.) (1992). *The handbook of emotion and memory: Research and theory*. Hillsdale, NJ: Erlbaum.
- Curran, T. (2000). Brain potentials of recollection and familiarity. *Memory and Cognition*, *28*, 923–938.
- Danion, J., Kauffmann-Muller, F., Grange, D., Zimmermann, M., & Greth, P. (1995). Affective valence of words, explicit and implicit memory in clinical depression. *Journal of Affective Disorders*, *34*, 227–234.
- Davidson, R. J. (2003). Affective neuroscience and psychophysiology: Toward a synthesis. *Psychophysiology*, *40*, 655–665.
- Dewhurst, S. A., & Parry, L. A. (2000). Emotionality, distinctiveness, and recollective experience. *European Journal of Cognitive Psychology*, *12*, 541–551.

- Dolan, R. J. (2002). Emotion, cognition, and behavior. *Science*, 298, 1191–1194.
- Dougal, S. (2003). *A dual process approach to emotional memory: Effects of emotion on familiarity and retrieval processes in recognition*. Unpublished doctoral dissertation, University of Pittsburgh.
- Eichenbaum, H. (2000). A cortical–hippocampal system for declarative memory. *Nature Reviews Neuroscience*, 1, 41–50.
- Ekman, P., & Friesen, W. V. (1975). *Unmasking the face*. Englewood Cliffs: Prentice-Hall.
- Fried, I., MacDonald, K. A., & Wilson, C. L. (1997). Single neuron activity in human hippocampus and amygdala during recognition of faces and objects. *Neuron*, 18, 753–765.
- Friedman, D., & Johnson, R. (2000). Event-related potential (ERP) studies of memory encoding and retrieval: A selective review. *Microscopy Research and Technique*, 51, 6–28.
- Gardiner, J. M., & Richardson-Klavehn, A. (2000). Remembering and knowing. In E. Tulving & F. I. M. Craik (Eds.), *The Oxford handbook of memory* (pp. 229–244). New York: Oxford University Press.
- Hamann, S. B. (2001). Cognitive and neural mechanisms of emotional memory. *Trends in Cognitive Sciences*, 5, 394–400.
- Hamann, S. B., Cahill, L., McGaugh, J. L., & Squire, L. R. (1997). Intact enhancement of declarative memory for emotional material in amnesia. *Learning and Memory*, 4, 301–309.
- Hamann, S. B., Ely, T. D., Grafton, S. T., & Kilts, C. D. (1999). Amygdala activity related to enhanced memory for pleasant and aversive stimuli. *Nature Neuroscience*, 2, 289–293.
- Kawasaki, H., Kaufman, O., Damasio, H., Damasio, A. R., Granner, M., Bakken, H., Hori, T., Howard, M. A., 3rd, & Adolphs, R. (2001). Single-neuron responses to emotional visual stimuli recorded in human ventral prefrontal cortex. *Nature Neuroscience*, 4, 15–16.
- Leiphart, J., Rosenfeld, J. P., & Gabrieli, J. D. (1993). Event-related potential correlates of implicit priming and explicit memory tasks. *International Journal of Psychophysiology*, 15, 197–206.
- Maratos, E. J., Allan, K., & Rugg, M. D. (2000). Recognition memory for emotionally negative and neutral words: An ERP study. *Neuropsychologia*, 38, 1452–1465.
- McCarthy, G., & Wood, C. C. (1985). Scalp distributions of event-related brain potentials: An ambiguity associated with analysis of variance models. *Electroencephalography and Clinical Neurophysiology*, 62, 203–208.
- McClelland, J. L., McNaughton, B. L., & O'Reilly, R. C. (1995). Why there are complementary learning systems in the hippocampus and neocortex: Insights from the successes and failures of connectionist models of learning and memory. *Psychological Review*, 102, 419–457.
- McGaugh, J. L., & Cahill, L. (2003). Emotion and memory: Central and peripheral contributions. In R. J. Davidson, K. R. Scherer, & H. H. Goldsmith (Eds.), *Handbook of affective sciences* (pp. 93–116). New York: Oxford University Press.
- McNeely, H. E., Dywan, J., & Segalowitz, S. J. (2004). ERP indices of emotionality and semantic cohesiveness during recognition judgments. *Psychophysiology*, 41, 117–129.
- Mecklinger, A. (2000). Interfacing mind and brain: A neurocognitive model of recognition memory. *Psychophysiology*, 37, 565–582.
- Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience*, 24, 167–202.
- Morris, J., Friston, K., Buchel, C., Frith, C., Young, A., Calder, A., & Dolan, R. J. (1998). A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain*, 121, 47–57.
- Nessler, D., & Mecklinger, A. (2003). ERP correlates of true and false recognition after different retention delays: Stimulus and response related processes. *Psychophysiology*, 40, 146–159.
- O'Reilly, R. C., & Norman, K. A. (2002). Hippocampal and neocortical contributions to memory: Advances in the complementary learning systems framework. *Trends in Cognitive Sciences*, 6, 505–510.
- Ochsner, K. N. (2000). Are affective events richly recollected or simply familiar? The experience and process of recognizing feelings past. *Journal of Experimental Psychology: General*, 129, 242–261.
- 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.
- Oken, B. S., & Chiappa, K. H. (1986). Statistical issues concerning computerized analysis of brainwave topography. *Annals of Neurology*, 19, 493–494.
- Pratto, F., & John, O. P. (1991). Automatic vigilance: The attention-grabbing power of negative social information. *Journal of Personality and Social Psychology*, 61, 380–391.
- Rajaram, S. (1996). Perceptual effects on remembering: Recollective processes in picture recognition memory. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, 22, 365–377.
- Reed, J. M., & Squire, L. R. (1997). Impaired recognition memory in patients with lesions limited to the hippocampal formation. *Behavioral Neuroscience*, 111, 667–675.
- Roediger, H. L., & McDermott, K. B. (1995). Creating false memories: Remembering words not presented in lists. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 21, 803–814.
- Rugg, M. D., & Allan, K. (2000). Event-related potential studies of memory. In E. Tulving & F. I. M. Craik (Eds.), *The Oxford handbook of memory* (pp. 521–537). New York: Oxford University Press.
- Rugg, M. D., & Coles, M. G. H. (1995). The ERP and cognitive psychology: Conceptual issues. In M. D. Rugg & M. G. H. Coles (Eds.), *Electrophysiology of mind: Event related brain potentials and cognition* (Vol. 25, pp. 27–39). Oxford: Oxford University Press.
- Rugg, M. D., Mark, R. E., Walla, P., Schloerscheidt, A. M., Birch, C. S., & Allan, K. (1998). Dissociation of the neural correlates of implicit and explicit memory. *Nature*, 392, 595–598.
- Rugg, M. D., & Wilding, E. L. (2000). Retrieval processing and episodic memory. *Trends in Cognitive Sciences*, 4, 108–115.
- Sharbrough, F., Chatrian, G., Lesser, R. P., Lüders, H., Nuwer, M., & Picton, T. W. (1990). *Guidelines for standard electrode position nomenclature*. Bloomfield, MI: American EEG Society.
- Shastri, L. (2002). Episodic memory and cortico-hippocampal interactions. *Trends in Cognitive Sciences*, 6, 162–168.
- Shimamura, A. P. (2000). The role of the prefrontal cortex in dynamic filtering. *Psychobiology*, 28, 207–218.
- Snodgrass, J. G., & Corwin, J. (1988). Pragmatics of measuring recognition memory: Application to dementia and amnesia. *Journal of Experimental Psychology: General*, 117, 34–50.

- Treese, A.-C., Brinkmann, M., & Johansson, M. (2003). *Picture database of emotional facial expressions* (Tech. Rep. No. 87). Retrieved November 14, 2003, from Saarland University Web site: <http://psydok.sulb.uni-saarland.de/volltexte/2003/87/>.
- Treves, A., & Rolls, E. T. (1994). Computational analysis of the role of the hippocampus in memory. *Hippocampus*, *4*, 374–391.
- Tulving, E. (1985). Memory and consciousness. *Canadian Psychology*, *26*, 1–12.
- Windmann, S., & Kutas, M. (2001). Electrophysiological correlates of emotion-induced recognition bias. *Journal of Cognitive Neuroscience*, *13*, 577–592.
- Windmann, S., Sakhavat, Z., & Kutas, M. (2002). Electrophysiological evidence reveals affective evaluation deficits early in stimulus processing in patients with panic disorder. *Journal of Abnormal Psychology*, *111*, 357–369.
- Winer, B. (1971). *Statistical principles in experimental design* (2nd ed.). New York: McGraw-Hill.
- Yonelinas, A. P. (2002). The nature of recollection and familiarity: A review of 30 years of research. *Journal of Memory and Language*, *46*, 441–517.