

Emotion and Memory:
The modulation of encoding, consolidation, and
retrieval processes as revealed by event-related
potentials (ERPs)

Dissertation

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1. Introduction

In the morning you see a car accident on your way to work; the pizza at lunch tastes unexpectedly good; a photograph of a plane crash in the evening news on television makes you wince. Everyday life is punctuated by events that elicit myriad nuances, crescendos, and plateaus of feelings. What happens when we attempt to make contact to memories of these events? How is later recognition or recall of the car accident, lunch, or television news changed because these experiences elicited affective reactions when they first occurred?

Many different, although related, scientific approaches (cognitive, neuroscientific) have been taken to address this issue in recent years. Starting point for these considerations was the debate about the relation of emotion and cognition (Zajonc, 1980, 1984; Lazarus, 1981, 1984). With the progress of cognitive neuroscience, and very influential work by LeDoux (1996) this debate could be answered at least with respect to compatibility. Thus, it has to be stated that both are right, the neural systems of emotion and cognition are independent and interdependent. The exact meaning of this will be elucidated in the course of the present thesis.

The question asked with respect to emotion and memory mostly concerned if emotional memories are remembered more accurately or vividly than neutral ones (e.g. Ochsner, 2000), if central or peripheral details of memories are promoted by emotion (e.g. Christianson, 1992; Safer, Christianson, Atry, & Österlund, 1998), if it is the emotional valence or the degree of arousal that determines how well an emotional episode is remembered (e.g. Matlin & Stang, 1978). The data (self-reports, behavioral, neuroimaging) collected with these approaches thus describe the conditions under which memories for affective events and stimuli become distorted and inaccurate (e.g. Schacter, 1996), the kinds of information and details that most resist distortions (e.g. Heuer & Reisberg, 1992), and how valenced stimuli, mood states, or levels of arousal modulate these effects (e.g. Bradley, Greenwald, Petry, & Lang, 1992; Christianson, 1992). Yet it remains to be fully elucidated and is of enormous interest what exact circumstances lead to memory enhancements and impairments on the other side.

As in other domains of cognitive neuroscience, studies of brain-lesioned patients provide a core foundation to delineate structure-function relationships, in this case determining which aspects of emotional memory depend on the integrity of the amygdala. In humans, organic syndromes rarely affect the amygdala selectively. Key insights have been provided by post-surgical studies of temporal lobectomy patients with unilateral damage to the MTL due to epilepsy, as well as case studies of patients with selective bilateral amygdala pathology due to Urbach-Wiethe syndrome.

Since the early behavioral findings of Kleinsmith and Kaplan (1963), behavioral studies in healthy adults have shown that memory advantages for emotional materials are sometimes augmented over time. For example, retention advantages for emotionally arousing words relative to neutral ones are greater when memory is tested after long (1 hour to one day) than after short (immediate) delay intervals (LaBar & Phelps, 1998; Sharot & Phelps, 2004). Such observations provide evidence that emotional arousal enhances memory in part by facilitating consolidation processes, which take time to emerge. Temporal lobectomy patients do not show enhanced arousal-mediated memory consolidation but instead show parallel forgetting rates for arousing and neutral words from immediate to 1 hour retention intervals (Phelps et al., 1998). Urbach-Wiethe syndrome patients show comparable impairments in recall or recognition of emotional words, pictures, and stories (Markowitsch et al., 1994; Adolphs, Cahill, Schul, & Babinsky, 1997). Thus the amygdala has proven to be highly relevant for memory enhancement effects.

Emotional arousal has also complementary, immediate effects during encoding that are time invariant and interpreted to reflect attentional influences on memory (Hamann, 2001). One additional consequence of emotional arousal is the focusing of attention on central information of a scene at the expense of peripheral details for complex events, as exemplified in the weapon focus of eyewitness testimony research (Steblay, 1992). Attentional focusing ensures that emotionally salient features of complex events are preferentially retained in memory, which confers evolutionary advantages. Patients with amygdala damage do not focus on central gist information when memory is tested for audiovisual narratives that describe emotionally arousing events (Adolphs, Tranel, & Buchanan, 2005).

The high relevance of researching the topic of emotion and memory is also given in the desired understanding of psychiatric disorders concerned with these two concepts. Of great importance here is the post-traumatic stress disorder (PTSD). It emerges after

exposure to a traumatic stressor that elicits fear, horror or helplessness and involves bodily injury or threat of injury or death to one's self or another person. Diagnostic symptoms include persistent re-experiencing of the traumatic event, avoidance of reminders, numbing of responsiveness and heightened arousal. Neurobiological models of PTSD have focused on brain regions and stress hormone systems that are involved in fear, arousal and emotional memory. Chronic stress in PTSD contributes to smaller hippocampal volume and declarative memory deficits (Bremner, Krystal, Southwick, & Charney, 1995). However, as pointed out by Gilbertson et al. (2002), small hippocampi predict symptom severity in PTSD. Therefore, it is not quite clear what exactly causes what. In order to apply goal-oriented treatments for this disorder it is of high interest to understand the basic functioning of memory in connection with emotion to a deeper extent. Not only therefore the present thesis tries to resolve open issues regarding the detrimental and augmented effects of emotion on memory processes. Hereby it is of special interest to tap the exact conditions, i.e. situational factors and personal factors that can lead to pathological emotion processing.

Following this introduction, I will give a theoretical introduction as well as a short review on the current state of research on the modulations of encoding, consolidation, and retrieval processes by emotion (chapter 2). Therefore, at first a general introduction into the topics emotion and memory will be given separately before converging in the influence of emotion on memory processes. Then, I will describe the main research questions of my work following from this state of the art in chapter 3. Afterwards, the results of four studies (two behavioral and two combined behavioral-ERP studies) investigating encoding, consolidation and retrieval processes and their neural correlates will be presented (chapter 4). Experiment 1 deals with encoding and retrieval processes for positive and negative pictures, as well as their binding to neutral contextual features. In Experiment 2 the assumed encoding mechanisms found in Experiment 1 are further examined in a behavioral companion study. Experiment 3 then tries to address the issues still open from the preceding two studies by using incidental encoding, high and low arousing negative stimulus classes, and two retention durations. In Experiment 4 the tunnel memory phenomenon (Safer et al., 1998) is researched in specific detail. In the next chapter I will discuss the results of the studies with regard to the current state of research and moreover give an outlook for future perspectives. In the end (in chapter 6) an illustrative summary of this thesis will be provided in German language.

2. Theoretical background

2.1 Emotion and cognition

Early cognitive psychology let the concept emotion relatively untouched. But when asking the question what characteristics a cognitive system must contain to flexibly act in and adapt to a complex environment, emotional phenomena have to be considered. The concept of attention is closely linked to the investigation of these phenomena. Therefore, at this stage it is of high relevance to introduce the three major theories about the influence of emotion on attention, namely the categorical negativity theory (Pratto & John, 1991), evolutionary threat theory (Öhman, Flykt, & Esteves, 2001), and arousal theory (Lang, Bradley, & Cuthbert, 1995; Anderson, 2005).

Pratto and John (1991) proposed that people constantly evaluate stimuli in their environment. These evaluations are supposed to take place automatically, outside of conscious awareness. Moreover, they are thought to be relatively simple, leading to mere categorical distinction between positive and negative stimuli. Those evaluated as negative automatically attract attention because the detection of negative stimuli is more critical for survival as the detection of positive ones. Clearly not all negative stimuli threaten survival, but it may have been easier to evolve a simple detection mechanism for all negative stimuli than a specific detector of threatening ones. It is assumed that attention is guided by an initial evaluation of valence, and only those evaluated as negative attract attention. This mechanism does not provide information about the degree of unpleasantness along the valence dimension, but rather the categorical information. Thus, mild and strong negative stimuli have the same effect on attention.

The evolutionary threat theory is based on the same evolutionary argument, the detection of stimuli that threaten survival has more adaptive value than the detection of other stimuli. However, it is assumed that this adaptive pressure has resulted in a specific detection mechanism for threat stimuli. The influence of emotion on attention should be limited to stimuli that signal a threat to survival during evolution, such as angry faces, snakes, and spiders.

Arousal theory suggests that responses to affective pictures form two factors that vary with the level of valence and arousal of the stimulus. I will give further explanations on this in the next section considering the dimensional approach to study emotion.

Since the present thesis is based on experimental neuropsychological studies that focus on underlying brain mechanisms of the interaction of emotion and memory, the evolutionary perspective seems most appropriate here. In this framework, neurological theories assume that emotions are generated by specific brain regions that are specialized for emotional processes (LeDoux, 1996). The evolutionary perspective views emotions as phylogenetical inheritance that developed in order to facilitate the survival of individuals (Bradley & Lang, 2000). The ability to infer intentions of potential perpetrators from distance by being able to understand e.g. the facial expressions the person displays has been highly advantageous. Moreover, in our evolutionary past the ability to perceive emotional signals of our offspring ensured the satisfaction of their needs and thereby the propagations of our genes.

In sum, at a cognitive level, emotions serve the evaluations and affective appraisal of events in their specific context. Early perceptual processes identify the event with its emotional value and activate the organism for action. Later cognitive processes verify the value of an event in relation to its context and in relation to long-term goals of the individual. Thus, emotions allow rapid and flexible action, but also provide information about the individuals' inner state to others and thereby also have a communicative function. In sum, emotions can be seen as an interface between constantly changing environmental conditions and the individual. They have a regulatory role in preparing us for action, shaping future behavior and helping us to interact in social context.

2.1.2 A conceptual definition of emotion

At a behavioral level emotions can be characterized mainly by two different approaches (namely the categorical and dimensional approach which will be introduced one after the other). Happy, sad, fearful, anxious, disappointed, angry, pleased, disgusted, guilty and excited are just some of the terms we use to describe our emotional life. Unfortunately, our rich language of emotion is difficult to translate into discrete states and variables that can be studied in the laboratory. Since Darwin's work on the evolutionary basis of human behavior, it was proposed to define a finite set of universal, basic emotions. One of the more recent attempts to characterize basic emotions comes from the study of the universality of facial expressions (Ekman & Friesen, 1971). By examining different cultures around the world, Ekman and others concluded that anger, fear, disgust,

happiness, sadness, and surprise are the six basic human facial expressions representing emotional states. Although there is still considerable debate as to whether any is adequate to capture emotional experience, it is widely accepted to investigate the different neural systems underlying these reported emotional states or moods.

Another way of approaching the categorization of emotions is not to describe them as discrete states but as reactions to events in the world that vary along a continuum (Lang, Greenwald, Bradley, & Hamm, 1993). This widely accepted dimensional framework proposes that affective experiences are best characterized by a two-dimensional space (Osgood, Suci, & Tanenbaum, 1957; Russell, 1980; Lang et al., 1993). The dimension of valence ranges from highly positive to highly negative, whereas the dimension of arousal ranges from calming or soothing to exciting or agitating. The interactions between the two dimensions are specified in the following paragraph when introducing the International Affective Picture System (IAPS). Depending on these two dimensions, some emotions call for action (e.g. anger, joy) and others do not (e.g. sadness). Thus, emotions can be seen as action sets that prepare the organism to act in specific ways (Öhman, Flykt, & Lundqvist, 2000). Emotions associated with action lead to either approach towards or avoidance of the event. As action tendencies, emotions allow a unique flexibility in the interaction between the individual and its environment. A vast majority of studies investigating declarative memory for emotional events have compared memory for neutral experiences (i.e. events that are neither highly positive or highly negative; and that are not exciting or agitating) with those that are both arousing (i.e. exciting or agitating) and at an extreme valence dimension (positive or negative). Clearly the abovementioned approaches to define emotions are not adequate to capture all emotional experiences. However, they are able to provide a beginning framework to be used in scientific investigations. Depending on the question or issue being addressed, one of the described approaches here, or even another, may be preferable. For several reasons of comparability to existing data, experimental designing and their relation to the to-be-addressed concepts of attention and memory, in the following I will rely on the dimensional approach.

2.1.3 The International Affective Picture System (IAPS)

The International Affective Picture System, originally developed by Bradley and Lang (1999), is a stimulus collection that in a second version (Lang, Bradley, & Cuthbert, 2005)

consists of by now 900 color photographs which can be used in the study of emotion. Affective ratings for male and female, as well as children and elderly have been conducted in order to get affective norms for these subgroups. Since the IAPS comprises material ranging from very pleasant (babies, sports, nature) to very unpleasant scenes (mutilation, death), as well as from very calm, neutral (household objects) to highly arousing pictures (guns, erotica), the affective norms also range along the lines of these dimensions. Pictures were rated on a scale from 1 to 9 each, with 1 = very unpleasant and 9 = very pleasant for valence ratings, and 1 = very calm to 9 = very excited for arousal ratings. As can be seen in Figure 2.1.2, due to its mean valence and arousal ratings each picture of the IAPS can be assigned within the coordinate plane that is defined by the dimensions of valence and arousal. There are several interesting aspects that characterize the shape of these distributions. By looking at the boomerang-shaped distribution of the IAPS norms, it is obvious that affective pictures evoke normative valence and arousal ratings along the whole range of these dimensions, for pleasure as well as arousal. Considering the different pleasantness levels, it can be seen that pleasant pictures are accompanied by high as well as low arousal ratings, a fact that confirms the orthogonality of the dimensions. Unpleasant pictures, however, seem to accumulate in the high arousing part of the panel, suggesting that the more unpleasant the picture is, the higher the arousal rating will be. Neutral slides do not evoke as high arousal ratings as do emotionally valenced pictures.

International Affective Picture System (IAPS, 2005)
All Subjects

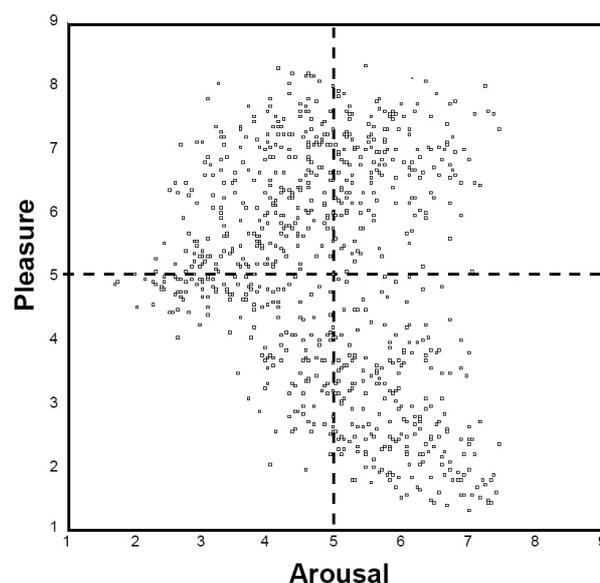


Figure 2.1.3: Normative ratings to IAPS pictures on valence and arousal dimensions (Lang et al., 2005).

In addition to affective norms, Bradley and Lang have conducted a number of studies with the aim to scrutinize the effects of the photographic material on physiological variables. With regard to facial muscle activity the corrugator muscle, which is responsible for frowning, shows significant contraction when negative pictures are seen, whereas it is relaxed when positive pictures are shown. Zygomatic activity is increased when viewing positive pictures, since this muscle is involved in the smile response. However, there is also a tendential increase in the increase of the muscle while viewing extremely negative pictures, which can be explained by the fact that very likely a facial grimace will be prompted (Bradley & Lang, 2000). The classical pattern in picture presentation involves a triphasic response of the heart rate: First, the heart rate decelerates, which is usually interpreted as an orienting process, and then there is acceleration, followed by a final deceleration. When viewing affective pictures, however, an enhanced initial deceleration for negative, and acceleration for positive material can be found (Bradley & Lang, 2000). Skin conductance response is supposed to be based on the sympathetic nervous system and has thus been shown to be influenced by the arousal level of the stimulus material. Skin conductance levels are higher for emotionally valenced, i.e. for pleasant or unpleasant pictures compared to neutral ones (Bradley & Lang, 2000). Several studies using electrophysiological measures (Cacioppo & Berntsen, 1994; Cuthbert et al., 1998) have shown that there are cortical event-related potentials (ERPs) that can be elicited by affective picture viewing. Especially positive-going ERPs tend to be more pronounced for emotionally arousing compared to neutral pictures. Moreover, in PET and fMRI studies, a significant activation for affective compared to neutral pictures in the occipital and extrastriate cortex could be found (Bradley & Lang, 2000). All these effects will be further introduced and discussed in the upcoming sections on electrophysiology and emotion. Therefore, in order to get a deeper understanding of the brain mechanisms that underlie these modulations, the next paragraph will be on the neural structures that have to be found crucial for the processing of emotional stimuli.

After this short theoretical framework, an introduction into the brain mechanisms underlying emotion processing will be given. They aid the understanding on how the privileged processing of emotional content results in an appropriate guidance of behavior.

2.2 Neural mechanisms of emotion processing

2.2.1 The limbic system

Early research on the brain mechanisms of emotion tended to see emotion as a unitary concept and tried to describe the location of emotion in the brain. The early work of Papez (1937) defined specific interconnected neuronal structures that were thought to control the expression of emotion, named limbic system. Based on knowledge from clinical effects of damaged brain regions and speculations of the nature of the connections within this circuit, the experience of emotion was explained as a flow of information in a specific circuit, the Papez circuit. According to this theory, sensory information reaches the thalamus and is directed to the cerebral cortex and hypothalamus. Information that enters the hypothalamus is further directed to the anterior thalamic nucleus which connects the mammillary bodies with the cingulate cortex, and last the cingulate cortex. The latter sends its outputs to the hippocampus which directs the information back to the hypothalamus. It was suggested that emotional experience could be generated via two pathways: through a path from the limbic system to the cortex (stream of thinking), and through a path within the limbic system (stream of feeling) (LeDoux, 1996). The theory of the limbic system was then expanded by MacLean (1952) who proposed that the amygdala, the hippocampus, the limbic cortex, and the area septalis compose major constituents of the limbic system (see Figure 2.2.1). The experience of emotion was supposed to involve the integration of sensations from the body, occurring in the limbic system. Despite the later criticism towards this theory, it is still held on to the idea that there exists a key structure that mediates a number of basic aspects of emotion processing, the amygdala (LeDoux, 1996). This structure will be described in the following, and its high relevance for emotion processing will be pointed out undoubtedly.

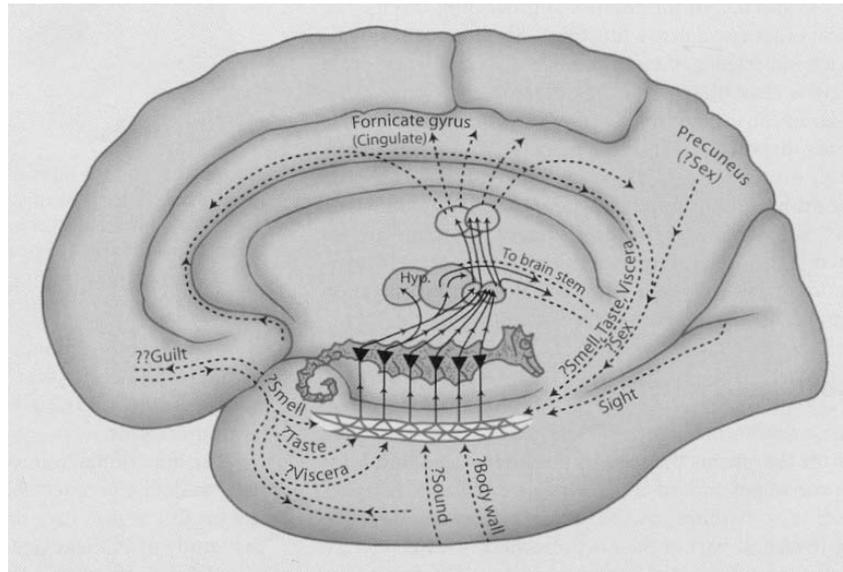


Figure 2.2.1: The limbic system (MacLean, 1949).

2.2.2 The amygdala

The amygdala is a small region in the medial temporal lobe adjacent to the anterior portion of the hippocampus, named by early anatomists for its almond shape (Nieuwenhuys, 1988). It functionally belongs to the limbic system and forms a large nuclear complex (Figure 2.2.2). Specifically, two parts of the amygdala are responsible for the perception of and the response to an emotional stimulus. The lateral nucleus receives sensory information from the thalamus, primary sensory and association cortices, as well as the hippocampal formation. Therefore, this part is regarded as the sensory interface that modulates the output response to the central nucleus, which is connected to different subsystems such as the autonomic nervous system and systems that control the release of stress hormones and initiate behavioral responses (Nieuwenhuys, 1988; LeDoux, 2000). Via connections to the hippocampus, the amygdala is able to influence hippocampal input as well as output. Clinicopathological evidence suggests that the hippocampus is involved in learning and memory processes. One suggested function of the connection of the amygdala to the hippocampus is that the former provides the emotional significance of an event to the latter. This information is then used in addition to other to build an episodic memory trace (Emery & Amaral, 2000).

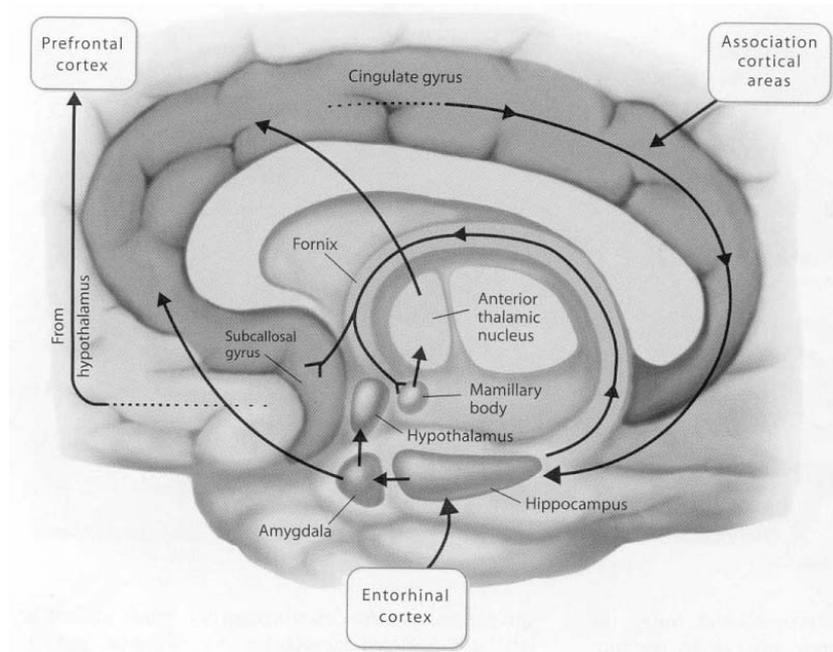


Figure 2.2.2: Location of the amygdala and its connections to the limbic system.

In a series of experiments LeDoux (1996, 2000) identified differential functions of the amygdala nuclei in the underlying systems underlying fear conditioning. The auditory pathways of rats were lesioned experimentally in order to assess the specific functions of the neural structures involved in auditory fear conditioning. Bilateral lesions of the corpus geniculatum mediale block fear conditioning towards a tone. Contrarily, bilateral lesions of the auditory cortex do not. It was concluded that the transmission of signals to the geniculatum mediale is a necessary condition for fear conditioning, whereas it is not to the auditory cortex. Since lesions of the amygdala block fear conditioning, the connection from the corpus geniculatum mediale to the amygdala was interpreted as essential. Based on this, LeDoux inferred that two pathways are taken: the low and the high road. The low road (or subcortical pathway) passes directly from the corpus geniculatum mediale to the amygdala and can by itself support rapid learning of conditioned responses on crude perceptual stimuli. The high road (or cortical pathway) passes from the corpus geniculatum mediale to the auditory cortex, leading finally to the amygdala. This road allows the discrimination of stimuli on the basis of complex analyses of their distinctive features, as well as the acquisition of differential conditioned responses to them (Figure 2.2.3). Studies using single-cell recordings have shown that learning through the thalamic way occurs faster than through the cortical way (Quirk, 1995). This led LeDoux to assume that the subcortical pathway provides a quick analysis of the affective properties of stimuli that serves as an initial template for subsequent processing. The low road thus can be very

useful in dangerous situations where it is important to react fast on a potentially dangerous stimulus. The amygdala is able to process both, the emotional significance of simple stimuli and complex situations. With respect to the interaction of emotion and episodic memory, this could be translated to the fact that the reoccurrence of a past perpetrator would be identified quickly without the retrieval of any detailed information but sufficient to gain the information that this person has been dangerous and allowing immediate preparedness. By means of high road memories rich and detailed information would be retrieved in order to evaluate details of the episode in which this person has been met.

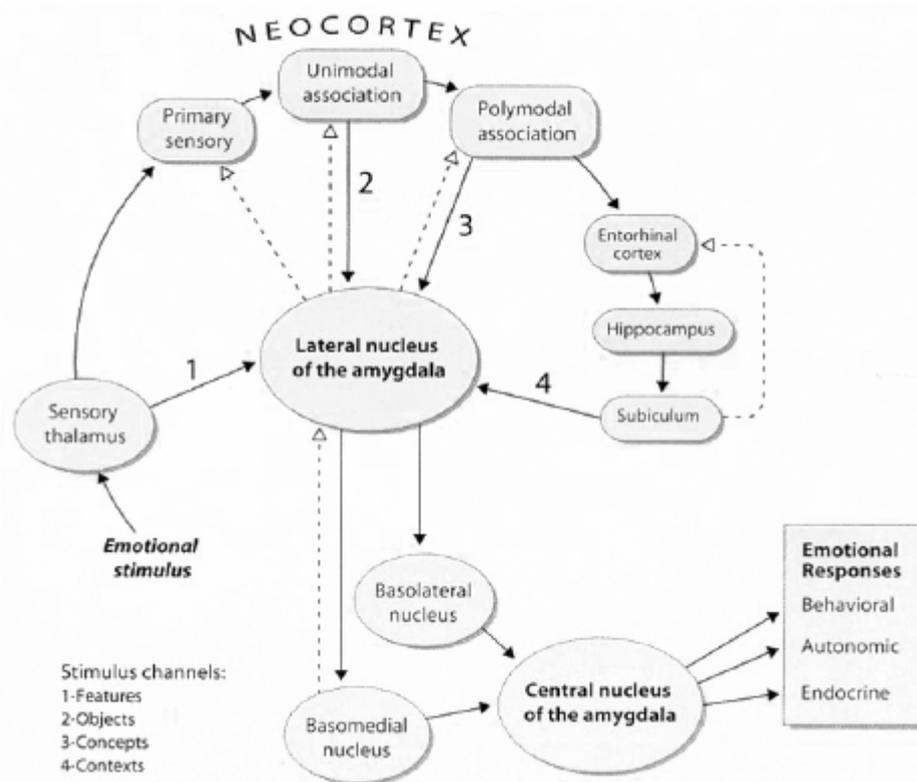


Figure 2.2.3: The high (1, 2, 3, 4, amygdala) and low road (1, amygdala) to the amygdala (according to LeDoux, 1995).

In neuropsychological research, a special patient group has provided new information about the amygdala in humans, the Urbach-Wiethe disease, a rare genetic disorder that results in pathology centered in the amygdala. Patients are characterized by an increase in emotional lability and childlike affect. Neuropsychological studies have shown that these patients have deficits in identifying emotional facial expressions and rate them less intense than healthy control subjects do. However, they are able to recognize personal identity.

Additionally, they are not able to describe fearful situations or draw fearful expressions. These deficits have been interpreted as a general lack of the concept of fear (Aggleton & Young, 2000). The finding that the amygdala has a crucial role in the recognition of fearful expressions is further supported by the findings of functional imaging studies. Morris et al. (1998) found left amygdala activity in healthy subjects while viewing fearful as compared to happy faces. By means of a regression analysis Morris et al. (1998) found that the connection between the amygdala and extrastriate cortex varied as a function of the facial expression being perceived. It was further suggested that the amygdala enhances the activity in extrastriate cortex when fearful faces are encountered. A comparable pattern of activation is also present when participants were not aware of the facial expressions (Morris, Öhman, & Dolan, 1999). This is in line with the animal model of fear conditioning by LeDoux (1996).

In conclusion, the amygdala seems to process initial associations between the appearance of a stimulus and the physiological responses that the stimulus or events elicits and furthermore modulates perceptual processing in other brain regions when an emotional stimulus occurs. Moreover, the amygdala has a key role in emotional learning processes. Another brain region, the orbitofrontal cortex, seems to be involved in the representation and control of stimuli that already have acquired positive or negative value (Adolphs, 2002) and will be discussed in the upcoming section.

2.2.3 The orbitofrontal cortex

The orbitofrontal cortex (OFC) is a region within the prefrontal cortex (PFC) situated on the orbital surface of the frontal lobe (Figure 2.2.4). Together with lower mesial sectors the OFC is also described as ventromedial prefrontal cortex. The OFC is interconnected with limbic structures, including connections with the hippocampus, the amygdala, and the hypothalamus (Miller & Cohen, 2001). Moreover, it receives input from all sensory modalities (auditory, somatosensory, and visual), and from other areas of the frontal and temporal lobes that integrate and associate information from many modalities (Nieuwenhuys, 1988). Therefore anatomically, the OFC is well suited to integrate information about the affective value of a stimulus and information about situational factors that might indicate a change in those values. According to Miller and Cohen (2001) the PFC is not critical for performing automatic behaviors, such as orienting to an unexpected dangerous object. These automatic behaviors are innate or develop with

experience. These bottom-up processes have the advantage that they can be executed very quickly without the need of attention. The PFC in contrast is critical for top-down processes, when behavior must be guided by internal states, or when actions are weakly established and must be adjusted to changing external conditions. In their biased competition model the PFC is able to bias processes in visual and sensory modalities, as well as systems for response execution, memory retrieval or emotional evaluation. The bias signals are very important when stimuli are ambiguous, when they activate more than one representation, or when multiple output channels are possible. This is of special importance in the domain of emotions since automatically elicited response tendencies must be evaluated in relation to their appropriateness in the given context. It is assumed that cues in the environment activate internal representations in the PFC that allow the selection of appropriate actions in situations that are uncertain and when one alternative is stronger because it is more habitual or salient. In sum, an important function of the OFC is the selection or inhibition of behavior according to environmental constraints. In most situations bottom-up emotional responses that are directly mediated by the amygdala are not always appropriate. Thus, irrelevant processing of emotional stimuli and automatically elicited responses have to be controlled in order to behave adequately. These control processes mediated by the OFC enable efficient cognitive functioning while inhibiting irrelevant responses.

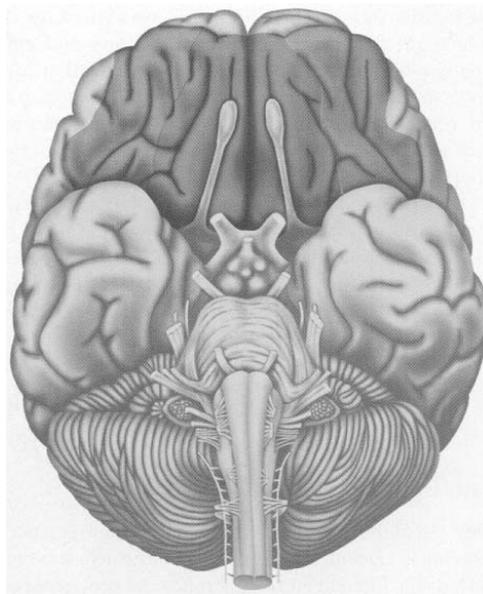


Figure 2.2.4: Location of the orbitofrontal cortex (dark grey). Adopted from Davidson et al., 2000.

The complex functional role of the OFC in guiding behavior can be well understood when examining patients with lesions in this region. Interestingly, a number of symptoms that these patients show can be related to impairments in altering behavior adequately when reinforcement contingencies change. The most famous patient described in the literature is Phineas Gage by the Damasio (1994). After an accident where an iron bar blew up into his head he could recuperate normal intelligence, memory, speech, sensation, and movement. Despite this, Gage showed a dramatic change in personality and social conduct, becoming irresponsible, behaving rudely, impatiently, and showed inappropriate emotional reactions, unable to organize his life (Damasio, 1994; Tranel, 2002). Remarkably, these patients are not impaired in their general knowledge about social conventions or moral reasoning. Thus, their impairment seems to result from a failure to apply emotional reasoning in real-life situations, especially in those that involve ambiguity and social contingencies (Tranel, Bechera, & Damasio, 1999). After the examination of several such patients, Tranel and colleagues developed the somatic marker hypothesis, in which they propose how emotional decision-making is mediated by the OFC. According to Damasio (1994) the OFC provides access to feeling states in relation to past decisions, which can then influence considerations of future decisions. They developed an experimental task that tests real-life decision-making situations, the Gambling task. Here, reward and punishment are unpredictable and delayed response gratifications are required. Card decks vary according to their risk, one providing large rewards but also penalties and the other lower rewards but also lower penalties. The goal of the game is to maximize profit on play money and response selection is guided by immediate monetary reward or delayed penalties. Testing this procedure in OFC patients and healthy control subjects revealed the latter learning quickly whereas the patients failed to shift to low risk decks, persisting on high risk ones. Measurements of skin conductance responses (SCRs) were taken as index of somatic state activation and revealed that both patients and controls showed increases in SCR when turning over a card related to reward or penalty. The SCR increased over trials for control subjects and became anticipatory before they turned over a card from the high risk deck. This was not true for the patients, which was taken as a physiological correlate for their insensitivity to future outcomes (Tranel, 2002). OFC patients performed that bad on this game not because they failed to generate affective reactions to analyses of their response options, but because they failed to activate biasing signals to use as value markers to differentiate choices with good or bad future outcomes. To assess the functional role of the amygdala in these processes,

bilateral amygdala patients were given the Gambling task. They failed to learn to focus on the low risk deck and to avoid the high risk one, and as the OFC patients did not generate anticipatory SCRs. But in contrast they additionally failed to generate punishment and reward SCRs, which was interpreted as a more basic deficit in coupling stimulus configurations with somatic states triggered by reward or punishment. The pattern of response of the OFC patients was instead interpreted as impairment in acquiring higher order conditioning (Tranel et al., 1999).

In conclusion, the amygdala and OFC seem to be two important components in a neural network responsible for detecting the emotional significance of external and internal events, but also for guiding behavior according to changes in the specific value of these events. Both components couple external events with internal somatic states, but they involve different types of information. Most importantly, the effects of the amygdala modulating hippocampal consolidation processes appear to be mediated by arousal (Hamann, Ely, & Grafton, 1999). This is of high relevance in the current study of the electrophysiological correlates of memory for emotional events which will be introduced in the following.

2.3 Emotion and ERP components

2.3.1 The electroencephalogram (EEG)

The electroencephalogram (EEG) was first measured in humans more than 75 years ago (Berger, 1929). It is a non-invasive technique with high temporal resolution, but low spatial resolution for evaluating brain activity underlying different brain functions. Recordings are possible from scalp or cortex surface and within certain brain regions. The latter two are designated as electrocorticogram and intracranial or intracerebral recordings. As neuronal basis, the EEG at the surface of the scalp is considered to reflect the extracellular current flow. The extracellular current flow is associated with summated postsynaptic potentials in synchronously activated, vertically oriented pyramidal cells. Action potentials from firing pyramidal cells, however, contribute only minimally because of geometrical reasons and extreme extracellular attenuation (Barlow, 1993). The action potential is transmitted within neurons. It induces the release of neurotransmitter at the connection to an adjacent neuron – the synapse. The neurotransmitter induces a change in the resting potential (approximately 70 mV) at the postsynaptic membrane of the adjacent neuron. Dependent on the type of neurotransmitter, the resting potential will increase (hyperpolarisation, i.e. caused by acetylcholine, adrenalin, or glutamate) or decrease (depolarization, i.e. caused by g-amino butric acid or glycine) (Kolb & Wishaw, 1996). The hyperpolarisation is called an inhibitory postsynaptic potential (IPSP), the depolarization excitatory postsynaptic potential (EPSP). The EPSP will elicit an action potential if the membrane potential is lowered below a certain threshold (approximately -50 mV). Electric fields caused by IPSPs or EPSPs can be recorded in the EEG. To measure an electric field at the scalp about 10^3 neurons have to be active in synchrony and need to be aligned in parallel to cause a detectable open electric field (Regan, 1989). If neurons are not aligned in parallel the resultant field is a closed one. It has the distribution of a sphere with zero potential and no field is generated outside. Thus, the electric activity from such closed fields cannot be recorded at the scalp. The condition of parallel alignment and synchronized activation establishes pyramidal cells as the origin of the EEG. They are organized in parallel in the outer cortical layers and represent 75% of neurons in the cerebral cortex (Braitenberg, 1977).

2.3.2 Event-related potentials (ERPs)

Changes in the EEG which follow or precede a certain classified event with a more or less potential course are called event-related potentials. They can be built from the background activity of the EEG which fluctuates between 0.1 to more than 40 Hz in the silent wakeful state (Berger, 1929). ERPs are repeatable potential shifts of the EEG (around 5 μ V). The remaining activity, not specific to the stimulus event, reflects randomly distributed background noise (around 50 μ V). To separate ERP and random background noise, the background noise is reduced by averaging the EEG of identical or similar trial repetitions, i.e. from one experimental condition (Rugg & Coles, 1995). The averaged EEG time epochs are usually time-locked to the stimulus onset. The averaged ERP consists of a pre-stimulus, not condition specific, baseline and a time window which covers the time of certain stimulus processes. This condition specific time window shows characteristic deflections or components. To discuss such ERP components, one has to take into account that not all neural structures are reflected in the EEG, but may modulate it (i.e. subcortical structures); scalp potentials allow only for vague source localization in the brain; and component overlap may be possible as a component is the summation of electrical potentials of different sources. These restrictions have to be considered and demand careful analyses of ERP components with regard to physiological and psychological characteristics. The physiological characteristics are polarity (positive or negative), latency (usually measured after stimulus onset as peak latency or component onset in milliseconds), amplitude (maximum or surface integral of the component relative to baseline), topography (spatial distribution over the scalp), and duration (overhead time from component onset to offset) of the component. Component labels are usually composed of polarity and latency, i.e. N100/P100 (negativity/positivity at 100 ms), or their order of appearance, i.e. N1/P1 (first negativity/positivity). ERP components can be categorized as exogenous or endogenous. Although this distinction is under discussion and is not strictly dichotomic, components which change only or mainly after physical stimulus modifications (e.g. loudness, frequency, color, contrast, etc.) are defined as exogenous, whereas components which change with respect to psychological factors (e.g. relevance, task, probability of occurrence) are defined as endogenous. Especially components between 100 and 200 ms after stimulus onset may be determined by physical and psychological stimulus characteristics.

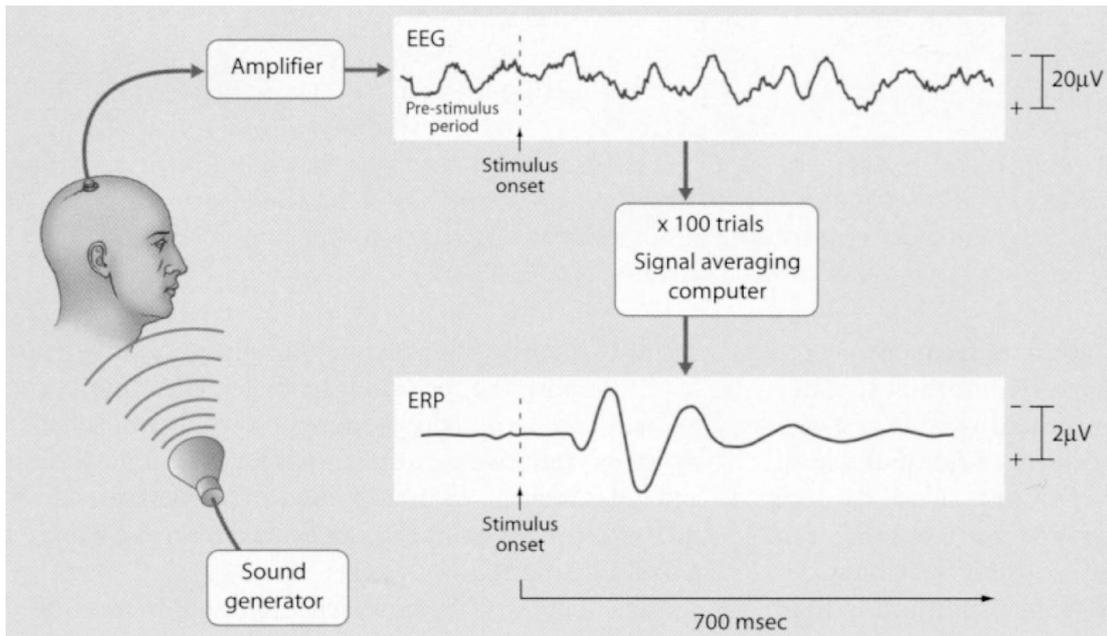


Figure 2.3.2: Example of EEG recording and ERP components.

2.3.3 Basic ERP components

In visual tasks, P1, N1, and P2 effects are usually studied in selective attention paradigms. In various studies the parieto-occipitally distributed P1 (90-120 ms) and N1 (around 170 ms) seem to reflect modality-specific processing in the visual pathways that is sensitive to the direction of attention (Hillyard & Münte, 1984; Heinze, Mangun, & Hillyard, 1990). Both are enhanced in attended stimuli. The N1 effect is thought to reflect stimulus intake processes and depends on the strength of a visual stimulus. The N1 and P2 vary in amplitude and latency as a function of stimulus intensity, presentation rate, and attention variation (Näätänen & Picton, 1987). The visual P2 peaks around 200 ms after stimulus onset, and is assumed to be exogenous as it varies with the complexity of stimuli.

The P300 is usually observed in a time window of 300 to 700 ms, and is distributed fronto-centrally (P3a) or centro-parietally (P3b) dependent on the experimental manipulation. The P3b is elicited by task-relevant stimuli with low probability and assumed to index brain activity required to update or modify the contents of working memory (Polich, 1990). The latency of the P3b is considered to be a measure of stimulus classification speed that is independent from overt responses. The P3a can be recorded in so-called three-stimulus paradigms in which rare targets have to be discriminated from frequent standards and rare distractor events. The P3a has a shorter peak latency than the

P3b and can be elicited by distractor events of different kinds and modalities (Mecklinger, Koenig, Ruffing, Reith, Mueller, Kaul, Becker, & Roell, 2006).

2.3.4 ERP components and emotion

In general, ERPs from affective stimuli suggest that more attention is garnered by affective content compared to neutral conditions, with amplitude modulations in early and late components (Schupp, Cuthbert, Bradley, Birbaumer, & Lang, 1997; Schupp et al., 2000; Carretie, Martin-Loeches, Hinojosa, & Mercado, 2001; Carretie, Martin-Loeches, Mercado, & Tapia, 2004; Delplanque, Silvert, Hot, Rigoulot, & Sequeira, 2006). These effects can be obtained in passive viewing as well as active response tasks (Cuthbert et al., 2000). Thus, affective processing can be described as an automatic feature of perception (LeDoux, 1989; Öhman & Soares, 1998). Support for this hypothesis comes from findings suggesting that valence category reflects initial selective attention capture by salient image content, whereby unpleasant stimuli generally produce stronger effects than pleasant ones (Cacioppo, Gardner, & Berntsen, 1999), and such a ‘negativity-bias’ may reflect rapid amygdala processing of aversive information (LeDoux, 1995; Morris et al., 1998). The arousal level of a stimulus is thought to determine attentional resource allocation for emotional picture processing, which has been explained in terms of high intrinsic motivational properties of picture stimuli. These appear to facilitate encoding and memory storage of the emotional event (Bradley et al., 1992; Lang et al., 1993).

At a short latency (100-200 ms) many emotion-related ERP modulations have been reported. The P1 and subsequent N1 components are sensitive to physical stimulus properties and index early sensory processing within the extrastriate visual cortex. When a stimulus discrimination task is administered, these potentials respond to manipulations of selective attention (Clark & Hillyard, 1996; Mangun, Hopfinger, Kussmaul, Fletcher, & Heinze, 1997). The P1 was found to be sensitive to the valence dimensions with unpleasant pictures eliciting larger components than pleasant ones over occipital sites (e.g. Smith, Henson, Rugg, & Dolan 2005). These results were interpreted in the way that negative pictures engage more focal attentional processing than positive pictures, i.e. negative pictures seem to preferentially attract attention early in the information processing stream.

The middle latency range (200-300 ms) is thought to reflect early stimulus discrimination and response selection processes (Di Russo, Tadei, Apnile, & Spinelli, 2006). An EPN (early posterior negativity) has here been reported for arousing as compared to neutral stimuli (Schupp, Junghöfer, Weike, & Hamm, 2003; Schupp et al., 2004; Schupp, Flaisch, Stockburger, & Junghöfer, 2006). Theoretically it is interpreted as an index of natural selective attention, such that evaluation of image features is guided by perceptual qualities that select affectively arousing stimuli for further processing (Dolcos & Cabeza, 2002; Schupp et al., 2004). Its amplitude is modulated by the arousal level of a stimulus (Schupp et al., 2003), independent of valence. The EPN is found across different tasks and stimulus durations, probably occurring automatically also when processing resources are limited by rapid presentation rate (Junghöfer, Bradley, Elbert, & Lang, 2001; Schupp, Junghöfer, Weike, & Hamm, 2003). This sensitivity may reflect rapid processing of aversive information of the amygdala (LeDoux, 1995; Morris et al., 1998). Theoretically, the underlying factor determining these modulations is selective attention to objects within the affective image that are assumed to be of intrinsic relevance (Schupp et al., 2006). This is indirectly supported by studies demonstrating non-affect perceptual and category-related ERP modulations in this time window which were attributed to selective attention mechanisms (Codispoti, Ferrari, & Bradley, 2006; Bradley, Hamby, Low, & Lang, 2007). The long latency (300 ms-...) segment is dominated by the P300 component and subsequent positive slow wave. This ongoing positivity is sometimes labeled LPP (late positive potential) elicited by arousing stimuli (Cuthbert et al., 2000). Major determinants of the P300 amplitude are task-relevance, motivational significance, arousal level, and the influence of these factors on mental resource allocation (Duncan-Johnson & Donchin, 1977; Polich & Kok, 1995). More specifically, this means that task-relevance, the more motivationally significant a stimulus is, and the higher the arousal of a stimulus, the larger the P300 amplitude. It was recently proposed that the P300 reflects noradrenergic modulatory effects exerted by phasic activity of the locus coeruleus-norepinephrine system associated with decision-making processes (Nieuwenhuis, Aston-Jones, & Cohen, 2005). Emotional arousal effects have been found for passive and active procedures for stimuli presented as distractors or targets in an oddball paradigm (Keil et al., 2002; Delplanque, Lavoie, Hot, Silvert, & Sequeira, 2004; Delplanque, Silvert, Hot, & Sequeira, 2005).

Thus, there is compelling evidence that arousal and valence modulate cognitive processes like e.g. attention allocation and encoding. The ERPs associated with these processes

represent indirect measures of the dimension of emotion. An even more detailed description and discussion of these emotion-related components will be given in the section on emotion and encoding processes, where they are considered highly relevant.

The upcoming chapter will first of all give an introduction into episodic memory for neutral materials, its neural substrates, and ERP correlates. This is of particular relevance when trying to understand the interplay of emotion and memory in the guidance of our behavior.

2.4 Episodic memory

Information maintained for a significant time is referred to as long-term memory. There are two major divisions that reflect the characteristics of the information that is stored, and that take into account the observable fact that not all stored knowledge is the same. The key distinction is between declarative and non-declarative memory. The former refers to knowledge to which there is conscious access to (world and personal knowledge), whereas the latter does not imply knowledge with conscious access (motor and cognitive skills called procedural knowledge, priming, and simple learned behaviors). In the following I will focus on declarative memory processes. These are further subdivided into episodic and semantic memory (Tulving, 1985). Episodic memory involves conscious awareness of past events, i.e. personal autobiographical memory. Contrarily, semantic memory reflects knowing facts, like world knowledge, language knowledge, and object knowledge. As argued by cognitive theory and supported by neuroscientific evidence memory therefore is supported by multiple cognitive and neural systems which support different aspects of memory (e.g. Squire, 1998; Aggleton & Brown, 1999). The proposed model by Squire (2004) is exemplified in Figure 2.4. The underlying brain structures of the different subprocesses also differ depending on the type of information to be retained and how it is encoded and retrieved. Hereby, the medial temporal lobe forms and consolidates new episodic and semantic memories, the prefrontal cortex is involved in encoding and retrieval of information, the temporal cortex stores episodic and semantic knowledge, and the association sensory cortices are responsible for the effects of perceptual priming (Squire, 2004).

In the following, I will go into more detail in the domain of episodic memory, whereby a way of experimentally investigating episodic memory (especially with ERPs) has been found great support, the so-called dual process theory of recognition memory.

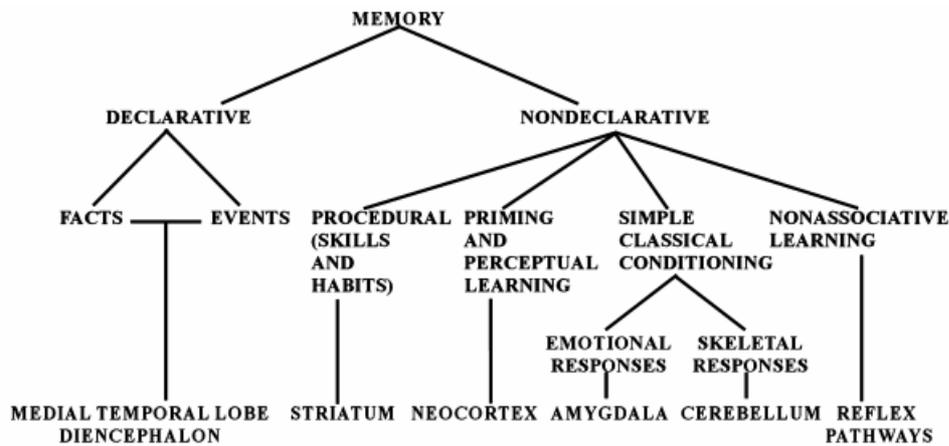


Figure 2.4: Taxonomy of long-term memory systems including responsible brain structures, proposed by Squire (2004).

2.4.1 Two-process models of recognition memory

When talking about dual process models of recognition memory, it seems necessary to shortly mention that there also exists another view, namely single process models. According to single process accounts recognition memory judgments are based on the evaluation of a single type of evidence, and a positive judgment is made when the strength of the evidence exceeds a criterion level (Mandler, 1980). Thus, recognition is supported by an undifferentiated, strength-like form of information. Dual process models, on the other hand, suggest that recognition memory is based on two distinct processes: familiarity and recollection. While recollection refers to the conscious retrieval of a prior study episode, including specific details such as spatial, temporal, or other contextual features, familiarity is assumed to reflect the fast assessment of global study-test similarity. It thus refers to an acontextual form of memory which does not imply any details of a prior encounter of a stimulus or event. A considerable body of evidence has been obtained in the support of proposals of the dual-process account (Yonelinas 2002; Aggleton & Brown, 2006). There are several techniques and operational definitions that derive behavioral estimates of familiarity and recollection from performance parameters. The most important of these techniques involve the remember/know procedure (Tulving, 1985), the process-dissociation procedure (Jacoby, 1991), and the receiver operating characteristics (ROC) procedure (Yonelinas, 1997).

Recollection and familiarity were distinguished on a physiological level, probably relying on partly non-overlapping neuronal networks. The medial temporal lobe (MTL) generally is critical for declarative long-term memory. The hippocampus therein is assumed to be essential for recollection-based remembering. Familiarity-based remembering, on the other hand, is supported by the surrounding parahippocampal region, especially the perirhinal cortex (Gonsalves, Kahn, Curran, Norman, & Wagner, 2005; Aggleton & Brown, 2006). Further support for this dissociation comes from neuropsychological studies with brain-lesioned patients. Lesions comprising the whole MTL disrupt both recollection and familiarity, whereas selective hippocampal lesions seem to affect recollection selectively while leaving familiarity relatively intact (Yonelinas et al., 2002; Quamme, Yonelinas, & Kroll, 2006). In the integrative neural network model (Norman & O'Reilly, 2003) the physiological properties of the abovementioned structures are taken as constraints for computational principles. Familiarity judgments are supported by the perirhinal cortex on the basis of the relative sharpness of item representations. While encoding an item, a sharpening process results in a smaller number of perirhinal neurons that are specifically tuned to represent a particular stimulus whereas other neurons are inhibited. This decreases the total perirhinal activity and at test, in response to a familiar compared to a new item, thus enables familiarity-based recognition judgments (Grill-Spector, Henson, & Martin, 2006). It is furthermore assumed that the same perirhinal structures are involved in both representing and extracting stimulus features and computing familiarity signals. The hippocampus, on the other hand, with its sparse level of neural firing (Aggleton & Brown, 1999), is proposed to be critical for recollection-based remembering, as it can establish associations between overlapping, arbitrarily paired items that are themselves represented in the perirhinal cortex. More specifically, the hippocampus creates pattern-separated representations of to-be-associated items in region CA3 that are linked to each other and to a copy of the perirhinal input pattern via region CA1. At retrieval, the hippocampus enables pattern-completion and retrieves a complete studied pattern in response to a partial cue. This mechanism may break down when the overlap between the to-be-associated information is too high, as pattern-separated representations cannot be established in this case (Schacter, Norman, & Koutstaal, 1998).

To conclude, the dissociation of familiarity and recollection as two qualitatively different mechanisms underlying recognition memory is supported by considerable evidence from behavioral, neuropsychological, and neuroimaging studies. The perirhinal cortex and

hippocampus seem to be the critical underlying neural substrates of the two processes. Additional activation in parietal and prefrontal regions that are frequently found in such tasks do not seem to be specific for either process, but are likely engaged in monitoring or top-down processes supporting familiarity- and recollection-based retrieval.

The next section will review recent ERP findings supporting dual process models of recognition memory. They provide a very useful insight into the spatio-temporal dissociation of the two qualities of remembering.

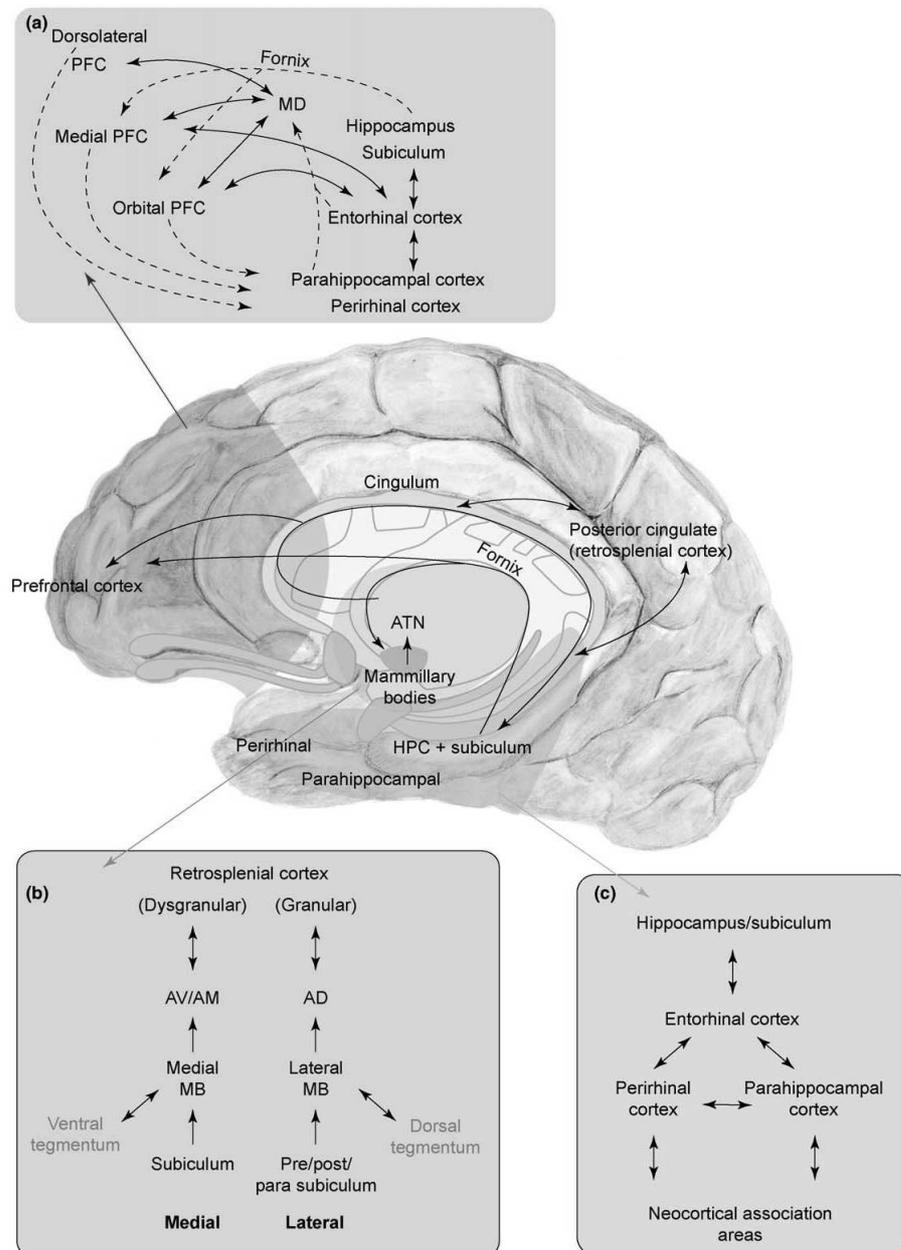


Figure 2.4.1: Schematic drawing of the main connections between the brain regions that underlie episodic memory. Adopted from Aggleton & Brown, 2006.

2.4.2 Electrophysiological correlates of recognition memory

Recollection and familiarity have been found to be associated with dissociable electrophysiological correlates. This lends further support to the abovementioned functional differentiation of the two cognitive processes. There is general consensus that familiarity is associated with an early (300-500 ms) mid-frontal old/new effect, i.e. more positive-going ERPs for previously studied as compared to new items. Recollection, on the other hand, seems to be reflected in a late (400-800 ms) (left) parietal old/new effect (Mecklinger, 2000; Friedman & Johnson, 2000; Rugg & Yonelinas, 2003; Wilding & Herron, 2006; Mecklinger & Jäger, in press).

There is compelling evidence from a large amount of studies that supports the distinction of spatio-temporally dissociable ERP components related to familiarity- and recollection-based retrieval. Of great importance here are the early findings of Rugg et al. (1998) who could demonstrate that the mid-frontal old/new effect is insensitive of depth of processing effects at encoding, whereas the late parietal old/new effect was of greater magnitude for deeply as compared to shallowly encoded items. Curran (2000) found that the mid-frontal old/new effect was of same size for studied words and plurality-reversed lure words that were judged as old. The late parietal old/new effect instead differentiated between the two classes of stimuli. Moreover, Nessler, Mecklinger, and Penney (2001) reported the mid-frontal old/new effect to be similar for true and false recognition of semantically related but unstudied words, and the parietal old/new effect being greater for true recognition. Thus, false recognition of lures happens in cases of high familiarity which is either derived from perceptual or conceptual similarity between study and test items. Vilberg, Moosavi, and Rugg (2006) demonstrated that the parietal old/new effect is greater when larger amounts of information are recollected, as compared to the mid-frontal old/new effect not showing this sensitivity. This is compatible with a study by Woodruff, Hayama, and Rugg (2006) where words engendering feelings of familiarity in the absence of recollection gave rise to a mid-frontal old/new effect but no parietal one. Contrarily, words that were accompanied by the recollection of specific contextual details elicited a parietal old/new effect that was not modulated by familiarity.

In sum, the dissociation of the two old/new effects and their corresponding characteristics strongly suggests the existence of two functionally distinct mechanisms underlying recognition memory. Thus familiarity- and recollection-based remembering can be investigated by means of electrophysiology quite thoroughly.

2.4.3 Associative recognition, item-context bindings, and source memory

As dual process models assume that item recognition is supported by both familiarity and recollection, traditionally only recollection is thought to be relevant to support associative recognition judgments (Yonelinas, 2002). Familiarity is not seen powerful enough to discriminate between same and rearranged pairs of which the constituting stimuli are all familiar; therefore recollection seems to be needed. Moreover, only the hippocampus is assumed to support such recognition judgments. However, these points are also controversially discussed (Mecklinger, 2006; Aggleton & Brown, 2006). The hypothesis initially formulated by Yonelinas and colleagues (Yonelinas, Kroll, Dobbins, & Soltani, 1999; Quamme, 2004; Quamme, Yonelinas, & Norman, 2007) states that familiarity, when the to-be-associated stimuli are encoded as a coherent whole and form a bound or 'unitized' representation, can contribute to associative recognition memory. In addition, it is inferred that associations can be retrieved independent of the hippocampus, only relying on the perirhinal region of the MTL. There are a line of ERP studies that support this general idea (Opitz & Cornell, 2006; Jäger, Mecklinger, & Kipp, 2006; Greve, van Rossum, & Donaldson, 2007). Pre-experimentally unitized associations (like rain-storm) and those that were unitized by encoding instructions can thus form familiarity-supporting representations.

How can this be referred to item-context bindings, i.e. is there also familiarity for contextual information? At least some ERP studies indicate that familiarity is sensitive for such influences, which is in contrast with the assumption that it represents an acontextual, item-specific form of recognition memory. Tsivilis, Otten, and Rugg (2001) found that the mid-frontal old/new effect was attenuated when studied objects were superimposed on novel, task-irrelevant backgrounds. In addition, Ecker, Zimmer, Groh-Bordin, & Mecklinger, (2007) reported that these contextual influences on the ERP-familiarity-effect disappeared when subjects were instructed to prevent directing attention to the backgrounds and therefore focus on the objects. It is thus likely that attentional and perceptual factors play a key role in establishing familiarity-based memories, consistent with the theoretical view that familiarity subserves genuinely acontextual forms of recognition memory.

A special way of testing contextual recognition is source memory. Source memory refers to the memory for the episode or context in which some information was presented or acquired (for a review, see Johnson, Hashtroudi, & Lindsay, 1993). Any aspect of context

can be considered in testing source memory accuracy (e.g., whether an event was actually experienced vs. imagined; whether a sentence was spoken by a male or female voice; whether a written word was presented in a blue or red font). Such information can be obtained in an incidental instruction or with the intention to learn, i.e. intentional encoding. Numerous studies have shown that, in general, memory for source is less accurate than item recognition memory (i.e., remembering simply whether one experienced an item or not) and involves more intentional processing and attention (Troyer, Winokur, Craik, & Fergus, 1999). Because source monitoring involves more intentional processing, and likely depends on frontal-lobe executive functions (Cycowicz, Friedman, Snodgrass, & Duff, 2001; Troyer et al, 1999), it should be more vulnerable than item recognition, especially in situations involving divided attention. It should be noted, however, that source monitoring performance varies depending on the type of source monitoring involved (e.g., internally- vs. externally- generated, voice, modality, font color, etc.), the type and difficulty of the secondary task, prior experience with the source differences that are being tested and a number of other factors (Dornbush, 1968; Farivar, Silverberg, & Kadlec, 2001; Toth & Daniels, 2002).

As mentioned above, source memory depends on the integrity of the frontal lobes, which could be demonstrated in several patient and neuroimaging studies (Janowsky, Shimamura, & Squire, 1989; Glinsky, Polster, & Routhieaux, 1995). The additional putative electrophysiological correlate of source memory retrieval, the LPN (late posterior negativity), is a posteriorly distributed negative slow wave and frequently obtained in the test phases of source memory tasks. Former studies have shown that the LPN has a parieto-occipital maximum, onsets at around the time at which a response is given, and is of equal amplitude for correct and incorrect source judgments (Johansson & Mecklinger, 2003; Friedman, Cycowicz, & Bersick, 2005; Herron, 2007). It was proposed that the LPN reflects the search for and retrieval of contextual features in tests of source memory, and retrieval processes that may act to reconstruct a prior study episode when item-context features are not sufficiently recovered or need continuous evaluation. The likely generator of this component is the parietal lobe, which has recently been shown to be critically involved in episodic memory retrieval (Wagner, Shannon, Kahn, & Buckner, 2005). The authors propose three hypotheses concerning how parietal cortex might contribute to memory. In case of the retrieval of item-context bindings the ‘output buffer hypothesis’ seems especially important. It is assumed that regions of the parietal cortex dynamically represent retrieved information in a form accessible to decision-making

processes. Although long-term memories are not stored in neuronal firing patterns, to influence decision-making, such memories must be expressed in active neuronal response patterns. The parietal cortex could act as the buffer into which stored information is transferred. Moreover, the phenomenon of reinstatement suggests that at least part of the retrieved information is represented in the corresponding sensory areas. Linking these thoughts to the electrophysiology of source memory retrieval, the LPN seems to be another piece of evidence that traditional cognitive-control-PFC models (e.g. Miller & Cohen, 2001) are not sufficient to explain episodic memory retrieval processes.

After focusing on memory retrieval processes, the following paragraphs will deal with memory encoding. Especially with respect to the study of emotion and memory, there are a line of studies that exclusively investigated encoding mechanisms. These are supposed to represent the hallmark for our behavior and later memory relevance. Thus, it is of particular relevance to first explain how neutral stimuli are thought to be encoded.

2.4.4 Encoding processes

Episodic encoding refers to the initial information processing steps whereby a memory trace is created such that it can subsequently support the conscious recollection of the past (Tulving, 1983).

For information to be encoded intentionally, it is processed by unimodal and polymodal cortical areas before being transmitted to the medial temporal lobe. As processing proceeds along these pathways, progressively higher-level representations of the perceived information are formed, integrating and associating different features of the to-be-remembered material into a bound representation (Simons & Spiers, 2003). At this stage, the interaction of the mentioned structures with the prefrontal cortex becomes important in providing top-down control of encoding processes, guiding, modifying, and elaborating representations in the medial temporal lobe on the basis of the current goals and task demands, and ensuring that representations are sufficiently non-overlapping to be amenable for long-term storage (Henson, Rugg, Shallice, Josephs, & Dolan, 1999). The interaction will involve differential recruitment of prefrontal regions depending on the type of top-down processing required, and its relative lateralization will depend on the verbal or non-verbal nature of the information being encoded (Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998).

Automatic (incidental) encoding of information, being related to bottom-up processing of stimuli, happens quite independent of the prefrontal cortex (Miller & Cohen, 2001). The PFC is not critical for performing simple, automatic behaviors. These behaviors can be innate or they can develop gradually with experience as learning mechanisms potentiate existing pathways or create new ones. These “hardwired” pathways are advantageous because they allow highly familiar behaviors to be executed quickly and automatically, without demanding attention. However, these behaviors are inflexible, stereotyped reactions elicited by just the right stimulus. They do not generalize well to novel situations, and they take extensive time and experience to develop. Bottom-up thus means that behaviors are determined largely by the nature of the sensory stimulus and well-established neural pathways that connect these with corresponding responses. In the case of encoding, sensory areas and the MTL memory system play a significant role for memory storage.

A special method of investigating encoding processes via fMRI and ERPs with regard to their direct mnemonic outcome is the subsequent memory paradigm which will be introduced in the next section.

2.4.5 The subsequent memory paradigm

To investigate the neural correlates of memory encoding in combination with the mnemonic outcome at retrieval the subsequent memory paradigm is used. In general, neural responses to distinct stimulus events are recorded and then classified based on testing the subject’s memory for the stimuli at a later time. The key contrast is typically between neural responses to stimuli later remembered and to those later forgotten (Paller et al., 1987). Differential neural activity based on memory sometimes referred to as ‘Dm’ (difference due to memory) provides an index of neural computations at the time of encoding that are predictive of accurate recall or recognition. Subsequent memory effects presumably index pivotal operations at the time of learning that influence what will be remembered, and constitute some of the tightest correlations between neural function and encoding (Paller & Wagner, 2002; see Figure 2.4.1 for a schematic description of the procedure and typical results in the ERP domain).

The configuration of neocortical modules that mediate encoding varies with the nature of the stimulus (e.g. Sommer, Schweinberger, & Matt, 1991; Mecklinger & Müller, 1996),

and with how attention is allocated to different stimulus features and types of processing. A central theoretical focus in memory research has concerned the influence of goal-directed attentional orientation on encoding, as can be manipulated by instructions to process stimuli for meaning, phonology, or structural form (Craik & Tulving, 1975). In one study by Paller (1987) ERPs were examined for words studied under four different attentional orienting conditions, using two structural and two semantic tasks. Dm effects, i.e. enhanced posterior positivity at a latency of 400-800 ms for subsequently remembered words, were greater during semantic than non-semantic orienting. Together with findings of Otten & Rugg (2001), this suggests that some Dm effects reflect processing variations that come into play when subjects maintain a meaning-based attentional orientation, and that different meaning-based goals can differentially influence encoding. On the other hand, associative or elaborative item processing, which probably demands strategic rehearsal and manipulations of actively maintained representations may likewise underlie frontal Dm findings in ERP studies (Mangels, Picton, & Craik, 2001). In their study the authors found the early N340 to be sensitive to attention and subsequent memory, indicating that it represents an attentionally modulated process that is also predictive of successful encoding. In addition, a posterior sustained potential demonstrated a clear association with subsequent memory, which was related to sustained activation of object representations just processed. Subsequently remembered words also elicited a robust sustained frontal positivity similar to that found in previous studies where encoding processes were explicitly biased towards elaborative strategies (Fabiani, Karis, & Donchin, 1990; Weyerts, Tendolkar, Smid, & Heinze, 1997). A previous study by Karis, Fabiani, and Donchin (1984) exemplifies the data quite well. Subjects reporting simple strategies while encoding words, larger P300s for subsequently recalled than not recalled items was found. The group of subjects reporting the use of elaborative strategies instead demonstrates a memory-sensitive frontal slow wave. This also receives support from studies with patients with focal lesions demonstrating the importance of this region for strategic processing and successful encoding (Stuss et al., 1994).

Thus it seems that there exists a topographical distinction for Dm effects being anteriorly and posteriorly focused, and reflecting strategic encoding operations usually obtained in intentional tasks versus automatic attentional operations in incidental tasks, respectively. Timing issues, however, are less well understood until now and remain to be classified in the abovementioned distinction.

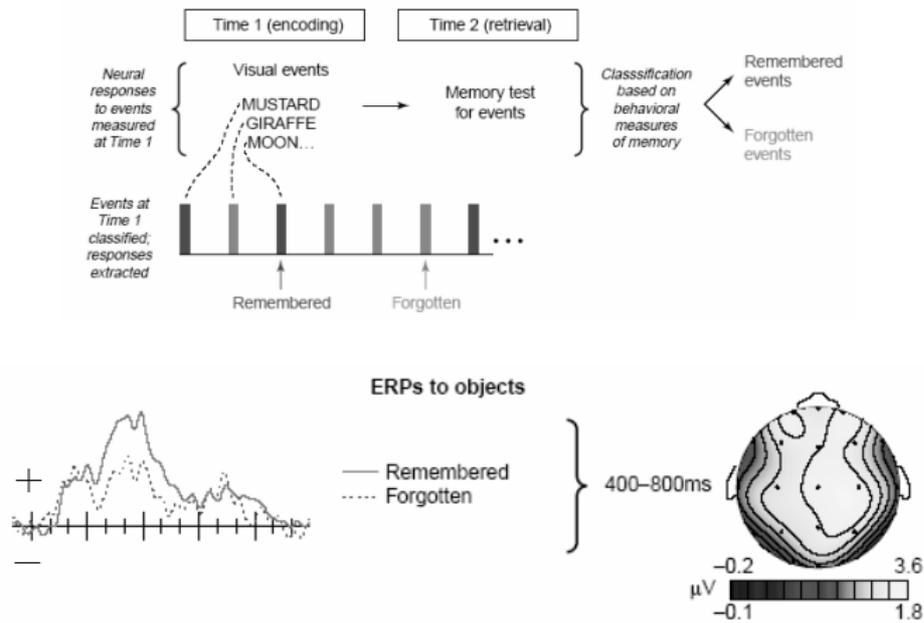


Figure 2.4.5: Procedure of the subsequent memory paradigm adapted from Paller & Wagner, 2002.

2.4.6 Summary

Episodic memory and its electrophysiological correlates are fairly well researched with dissociable ERP old/new effects for two qualitatively distinct types of remembering, familiarity (early frontal old/new effect) and recollection (late parietal old/new effect). These are supposed to reflect the different involvement of underlying neural structures of the MTL memory system, being the perirhinal cortex and hippocampus, respectively. Encoding phenomena have additionally been investigated to a large extent and point to a significant role of encoding instruction for later memory processing and relevance. Hereby, it is of further importance to look at automatic and controlled processes supporting the encoding of information into memory, revealed in topographically distinct subsequent memory effect in the EEG.

In the following it will be of special interest how the abovementioned processes are affected by the emotional valence and arousal of a stimulus. Are there emotion-specific brain regions and networks? Therefore, I will shed light on the processes of encoding, consolidation, and retrieval in interplay with emotional arousal.

2.5 Emotional influences on encoding processes

2.5.1 Attentional and strategic modulations

As already introduced in the last section on episodic memory and encoding, there are at least two ways of encoding events, namely bottom-up (i.e. relatively automatic) and top-down (i.e. under the engagement of strategic operations) driven processing. At the point of the first encounter, emotionally arousing stimuli are usually processed prioritized, i.e. relatively automatic. Attention may be directed towards threatening or aversive stimuli and these may benefit from facilitated processing (Pratto & John, 1991; Wentura, Rothermund, & Bak, 2000; Öhman et al., 2001; Anderson & Phelps, 2001; Kensinger & Corkin, 2004). There is increasing evidence that this is realized by the modulatory effects of the amygdala on the MTL memory system and lower sensory areas (e.g. reviewed in LaBar & Cabeza, 2006). There are relatively few studies that investigated the effect of only valenced stimuli or directly compared those to additionally arousing ones, but there are reports that the valence dimension is sufficient to boost (i.e. better and richer) memory performance (LaBar & Phelps, 1998; Ochsner, 2000; Kensinger & Corkin, 2004). The processes contributing to this enhancement, however, seem to be distinct from the former. These stimuli are found to profit from self-generated and controlled encoding strategies that on a neurophysiological level are seemingly realized by a network engaging the prefrontal cortex (PFC) and hippocampus (Kensinger & Corkin, 2004). Using the subsequent memory paradigm with neutral and negative words as test stimuli in a later recognition memory test, the authors identified this network in successful encoding of negative non-arousing words. Contrarily, for the successful encoding of negative and high arousing words the amygdala and hippocampus proved to be highly relevant. Kensinger and Corkin were thereby able to find a dissociation of two encoding mechanisms related to valence and arousal in one experiment, which is summarized in Figure 2.5.1. Panel A shows that the left amygdala only proved to predict subsequent memory performance for negative words with high arousal, whereas panel B implicates that the left hippocampus is relevant for the successful formation of memories of all kinds of stimuli. The left inferior PFC (panel C) demonstrated a further dissociation with only being sensitive to later memory performance for negative non-arousing words and neutral ones, and not for arousing ones. Thus, the latter two classes of stimuli engaged a similar network, whereas on a behavioral level this only led to a memory enhancement for negative words. Probably

strategic encoding operations are more efficiently engendered for these stimuli only. This elaborative processing could at least take two forms: autobiographical and semantic (Kensinger, 2004). Autobiographical elaboration involves processing stimuli with regard to the subject who is seeing it, linking the stimulus to autobiographical experiences or undertaking self-introspection. This is more likely to happen for valenced as for neutral stimuli. Semantic elaboration means that subjects semantically elaborate on the items, i.e. think about their meanings or their relation to other items. Especially the latter is supposed to be enhanced for valenced items that usually share stronger inter-item associations than neutral ones.

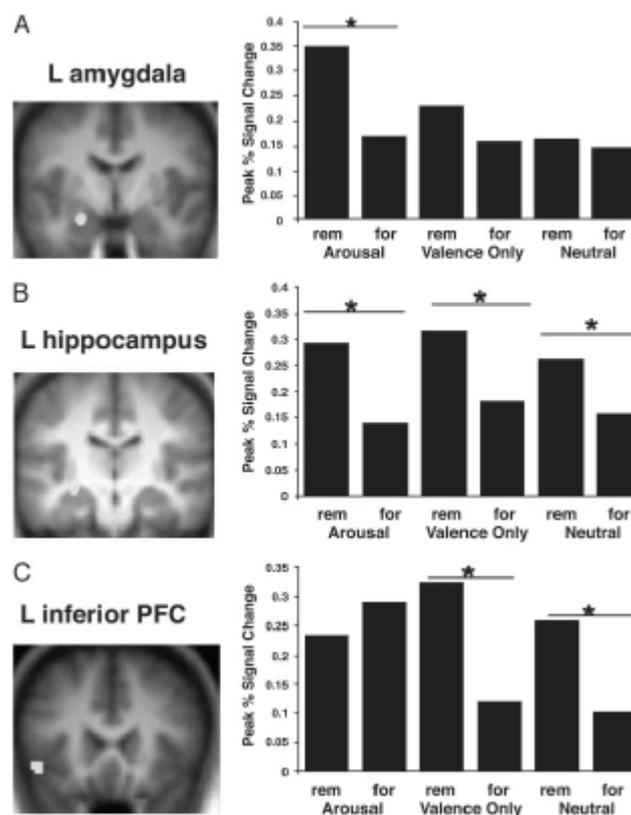


Figure 2.5.1: Subsequent memory data from Kensinger & Corkin, 2004. A represents the results for the left amygdala, B the left hippocampus, and C the left inferior PFC.

There is a current debate about the role of the amygdala in encoding neutral contextual information (Kensinger, 2004; Adolphs et al. 2005). Although amygdala activity corresponds with memory for some details (whether an item was seen or imagined; Kensinger & Schacter, 2005 a, b), it does not for others, e.g. the task performed

(Kensinger & Schacter, 2006). The authors assume that contextual information has to be task-relevant to reach the amygdala and moreover gain special mnemonic relevance. Another piece of evidence with respect to encoding processes of emotional stimuli comes from EEG studies.

As already introduced in the paragraph on electrophysiology, event-related potential (ERP) studies consistently found that emotional pictures from the International Affective Picture System (IAPS; Lang et al., 2005) evoke a late positive potential (LPP) in stimulus classification paradigms (Schupp et al., 2006). This component is additionally modulated by the level of arousal, with more arousing pictures eliciting greater positive potentials than low arousing ones (Schupp et al., 2000). During intentional encoding of a recall test, Dolcos and Cabeza (2002) found the positivity for emotional stimuli (here positive and negative arousing) to be modulated by arousal at parietal and by both arousal and valence at fronto-central sites. The authors related this to the abovementioned distinct neural systems for arousal (amygdala-hippocampus) and valence (PFC-hippocampus) processing. However, the specific functional significance of the posterior positivity in the domain of memory remains an open issue. On the basis of findings that show that the posterior positivity is associated with the amount of attention paid to the emotional stimulus being processed (Diedrich, Naumann Maier, & Becker, 1997) and that the amplitude of the posterior positivity is positively correlated with the number of subsequently remembered emotional events (Palomba, Angrilli & Mini, 1997), one could assume that it reflects some kind of ‘attentional capturing’ that leads to better memory for stimuli that contain this attention grabbing properties. Moreover going a step further, this attentional capturing mechanism could also modulate the build up of memory-relevant associations (bindings) between stimuli and context features and thus lead to impairment effects in the domain of source memory.

In conclusion, it has to be noted that already at encoding valence and arousal seem to have dissociable effects contributing to a memory advantage for emotional stimuli which can be inferred from fMRI and ERP studies. It, however, remains open how the correlates of the two methods of investigation are related to each other, and how arousal and valence are to be dissociated specifically.

2.5.2 The tunnel memory phenomenon

A frequently discussed phenomenon in the domain of encoding and processing emotional stimuli is the tunnel memory phenomenon. It states that central aspects of an emotionally arousing scene are usually better remembered than those of neutral and non-arousing ones. Moreover, neutral and non-arousing peripheral aspects tend to be remembered less well when they are part of an emotionally arousing scene as compared to being part of a neutral non-arousing scene (e.g., Safer et al., 1998). This phenomenon is often also referred to as weapon focus (Stebly, 1992) and more directly describes the fact that witnesses of a crime mostly are able to give details about the assailant's weapon, but not e.g. about his clothes. Another distinction is made within the terms of boundary restriction and extension. According to Intraub, Bender, and Mangels (1992), while viewing a picture people automatically activate a perceptual or mental schema that extends the arbitrary boundaries of the picture. This is supposed to happen to neutral scenes, whereas the opposite should be true for emotionally arousing ones (Christianson, 1992).



Figure 2.5.2: Examples of neutral (top) and traumatic (bottom) stimuli used by Safer et al., 1998.

This effect is usually explained through two different mechanisms. The first is supported by the special attentional properties of emotionally arousing stimulus material (Easterbrook, 1959). Attention is focused on the central arousing emotional object in a scene and may therefore result in better encoding of information in that location, at the expense of other less well attended locations. This is often called a narrowed focus of attention (Baddeley, 1972) or attentional capturing (Pratto & John, 1991) of emotional material. This finding can be related to bottom-up processing introduced at the beginning of this paragraph. The second mechanism relies on top-down driven processing and is reflected in a greater elaboration of the meaning of emotional scenes and a direct enhancement of memory trace encoding as a result of emotional arousal at the time of processing (Cahill & McGaugh, 1995).

To get closer to the underlying mechanisms of the special encoding characteristics of tunnel memory phenomenon and to further validate the general phenomenon, most recent behavioral studies used quite diverging experimental designs. Moreover, a relatively small amount of stimulus material was taken into investigation and no really converging patterns of results on the tunnel memory phenomenon are reported as will be described in the following. Safer et al. (1998) concluded that their series of experiments, while using two different sets of stimuli and three different methods of testing recognition, provides considerable support that subjects remember traumatic scenes as more focused than neutral ones. However, these claims are build on the use of two test items per subject that only restrictedly point to the tunnel memory phenomenon. Candel, Merckelbach, and Zandbergen (2003), who tried to validate Safer et al.'s conclusions, investigated the aforementioned phenomenon with a drawing test and the camera distance paradigm (according to Intraub et al., 1992). Their results suggest that boundary extension for neutral and emotional photographs is a more robust finding than boundary restriction. Mathews and Mackintosh (2004) brought an important influence factor into discussion that might at least partially account for the diverging results in the domain of the tunnel memory phenomenon. In a well-designed experiment using a much wider range of stimuli (32 out of the IAPS; Lang et al., 1995) than all abovementioned studies, they could show that boundary extension was reduced in high trait-anxious individuals for negative scenes as compared to neutral ones. This was explained through the association of high trait anxiety with selective attention focused on threat content, together with a neglect of processing other more peripheral details, consistent with bottom-up processing. This is in accordance with early findings that increased anxiety or threat leads to reduced attention

and responsiveness to peripheral cues (e.g. Erdelyi & Blumenthal, 1973) together with heightened attention and responsiveness to central cues that were the source of the increased anxiety (Christianson, Nilsson, Mjörndal, Perris, & Tjellén, 1986; Derryberry & Reed, 1998). Previous research has suggested that threatening stimuli are more likely than emotionally neutral ones to capture attention. This particularly is the case in anxiety-prone individuals (Mathews & MacLeod, 1994). Two main sources of evidence build the basis for this conclusion. First, in interference tasks such as the emotional Stroop, words with a threatening meaning often cause slowed color naming relative to matched neutral words (Williams, Mathews, & MacLeod, 1996). Second, in attentional search tasks, targets may be detected faster when they occur in the same location as threatening words than in the location of neutral ones (Broadbent & Broadbent, 1988; Yiend & Mathews, 2001). Preferential attention capture by threat stimuli has been reported in both clinically anxious groups and in high-trait anxious non-clinical groups, especially when under stress. Typically, low-trait anxious individuals do not show the same response to such stimuli and, indeed, have sometimes tended to show the reverse effect, suggestive of avoidance (Mogg, Bradley, & Hallowell, 1994). These results have been used to argue that individual variations in selective attention to threatening cues when under stress may underlie vulnerability to anxiety states, by enhancing the acquisition of information about potential dangers in some people and minimizing it in others (Mathews & MacLeod, 1994). This argument implies that the finding with threatening stimuli leading to selective intake of information about danger by anxiety-prone individuals in everyday life, and thus representing a causal factor in anxiety disorders.

Very recently, Kensinger, Garoff-Eaton, and Schacter (2007) tried to disentangle different memory trade-off effects with regard to memory for emotionally arousing scenes. The authors first defined two types of such trade-off effects which correspond with the aforementioned mechanisms: the central/peripheral trade-off and the gist/detail trade-off. The former refers to the fact that subjects are more likely to remember the negative visually arousing objects than the neutral objects in the center of a scene, and are less likely to remember background information shown with negative arousing objects than with those shown with neutral objects. The latter is described as an enhancement of the likelihood that the gist or general theme of an experience is remembered, while reducing the probability that specific visual details of that event are remembered. In four behavioral experiments they demonstrate that the central/peripheral trade-off is a very robust phenomenon whereas the gist/detail trade-off could only be found with special encoding

tasks and only for memory for the nonemotional background of a scene. With regard to the tunnel memory phenomenon this means that it most likely is based on the attentional capturing mechanism introduced by Easterbrook (1959), supported by bottom-up processing.

2.5.4 Summary

There are a few ways by which emotional arousal can affect encoding. The first is by modulating the selectivity of attention (Easterbrook, 1959). It is proposed that arousal will lead to the narrowing of attention, i.e. a decrease in the span of cues to which an organism is sensitive. When observing an emotional event, attention will be focused primarily on the arousing details of the stimulus, resulting in better encoding of those details and impaired encoding of less relevant ones, resulting in a general memory failure. This is what is supposed to underlie the tunnel memory phenomenon. The contrary finding, boundary extension, is usually observed for neutral stimuli.

Emotional stimuli may also benefit from conscious top-down encoding strategies, such as elaboration. This is supposed to be mostly true for non-arousing negative stimuli. Elaboration refers to the process of establishing links between newly acquired information and previously stored one. This elaborative processing could at least take two forms: autobiographical and semantic (Kensinger, 2004).

On a neural level, the first modulation of encoding processes is realized by the amygdala (e.g. Morris et al., 1998). With its activation it appears to also bias sensory processing, due to its connections with lower-level sensory areas (Amaral et al., 2003). Moreover, a further influence on hippocampal activity seems to be responsible for the often reported later memory advantage (Kensinger & Corkin, 2004). Contrarily, elaborate processing is more likely to be mediated by the prefrontal cortex and its connections to the hippocampus.

Emotion may moreover affect memory in other ways, i.e. by influencing retention or consolidation. Therefore, the upcoming section deals with these possible mechanisms.

2.6 Modulation of consolidation processes by emotion

2.6.1 Effects of stress hormones

In the context of consolidation processes of emotional stimuli, stress hormones have been discussed as highly relevant. This is inferred from a line of experimental studies with animals and humans. Stress-hormone systems activated by emotional situations serve the immediate adaptive needs of an organism (Frankenheuser, 1975). Additionally, extensive evidence suggests that they influence memory storage (McGaugh, 1992; Cahill, McGaugh, & Roozendaal, 1996). Initial animal studies examined the effects of post-training injections of the adrenal medullary hormone adrenaline on memory for inhibitory-avoidance training (Gold & Van Buskirk, 1975). Adrenaline enhanced memory in a dose-dependent way and the effects were time-dependent. Memory was only enhanced when adrenaline was administered shortly after training, which was also found in discrimination learning and appetitively motivated tasks (McGaugh, 1992). These effects seem to be mediated by the activation of peripheral β -adrenergic receptors and additionally might involve the release of glucose (Gold, 1995).

These studies imply that activation of β -adrenergic receptors in humans could influence long-term declarative memory formation for emotionally arousing events, which is supported by several recent studies (Cahill, Prins, Weber, & McGaugh, 1994; Nielson & Jensen, 1994; Van Stegeren, Everead, Cahill, McGaugh, & Gooren, 1998). Emotional arousal also activates adrenocortical hormone release (cortisol in humans). The adrenocortical response is generally viewed as the second wave of the endocrine response to an emotional event (Lupien & McEwen, 1997). Most studies have examined the impairing effects of high, sustained doses of the hormones. However, the well-known inverted-U relationship between dose and retention performance (i.e. memory performance after a given retention interval) suggests that lower, acute doses of corticosterone-receptor antagonists should enhance memory consolidation (Roozendaal & McGaugh, 1996). Furthermore, adrenomedullary and adrenocortical hormones on memory interact in influencing memory storage (Roozendaal, Carmi, & McGaugh, 1996). Thus, the adrenal hormones adrenaline and corticosterone enhance declarative memory of arousing experience.

It is documented in several lines of research that the amygdala modulates memory storage for emotional stimuli. Goddard (1964) was the first to show that stimulation of the

amygdala influences memory consolidation processes. The amygdala is crucial for memory-modulating influences of stress hormones. Lesions block the memory-enhancing effects of adrenaline and glucocorticoids (McGaugh, 1992; Cahill et al., 1996). The basolateral nucleus of the amygdala seems to be the nucleus most crucially involved in these modulations (Roosendaal & McGaugh, 1997). It projects prominently to the hippocampus and entorhinal cortex, which are critically involved in memory processes (Ikegaya, Saito, & Abe, 1996). Moreover, the amygdala modulates memory storage processes in the neocortex via projections to several cortical regions (Iwai & Yukie, 1987).

Considerable evidence from both animal and human studies lends support to the perseveration-consolidation hypothesis first introduced by Müller & Pilzecker (1900). It states that neural processes initiated by an experience persevere and consolidate over time with emotional arousal activating neurobiological processes that modulate the consolidation of memories of recent experiences. The adrenal stress hormones, adrenaline and corticosterone (cortical in humans), normally released by emotional arousal enhance long-term memory when administered to rats or mice shortly after a training experience (McGaugh & Roosendaal, 2002). These stress hormones influence noradrenergic activation within the basolateral region of the amygdala, and amygdala activity in turn modulates memory processing in other brain regions, e.g. the hippocampus via long-term potentiation (Ikegaya et al., 1996; Cahill & McGaugh, 1998). Human studies have also reported that memory is enhanced by administering adrenaline shortly after learning or by inducing stressful conditions that release adrenaline (Cahill & Alkire, 2003). Drugs that prevent the actions of adrenaline (β -adrenergic antagonists) block the memory enhancement by emotional arousal (see Figure 2.6.1).

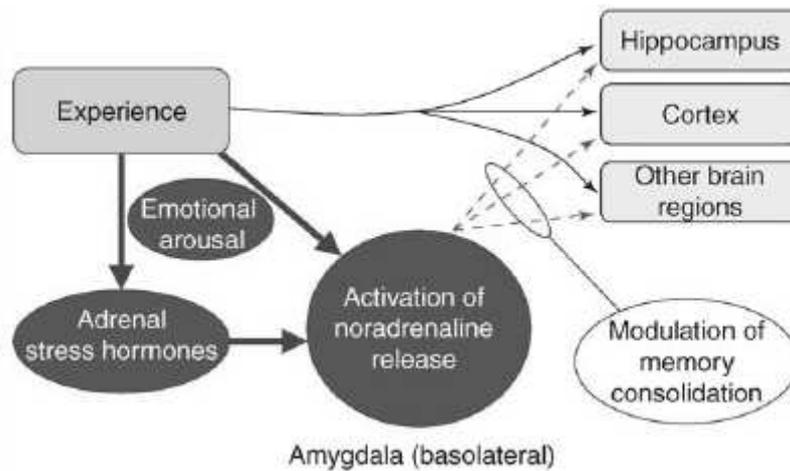


Figure 2.6.1: Schematic representation of modulation of memory consolidation by emotional arousal-induced release of stress hormones and noradrenergic activation of the amygdala (McGaugh, 2006).

2.6.2 Retrograde memory enhancement (RME) and retention duration

When discussing effects of emotional arousal on consolidation processes, it seems worth mentioning that there are a few studies that could demonstrate the modulatory power of arousal on memory for neutral events when administered timely associated. Livingston (1967) proposed that memory for neutral items preceding emotionally arousing items are enhanced. In many studies influences on attention at encoding and those on consolidation are confounded, especially when emotional items are used as test probes. In a recent study (Anderson, Wais, & Gabrieli, 2006) the authors tried to research consolidation effects selectively, i.e. unconfounded by encoding processes. Subjects encoded neutral and emotional (both positive and negative) pictures. The former were presented either 4 or 9 seconds before arousing (or neutral) stimuli. During a recognition test administered one week later, remember/know judgment had to be given. Memory performance for the emotional stimuli varied directly as a function of subjectively experienced arousal with more arousing pictures remembered to a greater extent than low arousing ones. Additionally, memory for neutral pictures preceding the emotional ones by 4 seconds (not by 9 seconds) also varied with the emotional intensity of the emotional pictures, i.e. the greater the emotional arousal of the emotional picture, the better the memory performance of the preceding neutral one. This was termed ‘retrograde memory enhancement’ (RME) by the authors. Moreover, specific recollection of the neutral pictures, but not judgments

of familiarity, was directly related to the degree of arousal of the pictures. The authors pointed out that it is unlikely that adrenal stress hormones played a role in mediating these effects, because stress hormone release is probably too slow to influence amygdala's functioning within the 4 second window of effectiveness. Also, as peripherally released stress hormones remain active for many minutes, they would have been influential during the presentation of neutral as well as emotional stimuli.

Retention duration seems to be a critical experimental factor for proving that consolidation processes are highly relevant in the topic of emotional arousal (LaBar & Phelps, 1998; Sharot & Phelps, 2004; Sharot & Yonelinas, 2008). These studies showed that a recognition advantage for negative arousing stimuli as compared to neutral ones could only be observed after a great delay (at least several hours), but not in immediate testing. This effect could be observed for recall and recognition memory tests using words and pictures as stimulus materials. Moreover, Sharot and Yonelinas (2008) demonstrated partially no forgetting or even enhancements for arousing stimuli over a 24 hour interval as compared to immediate testing. This means that ongoing consolidation processes are beneficial for emotional stimuli to be stored in memory and later facilitate retrieval operations. However, these studies did not investigate the underlying neural correlates of this phenomenon which seems to be highly relevant for obtaining an association with the abovementioned modulatory effects of stress hormones on consolidation processes for emotional stimuli. Moreover, these studies lack to find differences in the valence and arousal characteristics of different stimulus materials.

In sum, there is compelling evidence that stress hormone systems and the amygdala play a key role in the modulation of consolidation processes mediated by emotional arousal. Such modulations engage ongoing central as well as peripheral neurohormonal systems and seem to promote memory for emotional stimuli, as exemplified in a retrieval advantage over time.

2.7 Emotional influences on retrieval processes

2.7.1 Quantity of remembering

The emotional salience of an event has proven to be an important modulator of memory performance, as it is usually more likely to remember events containing emotional relevance than those that do not. This memory enhancement effect has been shown for a large class of stimuli in diverse tests of memory. A robust pattern in free recall tests is that emotional stimuli are recalled to a greater extent than neutral stimuli (Cahill et al., 1996; Hamann, 2001; Buchanan & Adolphs, 2002). Similar effects have been noted within the autobiographical memory literature. When individuals are asked to generate memories in response to a cue word, the retrieved memories will often be rated as personally significant and emotional (e.g. Conway, 1990). A topic of further investigation is the extent to which the valence of an event (positive or negative) differentially influences the likelihood that an event is remembered. Often, the boost in recall or recognition is comparable for both kinds of stimuli (Bradley et al., 1992; Kensinger, Brierley, Medford, Growdon, & Corkin, 2002). However, in some studies negative items are more likely to be recalled than positive ones (e.g. Charles, Mather, & Carstensen, 2003). Yet other studies, those on autobiographical memories, revealed the opposite pattern, an advantage for positive events (D'Argembeau, Comblain, & Van der Linden, 2005).

However, recognition memory enhancements are less consistently reported (reviewed in Christianson, 1992). In a behavioral study Ochsner (2000) reported higher old-new discrimination for negative pictures than for both positive and neutral ones after a two-week test delay. Moreover, he obtained more liberal response biases for negative and positive pictures as compared to neutral ones. In most cases, hits and false alarms are enhanced for emotional material. Moreover, the so-called 'emotion-induced recognition bias', i.e. a more liberal response criterion for emotional as compared to neutral stimulus materials often is accompanied by comparable d' values (i.e. old/new discrimination performance) for neutral and emotional stimuli (Windmann & Kutas, 2001; Johansson, Mecklinger, & Treese, 2004), or even worse performance for negative words (Maratos, Allan, & Rugg, 2000). The latter study examined their proposed underlying electrophysiological mechanism that emotional stimuli share stronger inter-item association strength than neutral ones and by this lead to illusory recollection. This phenomenon could be demonstrated behaviorally, and the examination of ERPs in the

recognition phase of their experiment supported their view that memory for emotional and neutral words is not mediated by different cognitive systems and operations. In contrast, after having made an effort to equalize the inter-item relatedness for the stimulus classes, and still obtaining a more liberal response bias for negative as compared to neutral words, Windmann and Kutas (2001) argued that the difference in response bias rather reflects flexible criterion setting triggered by emotional valence that works to ensure that especially negative stimuli are not missed or taken as irrelevant. This was inferred by the finding that, although ERP old/new effects were not different for negative and neutral words, waveforms for 'old' responses (hits and false alarms) revealed ERP differences in an early time window (300-500 ms) only for neutral items at frontal sites. This was interpreted as a reflection of response bias effects on ERPs linked to recognition memory. The authors proposed that the non-existing difference for negative words reflects a disinhibition of prefrontal control mechanisms which thus leads to an enhanced false alarm rate for these stimuli. A further study with negative, positive, and neutral faces as stimuli (Johansson et al., 2004) supported this interpretation. Again, emotional valence did not influence old/new discrimination accuracy, but response bias. In addition a similar frontal ERP modulation as in the Windmann & Kutas (2001) study could be observed. Some of these conflicting findings may be explained by the proposal that memory mechanisms evolved to facilitate the encoding and retrieval of the affective information that is most relevant to one's goals (e.g. LeDoux, 1996). Remembering a negative experience often may be more relevant to survival or well-being. In these instances, more attention may be paid to the negative item, enhancing memory for this kind of information. However, there likely are instances in which positive events are just as relevant as or even more relevant than negative ones. In support of this is evidence that individuals (e.g. older adults) who seek positive goal states show enhanced memory for positive as compared to negative items (reviewed by Mather & Carstenson, 2005). To reflect this of an experimental point of view, all abovementioned studies used diverse kinds of test materials (words, pictures, faces), different encoding instructions (intentional, incidental), and methods to test recognition performance (pure old/new discrimination, old/new discrimination together with the remember/know procedure). Moreover, they did not disentangle effects of valence and arousal, and did mostly use immediate testing, not delayed (where advantageous effects for emotional stimuli are found to be extremely pronounced (e.g. Sharot & Phelps, 2004)). Especially the last two points seem to be of high importance and may account for the inconsistency in results. Thus in the following,

the quantity of remembering for emotional pictures will be researched. This kind of stimulus material is not used very often in mere recognition memory paradigms, but seemingly has several advantages as compared to words. Photos of real-life objects and situations are far more realistic to induce emotional arousal and therefore deserve special attention in the following research.

The next section will present results on the quality of remembering, which will provide a valuable tool for a deeper understanding of the mechanisms by which emotion modulates recognition processes.

2.7.2 Quality of remembering

Although quantitative assessments of memory have been instrumental in laying the groundwork for investigations of emotion-memory interactions, they may underestimate the influence of emotion. Not all remembrances are created equal. Many of emotion's effects on memory become apparent only when the quality of a memory is considered. Thus, in addition to a change in the quantity of remembering, modulatory effects are also described as a boost of recollective experience (Ochsner, 2000; Sharot & Yonelinas, 2008; Sharot, Verfaellie, & Yonelinas, 2007) for emotionally arousing stimulus materials as compared to neutral ones. This means that emotional memories are usually experienced more vividly than neutral ones. Ochsner (2000) interpreted this finding from an evolutionary point of view, where it might be advantageous to reexperience negative events more detailed than positive or neutral ones. Moreover, he pointed out that the immediate personal relevance of the (picture) material might play an important role, having negative scenes containing the most survival-relevant information. Neuroimaging studies (Sharot, Delgado, & Phelps, 2004; Dolcos, LaBar, & Cabeza, 2005) have provided evidence that this enhanced feeling of remembering for emotionally arousing stimuli is dependent on activity of the amygdala and the MTL memory system and accompanied by a feeling of arousal and enhanced perceptual fluency.

An ERP study (Johansson, et al., 2004) using emotional faces selectively found the (left) parietal old/new effect, the assumed correlate of recollection-based remembering (Mecklinger, 2000; Friedman & Johnson, 2000), for negative faces as compared to positive and neutral ones that only elicited an early frontal old/new effect, the supposed reflection of familiarity-based remembering (Curran, 2000; Mecklinger, 2006). Figure

2.7.2 shows this finding at frontal and parietal electrodes separately for the three stimulus classes. This is in concert with the findings and interpretation of Ochsner (2000). However, in addition with other studies (Maratos, et al., 2000; Windmann & Kutas, 2001) ERP data have provided a less consistent picture as the fMRI data, as the latter two studies did not find different ERP old/new effects for neutral as compared to negative words. There moreover is no study that compared the recognition memory ERP correlates for emotionally arousing stimuli at two different time points of retrieval, which is thought to be an important condition to elicit memory advantages for emotional stimuli. Additionally, as with regard to consolidation, there is no clear distinction between emotionally arousing and nonarousing only valent stimuli to be found in the literature. As encoding processes are affected by this point to a great extent, it seems likely that retrieval is based on a similar differentiation.

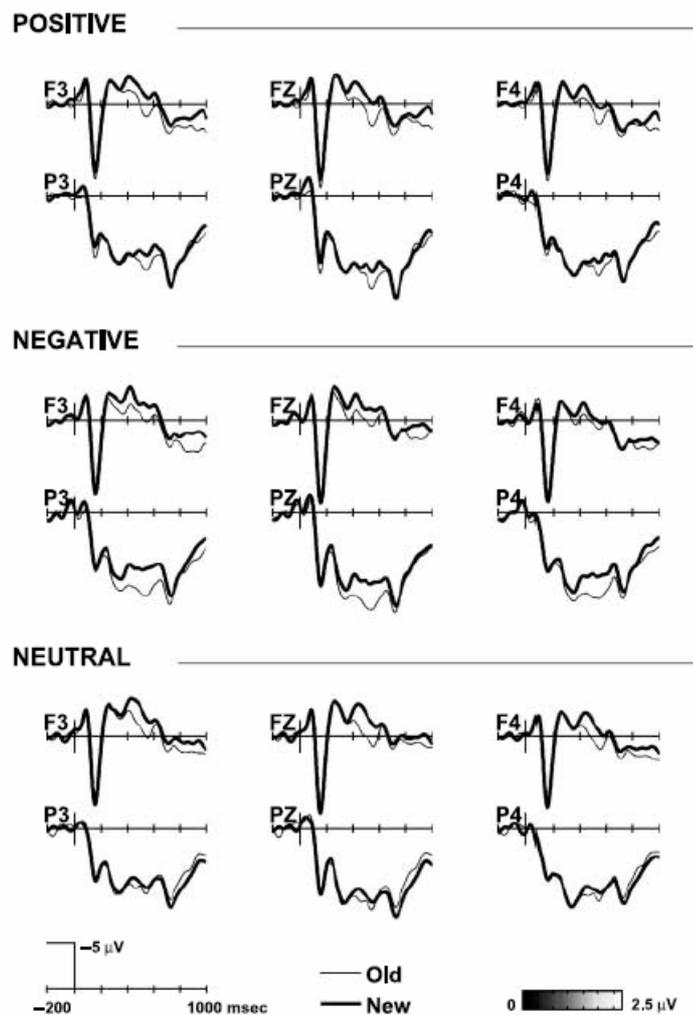


Figure 2.7.2: ERP old/new effects in the Johansson et al. (2004) study for neutral, negative and positive pictures.

A recent study on the retrieval of valent contextual information found associated enhanced effective connectivity from hippocampus to amygdala (Smith, Stephan, Rugg, & Dolan, 2006), which provides a strong proof for dynamic interactions between these regions. Importantly, there are a number of studies on emotional source memory in which neutral items are presented in either neutral or emotional contexts (Maratos & Rugg, 2001; Smith et al., 2004; Smith et al., 2006). These constitute either presenting a neutral picture in context of an emotional one, or presenting a neutral word in an emotionally valenced sentence. On the one side, these studies reliably demonstrate a positive effect of the emotional content of information on source memory, i.e. when the contexts to be retrieved are themselves emotional (Smith et al., 2006). On the other side, specific ERP effects are observed for correctly retrieved emotional contexts (Maratos & Rugg, 2001; Smith et al. 2004). The question arises if this is also true for non-emotional contextual information. In behavioral tests of source memory there are reports of enhancement and impairment effects. The former have been shown in studies in which the contexts used to test were themselves emotional (e.g. Smith et al., 2006). Source memory impairments refer to the fact that peripheral elements of a scene or other non-emotional elements of a study episode are remembered less well when they were presented together with emotionally arousing information (Kensinger, Piguet, Krendl, & Corkin, 2005; Adolphs, Tranel, & Buchanan, 2005). Thus far, all studies have tested source memory only after a short while after encoding and it remains open what happens after a long retention interval.

2.7.4 Summary

The ways in which retrieval processes are affected by emotional arousal are not well understood. Although there is the general notion of enhancement effects of memory for emotional materials, there are several points that bring doubt to the generability of this claim. First, it seems to be of special relevance to test memory after a delay, as immediate testing showed a mixed pattern of results, from enhancement to decrement effects (Sharot & Phelps, 2004). Moreover, the kind of test procedure plays an important role, as recent studies imply that the lack of memory enhancement by arousal at immediate test may be specific to cued recall and recognition tests (Richardson, Strange, & Dolan, 2004) rather than to free recall (Strange, Henson, Friston, & Dolan, 2000). In addition to this, the enhancement of recollective experience for emotionally arousing stimuli is a more robust

pattern. Nevertheless, it remains an open issue if emotional arousal enhances (Smith et al., 2006) or impairs (Kensinger et al., 2005; Adolphs et al., 2005) the binding to context features (tested in source memory tasks).

In the present thesis these issues are to be clarified to a greater extent via the use of behavioral and event-related potential measures using pictures of differing valence and arousal for two different retention durations.

3. Research Questions

Following this empirical background of the modulating effects of emotion on memory processes, many questions remain open and need further elucidation. Therefore, the focus of the upcoming four experiments is on the exact interplay of encoding, consolidation, and retrieval processes when emotional valence and arousal are considered.

More specifically, the experiments seek to find the electrophysiological correlates of encoding emotional events and to directly set them into relationship with recognition and source memory performance. If special attentional focusing mechanisms for emotional materials are set in train at a first encounter, they should be visible in their ERP correlates as compared to neutral materials. This is examined with respect to manipulations in encoding instruction (intentional vs. incidental), the amount of arousal and valence of the stimuli (neutral vs. positive vs. negative), the context features of the study episode used to test later source memory performance (study location, study time, study task), and the retention duration being immediate or 24 hours later. For this purpose, event-related potential measures are obtained for the encoding and retrieval phase of Experiments 1 and 3. These are fairly researched for emotional pictures and therefore supposed to give a deeper insight into the mechanisms that underlie the abovementioned phenomena.

In more detail, Experiment 1 investigates the ERP correlates of encoding and retrieving emotional events, i.e. negative and positive as compared to neutral pictures. Using a source memory test procedure, it is the aim to find out if recognition memory performance on an item level is enhanced for emotional as compared to neutral pictures. If so, it remains to clarify if this happens as a consequence of attentional capturing at encoding or via the engagement of controlled encoding operations. That is, I will take a look at encoding activity via the use of event-related potentials which up to now has been fairly done. Additionally, the question how emotion modulates ERP recognition memory old/new effects expressing differences in the quality of remembering remains open from the introduced studies that used words and faces as stimulus materials. Moreover, I will examine the binding mechanisms by which the emotional pictures are supposed to be bound to the neural context features study location and study time. From the current state of research it is not clear if these associations can be enhanced or if emotional arousal leads to attenuations.

Experiment 2 is then supposed to test the contribution of controlled processing to the encoding of positive and negative events while using a divided attention manipulation at encoding. This is done to prevent the engagement of controlled encoding operations and aims at resulting in the receipt of effects that can even be obtained under capacity-limited conditions. These are to be different for high and low arousing stimuli due to their assumed different ways on encoding.

Experiment 3 is concerned with disentangling the effects of valence and arousal on encoding processes and recognition memory performance like Experiment 1 did. To answer the remaining open questions experimental conditions are applied that presumably influenced the unexpected findings of Experiment 1. Specifically, retention duration is manipulated as being either immediate or 24 hour recognition to test if consolidation processes are needed to lead to memory enhancement for negative pictures. Moreover, as opposed to Experiment 1, I will use incidental encoding instructions to allow for automatic attention-driven effects. Additionally, the context feature ‘study task’ is used to test the binding of negative high and low arousing pictures to a different neutral part of the study episode. Thus, Experiment 3 tries to give some answers to the unresolved issues of Experiment 1.

Finally, in Experiment 4 the detailed investigation of the encoding phenomenon tunnel memory and attentional capturing mechanisms are on the scope. We designed a new experimental paradigm and took individual factors such as trait anxiety of the subjects into account to examine the focusing on emotionally arousing aspects of a scene while neglecting neutral ones in the periphery. If attentional mechanisms are responsible for this effect, high trait-anxious individuals should demonstrate it very clearly as these individuals are said to be especially affected in their attentional capacities.

Even detailed descriptions of the single objectives of the experiments are to be found in the corresponding section ‘Question’ inherent in the story in each of the four studies.

4. Experiments

4.1 Experiments 1A and 1B

4.1.1 Questions

In the first experiment I set out to investigate the impact of emotional content on encoding and retrieval processes in more detail, trying to link the electrophysiological correlates of those processes with memory performance. Specifically, three issues are addressed: First, it is of special interest to find out whether the posterior positivity for emotional pictures during encoding is directly associated with enhanced item memory on the one side and attenuated source memory performance on the other. More specifically, it is predicted that to the extent to which the posterior positivity reflects attentional capturing mechanisms for emotional events, it should result in facilitated encoding for positive and negative pictures relative to neutral pictures. Simultaneously, attentional capturing by emotional pictures could attenuate the binding between these pictures and the features of the context in which they are presented and lead to impaired source memory performance. Second, it is of question to what extent the ERP old/new effects in the test phase are modulated by valence and arousal of the studied material. Consistent with the findings of Johansson et al. (2004) and Ochsner (2000), a larger amount of recollection-based memories for negative as compared to positive and neutral events is predicted. This should be evident in a larger (left) parietal old/new effect, i.e. the putative ERP correlate of recollection (Friedman & Johnson, 2000; Mecklinger, 2006). Third, with regard to source memory it should be examined how the late posterior negativity (LPN) is modulated by source retrieval demands for emotional events (Johansson & Mecklinger, 2003; Herron, 2007). This component is repeatedly found in source memory tasks and has been associated with search for and retrieval of attribute conjunctions in the retrieval phase of these tasks. Two source retrieval conditions, which are frequently used in experimental and clinical studies on memory (Mayes et al, 2004) are examined: Time and location. These features constitute core elements of every experienced episode and are both derived from the external world (Simons, Gilbert, Owen, Fletcher, & Burgess, 2005), but should recruit differential posterior brain circuitries, in reconstructing of context-specific features from a study episode (Johansson & Mecklinger, 2003).

4.1.2 Methods

Participants

Twenty volunteers (10 female) between 18 and 23 years of age (mean 21 years) participated in this study. They were students at Saarland University, native German-speakers, right-handed (as assessed by the Edinburgh Handedness Inventory; Oldfield, 1971) and had normal or corrected-to-normal vision. Data of four other participants were excluded due to excessive eye-movement artefacts. All participants gave written informed consent.

Experimental material

Stimuli consisted of 480 pictures taken from the International Affective Picture System (Lang et al., 2005) which were divided into three categories: negative, neutral and positive. They all differed with regard to valence (negative: 2.97; neutral: 5.09; positive: 7.13). Positive and negative pictures were equally arousing (positive: 5.04; negative: 5.2) and more arousing than neutral pictures (3.43). An ANOVA on the valence scores yielded a significant main effect of valence [$F(2,318) = 2394.15, p < .0001$], and post hoc tests showed significant differences between the valence scores of all three categories ($p < .0001$). A second ANOVA on the arousal scores of negative, neutral, and positive pictures revealed a significant main effect of arousal [$F(2,318) = 255.14, p < .0001$], and post hoc tests showed significant differences between the arousal scores of positive and negative pictures with those of neutral pictures ($p < .0001$), but no significant differences between positive and negative pictures ($p > .05$).

Procedure

Participants took part in two sessions separated by at least three but not more than seven days. In each session they completed one of two source memory tests each consisting of a study and a test phase. Before starting the experimental session, each participant passed a practice run. Pictures used here were not used during the experimental session. Subjects were comfortably seated in a dimly lit chamber in front of a monitor at a distance of 100 cm on which they saw the pictures. In the ‘time’ session they saw two lists of 60 pictures each with a break of 7,5 min in between in which they performed a visuo-motor tracking task. During study pictures appeared in the centre of the screen for 2 s and the participant’s task was to memorize the picture plus the list in which it was presented

(before or after the break, i.e. list 1 or list 2). Additionally, the participants had to indicate via button press whether the depicted scene happened indoor or outdoor. This procedure was used to constrain the variability of possible mnemonic strategies during study and to ensure an appropriate encoding for each picture. In the test phase (administered 2,5 min later) the 120 old and 120 new pictures were presented for 500 ms each. The participants made an old/new decision. In case of an ‘old’ response a source decision (list 1 or list 2) was triggered by the appearance of three ‘?’ in the centre of the screen. After a ‘new’ response, a fixation cross appeared to initiate the next trial. The test phase of the ‘location’ session was identical to the ‘time’ session and took place at the same computer. But during study we placed participants in one of two booths. These chambers were two small rooms sized about 3 m² equipped with a desk and a comfortable chair. To rule out the possibility that time would be entirely predictive of location participants had to change between the two booths three times so that they sat in each of them twice. Booth order, source task order and response buttons were counterbalanced across subjects. For a schematic illustration see Figure 4.1.2.

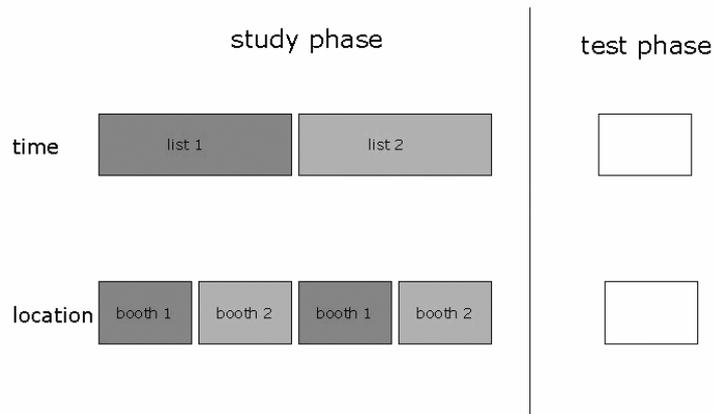


Figure 4.1.2: Schematic illustration of the study and test phases.

EEG recordings

EEG was recorded using Ag/AgCl electrodes mounted in an elastic cap from 60 scalp sites at locations of the extended 10-20 system (Sharbrough et al., 1990). The ground electrode was placed at AFz. 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. The vertical and horizontal EOG were recorded from electrodes located below and above the right eye and at the outer canthus of each eye. Electrode impedance was kept below 5 kOhms. EEG and EOG were recorded continuously with a band pass from DC to 70 Hz and were sampled at a rate of 500 Hz.

Data analysis

Data were analyzed with repeated measures analyses of variance (ANOVA) using a significance level of $\alpha = .05$. For all effects with two or more degrees of freedom in the numerator, I adjusted for violations of sphericity which are inherent in analyses of variances (ANOVAs) according to the formula by Greenhouse and Geisser (1959) when appropriate.

Behavioral data

The data analysis was based on reaction time measures (RT) for all correct responses, i.e. item hits and correct rejections. Item hits were defined as correct 'old' responses at test to pictures already presented during study, irrespective of the correctness of the subsequent source judgment. Correct rejections were defined as correct responses to new items presented at test for the first time. Recognition accuracy was estimated by means of Pr values (Snodgrass & Corwin, 1988). Pr is a measure that estimates the degree of true memory judgments by subtracting the false alarm rate, as an estimate of guessing, from the hit rate. Therefore, a Pr value of 1 indicates perfect recognition performance, whereas a Pr value of 0 indicates chance performance.

For the second (source memory) response accuracy was calculated by dividing the probability of a correct source judgment by the probability of a correct 'old' response [$p(\text{correct source})/p(\text{correct source} + \text{incorrect source})$].

ERP data

ERPs were computed separately for each subject at all recording sites with epochs extending from 200 ms before stimulus onset until 1000 (study phase) or 2000 ms (test phase) thereafter. The 200 ms before stimulus onset served as a baseline. EEG trials with artefacts (criterion: ± 40 mV) were rejected. Eye blink artefacts were corrected using a linear regression approach (Gratton, Coles, & Donchin, 1983) implemented in the EEProbe software package (A.N.T. Software BV).

For statistical analysis, a hypothesis-driven approach was chosen. On the basis of prior studies, for the evaluation of the posterior positivity and other emotion-specific effects in the encoding phase, I employed the mean amplitudes in three different time windows that were derived by visual inspection of the grand-average waveforms: 250 to 450 ms, 450 to 650 ms and 650 to 850 ms. The mean amplitudes in the 250 to 450 ms time interval will be referred to as posterior positivity in the following. For the quantification of the ERP old/new effects in the test phases, the mean amplitudes in two different time windows were used. Based on visual inspection of the grand average waveforms and consistent with prior studies (reviewed in Friedman & Johnson, 2000 and Mecklinger, 2006), the early frontal old/new effect was examined in a time window between 350 and 500 ms, whereas the parietal old/new effect was defined between 500 and 650 ms. This analysis aimed primarily at tapping the old/new effects related to familiarity and recollection, respectively. Consistent with prior studies (Friedman et al., 2005; Cycowicz & Friedman, 2003; Leynes & Bink, 2002), the LPN was examined in a late time window between 1000 and 2000 ms. For the statistical evaluation of the study and test phase ERPs I employed twelve electrode sites in the overall ANOVA: left anterior-frontal (AF3), middle anterior-frontal (FZ), right anterior-frontal (AF4), left fronto-central (FC3), middle fronto-central (FCZ), right fronto-central (FC4), left centro-parietal (CP3), middle centro-parietal (CPZ), right centro-parietal (CP4), left parieto-occipital (PO3), middle parieto-occipital (POZ), and right parieto-occipital (PO4). The LPN was examined at more electrode sites to allow a more sensitive analysis of possible topographical differences: AF3, AF4, FZ, FC3, FCZ, FC4, C3, CZ, C4, CP3, CPZ, CP4, P3, PZ, P4, PO3, POZ, PO4, O1, OZ, O2. In order to test whether the topography of the LPNs for the two source retrieval conditions differed, the ANOVAs were conducted on the rescaled difference waveforms (source hits minus correct rejections) such that amplitude differences between the two contrasted conditions were removed (McCarthy & Wood, 1997).

For the study phase, the overall repeated-measures ANOVA included the following factors: EMOTION (negative, neutral, positive), TASK (source task time, source task location), LATERALITY (left, middle, right), ANTPOS (anterior-frontal, fronto-central, centro-parietal, parieto-occipital) and WINDOW (250-450 ms, 450-650 ms, 650-850 ms). In the case of significant main effects and interactions involving the factors EMOTION or TASK, subsidiary one-way ANOVAs and planned pairwise comparisons were performed to examine the effects in more detail.

For the quantification of the old/new effects for the test phase, two repeated-measure ANOVAs (factors: EMOTION, TASK, LATERALITY, ANTPOS) were performed for each of the two time windows with the additional factor RESPONSE TYPE (hit, correct rejection). Again, in the case of significant main effects and interactions involving any of these factors, subsidiary one-way ANOVAs and planned pairwise comparisons were performed to examine the effects in more detail. For the calculation of the LPN, the ANOVA involved the factors EMOTION (negative, neutral, positive), SOURCE TYPE (source hit, correct rejection), TASK (source task time, source task location), LATERALITY (left, middle, right) and ANTPOS (frontal, fronto-central, central, centro-parietal, parietal, parieto-occipital, occipital).

4.1.3 Results

4.1.3.1 Behavioral data

An overview of item, source memory performance and reaction time data is given in Figure X and Table 4.1.3.

The ANOVA performed on the Pr values for the two source tasks (time, location) and the three emotional conditions (positive, negative, neutral) revealed a significant main effect of EMOTION [$F(2,38) = 5.33, p = .009$], suggesting that the emotional status of the pictures influenced participant's ability to accurately discriminate between old and new stimuli. The subsidiary one-way ANOVAs and planned pairwise comparisons showed that this effect was attributable to the fact that positive pictures were better remembered than both neutral [$F(1,19) = 9.70, p = .006$] and negative pictures [$F(1,19) = 7.24, p = .0145$].

The analysis of response bias measures (Br) revealed no significant effect involving the factors EMOTION and TASK.

The ANOVA on the reaction-time measures for hits and correct rejections gave rise to a main effect of RESPONSE TYPE [$F(1,19) = 32.95, p < .001$], confirming that correct rejections were faster than hits. There also was a main effect of EMOTION [$F(2,38) = 13.52, p < .001$]. Decomposition of this effect revealed that, irrespective of response type, responses to neutral [$F(1,19) = 40.43, p < .0001$] and positive items [$F(1,19) = 7.96, p = .011$] were given faster than to negative items.

source task	Pr			source performance		
	negative	neutral	positive	negative	neutral	positive
time	0.67 (.04)	0.65 (.04)	0.71 (.03)	0.60 (.03)	0.60 (.03)	0.63 (.03)
location	0.60 (.04)	0.65 (.04)	0.69 (.04)	0.57 (.03)	0.55 (.02)	0.57 (.02)

source task	hit			correct rejection		
	negative	neutral	positive	negative	neutral	positive
time	978 (34)	948 (34)	962 (41)	884 (26)	846 (25)	861 (25)
location	1044 (44)	978 (34)	985 (40)	908 (30)	864 (28)	895 (28)

Standard errors of the mean (SEM) are given in parenthesis.

Table 4.1.3: Pr, source performance data and reaction times for the test phases separately for negative, neutral, and positive pictures. Reaction times are displayed in milliseconds.

For source memory performance an ANOVA with the factors TASK and EMOTION revealed a marginally significant effect for TASK [$F(1,19) = 3.03, p = .098$], suggesting that performance tended to be better in the ‘time’ task than in the ‘location’ task. The emotional status of an item did not seem to modulate source memory performance which was also well above chance level (i.e. $> .50, p\text{-values} < .05$) in both tasks. ¹In light of the tentatively higher source memory performance in the time task, it could be argued that source discrimination in the time task may have been facilitated especially for those items presented at the extremes of time, i.e. at the beginning of the first and the end of the second list. To examine this, I compared source memory performance for high separated items (the first 20 trials of list 1 plus the last 20 trials of list 2) and low separated items (last 20 items of list 1 plus the first 20 items of list 2). Source memory performance was .62 and

.59, for the high and low separated items, with this difference not being significant, $p > .05$. On the basis of this post hoc analysis I feel save to conclude that source discrimination was not selectively facilitated for highly distant items.

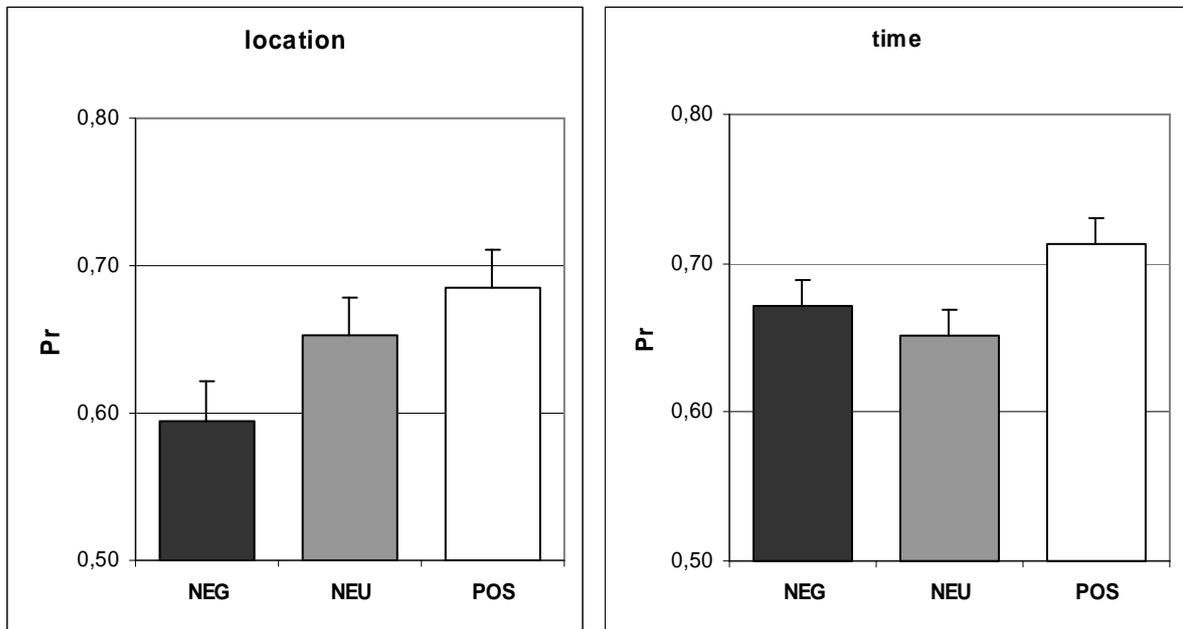


Figure 4.1.3: Pr results in the location and time task for negative, neutral, and positive pictures.

4.1.3.2 ERP data

Encoding phase

The grand average ERP data of the encoding phase, separately for the two source tasks and the three emotion conditions, are depicted in Figure 4.1.4. The overall morphology of the waveforms was similar for positive, negative and neutral pictures in both the time and location task and was characterized by a N300-P300-SW complex. More specific examination of the grand average ERPs reveals three distinct effects:

The first effect starts at around 250 ms post-stimulus onset at frontal sites and lasts until the end of the recording epoch (1000 ms). In this interval, the ERPs were more positive-going for positive as compared to negative and neutral pictures at anterior-frontal and fronto-central recording sites in both source tasks, albeit smaller in the time than in the location task.

The second effect is manifested in more positive-going waveforms for positive and negative pictures as compared to neutral ones in the location condition at parieto-occipital

sites in an early time window (lasting from 250 to 450 ms) which is consistent with our previous definition of the posterior positivity.

The third effect is characterized by a posteriorly distributed positive slow-wave that was only obtained for positive pictures in the location task, starting at around 450 ms and lasting until the end of the epoch.

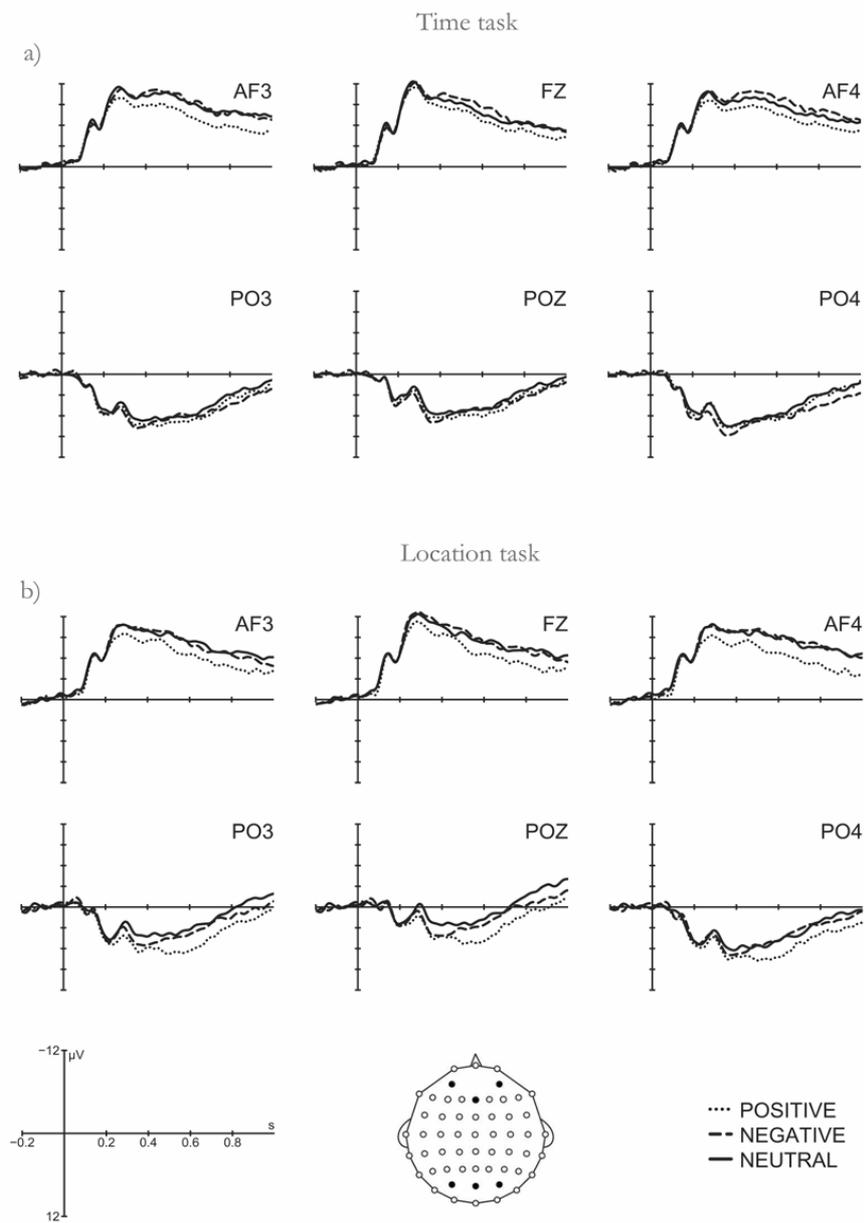


Figure 4.1.4: Encoding ERPs for the time (a) and location task (b) elicited by positive, negative, and neutral pictures at anterior and posterior electrodes.

Table 4.1.4 shows the results of the initial ANOVAs performed for the encoding phase. Significant main effects for the factors EMOTION, LATERALITY, and WINDOW were obtained. Additionally, two interactions emerged: EMOTION by ANTPOS, and EMOTION by WINDOW. For the first interaction, subsidiary ANOVAs and planned pairwise comparisons revealed that a main effect of EMOTION was present at anterior-frontal [$F(2,38) = 14.61, p < .0001$] and fronto-central sites [$F(2,38) = 13.28, p < .0001$]. It reflects significant differences between the waveforms elicited by positive and neutral ($p < .05$) and positive and negative pictures ($p < .05$), with no differences between negative and neutral pictures ($p > .05$). Investigation of posterior sites revealed an EMOTION by WIN [$F(2,38) = 9.49, p = .0005$] and an EMOTION by TASK [$F(2,38) = 3.61, p = .039$] interaction. Decomposition of these effects showed that in the time window of the posterior positivity as well as in the two other time windows, there was a main effect of EMOTION in the location task ($p < .05$), but not in the time task ($p > .05$). Further analyses of the EMOTION effect in the location task revealed that in the time window of the posterior positivity, the waveforms elicited by positive and negative pictures were more positive-going than those to neutral pictures ($p < .05$). In the middle and late time window I found that in the location task positive pictures gave rise to more positive-going waveforms than both negative and neutral pictures (with no difference between the two) ($p < .05$). Contrasting the two task versions revealed that in all of the three time windows, waveforms for positive pictures were comparable in the location and time task ($p > .05$), whereas those of neutral and negative pictures were more positive-going in the time task than in the location task ($p < .05$).

Effect	df	F	p
EMOTION	2,38	10.85	.0004
LATERALITY	2,38	6.22	.0046
ANTPOS	3,57	78.69	<.0001
WINDOW	2,38	22.04	<.0001
EMOTION X ANTPOS	6,114	3.05	.036
EMOTION X WIN	4,76	3.56	.019

Standard errors of the mean (SEM) are given in parenthesis.

Table 4.1.4: ANOVA results for the study phase.

Retrieval phase

Grand averages for correct responses to old and new pictures in all three emotion conditions for the ‘time’ and ‘location’ task are displayed in Figure 4.1.5. As expected, correctly recognized old pictures elicited more positive-going ERPs than correctly rejected new pictures. This old/new effect starts at around 250 ms post-stimulus and lasts until 700 ms at posterior electrodes. Remarkably, these effects appear to vary as a function of emotional condition, time, and task with neutral and positive pictures showing an early frontal and a late parietal old/new effect irrespective of task and negative pictures eliciting only a frontal old/new effect in the location task while showing the same effects as neutral and positive pictures in the time task.

Table 4.1.5 shows the results of the initial ANOVAs performed for each time window.

Time window and Effect	df	F	p
350-500 ms			
EMOTION	2,38	14.81	<.0001
RESPONSE TYPE	1,19	31.09	<.0001
LATERALITY	2,38	4.56	0.018
ANTPOS	3,57	66.12	<.0001
EMOTION X ANTPOS	6,114	14.54	<.0001
RESP TYPE X ANTPOS	3,57	33.42	<.0001
500-650 ms			
EMOTION	2,38	14.36	<.0001
RESPONSE TYPE	1,19	81.36	<.0001
ANTPOS	3,57	40.33	<.0001
EMOTION X TASK	2,38	3.31	.059
EMOTION X ANTPOS	6,114	3.64	.019
RESP TYPE X ANTPOS	3,57	14.24	<.0001
1000-2000 ms			
SOURCE TYPE	1,19	46.21	<.0001

Standard errors of the mean (SEM) are given in parenthesis.

Table 4.1.5: ANOVA results for the test phase.

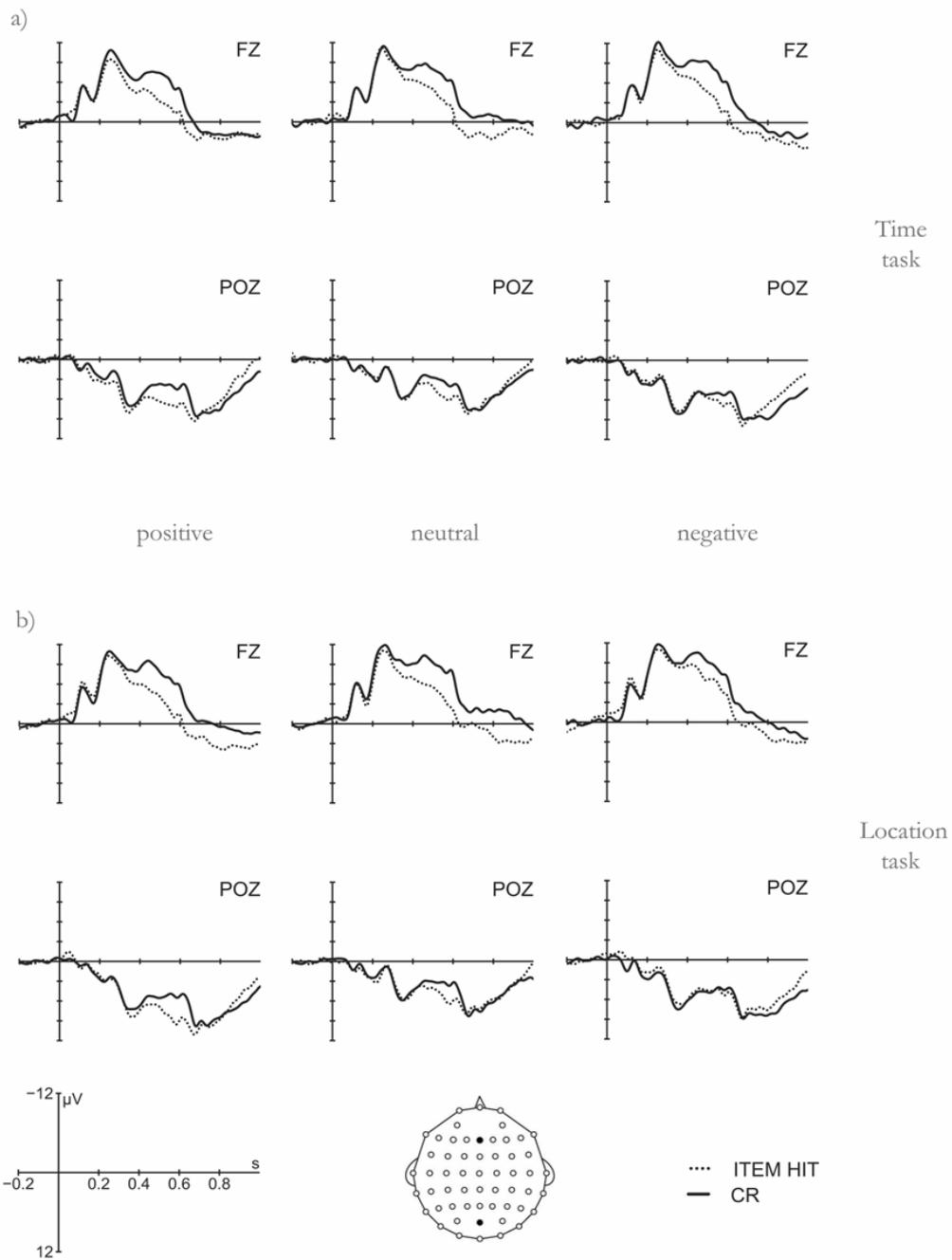


Figure 4.1.5: Retrieval ERPs for the time (a) and location (b) task for positive, neutral, and negative pictures at a fronto-central and middle parieto-occipital electrode.

Analyses performed on the early time window (350 to 500 ms) revealed main effects of EMOTION, RESPONSE TYPE, LATERALITY and ANTPOS. Additionally, two interactions emerged: EMOTION by ANTPOS and RESPONSE TYPE by ANTPOS. For the first interaction, subsidiary ANOVAs revealed main effects of EMOTION at all levels

of the ANTPOS factor ($p < .05$) and of RESPONSE TYPE ($p < .05$) at all sites besides parieto-occipital. In this early time window old/new effects seem to be prominent at anterior-frontal, fronto-central and centro-parietal electrodes for all of the emotion conditions in both source tasks.

For the late time window (500 to 650 ms) the following main effects were obtained: EMOTION, RESPONSE TYPE and ANTPOS. Here, additional interactions involved the factors EMOTION by TASK, EMOTION by ANTPOS and RESPONSE TYPE by ANTPOS. On the basis of these interactions three-way ANOVAs (EMOTION, TASK, and RESPONSE TYPE) were performed for each level of the ANTPOS factor. At parieto-occipital electrodes, I found interactions of the factors EMOTION by TASK [$F(2,38) = 4,56, p = .025$] and EMOTION by RESPONSE TYPE [$F(2,38) = 3.32, p = .053$]. Decomposition of these interactions confirmed the visual impression that the late old/new effect was present for all emotional conditions in the time task ($p < .05$), whereas in the location task it was present for neutral and positive ($p < .05$) but not for negative events ($p > .05$).

Visual inspection of Figure 4.1.6 showing the ERPs in the test phase for a duration of 2000 ms reveals a large and posteriorly distributed LPN for source hits as compared to correct rejections in a time window from 1000 until 2000 ms in both tasks. This topographical distribution is well in agreement with earlier source memory studies (e.g. Johansson & Mecklinger, 2003; Friedman et al., 2005; Cycowicz & Friedman, 2003; Leynes & Bink, 2002) and ANOVAs performed on this effect reveal a highly significant main effect of SOURCE TYPE (source hits vs. correct rejections, Table 3). The LPN was not modulated by emotional context as none of the analysed factors revealed an interaction with the factor EMOTION.

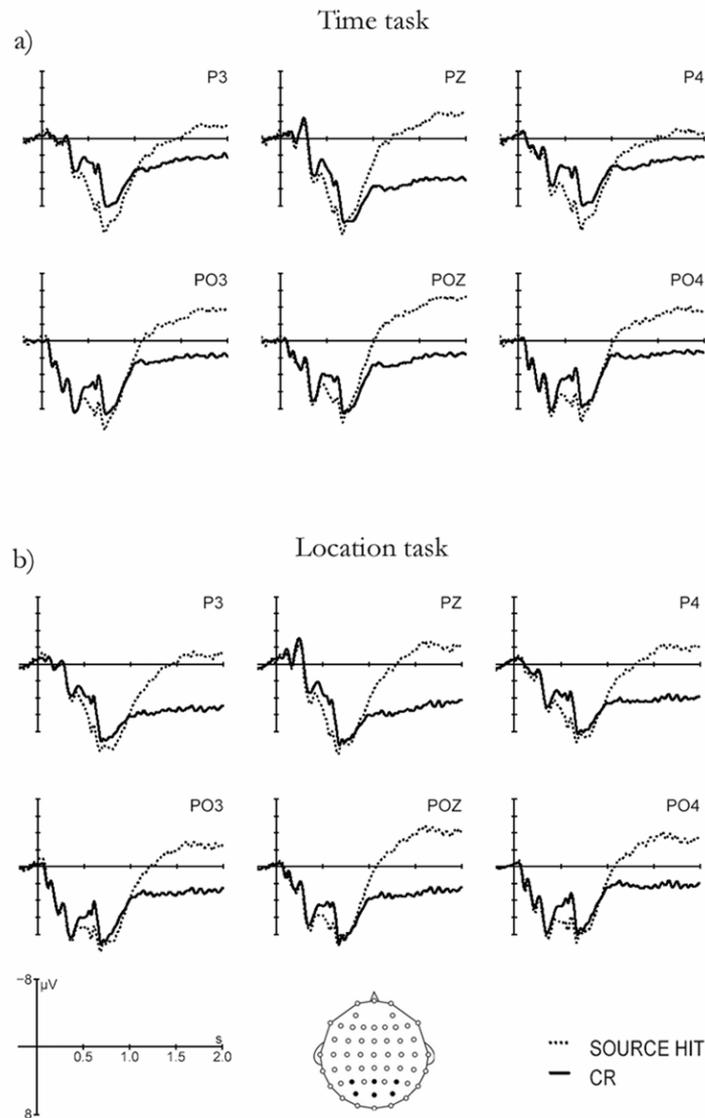


Figure 4.1.6: Retrieval ERPs for source hits compared to correct rejections in the time (a) and location (b) task at posterior electrodes.

Figure 4.1.7 depicts the topographic maps showing the distribution of the LPN for the time and location task in a time window from 1000 to 2000 ms. As can be seen in the figure, the distribution of the LPN is more fronto-centrally accentuated in the time task than in the location task, although the maxima of both effects seem to be at parieto-occipital sites. This observation is confirmed by a post-hoc ANOVA on the difference waveforms (source hits minus correct rejections) collapsed across the emotion factor with the factors TASK (time vs. location), ANTPOS (7 levels) and LATERALITY (left, middle, right) with amplitude normalized data (McCarthy & Wood, 1997). This analysis

revealed an interaction TASK by ANTPOS [$F(6,114) = 3.17, p = .03$], supporting the view that the LPN in both tasks was generated by different underlying neural circuits.

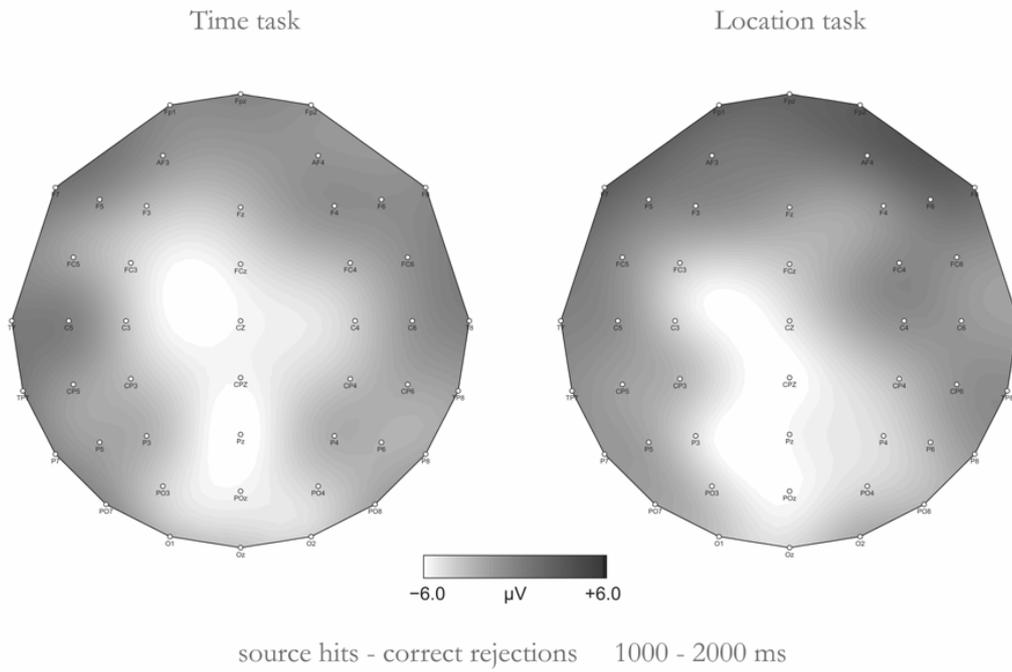


Figure 4.1.7: Topographical distribution of the LPN for the source tasks time and location separately.

4.1.4 Experiment 1C: Post-hoc rating study

Given the unexpected findings of no memory enhancement for negative pictures relative to neutral ones, in a first step, it was examined whether the valence and arousal induction via the IAPS stimulus materials influenced the group of participants of students at Saarland University in the intended way. Even though the arousal levels of positive and negative pictures were equated pre-experimentally by means of the IAPS ratings, on the basis of the present results it cannot be excluded that the individual arousal levels of our group of subjects were higher for positive than negative pictures.

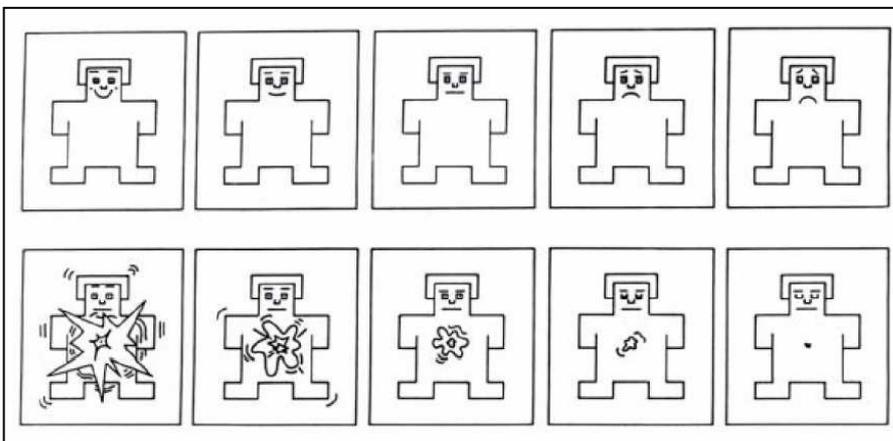


Figure 4.1.8: The self assessment manikins (SAM) used for the valence (top) and arousal (bottom) rating according to Lang et al., 2006.

The 20 subjects were reinvited to rate the 480 pictures used in the experiment using the SAM-procedure (Lang et al., 2005). In contrast to the IAPS ratings, the arousal ratings for negative and positive pictures differed in the way that positive pictures were far less arousing than negative pictures (3,23 vs. 5,73). In fact, positive pictures were only marginally significantly different from neutral pictures in their arousal ratings (3,23 vs. 2,56). This was confirmed by an ANOVA which indicated arousal differences between positive and negative ($p < .05$), negative and neutral ($p < .05$), and only a marginally significant difference between positive and neutral pictures ($p < .10$). In contrast to the arousal ratings, the valence ratings of our group of subjects were analogue to the one from the IAPS. This means that the effects of the present study may be attributable to differences in the amount of arousal experienced for positive and negative stimulus materials.

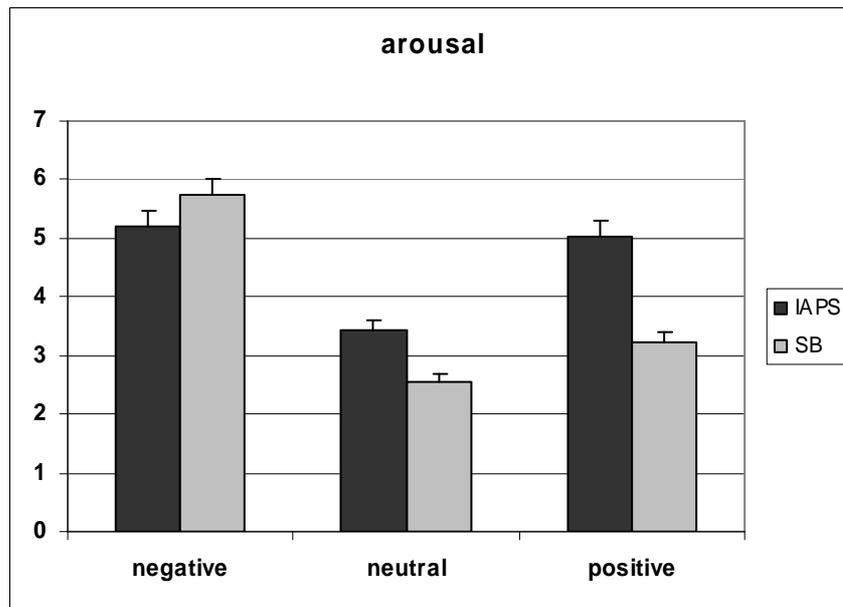


Figure 4.1.9: Results of the arousal rating from the group of subjects at Saarland University as compared to the normative rating of the IAPS.

4.1.5 Discussion

The electrophysiological correlates of encoding and retrieving emotional pictures and context features of the study episode were examined in this first experiment. Specifically, three issues were addressed: First, it was explored to which extent the posterior positivity for emotional pictures during encoding is associated with item memory and source memory performance. On the assumption that it reflects attentional capturing by emotional events, it was tested whether the posterior positivity at encoding is associated with enhanced item memory for emotional events on the one side, and attenuated source memory for neutral context features on the other side. Second, it was of high interest to what extent the old/new effects in the test phase of the recognition task are modulated by valence and arousal of the studied materials. Are the putative ERP correlates of familiarity and recollection differentially influenced by the emotional status of an item? Third, it was examined if the LPN is modulated by different source retrieval demands for emotional events.

The emotional status of the pictures affected recognition memory performance with better memory performance for positive pictures than neutral or negative ones. Unexpectedly, the predicted pattern of results of the posterior positivity being associated with enhanced item memory and attenuated source memory was not obtained. Rather, the posterior positivity was found in the 250 to 450 ms time interval for positive and negative pictures in the location task, whereas no such modulations were obtained in the time task. The finding that memory performance was enhanced for positive as compared to negative events irrespective of task, whereas the posterior positivity was obtained for positive and negative events in the location task only, is inconsistent with the attentional capturing view of the posterior positivity. A more direct correspondence between emotion-induced ERP effects at study and item recognition memory performance was obtained for the ERP effects in the middle and late time intervals (i.e. from 450 to 850 ms). At anterior recording sites, positive slow wave activity was obtained for positive stimuli in both tasks for which enhanced memory performance was obtained. A similar pattern was found at posterior recording sites, at which the better remembered positive events were associated with enhanced encoding related ERP positivities.

An additional albeit less direct link between emotion-induced ERP modulations at study and recognition memory performance can be derived from the analysis of the ERP old/new effects. While a parietal old/new effect was present for all positive and neutral

pictures irrespective of source task, no such ERP old/new effect was found for negative events in the location task, for which positive slow wave activity between 450 and 850 ms at anterior and posterior recording sites was significantly reduced (i.e. not present) in the encoding phase. It is generally assumed that the magnitude of the parietal old/new effect is associated with the amount of information of a study episode being retrieved on the basis of recollection (e.g. Wilding & Herron, 2006). However, in the present study subjects showed lower hit rates to negative pictures than to positive pictures in the location task (.67 and .75, respectively, $p < .05$). Also, the proportion of guess responses (estimated from the false alarm rates (Snodgrass & Corwin, 1988), which were .08 for negative pictures and .05 for neutral pictures ($p < .05$)) was presumably larger for negative than for neutral events. This suggests that the attenuated parietal old/new effect for negative pictures more likely reflects the smaller amount of negatively valenced items retrieved on the basis of recollection.

With respect to the third issue addressed in the current study, the ERP correlates of source retrieval requirements for emotional events, pronounced late posterior negative slow wave activity (i.e. the LPN) for correctly retrieved item-source associations was obtained in both tasks. While the amplitude of the LPN was not affected by source type or emotional status of the pictures, the LPN in the time task was more fronto-centrally distributed than in the location task. This suggests that even though performance differences in source memory were only marginally significant, a difference in underlying brain activity for the retrieval of item-context associations in the late phase of the retrieval phase could be observed.

Given the unexpected findings of no memory enhancement for negative pictures relative to neutral ones, in a first step, it was examined whether the valence and arousal induction via the IAPS stimulus materials influenced our group of participants in the intended way. Even though the arousal levels of positive and negative pictures were equated pre-experimentally by means of the IAPS ratings, for the group of subjects at Saarland University the arousal ratings for negative and positive pictures differed in the way that positive pictures were far less arousing than negative pictures (3.23 vs. 5.73). In fact, positive pictures were only marginally significantly different from neutral pictures in their arousal ratings (3.23 vs. 2.56). In contrast to the arousal ratings, the valence ratings of the group of students at Saarland University were analogue to the one from the IAPS. This means that the effects of the present study may be attributable to differences in the amount of arousal experienced for positive and negative stimulus materials.

A hint towards an interpretation of the present results in light of these valence and arousal ratings is given by a recent study by Kensinger & Corkin (2004). Using fMRI and behavioral measures, they found that distinct neurocognitive processes contribute to memory for highly arousing versus only mildly arousing emotion words. An amygdala-hippocampus network was active during the encoding of highly arousing words, whereas a prefrontal-hippocampal circuitry was engaged in the encoding of non-arousing words. This is in agreement with the interpretation of Dolcos & Cabeza's (2002) ERP results of an amygdala (related to arousal) and a prefrontal-hippocampus network (related to valence), and lends further support to a dissociation of valence- and arousal-related brain systems. An additional behavioral study by Kensinger & Corkin revealed that memory for highly arousing words was still enhanced even when a divided attention manipulation was used at study, whereas memory for low arousing words declined when encoding resources were devoted towards a secondary task. It is argued that memory enhancement for valenced but non-arousing materials relies on controlled and self-generated encoding processes such as elaboration and rehearsal whereas memory enhancement for arousing words occurs automatically. On an electrophysiological level, this is confirmed by the anterior positivity that was obtained for positive pictures irrespective of task, and only a late posterior positivity for positive pictures in the location task. Even though inferences from the scalp topography of ERP effects on underlying neural generators in most cases are problematic and comparisons can only be speculative, the anterior scalp distribution and the sustained nature of the anterior positive slow wave to positive pictures resembles the inferior PFC activity to low arousing emotion words in the Kensinger & Corkin (2004) study and may reflect enhanced PFC activation devoted to the encoding of positive and low arousing emotional stimulus materials. The high relevance of the PFC in situations in which the retrieval of emotional information is task relevant was recently also demonstrated in a study examining the effective connectivity between brain regions relevant for processing mnemonic and emotional information (Smith et al., 2006). In a condition in which emotional contexts of a study phase had to be discriminated, the authors found enhanced effective bidirectional connectivity between hippocampus and amygdala and enhanced activity in the orbitofrontal cortex which in turn increased the hippocampus-amygdala connectivity. This suggests that the requirement to retrieve emotional information constitutes a cognitive set that modulates retrieval in a top-down manner. An interesting issue to be pursued in further studies would be to examine whether the retrieval of high and low arousing emotional events is mediated by different cognitive sets and brain circuitries.

Negative and highly arousing pictures evoked a similar posterior positivity as positive pictures in the location task in an early, 250 to 450 ms time interval, suggesting that the initial attentional capturing mechanisms were highly similar for both classes of stimuli. However, while positive stimuli were subjected to elaborate encoding processes as revealed by sustained positive slow wave activity and enhanced recognition memory performance for these stimuli, negative pictures apparently did not enter this processing stage.

To further test the idea of controlled and top-down driven encoding processes for positive and low arousing pictures, I conducted a subsequent memory analysis (for a review see Paller & Wagner, 2002). In such an analysis, the ERPs at encoding are sorted according to memory performance at test (remembered vs. forgotten). There is some consensus that parts of ERP subsequent memory effects reflect top-down driven processing like attentional orienting towards events or elaborated mnemonic strategies in support of episodic encoding (Paller & Wagner, 2002; Mecklinger & Müller, 1996). If controlled and top-down modulated encoding strategies were engaged and are reflected in the anterior slow wave, then this component should be sensitive to the later memory status. To test this assumption, I sorted the trials according to their later memory status being either ‘remembered’ (hits at retrieval) or ‘forgotten’ (misses at retrieval). As *Pr* values were not significantly different between source tasks, the ERPs of both source tasks were collapsed for this analysis. It was found that the anterior positive slow wave (450 to 850 ms) was larger for later remembered positive pictures as compared to later forgotten ones, whereas the posterior positivity (250 to 450 ms) was not modulated by subsequent memory performance (see Figure 4.1.10). The anterior positivity elicited by positive pictures was tested in a repeated-measures ANOVA with the factor MEMORY STATUS (remembered, forgotten) in the 450-850 ms time window at FZ and revealed a significant main effect of MEMORY STATUS [$F(1,19) = 3.56, p < .05$]. The posterior positivity was tested in a repeated-measures design with the factor MEMORY STATUS (remembered, forgotten) in the 250-450 ms time window at POZ and revealed no significant result [$F(1,19) = 0.14, p > .71$].

This selective modulation of the anterior positive slow wave by subsequent memory performance confirms the view that it reflects top-down driven encoding processes for positive and low arousing events. In contrast, the posterior positivity may reflect the automatic bottom-up-driven attentional capturing of valent stimuli.

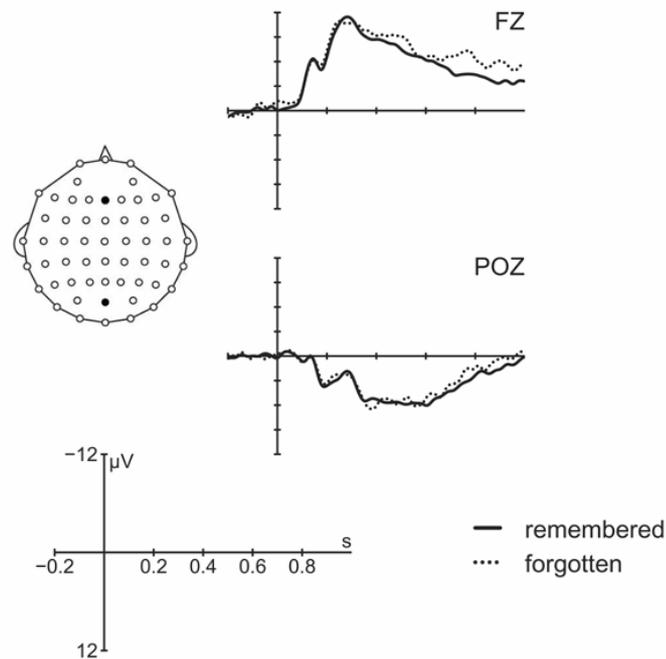


Figure 4.1.10: Dm effects for positive pictures at a fronto-central and middle parieto-occipital electrode.

The finding that no memory enhancement was obtained for negative stimuli, even though they were rated as highly arousing in the IAPS and the post-experimental rating studies, could also be accounted for by the characteristics of the memory task used in the present study. There is increasing evidence for the view that memory enhancement for highly arousing stimuli is especially pronounced in memory tests with a longer retention interval (LaBar & Phelps, 1998; Sharot & Phelps, 2004). As consolidation of memory occurs over a period of time, and in case of emotional materials involves noradrenergic mechanisms (McGaugh, 2006), the effect of arousal on memory consolidation will be apparent only following a delay. The exact duration of this consolidation process is uncertain, but behavioral effects may be evident as soon as 1 hour after encoding (LaBar & Phelps, 1998) and are expected to be visible at least 24 hours later (Sharot & Phelps, 2004). The combined item and source memory requirements in our study did not allow longer retention intervals than 2 to 3 minutes and by this may have wiped out arousal related memory enhancements.

Additionally, prior studies showed that encoding instructions can be a critical variable for the occurrence of memory enhancements and impairments for emotional materials. In support of this view is a recent study by Kensinger et al. (2005), which revealed that under incidental encoding instructions, where subjects are unaware that their memory will be

tested subsequently, young adults show good memory for arousing central elements of a scene and poor memory for non-arousing peripheral elements. This memory trade-off disappears under intentional encoding instructions, where young adults show same memories for peripheral features of emotional and neutral scenes. In light of these findings, the result that no impairments of source memory for emotional materials was found in the present study could be accounted for by controlled encoding strategies, set in train by the intentional encoding instructions. Subjects may have associated the emotional stimuli with the features of the source task (where and when was a particular event encountered) and this may have overwritten the attentional capturing effects for emotional events and detrimental effects on source memory performance. The finding of slow wave activity at frontal sites for positive material only, being related to subsequent memory performance, is consistent with this view.

The observation that the presentation of negative pictures initiated a similar early posterior positivity as the presentation of positive pictures may suggest that similar attentional capturing mechanisms were initiated during the encoding of both classes of stimuli. As no memory enhancement was obtained for negative pictures, it is conceivable that negative events due to their high arousing characteristics may have initiated the retrieval of autobiographic memories or personal experiences of task-irrelevant events (e.g. the last personal encounter with a given object) and by this were subjected to controlled encoding operations to a lower extent than positive and neutral events. This phenomenon could reflect the higher biological relevance of negative stimuli which in an evolutionary sense may guarantee that biologically relevant events are not ignored or taken as irrelevant. The fact that an attenuated parietal old/new effect was observed for negative pictures is consistent with such a memory distraction function of highly arousing events. This distraction function of highly arousing events observed in the present study may just be another instance of the automatic capture of attention by emotional events as for example observed in form of interference effects of emotionally valenced words in the emotional stroop paradigm (Pratto & John, 1991). The absence of a parietal old/new effect for negative events could also be due to an enhanced positivity to correct rejections that presumably elicited spurious or 'illusory' episodic memories (Maratos et al., 2000) and by this were indistinguishable from the hits.

There are a number of studies on emotional source memory in which neutral items are presented in either neutral or emotional contexts (Maratos & Rugg, 2001; Smith et al., 2004, Smith et al., 2006). On the one side, these studies reliably demonstrate a positive

effect of the emotional content of information on source memory, i.e. when the contexts to be retrieved are themselves emotional (Smith et al., 2006). On the other side, specific ERP effects are observed for correctly retrieved emotional contexts (Maratos & Rugg, 2001; Smith et al. 2004). As these studies consistently used neutral items (presented in either emotional or non-emotional contexts) and the present study employed emotional items in neutral context, the aforementioned studies and the present study differ in important aspects. By this the latter findings do not speak against the present interpretation of an attentional capturing function of negative and highly arousing events. Rather, the findings of both experimental approaches suggest, that depending on task characteristics and retrieval demands, the emotional content of information exerts differential mnemonic effects. It is conceivable that attentional capturing more likely occurs for high levels of arousal and the high salience and high arousal level of the negatively valenced pictures in the present study may have enhanced the attentional narrowing and mnemonic distortion effects of these stimuli.

A final issue addressed in the present study was the extent to which the LPN, a posteriorly distributed negative slow wave frequently obtained in the test phases of source memory tasks, is modulated by source retrieval requirements in case of emotional events. Former studies have shown that the LPN has a parieto-occipital maximum, onsets at around the time at which a response is given, and is of equal amplitude for correct and incorrect source judgments (Johansson & Mecklinger, 2003; Friedman et al., 2005; Herron, 2007). It was proposed that the LPN reflects the search for and retrieval of contextual features in tests of source memory, and retrieval processes that may act to reconstruct a prior study episode when item-context features are not sufficiently recovered or need continuous evaluation. Consistent with prior studies, the present study revealed a pronounced LPN in both source tasks, underlining the high relevance of this component in the search/retrieval of attribute conjunctions. Interestingly, even though LPN amplitude was not affected by the emotional contents to be associated with either time or location characteristics of the study episode, it differed in scalp topography between the two source memory tests. Retrieving/searching conjunctions between pictures and study time elicited a more widespread LPN than between pictures and their study location, suggesting that a wider range of contextual attributes are relevant for reconstructing the point of time when an item occurred as compared to where it occurred. However, it cannot be excluded that deeper brain circuitries were activated during time discrimination and that this may have contributed to the more wide spread scalp topography in the time task. Notably, as recently

pointed out by Urbach and Kutas (2006), inferences drawn from topographical differences of ERP effects on underlying brain generators in some cases (e.g. differences in pre-stimulus baseline potentials) have to be made with caution.

In conclusion, the present study sheds new light on the issue of how encoding mechanisms for emotional events affect subsequent item and source memory performance. Negative and positive events elicit a posterior positivity between 250 and 450 ms that presumably reflects attentional capturing of emotionally valenced stimuli. Positive events gave rise to additional anterior and posterior slow wave activity as compared to neutral and negative events and also showed enhanced recognition memory. In light of a post-experimental rating study that revealed that positive events in the present study were perceived as less arousing than negative events, I take the latter results to suggest that positive and low arousing events enter controlled and elaborated encoding processes which are beneficial for recognition memory performance. The high arousal of negative events however, may interfere with controlled encoding mechanisms and attenuate item recognition and the quality of remembering. Finally, topographically distinct LPNs were obtained in both source tasks, suggesting that this component reflects processes in service of reconstructing the study episode by binding together contextual details with an item, and these mechanisms vary with the kind of episodic detail to be retrieved.

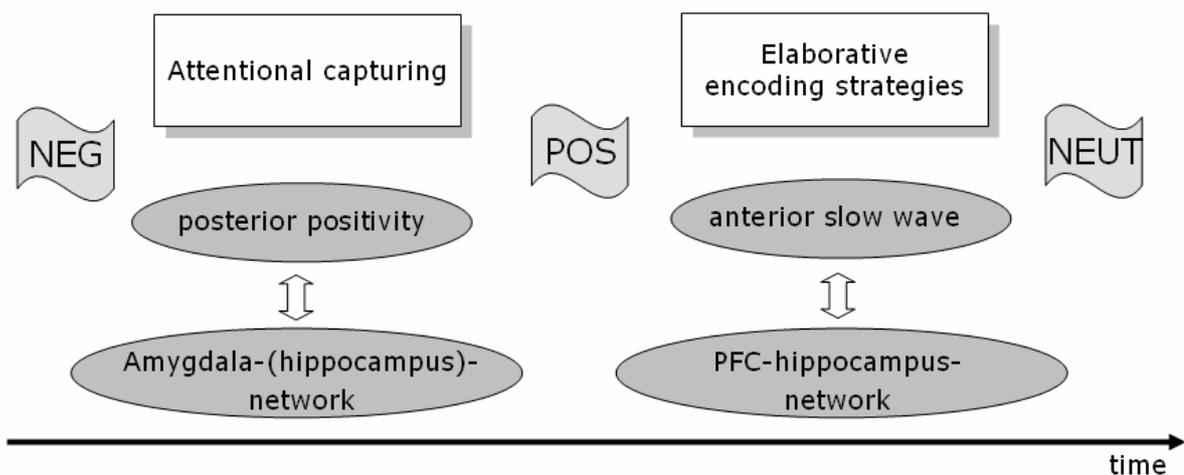


Figure 4.1.11: A proposed model derived from the data of Experiment 1. Initial attentional capturing mechanisms are engaged for both negative and positive pictures. However, additional elaborative encoding strategies are apparently necessary to lead to effective encoding promoting later recognition memory performance (found for positive pictures). Neutral pictures rely on elaborative encoding strategies that are not as powerful as those engaged by positive pictures due to the lack of emotional content.

4.2 Experiment 2

4.2.1 Questions

To further test the interpretation of the engagement of controlled encoding elaborations set in train by positive pictures, and leading to a recognition advantage, a divided-attention manipulation is employed. Dividing attention at study is supposed to limit the resources available for encoding (Craik, Govoni, Naveh-Benjamin, & Anderson, 1996) and has been shown to have a greater impact on self-generated strategic encoding processes and a less pronounced effect on relatively automatic processes (Yonelinas, 2002). Using fMRI and behavioral measures, Kensinger and Corkin (2004) found that distinct neurocognitive processes contribute to memory for highly arousing versus only mildly arousing emotion words. An amygdala-hippocampus network was active during the encoding of highly arousing words, whereas a prefrontal-hippocampal circuitry was engaged in the encoding of non-arousing words. This is in agreement with the interpretation of Dolcos and Cabeza's (2002) ERP results of an amygdala (related to arousal) and a prefrontal-hippocampus network (related to valence), and lends further support to a dissociation of valence- and arousal-related brain systems. An additional behavioral study by Kensinger and Corkin (2004) revealed that memory for highly arousing words was still enhanced even when a divided attention manipulation was used at study, whereas memory for low arousing words declined when encoding resources were devoted towards a secondary task. It is argued that memory enhancement for valenced but non-arousing materials relies on controlled and self-generated encoding processes such as elaboration and rehearsal whereas memory enhancement for arousing words occurs automatically. It is assumed that the same types of these self-generated controlled encoding processes are engaged while encoding neutral items, but that subjects are more likely to elaborate on or rehearse stimuli containing valent information as compared to those that do not. Thus, if controlled encoding operations were responsible for the enhancement effect for positive and low arousing pictures in Experiment 1, this enhancement should be disproportionately reduced by the divided-attention manipulation quite selectively for this class of stimuli. Neutral pictures may be inclined to a lesser degree, as well as especially negative high arousing ones that instead profit from automatic processing and encoding due to their arousal content.

4.2.2 Methods

Participants

Twenty volunteers (10 female) between 19 and 28 years of age (mean 24 years) participated in this study. They were students at Saarland University, native German-speakers, right-handed (as assessed by the Edinburgh Handedness Inventory; Oldfield, 1971) and had normal or corrected-to-normal vision. All participants gave written informed consent.

Experimental material

Stimuli consisted of 480 pictures taken from the International Affective Picture System (Lang et al., 2005) which were divided into three categories: negative, neutral and positive. They all differed with regard to valence (negative: 2.97; neutral: 5.09; positive: 7.13). Positive and negative pictures were equally arousing (positive: 5.04; negative: 5.2) and more arousing than neutral pictures (3.43). In contrast to the IAPS ratings, for the group of subjects in Experiment 1 the arousal ratings for negative and positive pictures differed in the way that positive pictures were far less arousing than negative pictures (3.23 vs. 5.73). In fact, positive pictures were only marginally significantly different from neutral pictures in their arousal ratings (3.23 vs. 2.56). In contrast to the arousal ratings, the valence ratings of our group of subjects were analogue to the one from the IAPS.

Procedure

Participants took part in two sessions separated by at least one but not more than seven days. In each session they completed a source recognition memory test each consisting of a study and a test phase. Before starting the experimental session, each participant passed a practice run. Pictures used here were not used during the experimental session. Subjects were comfortably seated in a dimly lit chamber in front of a monitor at a distance of 100 cm on which they saw the pictures. In the full attention (FA in the following) session during study participants were placed in one of two booths. These chambers were two small rooms sized about 3 m² equipped with a desk and a comfortable chair. To rule out the possibility that time would be entirely predictive of location participants had to change between the two booths three times so that they sat in each of them twice. Pictures

appeared in the centre of the screen for 2 s and the participant's task was to memorize the picture plus the list in which it was presented (booth 1 or booth 2). Additionally, the participants had to indicate via button press whether the depicted scene happened indoor or outdoor. This procedure was used to constrain the variability of possible mnemonic strategies during study and to ensure an appropriate encoding for each picture. In the test phase (administered 2.5 min later and at a computer outside of the two booths) the 120 old and 120 new pictures were presented for 500 ms each. The participants made an old/new decision. In case of an 'old' response a source decision (booth 1 or booth 2) was triggered by the appearance of three '?' in the centre of the screen. After a 'new' response, a fixation cross appeared to initiate the next trial. The study phase of the divided attention (DA in the following) session was run through as follows: Participants were instructed that they had three tasks (instead of only two in the FA session) which were of equal significance. One was to encode the picture plus its booth, the second considered the indoor/outdoor decision and three was about a number judgment. In the first 1000 ms in which they saw each picture, a four-digit number was shown left to the picture, whereas it disappeared in the last 1000 ms when another one was shown on the right of the picture. Afterwards, participants had to decide via button press whether the two numbers were identical. Half of the number pairs were identical and the other half were not. The test phase of the DA session was identical to the FA session. Booth order, encoding task (FA and DA) order and response buttons were counterbalanced across subjects.

Data analysis

Data were analyzed with repeated measures analyses of variance (ANOVA) using a significance level of $\alpha = .05$. For all effects with two or more degrees of freedom in the numerator, I adjusted for violations of sphericity which are inherent in analyses of variances (ANOVAs) according to the formula by Greenhouse and Geisser (1959) when appropriate.

The data analysis was based on reaction time measures (RT) for all correct responses, i.e. item hits and correct rejections. Item hits were defined as correct 'old' responses at test to pictures already presented during study, irrespective of the correctness of the subsequent source judgment. Correct rejections were defined as correct responses to new items presented at test for the first time. Recognition accuracy was estimated by means of Pr values (Snodgrass & Corwin, 1988). Pr is a measure that estimates the degree of true memory judgments by subtracting the false alarm rate, as an estimate of guessing, from

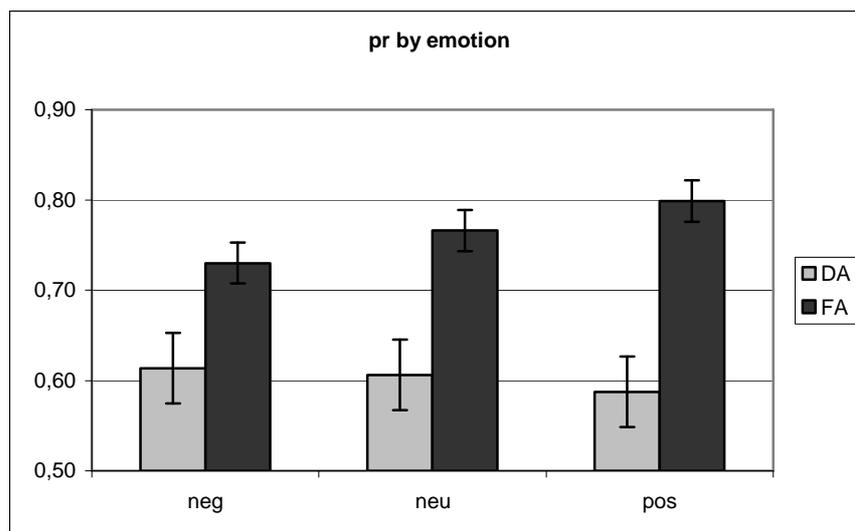
the hit rate. Therefore, a Pr value of 1 indicates perfect recognition performance, whereas a Pr value of 0 indicates chance performance.

For the second (source memory) response accuracy was calculated by dividing the probability of a correct source judgment by the probability of a correct 'old' response [$p(\text{correct source})/p(\text{correct source} + \text{incorrect source})$].

4.2.3 Results

The performance on the secondary number judgment task was .81 (.02). This suggests that participants were able to perform this task together with the other demands, but that it was not too easy to be completed.

An overview of the memory performance data by emotion and encoding task is given in figure 4.2.3. The repeated measures ANOVA on the Pr scores with the factors TASK (full attention, divided attention) and EMOTION (negative, neutral, positive) reveals a main effect of TASK [$F(1,19) = 34.52, p < .0001$] as well as an interaction TASK by EMOTION [$F(2,38) = 7.19, p < .003$]. This firstly reflects the fact that Pr values were higher in the FA task than in the DA task. Second, decomposition of the interaction brings up that in the FA task positive pictures were recognized to a greater extent than negative ones [$F(1,19) = 11.29, p < .0033$], with no differences for the other comparisons. Importantly, in the DA task the advantage of positive pictures disappears. This is even better reflected in the difference scores (Pr score FA- Pr score DA), where another analysis revealed significant differences between positive (0.21) and negative (0.12) [$F(1,19) = 12.32, p < .0023$] and positive and neutral (0.16) pictures [$F(1,19) = 5.50, p < .03$].



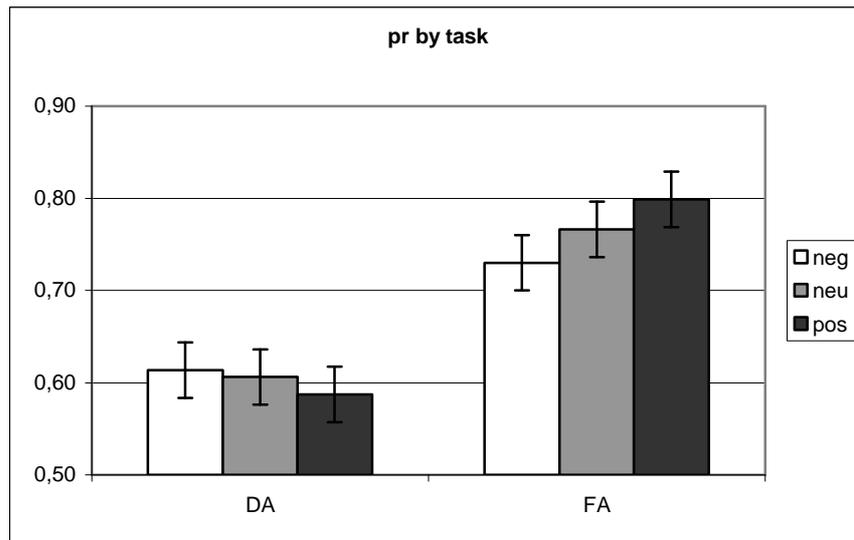
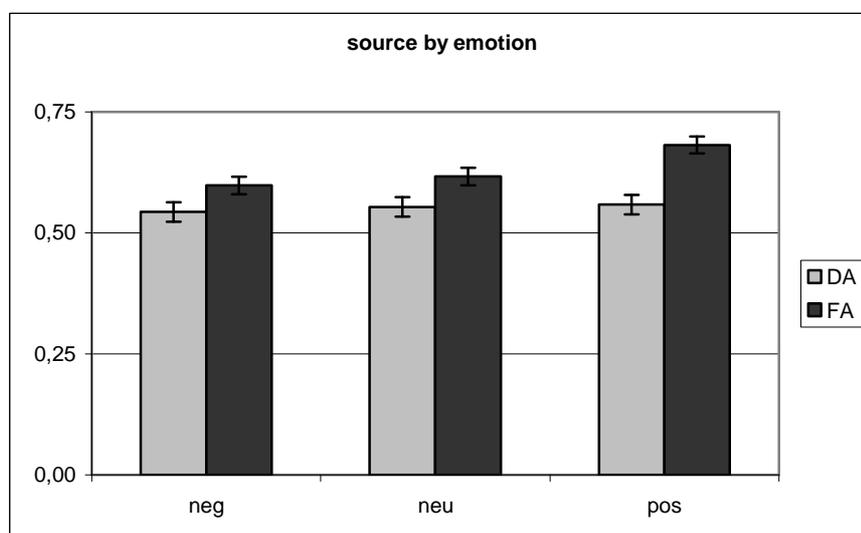


Figure 4.2.3: Pr results split by emotion (top) and attention task (bottom) at encoding for negative, neutral, and positive pictures.

Source memory performance, moreover, was additionally affected by diverting attention at encoding. A complementary ANOVA as for the Pr values revealed that there were main effects of TASK [$F(1,19) = 26.24, p < .0001$], EMOTION [$F(2,38) = 4.84, p < .016$], and an interaction between them [$F(2,38) = 3.30, p < .05$]. Source memory performance was generally better in the FA than in the DA session, and in the FA session it was highest for positive pictures, both compared to negative [$F(1,19) = 28.82, p < .0001$] and neutral ones [$F(1,19) = 7.82, p < .012$], with no difference between the latter. The DA session showed no differences.



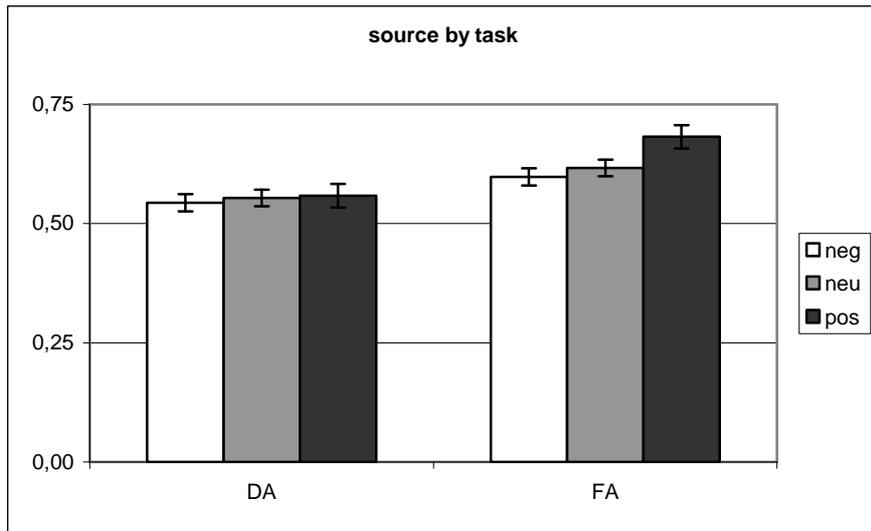


Figure 4.2.4: Source memory performance split by emotion (top) and attention task (bottom) at encoding for negative, neutral, and positive pictures.

4.2.4 Discussion

To further test the post-hoc interpretation of Experiment 1, I here looked at the effects of dividing attention at encoding on the recognition memory performance for negative and high arousing, positive and low arousing, and neutral pictures. In a within-subjects design, I let participants in the one session encode the pictures without a secondary task, and in the other with a secondary number judgment task. The latter was supposed to prevent participants to engage controlled encoding strategies, which were the putative means by which positive and low arousing pictures gained recognition advantage in Experiment 1. More specifically, it was predicted that with the use of elaborated encoding operations, positive and low arousing pictures will be recognized to a greater extent than both negative and high arousing and neutral ones in the full attention session. As follows, this effect should be diminished in the divided attention session.

I was successful in replicating the recognition memory performance for positive and low arousing as compared to negative and high arousing pictures in the full attention session (Experiment 1, Koenig & Mecklinger, 2008). Even more importantly, in the divided attention session there was no difference in the Pr scores of the three emotion conditions. Performance as a whole decreased for all the conditions as compared to the full attention session, but this was especially pronounced for positive pictures. This is clearly expressed in the higher difference scores of the two Pr values as compared to both negative and neutral pictures. Moreover, a comparable effect for source memory performance was obtained, which in the full attention session was highest for positive pictures, and not existing when attention was divided at encoding.

These results are in line with the interpretation of the results of Experiment 1. The anterior slow wave at encoding and the recognition memory advantage at test suggested that positive and low arousing events entered controlled and elaborated encoding processes which are beneficial for recognition memory performance. As recently demonstrated by Kensinger and Corkin (2004), dividing attention at encoding diminished the memory advantage for in their study negative nonarousing words. Kensinger and Corkin's fMRI data suggest that memory for nonarousing words was enhanced because of additional recruitment of the same types of self-generated controlled processes as are used to encode neutral words. Participants may be more likely to elaborate on, or to rehearse, the negative nonarousing words as compared with neutral ones. This hypothesis is supported by their fMRI data as activation in regions associated with controlled encoding processes (i.e. the

PFC) was greater for negative nonarousing words than for neutral ones, and the relation between activation and subsequent memory in these regions was stronger for the former than the latter. The same seems to be true in our study for positive low arousing pictures.

The same pattern of results was also obtained for source memory performance. I did not have hypotheses on this measure, as source performance in Experiment 1 was not modulated by the emotion status of the items. However, it fits the idea that source judgments require even more frontal lobe resources, and more "effortful processing" than item recognition judgments (Troyer et al., 1999). If these were engaged especially for positive low arousing pictures and their encoding context, source memory should be affected in a similar way as item recognition for these stimuli does.

For negative and high arousing pictures, I did not find an enhancement in recognition performance, but a reduction as compared to positive pictures in the full attention session, as in Experiment 1. This again is surprising, but fits to the early data by Kleinsmith and Kaplan (1963) and recent ones obtained by Sharot and Phelps (2004), who found that arousing words at immediate testing were recognized to a lesser extent than neutral ones. There are two possible explanations for this effect. The first is along the lines of the action-decrement theory by Walker (1958). The action decrement is a refractory state that follows performance of a response, correlating with the amount of learning that has accumulated at that same response over time. The superior consolidation due to high arousal is advantageous over time, but it produces a more intense refractory state in immediate tests. Thus, information learned under high arousal is relatively inaccessible at early test. The second explanation is according to Revelle and Loftus's tick-rate hypothesis (Revelle, 1989; Revelle & Loftus, 1990) which suggests that arousal increases the rate at which a scene is sampled, interfering with accessibility in immediate memory. However, an increase in the rate at which the to-be-learned material is linked with internal and external context may aid long-term retrieval. In addition to these two accounts, recent studies imply that the lack of memory enhancement by arousal at immediate test may be specific to cued recall and recognition tests (Richardson, Strange, & Dolan, 2004) rather than to free recall (Strange, Henson, Friston, & Dolan, 2000). It is thus hard to say what might have driven the decrement for negative and high arousing pictures in our study.

To summarize, I was able to replicate the results of item memory enhancement for low arousing positive pictures of Experiment 1 in the full attention session, and moreover and importantly, to show that this effect fades when attention is divided at encoding. In the divided attention session, *Pr* values were comparable for all three emotion conditions.

This is in line with the interpretation of strategic encoding operations that are supposed to be engaged for positive low arousing stimuli when attention is not limited by a secondary task. In accordance with the anterior slow wave found for these pictures in Experiment 1 and together with the prefrontal cortex activation of Kensinger and Corkin (2004), I feel safe to conclude that controlled operations were for the recognition advantage of positive and low arousing pictures.

4.3 Experiments 3A and 3B

4.3.1 Questions

The present study aims at investigating the impact of emotional arousal and retention duration on recognition memory and its neural correlates. While experiments 1 and 2 primarily shed light on the encoding and retrieval mechanisms supporting recognition memory for positive low arousing words, the obtained results for negative stimuli are not entirely understood by now. Therefore, the upcoming experiment focuses on this kind of stimulus material. More specifically, I will concentrate on the following five issues: The first concerns the differential effects of low and high negative arousal on encoding processes. Highly arousing negative stimuli are said to be processed fast and automatically while negative low arousing ones rely on controlled encoding operations, which should be dissociable on an electrophysiological level. The second issue deals with the question of how crucial a long retention duration is to build up a memory advantage of emotionally arousing stimuli, and how low and high arousal differ in this regard. These stimuli have proven to benefit from lasting consolidation processes (e.g. Sharot & Phelps, 2004) and result in a mnemonic advantage as compared to neutral materials through this mechanism. The question is if valence alone is sufficient to produce such advantage or if arousal is a necessary characteristic of the stimulus. Third, I want to clarify the topic of the quality of remembering of emotionally arousing events via the use of event-related potentials. I would like to find out if recollection-based remembering is unique to emotional stimuli and if a retention delay of 24 hours is necessary to produce differences as compared to neutral stimuli. Experiment 1 revealed recollection-based remembering (as revealed by the assumed underlying ERP correlates) only for neutral and positive pictures. Fourth, a subsequent memory analysis will be run on the data to see if the to-be-obtained dm-effects are different for valence and arousal. Is the successful encoding of valent and arousing information dissociable on an electrophysiological level as it is on a functional imaging one (Kensinger & Corkin, 2004)? The final point deals with source memory and possible influences of retention here. If memory is boosted for emotionally arousing stimuli due to enhanced consolidation, it might also modulate contextual details of the study episode.

4.3.2 Methods

Participants

Forty volunteers (20 female) between 19 and 28 years of age (mean 24 years) participated in this study. They were students at Saarland University, native German-speakers, right-handed (as assessed by the Edinburgh Handedness Inventory; Oldfield, 1971) and had normal or corrected-to-normal vision. Data of two other participants were excluded due to excessive eye-movement artefacts. All participants gave written informed consent.

Experimental material

Stimuli consisted of 300 pictures taken from the International Affective Picture System (Lang et al., 2005) and another source (Ecker et al., 2007) to equate for visual complexity between negative and neutral pictures. They were divided into three categories: neutral, negative and high arousing, negative and low arousing. As illustrated in Figure 4.3.1, a post-hoc rating experiment with the forty above-mentioned participants revealed that neutral and both negative picture conditions differed with regard to valence (negative and high arousing: 2.8; negative and low arousing: 3.3; neutral: 5.8) and arousal: negative and high arousing pictures (5.2) were more arousing than negative and low arousing pictures (4.1) and both of them more arousing than neutral pictures (2.2). An ANOVA on the valence scores yielded a significant main effect of valence [$F(2,198) = 521.91, p < .0001$], and post hoc tests showed significant differences between the valence scores of all three categories ($p < .0001$). A second ANOVA on the arousal scores of the pictures revealed a significant main effect of arousal [$F(2,198) = 292.42, p < .0001$], and post hoc tests showed significant differences between the arousal scores of all three categories ($p < .0001$).

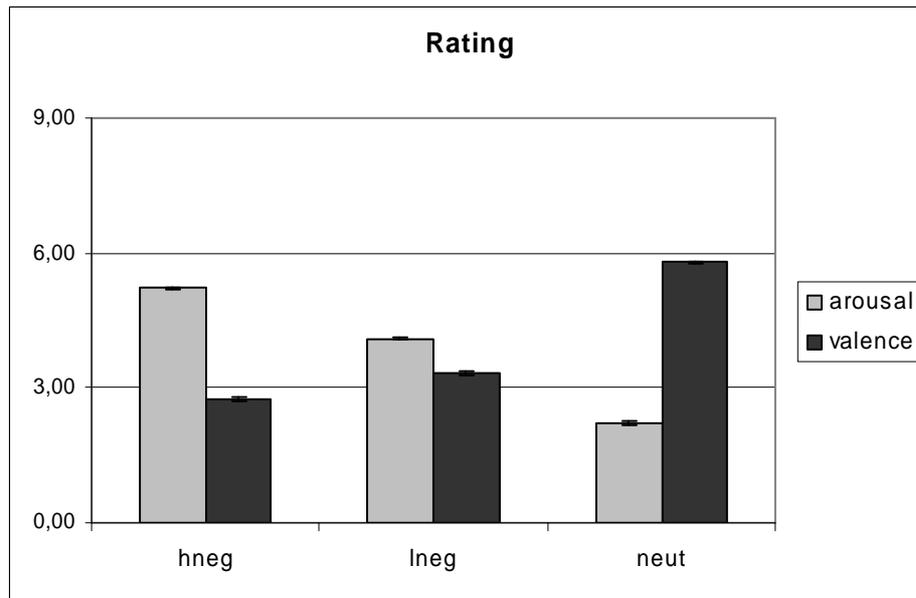


Figure 4.3.1: Results of the post-experimental rating of valence and arousal of the pictures used in the experiment.

Procedure

Participants were divided into two groups: the short retention group and the long retention group. The short retention group passed an incidental study phase and a test phase separated by 5 minutes in which they filled out the trait version of the State-Trait Anxiety Inventory (STAI; Laux, Glanzmann, Schaffner, & Spielberger, 1981). Subjects were comfortably seated in a dimly lit chamber in front of a monitor at a distance of 100 cm on which they saw the pictures. During incidental study, 150 (50 of each condition) pictures appeared in the centre of the screen for 1000 ms in random order and the participant's task was either to indicate via button press whether the depicted scene happened indoor or outdoor (the indoor/outdoor task) or if the displayed object was smaller or larger than the screen (the smaller/larger task). Both was demanded by trial by trial cuing in random order. This procedure was used to make the memory task non-predictable and to nevertheless ensure an appropriate encoding of each picture. In the test phase 150 old and 150 new pictures were presented for 500 ms each. The participants made an 'old-source task indoor/outdoor' / 'old-source task smaller/larger' / 'new' decision by pressing one of three buttons. Thereafter, they rated all the seen pictures according to the SAM-procedure (Lang et al., 2005). The long retention group received the very same tasks, but here study and test phase were separated by approximately 24 hours. In both groups subjects reported to be unaware that memory would be tested after the study phase.

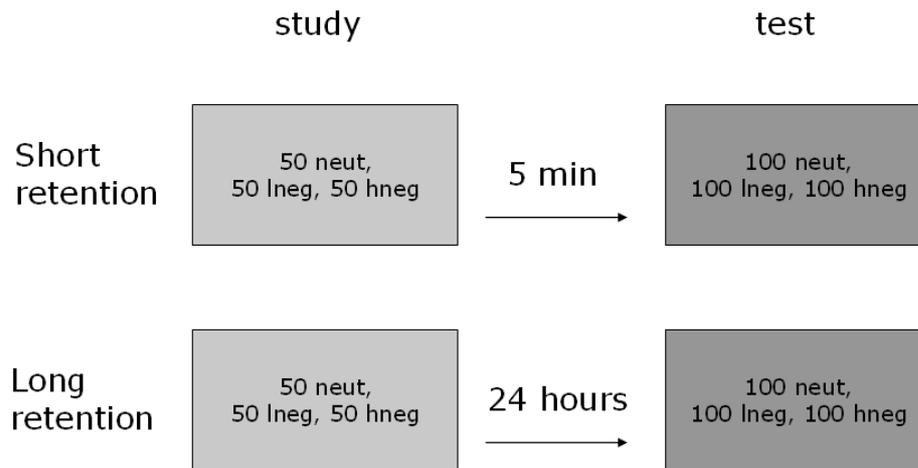


Figure 4.3.2: Schematic illustration of the study and test phases for the two groups of subjects.

EEG recordings

EEG was recorded using Ag/AgCl electrodes mounted in an elastic cap from 60 scalp sites at locations of the extended 10-20 system (Sharbrough et al., 1990). The ground electrode was placed at AFz. 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. The vertical and horizontal EOG were recorded from electrodes located below and above the right eye and at the outer canthus of each eye. Electrode impedance was kept below 5 kOhms. EEG and EOG were recorded continuously with a band pass from DC to 70 Hz and were sampled at a rate of 500 Hz.

Data analysis

Data were analyzed with repeated measures analyses of variance (ANOVA) using a significance level of $\alpha = .05$. For all effects with two or more degrees of freedom in the numerator, I adjusted for violations of sphericity which are inherent in analyses of variances (ANOVAs) according to the formula by Greenhouse and Geisser (1959) when appropriate.

Behavioral data

The data analysis was based on reaction time measures (RT) for all correct responses, i.e. item hits and correct rejections. Item hits were defined as correct 'old' responses at test to pictures already presented during study, irrespective of the correctness of the subsequent source judgment. Correct rejections were defined as correct responses to new items presented at test for the first time. Recognition accuracy was estimated by means of Pr values (Snodgrass & Corwin, 1988). Pr is a measure that estimates the degree of true memory judgments by subtracting the false alarm rate, as an estimate of guessing, from the hit rate. Therefore, a Pr value of 1 indicates perfect recognition performance, whereas a Pr value of 0 indicates chance performance.

For the second (source memory) response accuracy was calculated by dividing the probability of a correct source judgment by the probability of a correct 'old' response [$p(\text{correct source})/p(\text{correct source} + \text{incorrect source})$].

ERP data

ERPs were computed separately for each subject at all recording sites with epochs extending from 200 ms before stimulus onset until 1000 ms thereafter. The 200 ms before stimulus onset served as a baseline. EEG trials with artefacts (criterion: +/- 40 mV) were rejected. Eye blink artefacts were corrected using a linear regression approach (Gratton et al., 1983) implemented in the EEProbe software package (A.N.T. Software BV).

For statistical analysis, a hypothesis-driven approach was chosen. On the basis of prior studies, for the evaluation of the late posterior positivity and other emotion-specific effects in the encoding phase, I employed the mean amplitudes in two different time windows that were derived by visual inspection of the grand-average waveforms: 350 to 600 ms and 600 to 850 ms. As incidental encoding should not differ between the short and long retention group, I averaged them for the analysis here. For the quantification of the ERP old/new effects in the test phases, the mean amplitudes in two different time windows were used. Based on visual inspection of the grand average waveforms and consistent with prior studies (reviewed in Friedman & Johnson, 2000 and Mecklinger, 2006), the early frontal old/new effect was examined in a time window between 300 and 500 ms, whereas the parietal old/new effect was defined between 500 and 700 ms. This analysis aimed primarily at tapping the old/new effects related to familiarity and recollection, respectively. For the statistical evaluation of the study phase ERPs I employed twelve electrode sites in the overall ANOVA: left frontal (F3), middle frontal

(FZ), right frontal (F4), left central (C3), middle central (CZ), right central (C4), left parietal (P3), middle parietal (PZ), and right parietal (P4). For the test phase the following electrodes formed an anterior and a posterior ROI: F3, FZ, F4, FC3, FCZ, FC4 (anterior), CP3, CPZ, CP4, P3, PZ, P4 (posterior). The analyses of the dm effects included the following two time windows: 400-600 ms and 600-800 ms. Three ROIs were established being anterior (F3, FZ, F4), central (C3, CZ, C4), and posterior (P3, PZ, P4).

For the study phase, the overall repeated-measures ANOVA included the following factors: EMOTION (negative and high arousing, negative and low arousing, neutral), LATERALITY (left, middle, right), ANTPOS (anterior, central, posterior) and WINDOW (350-600 ms, 600-850 ms). In the case of significant main effects and interactions involving the factor EMOTION, subsidiary one-way ANOVAs and planned pairwise comparisons were performed to examine the effects in more detail.

For the quantification of the old/new effects for the test phase, two repeated-measure ANOVAs (factors: EMOTION (negative and high arousing, negative and low arousing, neutral), LATERALITY (left, middle, right), ANTPOS (frontal, parietal), WINDOW (300-500 ms, 500-700 ms) were performed for each of the two retention groups with the additional factor RESPONSE TYPE (hit, correct rejection). Again, in the case of significant main effects and interactions involving the factor EMOTION or RESPONSE TYPE, subsidiary one-way ANOVAs and planned pairwise comparisons were performed to examine the effects in more detail.

In order to tap the dm effects, a repeated-measure ANOVA for each of the retention groups was conducted. It included the following factors: EMOTION (negative and high arousing, negative and low arousing, neutral), REMFOR (remembered, forgotten), LATERALITY (left, middle, right), ANTPOS (anterior, central, posterior), and WINDOW (400-600 ms, 600-800 ms). In the case of significant main effects and interactions involving the factors EMOTION or REMFOR, subsidiary one-way ANOVAs and planned pairwise comparisons were performed to examine the effects in more detail.

4.3.3 Results

4.3.3.1 Behavioral data

An overview of item (Pr and percent correct), source memory performance and reaction time data is given in Table 4.3.3.

ret group	Pr			hits			source mem		
	neg high arous	neg low arous	neut	neg high arous	neg low arous	neut	neg high arous	neg low arous	neut
short	0.63 (0.03)	0.63 (0.03)	0.62 (0.02)	0.76 (0.03)	0.70 (0.02)	0.74 (0.03)	0.66 (0.02)	0.62 (0.02)	0.67 (0.02)
long	0.46 (0.04)	0.44 (0.04)	0.36 (0.04)	0.66 (0.04)	0.56 (0.04)	0.52 (0.04)	0.56 (0.02)	0.56 (0.02)	0.56 (0.03)

retention group	correct rejections			hits		
	neg high arousing	neg low arousing	neutral	neg high arousing	neg low arousing	neutral
short	1166 (35)	1102 (37)	1121 (39)	1735 (56)	1672 (55)	1590 (50)
long	1097 (55)	1049 (53)	1015 (51)	1646 (110)	1640 (113)	1567 (94)

Standard errors of the mean (SEM) are given in parenthesis.

Table 4.3.3: Pr and source performance data as well as reaction times (displayed in milliseconds) for the short and long retention group.

The ANOVA performed on the Pr values for the three EMOTION conditions (negative high arousal, negative low arousal, neutral) with the between-subject factor RETENTION GROUP (short, long) revealed a significant main effect of RETENTION GROUP [$F(1,38) = 20.71, p < .0001$] and EMOTION [$F(2,76) = 3.68, p < .031$], and an interaction between the two [$F(2,76) = 2.41, p < .098$]. The subsidiary one-way ANOVAs and planned pairwise comparisons showed that the short retention group performed better than the long retention group, and that performance was better for negative high arousing pictures and negative low arousing than neutral ones (across groups) [$F(1,38) = 6.92, p < .012$], [$F(1,38) = 4.82, p < .034$], with no difference between the two negative conditions [$F(1,19) = 0.03, p > .85$]. In the short retention group all three Pr values were comparable [$F(2,38) = 0.12, p > .88$], but in the long retention group I obtained worse performance for neutral pictures than both classes of negative ones, negative high arousing: [$F(1,19) = 11.40, p < .003$], negative low arousing: [$F(1,19) = 6.51, p < .02$]. In each emotion condition there was a difference between the long and short retention group insofar as the latter performed on a higher level, negative high arousing: [$F(1,38) = 10.57, p < .003$], negative low arousing: [$F(1,38) = 14.24, p < .0005$], neutral: [$F(1,38) = 26.44, p < .0001$]. Running the same analysis on the hits (percent correct) showed that there were also differences between the two negative conditions (see Figure 4.3.3). I obtained as for the Pr values an effect of RETENTION GROUP [$F(1,38) = 13.17, p < .0008$] and one of EMOTION [$F(2,76) = 11.40, p < .0001$], as well as an interaction between them [$F(2,76) = 4.70, p < .013$]. Subsidiary one-way ANOVAs revealed the same results as for the Pr values except for the fact that both within the short and long retention group more hits were obtained for high arousing than low arousing negative pictures [$F(1,19) = 9.16, p < .007$], [$F(1,19) = 10.75, p < .004$].

The analysis of response bias measures (Br) revealed a main effect of EMOTION [$F(2,76) = 18.37, p < .0001$] which means that Br was higher for negative high arousing pictures (short: 0.36, long: 0.35) than neutral (short: 0.32, long: 0.25) [$F(1,38) = 5.04, p < .031$] and negative low arousing ones (short: 0.17, long: 0.20) [$F(1,38) = 47.76, p < .0001$], i.e. a more liberal response criterion for high arousing negative pictures than neutral and low arousing negative ones.

The ANOVA on the reaction-time measures for hits and correct rejections gave rise to a main effect of RESPONSE TYPE [$F(1,38) = 201.49, p < .0001$] and EMOTION [$F(2,76) = 19.02, p < .0001$] as well as an interaction between them [$F(2,76) = 3.73, p < .029$]. There were no interactions with the between subject factor RETENTION GROUP. This

means that overall correct rejections were given faster than hits. This is probably due to the additional source decision inherent in the ‘old’ responses. Moreover, post-hoc tests revealed that responses to neutral items were given faster than those to negative low arousing [$F(1,38) = 8.69, p < .017$] and negative high arousing ones [$F(1,38) = 37.04, p < .0001$] with the latter even slower than the former [$F(1,38) = 19.66, p < .002$]. This means that the emotionally arousing status of the pictures influenced the reaction times of the subjects.

For source memory performance I only obtained an effect of RETENTION GROUP [$F(1,38) = 11.77, p < .002$]. Source memory performance was better for the short retention group than the long retention group irrespective of the emotional status of an item.

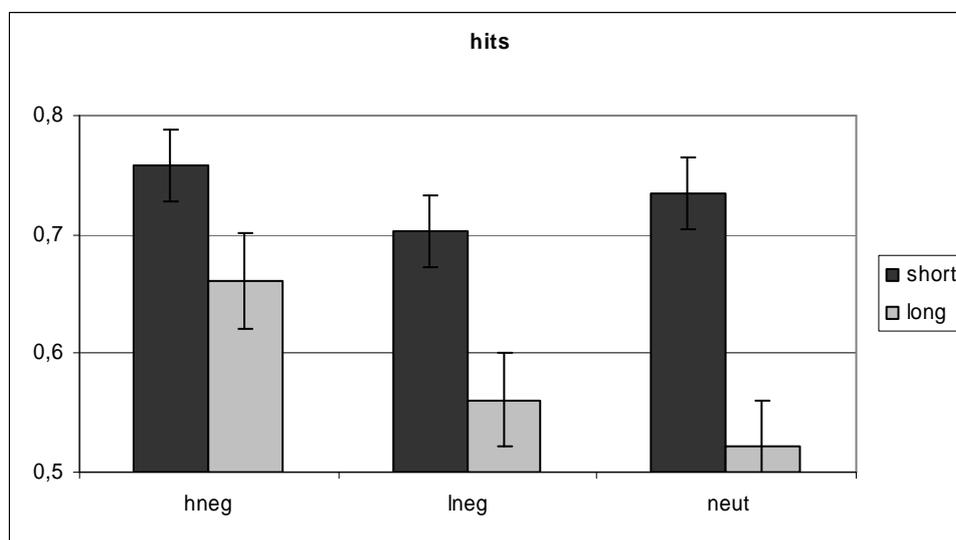


Figure 4.3.3: Proportion of correctly recognized old items for the short and long retention group for negative high arousing, negative low arousing, and neutral pictures.

4.3.3.2 ERP data

Encoding phase

The grand average ERP data of the encoding phase, averaged across the two retention groups and separately for the three emotion conditions, are depicted in Figure 4.3.4. The overall morphology of the waveforms was similar for negative high arousing, negative low arousing and neutral pictures and was characterized by a N300-P300-SW complex.

More specific examination of the grand average ERPs reveals two distinct effects: The first effect is a large positivity for negative high arousing pictures (as compared to negative low arousing and neutral pictures) and starts at around 350 ms post-stimulus with a broad scalp topography and lasts until the end of the recording epoch (1000 ms). The second initiates at around 600 ms and can be described as a positivity for negative low arousing pictures as compared to neutral ones with a broad scalp distribution.

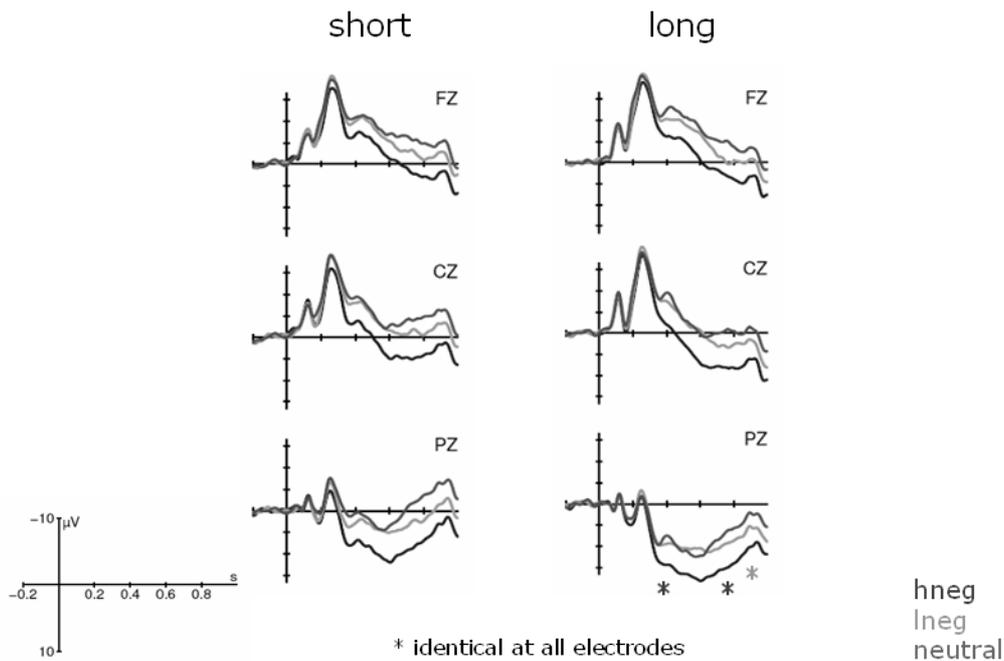


Figure 4.3.4: Encoding ERPs for the short and long retention group elicited by negative high arousing, negative low arousing, and neutral pictures at frontal, central, and parietal electrodes.

Table 4.3.4 shows the results of the initial ANOVA performed for the encoding phase. Significant main effects of EMOTION, LATERALITY, ANTPOS and WINDOW were obtained. Additionally, two interactions emerged: EMOTION by ANTPOS and EMOTION by WINDOW. For the first interaction, subsidiary ANOVAs and planned pairwise comparisons revealed that main effects of EMOTION and WINDOW, as well as an interaction between them, was present at frontal [$F(2,78) = 49.36, p < .0001$], [$F(1,39) = 77.03, p < .0001$], [$F(2,78) = 9.92, p < .0004$]; central [$F(2,78) = 79.54, p < .0001$], [$F(1,39) = 37.02, p < .0001$], [$F(2,78) = 11.65, p < .0001$]; and posterior sites [$F(2,78) = 70.52, p < .0001$], [$F(1,39) = 8.99, p < .005$], [$F(2,78) = 14.09, p < .0001$]. Further

examination showed that the second abovementioned interaction includes main effects of EMOTION and ANTPOS, as well as an interaction between them in both time windows, 350-600 ms: [$F(2,78) = 71.72, p < .0001$], [$F(2,78) = 132.91, p < .0001$], [$F(4,156) = 5.00, p < .005$]; 600-850 ms: [$F(2,78) = 68.49, p < .0001$], [$F(2,78) = 49.94, p < .0001$], [$F(4,156) = 3.58, p < .023$]. In more detail, this means that in both time windows and at all investigated electrode sites negative high arousing pictures give rise to more positive-going waveforms than both negative low arousing and neutral ones. Negative low arousing pictures are more positive-going than neutral ones in both time windows at frontal sites and in the late time window at central and posterior electrodes. This means that already at incidental encoding negative high and low arousing pictures seem to differ in topography and timing.

Effect	df	F	p
EMOTION	2,78	78.10	<.0001
LATERALITY	2,78	7.86	.0008
ANTPOS	2,78	94.51	<.0001
WINDOW	1,39	25.96	<.0001
EMOTION X ANTPOS	4,156	4.57	.0016
EMOTION X WINDOW	2,78	13.40	<.0001

Standard errors of the mean (SEM) are given in parenthesis.

Table 4.3.4: ANOVA results for the encoding phase.

Retrieval phase

Grand averages for correct responses to old and new pictures in all three emotion conditions for the short and long retention group are displayed in Figure 4.3.5. As expected, correctly recognized old pictures elicited more positive-going ERPs than correctly rejected new pictures. This old/new effect starts at around 250 ms post-stimulus at frontal sites and lasts until 700 ms at posterior electrodes. Remarkably, these effects appear to vary as a function of retention group and emotional condition with an early frontal and late parietal old/new effect for all three conditions in the short retention group

and early frontal effects for all conditions as well as a selective late parietal effect for negative high arousing pictures in the long retention group.

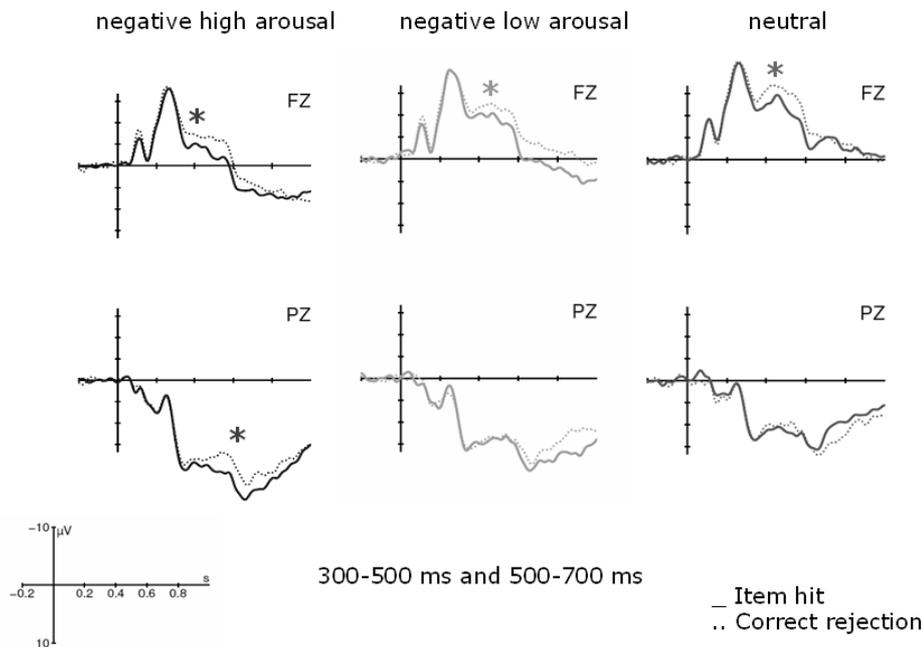
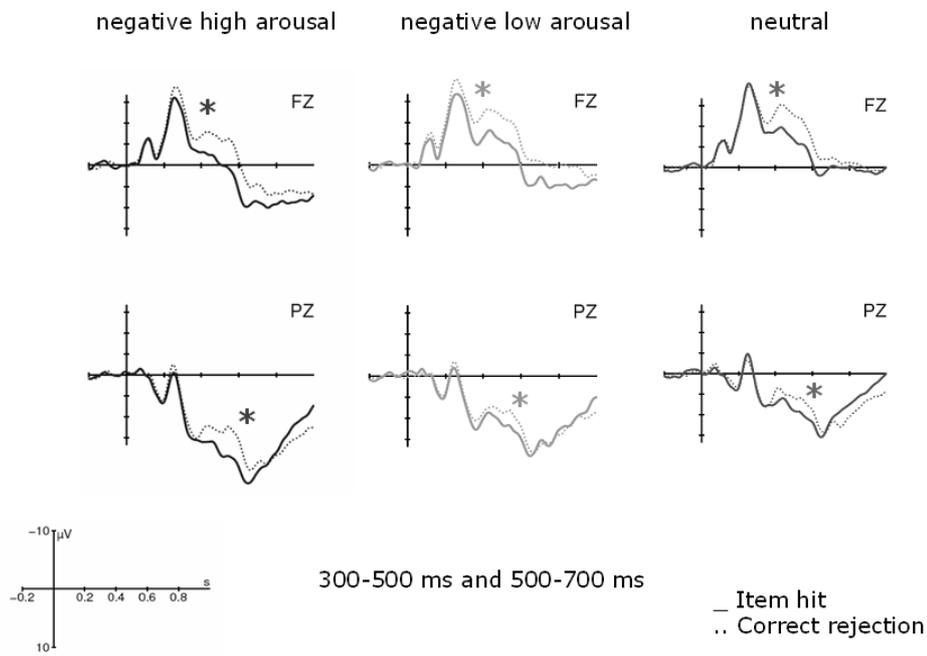


Figure 4.3.5: Retrieval ERPs for the short (top) and long retention group (bottom) elicited by negative high arousing, negative low arousing, and neutral pictures at a fronto-central and centro-parietal electrode.

Table 4.3.5 shows the results of the initial ANOVAs performed for both retention groups. Analyses performed for the short retention group revealed main effects of EMOTION, RESPONSE TYPE, ANTPOS and WINDOW, and a three-way interaction EMOTION by RESPONSE TYPE by WINDOW. For this interaction, subsidiary ANOVAs and planned pairwise comparisons showed that there was an early frontal as well as a late parietal old/new effect for negative high arousing [$F(1,19) = 30.09, p < .0001$], [$F(1,19) = 73.96, p < .0001$]; negative low arousing [$F(1,19) = 31.54, p < .0001$], [$F(1,19) = 5.57, p < .03$]; and neutral pictures [$F(1,19) = 24.99, p < .0001$], [$F(1,19) = 6.72, p < .02$]. For the long retention group I obtained significant main effects of EMOTION, RESPONSE TYPE, ANTPOS and WINDOW, and the following interaction: EMOTION by RESPONSE TYPE by ANTPOS by WINDOW. For this interaction, subsidiary ANOVAs and planned pairwise comparisons revealed an early frontal old/new effect for negative high arousing [$F(1,19) = 5.98, p < .02$], negative low arousing [$F(1,19) = 6.72, p < .02$] and neutral pictures [$F(1,19) = 4.82, p < .04$], and a selective late parietal old/new effect for high arousing negative pictures [$F(1,19) = 9.62, p < .006$].

Effect	df	F	p
short retention group			
EMOTION	2,38	99.84	<.0001
RESPONSE TYPE	1,19	81.59	<.0001
ANTPOS	1,19	85.86	<.0001
WINDOW	1,19	33.20	<.0001
EMO X RESP TYPE X WIN	2,38	9.37	.0005
long retention group			
EMOTION	2,38	55.59	<.0001
RESPONSE TYPE	1,19	18.00	.0004
ANTPOS	1,19	112.93	<.0001
WINDOW	1,19	35.28	<.0001
EMO X RESP TYPE X ANTPOS X WIN	2,38	4.46	.023

Standard errors of the mean (SEM) are given in parenthesis.

Table 4.3.5: ANOVA results of the retrieval phase.

Dm effects

To get even closer to the relationship between encoding activity and later memory performance, I additionally ran a dm-analysis for both retention groups. Therefore, I sorted the encoding trials according to their later memory status being either remembered (hits) or forgotten (misses).

As can be seen in Figure 4.3.6, ERPs to later remembered pictures were more positive-going than those to later forgotten ones. This effect, however, was differently pronounced for the three emotion conditions and two retention groups. Whereas no dm effect could be obtained for neutral pictures in either retention group, it was present for high and low arousing negative pictures at anterior and central sites in a time window from about 400 ms until the end of the epoch in both groups. At posterior electrodes, interestingly, high and low arousal as well as retention group could be dissociated.

The ANOVA for the short retention group thus revealed main effects of EMOTION, REMFOR, ANTPOS, and WINDOW, as well as an interaction EMOTION by REMFOR by WINDOW. Decomposition of this three-way interaction revealed dm effects for negative high and low arousing pictures at all sites in the late time window (all $p < .05$), but no such effect in the early time window at posterior sites ($p > .10$). Here, the effect was only prominent at anterior and central electrodes: high arousing anterior [$F(1,19) = 7.05, p < .016$], high arousing central [$F(1,19) = 6.28, p < .02$], low arousing anterior [$F(1,19) = 8.35, p < .009$], low arousing central [$F(1,19) = 5.23, p < .04$], as indicated by the interaction REMFOR by ANTPOS for the ANOVA of the early time window. No dm effects could be obtained for neutral pictures.

For the long retention group similar effects were obtained: main effects of EMOTION, REMFOR, ANTPOS, and WINDOW, as well as the interactions EMOTION by REMFOR by WINDOW and EMOTION by REMFOR by ANTPOS. Post-hoc tests showed that there were dm effects at anterior sites for both high and low arousing pictures in the two time windows: high arousing early time window [$F(1,19) = 7.88, p < .012$], high arousing late time window [$F(1,19) = 7.62, p < .013$], low arousing early time window [$F(1,19) = 5.65, p < .03$], low arousing late time window [$F(1,19) = 5.46, p < .03$]. For negative low arousing pictures, there was only an additional one at central sites in the early [$F(1,19) = 4.21, p < .054$] and late time window [$F(1,19) = 5.33, p < .03$], whereas for high arousing pictures, such effects were prominent at central sites in both time windows: early [$F(1,19) = 11.41, p < .003$], late [$F(1,19) = 12.43, p < .002$], as well

as at posterior sites in the late time window [$F(1,19) = 3.67, p < .07$]. Again, no dm effects could be obtained for neutral pictures.

Effect	df	F	p
short retention group			
EMOTION	2,38	10.01	<.007
REMFOR	1,19	9.30	.0003
ANTPOS	2,38	34.87	<.0001
WINDOW	1,19	7.39	<.014
EMO X REMFOR X WIN	2,38	5.05	<.013
long retention group			
EMOTION	2,38	12.49	<.0001
REMFOR	1,19	16.31	.0007
ANTPOS	2,38	89.66	<.0001
WINDOW	1,19	19.56	.0003
EMO X REMFOR X ANTPOS	4,76	5.61	.0005
EMO X REMFOR X WIN	2,38	2.74	0.80

Standard errors of the mean (SEM) are given in parenthesis.

Table 4.3.6: ANOVA results of the dm analysis.

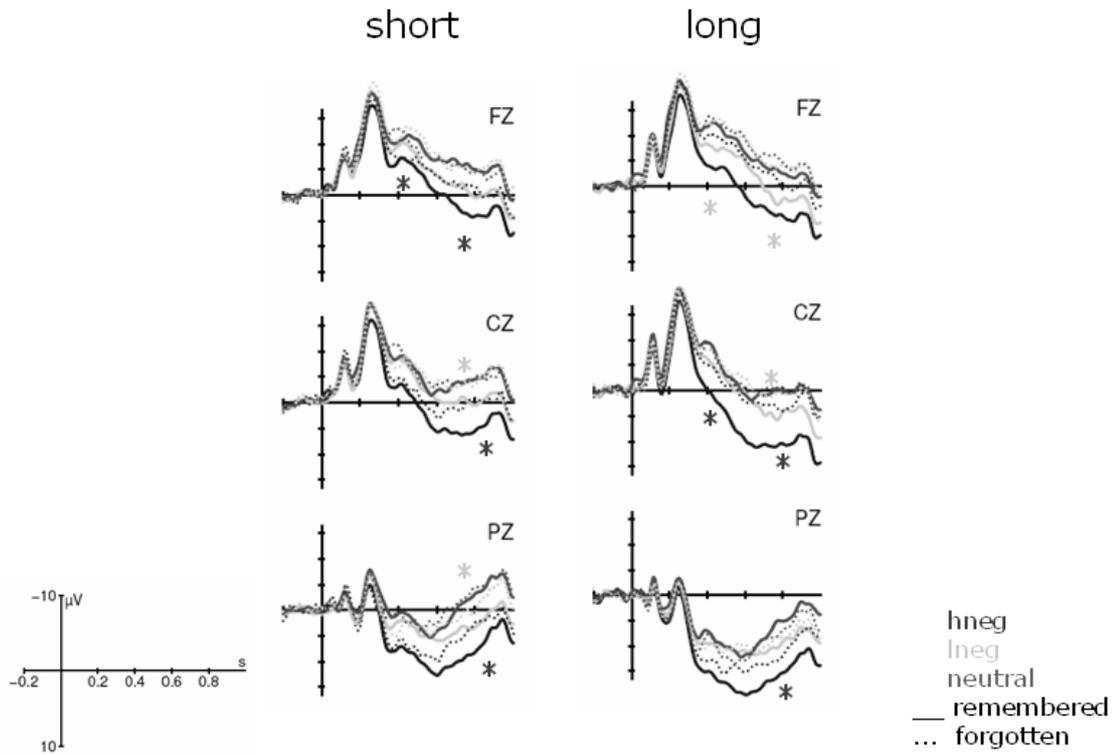


Figure 4.3.6: ERPs for the dm analysis in the short and long retention group for negative high arousing, negative low arousing, and neutral pictures at frontal, central, and parietal electrodes.

4.3.4 Discussion

Emotionally arousing events tend to be better and more richly remembered than neutral ones. This effect seems to be especially pronounced when testing memory after a delay. Here I tried to disentangle possible differential effects of valence and arousal at encoding, during consolidation and at retrieval via the use of behavioral measures and event-related potentials. In more detail, five issues were addressed: The first concerned the influences of low and high negative arousal on encoding processes. High arousing stimuli are said to be processed fast and automatically while only valent ones rely on controlled operations, which should be dissociable on an electrophysiological level. The second point dealt with the question of how necessary a long retention duration is to build up a memory advantage of emotionally arousing stimuli, and if high and low arousal produce differences here. The question was if valence alone is sufficient to produce such advantage or if arousal is a crucial characteristic of the stimulus. Third, I wanted to take a look at the quality of remembering of emotionally arousing events via the use of event-related potentials. I wanted to find out if recollection-based remembering is unique to emotional stimuli and if a retention delay of 24 hours is necessary to produce differences as compared to neutral stimuli. Fourth, a subsequent memory analysis was run on the data to see if the to-be-obtained dm-effects are different for valence and arousal, as well as for the short and long retention group. The final point dealt with source memory and their possible influences of retention. If memory is boosted for emotionally arousing stimuli on an item level due to enhanced consolidation, it might also modulate contextual details of the study episode.

Emotional arousal and retention duration had a modulatory effect on encoding, consolidation and retrieval processes. For the short retention group, I found that high arousing negative, low arousing negative and neutral pictures were equally well remembered as indexed by comparable Pr values. Taking a sole look at the hits however revealed a higher percentage of negative high arousing than neutral pictures. The long retention group, which on the whole performed worse than the short retention group, displayed a different pattern of results. Negative pictures (high and low arousing ones) exhibited a recognition advantage as compared to neutral pictures. This was revealed by higher Pr values that did not differentiate between the two negative conditions. Investigating the hit rates displayed more remembered items for negative high arousing than both low arousing and neutral pictures. This points to the fact that the former pictures

produced the highest false alarm rate and therefore the most liberal response bias (Br) in both retention groups. Source memory performance was better in the short than in the long retention group, but did not bring up any differences with regard to the arousal status of the items. Thus behaviorally, emotional arousal and retention duration had a converging effect on recognition memory performance. Event-related potential measures revealed an early frontal (supposed to index familiarity-based remembering) and late parietal old/new effect (the assumed correlate of recollection-based remembering) for hits as compared to correct rejections for negative high arousing, negative low arousing and neutral pictures in the short retention group which kind of resembles the behavioral results obtained in this group. Dissociable results could be found for the long retention group: an early frontal old/new effect for all three conditions and a late parietal old/new effect for high arousing negative pictures only. Remarkably, high negative arousal had a positive influence on the quantity and quality of remembering after a 24 hour retention interval. Encoding ERPs for negative high arousing pictures in both an early and a late time window and with a broad scalp topography gave rise to more positive-going waveforms than both negative low arousing and neutral ones. Negative low arousing pictures were more positive-going than neutral ones in both time windows at frontal sites and in the late time window at central and posterior electrodes. The subsequent memory analysis revealed dm effects for high and low arousing negative pictures at anterior and central sites in a time window from about 400 ms until the end of the epoch in both groups. At posterior electrodes, interestingly, high and low arousal as well as retention group could be dissociated. Whereas there were significant effects in the short retention group for both types of emotional stimuli in a late time window, this effect was not present in the high retention group for low arousing negative pictures, but for high arousing. Negative high arousing pictures thus seem to gain prioritized processing already at incidental encoding which then becomes memory-relevant at long retention duration.

The behavioral advantage for negative high and low arousing pictures as compared to neutral ones only exhibited over time, which is consistent with prior studies comparing two time points at test (LaBar & Phelps, 1998; Sharot & Phelps, 2004; Sharot & Yonelinas, 2008). These studies however did not compare high and low arousing stimuli which here seem to differ with regard to the amount of hits and false alarms. Both were given to a greater extent to high arousing items, which is consistent with prior studies on the emotion-induced recognition bias (Windmann & Kutas, 2001; Windmann, Sakhavat, & Kutas, 2002) that compared neutral with emotional stimulus materials. Moreover, the

quality of remembering was modulated by the arousal status of negative pictures as revealed by a selective parietal old/new effect for high arousing stimuli. This is consistent with the boost in recollective experience for such items in general, i.e. immediate (Kensinger & Corkin, 2003; Sharot et al., 2004) and delayed testing (Ochsner 2000; Sharot & Yonelinas, 2008; Sharot et al., 2007). Memories are said to produce an enhancement of vividness, as well as an increase in confidence, and consist of more detail (Ochsner, 2000; Sharot et al., 2004). However, a parallel boost in memory for the task performed during encoding was not observed. This suggests that emotion does not provide a general enhancement of recollection, but rather acts in a selective manner. Thus, given that the increase in recollective experience is not always accompanied by better recognition accuracy (Ochsner, 2000; Sharot et al., 2007) or memory consistency (Talarico & Rubin, 2003), emotional arousal may enhance this experience without necessarily improving memory for contextual features. The same results were obtained in a very recent study by Sharot and Yonelinas (2008) who also investigated study task as context information. Negative low arousing pictures exhibited the same recognition advantage on a behavioral level, but ‘only’ seem to be remembered familiarity-based (as revealed by the selective early frontal old/new effect). This is remarkable and provides evidence for a distinction between high and low arousing pictures for their mnemonic relevance, which has until now only been observed for encoding effects (Kensinger & Corkin, 2004). However, there are other reports that it is specifically arousal that is related to the boost in recollection-based remembering (Dolcos, LaBar, & Cabeza, 2005) which fits well to our data. Neutral pictures, that were remembered much less well than negative ones, seem to be done so on the basis of familiarity after the 24 hour delay. There are only two ERP studies that have investigated the effect of retention interval on neutral stimulus materials (Curran & Friedman, 2004; Wolk et al., 2006), and reported an early frontal and a late parietal old/new effect for both time points of testing. The discrepancy from our results might stem from the fact that these studies only used neutral materials and no additional emotionally arousing ones that may compete for processing capacities.

Encoding activity in our study using incidental instructions is comparable with the stimulus classification paradigms of Schupp et al. (2000; 2006). They consistently found the late posterior positivity to be modulated by the level of arousal with increasing arousal producing greater positivities. In a recent study using combined ERP and fMRI recordings (Sabatinelli, Lang, Keil, & Bradley, 2007) the late posterior positivity was shown to be a

reflection of activity in visual cortical structures demonstrating a higher perceptual sensitivity to the relevance of emotional visual scenes. Our ERP results seem to entirely fit to the data of Schupp (2000; 2006) with a larger late posterior positivity for negative high arousing than low arousing pictures, but additionally modulated anterior electrodes in the same manner. Hereby, a dissociation of low arousing pictures with regard to timing and topography was evident. I assume that even without the intention to encode the pictures, subjects felt different for low arousing than high arousing pictures that thus were processed in separable ways. This may be due to activity of the amygdala and the MTL memory system and accompanied by a feeling of arousal and enhanced perceptual fluency for high arousing stimuli only realized via the automatic attention capture of these stimuli. For the low arousing pictures subjects may be inclined to elaborate on this information or to rehearse it (Kensinger & Corkin, 2004). This may be reflected in the later onsetting posterior positivity and the long lasting anterior slow wave in our data, even though inferences from the scalp topography of ERP effects on underlying neural generators in most cases is problematic and comparisons can only be speculative. When comparing the current results with Experiment 1 (Koenig & Mecklinger, 2008) using intentional encoding instructions and positive and negative pictures as stimulus materials, they might make additional sense. Here, the anterior slow wave (elicited by low arousing positive stimuli) was assumed to be a reflection of controlled encoding strategies and the posterior positivity (present for low arousing positive and higher arousing negative pictures) one of attentional capturing mechanisms. The selective elicitation of the latter however did not lead to enhanced recognition memory performance for negative pictures after a short delay, whereas the additional anterior slow wave did for positive ones. For the current results this could mean that for high arousing negative pictures (even higher arousing than in the aforementioned study) attentional capturing mechanisms were initiated and in addition with anterior (most likely controlled PFC activity) operations were successful and led to the recognition memory advantage in quantity and quality. Low arousing negative pictures here produced a smaller anterior slow wave and a later onsetting posterior positivity which both may contribute to a recognition advantage as compared to neutral pictures that was nevertheless not as pronounced as for negative high arousing ones.

The dm effects obtained for high and low arousing pictures in the short and long retention group mirror the recognition memory performance. Whereas the anterior and central parts of the effect were comparable for the two groups and the two classes of negative stimuli,

the posterior part showed a dissociation. This is well in agreement with the findings of Dolcos and Cabeza (2002) who found an earlier onsetting subsequent memory effect for positive and negative pictures as compared to neutral ones. They conducted the first study of this kind and postulated that the emotional content granted a privileged access to processing resources that resulted in a better encoding of high arousing stimuli. This in turn, resulted in better retrieval of these pictures. Adapted to the present experiment, this could fit the finding of the more widespread and longer lasting dm effect for high arousing negative pictures in the long retention group that also showed the best memory performance. It can only be speculated about the neural generators of this ERP effect, but there is reason to believe that the amygdala, with its connections to several neocortical regions (Amaral et al., 1992) is responsible, together with other regions like the prefrontal cortex and parietal regions associated with emotional processing (LaBar et al., 1999; Lang et al., 1998). The similarity of the subsequent memory effect for high and low arousing pictures at anterior and central sites may suggest that these ERPs reflect comparable involvement of the same neural generators as those associated with successful encoding in fMRI studies (Brewer et al., 1998; Wagner et al., 1998).

In sum, it could be shown that the recognition advantage for emotionally arousing pictures and the enhancement in recollective experience benefit from the operation of a time-dependent process consistent with consolidation. The latter was only true for negative high arousing pictures and in addition with enhanced positivities during encoding for those pictures I assume that high arousal has a special influence of the processes underlying memory formation which is manifested at all stages of processing. Moreover, a 24 hour retention duration seems to be necessary to reveal such dissociations as immediate testing did not show up clear differences between negative high arousing, negative low arousing and neutral pictures.

4.4 Experiment 4

4.4.1 Questions

With the experimental approach of this study I want to once more focus on an encoding phenomenon. For this reason, I set out to clarify the existence of the tunnel memory phenomenon. A new experimental design is created and takes into account individual factors such as trait anxiety and individual stimulus ratings, as these seem to differently affect the processing of emotionally arousing stimuli. Previous studies used a variety of designs and testing procedures. Mostly only a few stimuli were used and thus conclusions drawn out of these data do not seem to be generalizable. Testing procedures also varied quite a lot, from forced-choice recognition (Safer et al., 1998) and drawing tests (Candel et al., 2003) to the camera distance paradigm (Intraub et al., 1992). Moreover, all existing experimental designs did not allow investigating reaction times (RT), which could be a crucial means to get closer to the underlying mechanisms contributing to the tunnel memory phenomenon. Therefore, it is of high interest to build up a test design that resembles common memory testing procedures in the literature.

To this end, it was predicted that neutral pictures will be remembered with extended boundaries while negative ones should result in a restriction of the pictures boundaries. However, as recently found by Mathews and Mackintosh (2004), negative pictures presumably only lead to a smaller boundary extension effect as neutral pictures do. Moreover, it is an open issue if averaging results for a high number of test pictures still lead to the early effects described for only one stimulus out of a story line.

4.4.2 Methods

Participants

36 volunteers (19 female) between 19 and 30 years of age (mean 25 years) participated in this study. They were students at Saarland University, native German-speakers, right-handed (as assessed by the Edinburgh Handedness Inventory; Oldfield, 1971) and had normal or corrected-to-normal vision. All participants gave written informed consent.

Experimental material

Stimuli consisted of 96 pictures taken from the International Affective Picture System (Lang et al., 2005) which were divided into two categories: negative and neutral (each containing 48 pictures). They differed with regard to valence (negative: 2,92; neutral: 5,38) and arousal (negative: 5,03; neutral: 3,52) as confirmed by ANOVA testing. Separate ANOVAs on the valence and arousal scores both yielded a significant main effect of valence [$F(1,47) = 840.81, p < .0001$] and arousal [$F(1,47) = 107.82, p < .0001$]. Each of the pictures was reproduced in three versions, i.e. three zoom levels. We created two additional versions from each original picture. First, we removed parts of the original picture's periphery. The resultant image was a first zoom of the original picture, focusing on its central objects. Second, we removed more parts of the periphery of this first zoom creating a second zoom. The percentage of the removed parts varied between the pictures, as it was individually adjusted to each picture. The mean size for the first zoom was 56% of the original picture and for the second zoom was 28% of the original picture. Then, the resultant images were expanded to the size of the original. Exemplars of each valence category are shown in Figure 4.4.2.

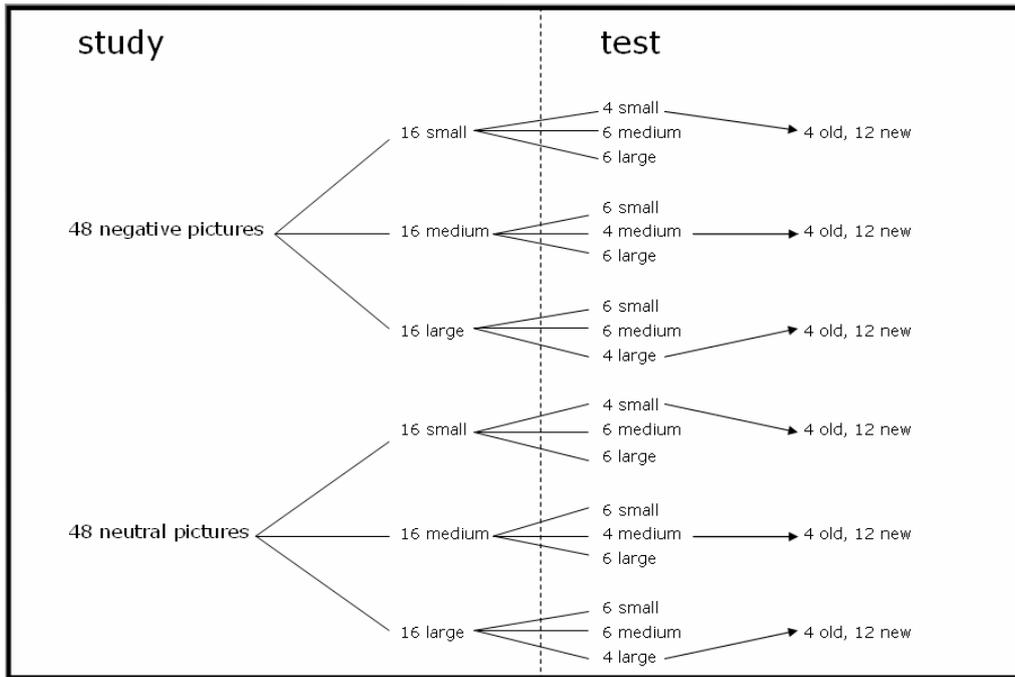


Figure 4.4.1: How stimuli were distributed to the different stimulus categories.

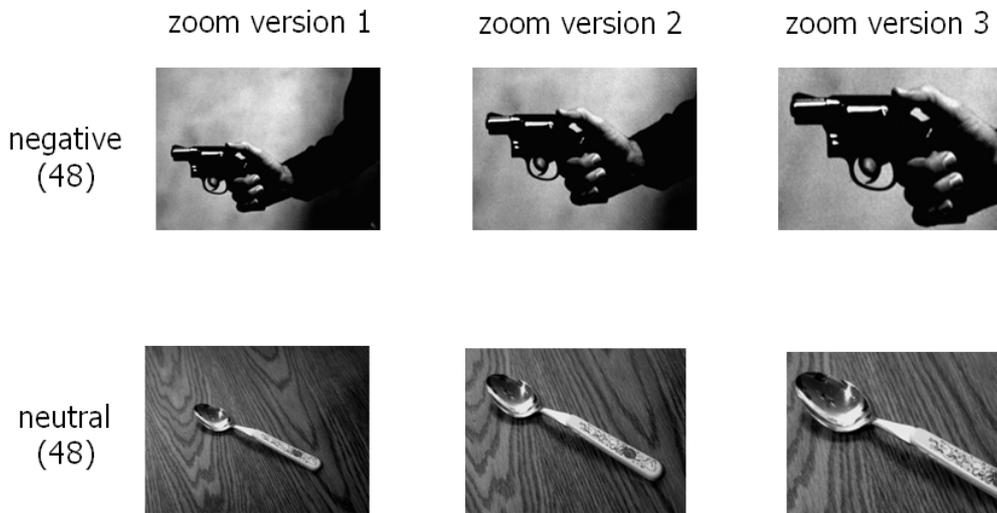


Figure 4.4.2: Examples of stimuli used in Experiment 4.

Procedure

Participants took part in a session comprising of a battery of several little tests. To run through it, subjects were comfortably seated at a desk and if necessary in front of a monitor at a distance of 100 cm on which they saw the pictures.

First, they filled out the shortened form (12 items) of the “Mehrdimensionaler Befindlichkeitsfragebogen” (MDBF; Steyer, Schwenkmezger, Notz, & Eid, 1994), a German multidimensional mood questionnaire to assess the effectiveness of mood induction. The MDBF assesses three mood dimensions: pleasantness (pleasant-unpleasant), calmness (calm-restless), and wakefulness (awake-sleepy). Using a 5-point Likert-scale, participants rated the degree to which mood was experienced at a particular point of time (here before and after the memory test).

Second, participants encoded the 96 pictures under incidental instructions to rate the pictures according to a three-point valence scale. One third of the pictures of each valence category were presented in each of the zoom versions (1, 2 and 3). Debriefing at the end of the entire experiment revealed that all subjects were not aware of the upcoming memory test.

Third, as a filler task subjects completed a questionnaire for about ten minutes to create a retention interval between study and test.

Thereafter, they underwent a surprise memory test. Participants were shown 24 pictures they already saw during study (old pictures) and the remaining 72 were presented in a different zoom version (to-be-called new pictures). After the appearance of each picture they had to decide whether they saw it in that exact same zoom level (old) or if the pictures was closer or farther than the one seen during study (new). A second response should tap the confidence of their judgment and was triggered through the appearance of ‘sicher/unsicher’ (certain/uncertain) on the screen. Two response buttons served as ‘old’ and ‘new’ and ‘certain’ and ‘uncertain’ response.

After filling out the MDBF for the second time, they completed the trait version of the State-Trait Anxiety Inventory (STAI; Laux et al., 1981).

Finally, subjects rated the 96 pictures used in the experiment plus 48 positive pictures (taken out of the IAPS, Lang et al., 2005) according to the SAM-procedure used by Lang et al. (2005) for arousal and valence. This was done to tap individual differences in these two dimensions and elucidate possible divergences from the normative IAPS rating. Positive pictures were included to prevent a bias for neutral pictures to be rated ‘positive’

as participants would likely use the entire nine-point scale ranging from very negative to very positive.

Data analysis

Data were analyzed with repeated measures analyses of variance (ANOVA) using a significance level of $\alpha = .05$. For all effects with two or more degrees of freedom in the numerator, I adjusted for violations of sphericity which are inherent in analyses of variances (ANOVAs) according to the formula by Greenhouse and Geisser (1959) when appropriate.

The data analysis was based on reaction time measures (RT) for hits, corrects rejections and false alarms. Hits were defined as correct 'old' responses at test to pictures already presented during study in this exact same zoom level. Correct rejections were defined as correct 'new' responses to items presented at test in a different zoom level. Recognition accuracy was expressed through the amount of hits and by means of Pr values (Snodgrass & Corwin, 1988). Pr is a measure that estimates the degree of true memory judgments by subtracting the false alarm rate, as an estimate of guessing, from the hit rate. Therefore, a Pr value of 1 indicates perfect recognition performance, whereas a Pr value of 0 indicates chance performance. In our study it is supposed to be interpreted with caution as on the one hand our test phase did not include the same number of old and new items and as on the other hand those 'new' items were not really new but a different version of an old item. Therefore, we take the hit rates as a more valid measure of recognition performance here. False alarms were further subdivided into restrictions (choosing a closer version of the original picture) or extensions (choosing a farther version of the original picture) of which the relative values are reported. Additionally, the 'extension value analysis' operates on coded values ranging from -2 (total restriction) to 2 (total extension). Here a value of -1 means that subject incorrectly classified an item as 'old' that was presented in zoom level 2 at study and in zoom level 1 at test. Likewise, positive values refer to the classification of such an item presented in a smaller zoom level at study than at test (see Figure 4.4.3). These analyses were run on the valence categories according to the individual ratings of each subject. The latter allows us a more specific and precise analysis. Additionally, I set them into relationship with the individual trait anxiety scores of each subject.

Study item	Test	Response „old“	Score
	Small	Hit	
Small	Medium	Extension	1
	Large	Extension	2
	Small	Restriction	-1
Medium	Medium	Hit	
	Large	Extension	1
	Small	Restriction	-2
Large	Medium	Restriction	-1
	Large	Hit	

Figure 4.4.3: Boundary scoring for the three zoom versions of pictures.

4.4.3 Results

Rating, STAI, and MDBF

The subjects' rating on arousal and valence of the stimuli revealed that negative and neutral pictures differed with regard to valence (2.87 vs. 5.03) [$F(1,47) = 479.37, p < .0001$] and arousal (5.13 vs. 2.31) [$F(1,47) = 2191.90, p < .0001$]. These rating scores did not significantly differ from those of the IAPS ($p > .05$).

The mean score of the trait scale of the State-Trait Anxiety Inventory (STAI; Laux et al., 1981) for our group of subjects was 38.5 (SD: 8.7). When performing a median split the critical value was 38, which created a low-anxiety group with a mean score of 31.8 (SD: 4.4) and a high-anxiety group with a mean score of 45.2 (SD: 6.5). This fits to the procedure performed by Mathews & Mackintosh (2004) who designated all subjects with a higher score than 40 as high-anxious.

The self-rated MDBF scores for the dimensions pleasantness, calmness and wakefulness for the two assessed time points were as follows: pleasantness (before the memory test: 15.6; after the memory test: 14.9), calmness (before: 15.2; after: 15.2), wakefulness (before: 13.3; after: 12.7). ANOVA testing revealed that subjects' pleasantness was affected by the memory test (before > after; [$F(1,35) = 5.25, p < .03$]), whereas there was no change in calmness [$F(1,35) = 0.00, p = 1$] or wakefulness [$F(1,35) = 1.57, p > .22$].

Reaction times

The reaction-times are listed in Table 4.4.3. An ANOVA on the reaction-time measures for hits, correct rejections and false alarms (extensions and restrictions) revealed a significant main effect of RESPONSE TYPE [$F(2,70) = 10.13, p < .0003$]. Decomposition of this effect revealed that, irrespective of emotion, hits were given faster than both false alarms [$F(1,35) = 7.29, p < .011$] and correct rejections [$F(1,35) = 14.22, p < .0006$], and false alarms faster than correct rejections [$F(1,35) = 5.51, p < .025$]. This indicates that boundary extension and restriction (false alarms) were not followed by an extremely long-lasting decision process, and thereby were not just the product of guessing, but of a relatively automatic and confidently given old response to a pictures in a different zoom version.

hits		false alarms		pr	
negative	neutral	negative	neutral	negative	neutral
.79 (.02)	.79 (.02)	.49 (.01)	.56 (.02)	.30 (.02)	.23 (.03)

hits		correct rejections		false alarms	
negative	neutral	negative	neutral	negative	neutral
930 (91)	1006 (83)	1308 (105)	1217 (109)	1159 (93)	1099 (89)

Standard errors of the mean (SEM) are given in parenthesis.

Table 4.4.3: Behavioral results and reaction time data (displayed in milliseconds).

Memory data analysis

An overview of the memory performance data is given in Table 4.4.3. The ANOVA performed on the hit rates for the factor EMOTION (negative, neutral) revealed no significant main effect [$F(1,35) = 0.02, p > .88$], which indicates that there was no difference between negative and neutral items. For the false alarms, the ANOVA demonstrated a significant main effect of EMOTION [$F(1,35) = 12.22, p < .001$], confirming that there was a higher rate of false alarms for neutral than negative items. Both these results lead to a higher Pr rate for negative than neutral items [$F(1,35) = 9.04, p < .005$]. Additional analysis with ANXIETY GROUP (high, low) as between subject factor did not reveal any significant effect with regard to memory performance.

When investigating the types of false alarms made, I performed an ANOVA with the factors EMOTION (negative, neutral) and ZOOM (extension, restriction). This revealed a main effect of EMOTION [$F(1,35) = 19.18, p = .0001$] and ZOOM [$F(1,35) = 20.79, p < .0001$], and an interaction between the two factors [$F(1,35) = 11.40, p < .002$]. This reflected the fact that extensions were more frequently made than restrictions, and that there were more false alarms for neutral than negative items. Moreover, planned pairwise comparisons revealed that more neutral than negative extensions were made ($p < .0001$), there was no difference among restrictions ($p > .10$), for neutral items there were more

extensions than restrictions ($p < .0001$) and no such differentiation for negative ones ($p > .10$). When taking ANXIETY GROUP (high, low) as a between subject factor into this ANOVA I did not obtain any interaction with false alarms.

An ANOVA on the confidence rating after each given response in the memory test with the factors EMOTION (negative, neutral) and TYPE (correct rejection, false alarm, hit) revealed two main effects. Responses to neutral items were given with more confidence than those to negative ones (0.74 vs. 0.69) [$F(1,35) = 8.73, p < .006$]. Moreover, the type effect [$F(2,70) = 68.24, p < .0001$] revealed that false alarms were given with higher confidence than correct rejections (negative: 0,69, neutral: 0,77 vs. negative: 0,55, neutral: 0,59) [$F(1,35) = 41.49, p < .0001$] and hits (negative: 0,82, neutral: 0,87) even more confident than both types of responses to new items [$F(1,35) = 37.28, p < .0001$] [$F(1,35) = 107.16, p < .0001$], all across emotion. This is an important finding since one cannot claim that boundary extension and restriction were not just given by high levels of uncertainty and additionally these results fit well to i.e. confirm the reaction time data.

Extension value analysis on individually valence-rated pictures

The extension value analysis revealed that there was boundary extension (and not restriction) for neutral and negative pictures (0,32 and 0,10), as both values were positive. Moreover, there was more boundary extension for individually as neutral rated than as negative rated pictures [$F(1,35) = 6.3, p < .017$]. This is well in agreement with the above-mentioned false alarm data analysis. When taking ANXIETY GROUP (high, low) as a between-factor into this analysis, a main effect of anxiety group [$F(1,34) = 7.44, p < .01$] and EMOTION [$F(1,34) = 6.64, p < .015$] was obtained and a marginally significant interaction between these factors [$F(1,34) = 2.92, p < .097$]. This means that the high-anxiety group all over has lower extension values than the low-anxiety group (0,08 vs. 0,33). Moreover, neutral pictures have comparable extension scores in both groups (low: 0,38; high: 0,26) [$F(1,34) = 1.15, p > .29$], whereas negative pictures differ extremely (low: 0,30; high: -0,10) [$F(1,34) = 7.92, p < .008$]. An illustration of this effect is given in figure 4.4.4. Thus I succeeded in obtaining a boundary restriction effect for negative pictures for the high-anxiety group selectively. An additional analysis revealed that for the over all group STAI score correlated with the extension score for negative pictures, $r = -.42, p = .01$. That is, the more trait-anxious the subjects are the less boundary extension

(and more boundary restriction) they show for negative pictures (see Figure 4.4.5). STAI did not correlate with the extension score for neutral pictures ($r = -.28, p > .10$).

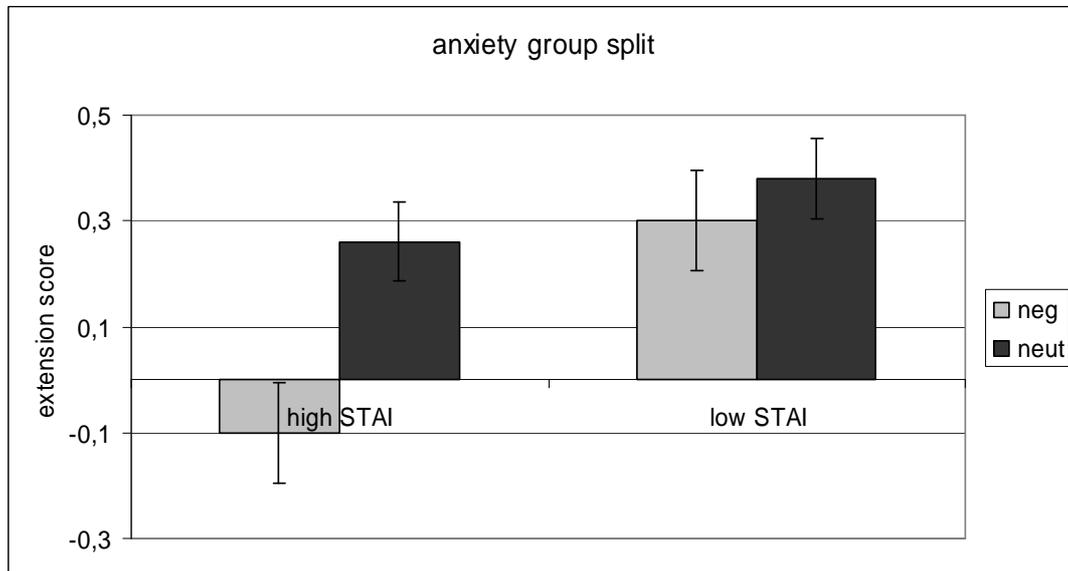


Figure 4.4.4: Results of the median split by STAI.

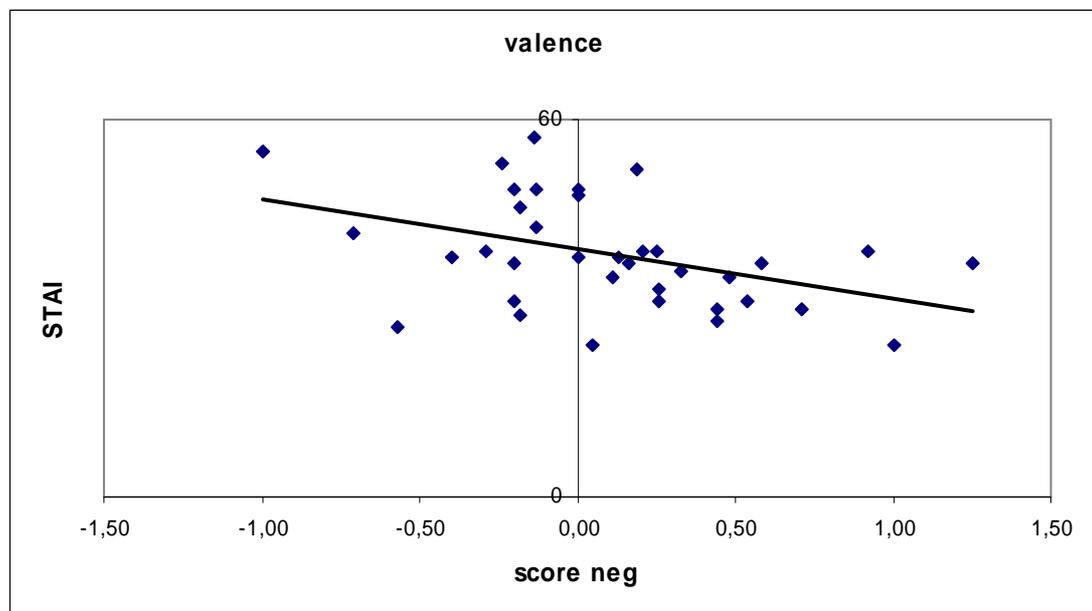


Figure 4.4.5: Correlation STAI and score negative.

4.4.4 Discussion

The present study aimed at investigating the tunnel memory phenomenon (also referred to as boundary restriction as compared to boundary extension) with a new design and taking individual factors like trait-anxiety into account. The main result was that the emotional content of a scene did have an impact on the boundary extension effect. Moreover, the emotional reactivity of the perceiver (trait anxiety) modulated this effect in a specific manner. In more detail, three main results were obtained. First, negative pictures were found to be remembered to a greater extent than neutral ones, which is well in line with studies on memory for emotional materials (e.g. Ochsner, 2000; Berntsen, 2002). Here, especially the central details seem to be recognized superiorly. Second, subjects showed reduced boundary extension to negative as compared to neutral scenes. This replicates the findings of Mathews and Mackintosh (2004) and extends them by showing that the effect is independent of the trait anxiety status of the subjects. Finally, only the group of subjects with high trait anxiety demonstrated boundary restriction for individually negative rated pictures. This finding further extends the data of Mathews and Mackintosh (2004) as they could only show reduced boundary extension, but no restriction in high trait-anxious individuals.

The modulation of processing by emotional arousal already happens at the point of the first encounter, at encoding. When confronted with an amount of sensory information attentional networks are required to select the relevant information to which one should attend. Critical effects of emotional arousal lead to a modulation of attention. Attention is focused on the emotionally arousing stimuli which are then processed facilitated and prioritized (Dolan & Vuilleumier, 2003). Therefore individuals are more likely to attend to emotional elements in a scene together with neglecting other neutral ones. This should lead to enhanced memory for the former parts of a picture (see Kensinger et al., 2005). In the present study this is revealed by the smaller amount of boundary extensions for negative arousing pictures as compared to neutral ones. Subjects less often demonstrate errors (i.e. false alarms to pictures changed in zoom version from smaller to larger) in this direction when encountering a negative than a neutral picture. However, hit rates were comparable for both types of pictures and thus general recognition performance does not seem to be affected by the emotional status of a picture.

Boundary extension seems to be a general phenomenon when remembering scenes (Intraub et al., 1992). According to the authors this effect is due to the fact that pictures

are perceived as being part of the real world with space beyond the limits of the picture, also known as the perceptual schema hypothesis (Intraub, Gottesman, & Bills, 1998). To bring this together with the effects of emotion, Safer et al. (1998) argued that selective processing of central emotional details should work against boundary extension (see also Christianson, 1992). Our results support this claim. The amount of boundary restriction, on the other hand, was not affected by the emotional status of the pictures in the analysis of occurrence of false alarms. However, when performing the extension value analysis (comparable to the one used by Mathews and Mackintosh, 2004) on individually negative rated pictures, I found a large overall difference between negative and neutral pictures (0.10 vs. 0.32). Nevertheless, as no negative values could be obtained, pure boundary restriction was not apparent when all participants were considered. However, the group of subjects with high trait anxiety showed boundary restriction (-0.10) and the negative correlation of the STAI and the extension score underpins this point: the higher trait-anxious the less boundary extension (i.e. restriction). In accordance with the abovementioned possible mechanisms underlying this phenomenon (Kensinger et al., 2007), it seems that attention in these individuals is more likely to be focused at the location of the central threat, in addition with a neglect of processing other more peripheral aspects. Individuals with low anxiety scores, on the other hand, may be more able to shift their attention away from such threat content and towards more peripheral aspects. This fits well to the results of other paradigms that have shown that individuals with high trait anxiety are more likely than others to selectively attend to and encode emotionally threatening stimuli (Mathews & MacLeod, 1994; Derryberry & Reed, 1998; Yiend & Mathews, 2001). Here, this happened while those individuals accept close up versions of negative arousing pictures as 'old' more pronounced than the reverse (accepting a more distant picture) and as compared to neutral pictures. Thus it seems that negative pictures were already encoded in a more focused format, whereas neutral ones with extended boundaries (Intraub et al., 1992). The second underlying mechanism considered in the theoretical background chapter is a greater elaboration of the meaning of emotional scenes and a direct enhancement of memory trace encoding as a result of emotional arousal at the time of processing (Cahill & McGaugh, 1995). It however seems to be quite neglectable as this should not have led to encoding failures (what boundary restriction really is). Hereby the results obtained in our study could not be explained via the tendency of emotion to enhance the likelihood that the gist (i.e. general theme) of a scene is remembered, while reducing the probability that specific visual details are

remembered (Adolphs et al., 2005). According to this line of argument, it is quite unlikely that high trait-anxious subjects may have elaborated the critical objects in a negative scene more thoroughly (because they were of special importance for them) and therefore at test accepted the close-up version of such pictures.

Altogether, this study shows that the tunnel memory phenomenon is not a stable effect but depends on several critical variables. The specific test design, test stimuli and method of analysis as well as the emotional reactivity of the spectators seem to modulate its occurrence. Here reduced boundary extension could be demonstrated for negative arousing pictures as compared to neutral ones in the whole group of subjects, as well as boundary restriction for negative arousing pictures only in those with high trait anxiety. This speaks for the fact that in these individuals attention is more likely to be focused on the location of the central threat and less likely to be developed elsewhere. I assume that these negative pictures are already encoded as being closer to the critical object of the scene.

5. General Discussion

5.1 Summary

The present thesis intended to lend contributions to several debates in the current research on emotion and memory. How does our cognitive system succeed in adaptive behavior? How are we guided by emotional experiences? What is the role of automatic attention? To answer these questions, it is of particular interest to find out how emotional stimuli achieve prioritized processing. Clearly it is functionally relevant not to miss threat signals and positive chances, but how does our cognitive system succeed in the guidance of adaptive behavior?

To gain a deeper understanding of this, I analyzed the modulation of memory processes by emotionally arousing stimuli. These memory processes form an essential means when examining the general influence of emotion on behavior. In the present four experiments, it was of particular motivation to create experimental conditions that test recognition memory performance for positive, negative and neutral events. Moreover, I wanted to find electrophysiological correlates of encoding emotional events and to directly set them into relationship with recognition memory performance. Under the assumption that attentional focusing mechanisms for emotional materials are set in train at a first encounter, they should be visible in their ERP correlates as compared to neutral materials. This was examined with respect to manipulations in encoding instruction, the availability of attentional resources for encoding, the amount of arousal and valence of the test stimuli, the context features of the study episode used to test later source memory performance, and the retention duration being immediate or 24 hours after encoding. Additionally, event-related potential measures were obtained for the encoding and retrieval phase of Experiments 1 and 3. These were supposed to give a deeper insight into the mechanisms that underlie the abovementioned phenomena, i.e. for the retrieval phases especially the contribution of familiarity- and recollection-based remembering. Of particular interest were the dissociation of valence and arousal of the processed stimuli in general, which proofed to be of significant relevance, but also particular difficulty.

Experiment 1 shed new light on the issue of how encoding mechanisms for emotional events affect subsequent item and source memory performance. Negative and positive

events elicited a posterior positivity between 250 and 450 ms that presumably reflected attentional capturing of emotionally valenced stimuli. Positive events gave rise to additional anterior and posterior slow wave activity as compared to neutral and negative events and also showed enhanced recognition memory. Yet, a post-experimental rating study revealed that positive events in the present study were perceived as less arousing than negative events for our group of subjects. With respect to this result it was suggested that positive and low arousing events enter controlled and elaborated encoding processes which are beneficial for recognition memory performance. The high arousal of negative events however, may have interfered with controlled encoding mechanisms and attenuated item recognition as well as the quality of remembering. Finally, topographically distinct LPNs in both source tasks were obtained, suggesting that this component reflected processes in service of reconstructing the study episode by binding together contextual details with a test item. These mechanisms may vary with the kind of episodic detail to be retrieved, but did not prove to be susceptible to the influence of emotion.

Experiment 2 was undertaken to test the interpretation of the engagement of controlled encoding strategies for positive low arousing stimuli selectively. By the implementation of a secondary task during encoding (i.e. a dividing attention manipulation), the capacities for these strategies were supposed to be diminished. To summarize, the results of item memory enhancement for low arousing positive pictures of Experiment 1 were replicated in the full attention session, whereas this effect faded when attention was divided at encoding. In the divided attention session, P_r values were comparable for all three emotion conditions. This is in line with the interpretation of strategic encoding operations that are supposed to be engaged for positive low arousing stimuli when attention is not limited by a secondary task. In accordance with the anterior slow wave found for these pictures in Experiment 1 and together with the prefrontal cortex activation of the fMRI study by Kensinger & Corkin (2004), it seems safe to conclude that controlled operations were responsible for the recognition advantage of positive and low arousing pictures in Experiments 1 and 2.

Experiment 3 revealed that the recognition advantage for emotionally arousing pictures and the enhancement in recollective experience benefit from the operation of a time-dependent process consistent with consolidation. The latter was only observed for negative high arousing pictures. Given enhanced positivities during encoding for those pictures, it

was assumed that high arousal has a special influence on the processes underlying memory formation which is manifested at all stages. Moreover, the 24 hour retention duration seemed to be necessary to reveal such dissociations as immediate testing did not show up clear differences between negative high arousing, negative low arousing and neutral pictures. This result was in line with the results of Experiment 1 and may explain the lacking of a recognition memory advantage for negative pictures.

In Experiment 4 it was shown that the special encoding phenomenon called ‘tunnel memory’ is not a stable effect but depends on several critical variables. The specific test design, test stimuli and method of analysis as well as the emotional reactivity of the spectators seemed to modulate the occurrence of the tunnel memory phenomenon. In Experiment 4 reduced boundary extension for negative arousing pictures as compared to neutral ones in the whole group of participants could be demonstrated, as well as boundary restriction for negative arousing pictures only in those participants with high trait anxiety. These individuals might focus their attention more on the location of the central threat and less on other parts of the scene. It was thus assumed that these negative pictures are already encoded as being closer to the critical object of the scene thereby leading to a later failure of memory.

In the upcoming sections, I will discuss these results in detail with respect to the general questions raised in the introduction. Moreover, a link to the current state of the literature is aimed at. This will be done separately for encoding, consolidation, and retrieval processes. In the final paragraph, prospects for future research will be outlined.

5.2 Emotion and encoding processes

With respect to the modulation of encoding processes by the valence and arousal of a processed stimulus, a multitude of behavioral and electrophysiological data was obtained in the abovementioned four studies. They will be discussed in the following by separation of different conceptual questions.

Are there separate mechanisms for valence and arousal?

Examining the neural correlates of encoding emotional events, a first dissociation could already be revealed in Experiment 1 where different neural correlates were obtained for positive low arousing pictures as compared to negative high arousing ones. The former elicited an early posterior positivity (250-450 ms) and additional anterior slow wave activity (250-1000 ms), whereas the latter only gave rise to the early posterior positivity. An interpretation of these results in light of the different arousal characteristics of the test material is given by a recent study by Kensinger and Corkin (2004). Using fMRI and behavioral measures, they found that distinct neurocognitive processes contribute to memory for highly arousing negative versus non-arousing negative words. An amygdala-hippocampus network was active during the successful encoding of highly arousing words, whereas a prefrontal-hippocampal circuitry was engaged in the encoding of non-arousing and only valent words. This moreover is in agreement with the interpretation of Dolcos and Cabeza's (2002) ERP results and the author's interpretation of an amygdala (reflected in a posterior positivity and related to arousal) and a prefrontal-hippocampus network (reflected in an anterior positivity and related to valence), and lends further support to a dissociation of valence- and arousal-related brain systems. On an electrophysiological level, this was confirmed in Experiment 1 by the anterior slow wave that was obtained for positive pictures, as well as a late posterior positivity. Even though inferences from the scalp topography of ERP effects on underlying neural generators in most cases are problematic and comparisons can only be speculative, the anterior scalp distribution and the sustained nature of the anterior positive slow wave to positive pictures resembles the inferior PFC activity to low arousing emotion words in the Kensinger and Corkin (2004) study and may reflect enhanced PFC activation devoted to the encoding of positive and low arousing emotional stimulus materials. Moreover, and more specifically, the anterior slow wave may at least in parts also reflect activity of the orbitofrontal cortex. This structure has been found to guide amygdala-hippocampal interactions at retrieval (Smith et al., 2006). In a

similar manner, the orbitofrontal cortex could guide the stimulus attributes that are attended and remembered already during encoding.

However, in addition to encoding strategies, the anterior positivity may also be a reflection of preference, as being raised by Dolcos and Cabeza (2002). This interpretation has ecological validity in the sense that, normally, people are more likely to show preference for positive than for negative stimuli (the Pollyanna effect; Matlin & Stang, 1978). Moreover, this seems to constitute a link to the concept of self-reference referred to by Gusnard, Akbudak, Shulman, and Reichle (2001). Here, the medial prefrontal cortex is associated with self-referential cognitive processing which could in our case mean that participants more likely and more often constituted a connection between themselves and positive pictures than negative or neutral pictures when they first encountered the picture during encoding. Moreover, and in line with the concept of preference, it appears to be of great importance to consider the goals of the participants. It could be shown that with respect to the current goal states, memory performance was enhanced for the congruent class of stimuli (Mather & Carstensen, 2005).

Negative and highly arousing pictures evoked a similar posterior positivity as positive and low arousing pictures in an early, 250 to 450 ms time interval, suggesting that the initial attentional capturing mechanisms were highly similar for both classes of stimuli. This is well in agreement with other recent studies proposing that valence processing comes first (as early as 150 ms), and thereafter the arousal dimension becomes relevant (Codispoti, Ferrari, & Bradley, 2007; Olofsson & Polich, 2007). Moreover, while positive stimuli were subjected to elaborate encoding processes as revealed by sustained positive slow wave activity and enhanced recognition memory performance for these stimuli, negative pictures apparently did not enter this processing stage. As no memory enhancement was obtained for negative pictures, it is conceivable that negative events due to their high arousing characteristics may have initiated the retrieval of autobiographic memories or personal experiences of task-irrelevant events (e.g. the last personal encounter with a given object) and by this were subjected to controlled encoding operations to a lower extent than positive and neutral events. This phenomenon could reflect the higher biological relevance of negative stimuli which in an evolutionary sense may guarantee that biologically relevant events are not ignored or taken as irrelevant. The fact that an attenuated parietal old/new effect was observed for negative pictures at retrieval is consistent with such a memory distraction function of highly arousing events. This distraction function of highly arousing events observed in the present study may just be another instance of the automatic capture

of attention by emotional events as for example observed in form of interference effects of emotionally valenced words in the emotional Stroop paradigm (Schimmack, 2005).

Encoding activity in Experiment 3 using incidental instructions is comparable with the stimulus classification paradigms of Schupp et al. (2000; 2006). They consistently found the late posterior positivity (LPP) to be modulated by the level of arousal with increasing arousal producing greater positivities. In a recent study using combined ERP and fMRI recordings (Sabatinelli et al., 2007), the late posterior positivity was shown to be a reflection of activity in visual cortical structures demonstrating a higher perceptual sensitivity to the relevance of emotional visual scenes. The ERP results of Experiment 3 seem to entirely fit to the data of Schupp et al. (2000; 2006) with a larger late posterior positivity for negative high arousing than low arousing pictures, but additionally modulated anterior electrodes in the same manner. Hereby, a dissociation of low arousing pictures from high arousing ones with regard to timing (longer lasting for the latter pictures) and topography (more widespread for the latter pictures) was evident. It was assumed that even without the intention to encode the pictures, subjects felt different for low arousing than high arousing pictures that thus were processed in separable ways. This may be due to activity of the amygdala and the MTL memory system and accompanied by a feeling of arousal and enhanced perceptual fluency for high arousing stimuli only realized via the automatic attention capture of these stimuli. For the low arousing pictures subjects may be inclined to elaborate on this information or to rehearse it (Kensinger & Corkin, 2004). This may be reflected in the later onsetting posterior positivity and the long lasting anterior slow wave in our data, even though inferences from the scalp topography of ERP effects on underlying neural generators is problematic and comparisons can only be speculative. When trying to link the current results with Experiment 1 using intentional encoding instructions and positive low arousing and negative high arousing pictures as stimulus materials, they might make additional sense. There, the anterior slow wave (elicited by low arousing positive stimuli) was assumed to be a reflection of controlled encoding strategies and the posterior positivity (present for low arousing positive and higher arousing negative pictures) one of initial attentional capturing mechanisms. The selective elicitation of the latter however did not lead to enhanced recognition memory performance for negative pictures after a short delay, whereas the additional anterior slow wave did for positive ones. For the current results this could mean that for high arousing negative pictures (even higher arousing than in Experiment 1 as revealed by the normative IAPS rating) attentional capturing mechanisms were initiated and in addition with anterior

(most likely controlled PFC activity) operations were successful, and thus led to the recognition memory advantage in quantity and quality for negative high arousing pictures. Low arousing negative pictures here produced a smaller anterior slow wave and a later onsetting posterior positivity which both may contribute to a recognition advantage as compared to neutral pictures that was nevertheless not as pronounced as for negative high arousing ones, but more likely resemble the data of Kensinger and Corkin (2004) using non-arousing negative words as stimulus materials.

Our results lend further support to this notion and provide evidence that not only the arousal characteristics, but also the valence (positive or negative) may be of high relevance when trying to interpret the obtained differences. To clearly disentangle the contributions of arousal and valence with respect to encoding processes, it is of particular interest to use all these kinds of stimuli (negative high arousing, negative low arousing, positive high arousing, positive low arousing) in one paradigm with intentional and incidental instructions separately.

Divided versus full attention during encoding of emotional stimuli

The term divided attention task refers to an experimental task in which participants learn information while performing a concurrent task that is easy (taking few resources from the encoding operation) or hard (shifting resources from the encoding operation) (Craik et al., 1996; Naveh-Benjamin, Craik, Gavrilesco, & Anderson, 2000). This manipulation is supposed to tax the general attention system and working memory capacity. Participant's performance is usually worse for items encoded with a hard than with an easy task. PET (positron emission tomography) studies using such a paradigm found less activation in regions of the prefrontal cortex with performance of a secondary task versus no secondary task (Shallice et al., 1994). These affected regions have been linked to episodic encoding (Wagner et al., 1998; Paller & Wagner, 2002). It is supposed that these regions have shown greater activation during encoding with no secondary task versus a secondary task because some encoding-related processes could not be performed with concurrent performance of the secondary task (Fletcher et al., 1995).

The additional behavioral study by Kensinger and Corkin (2004) revealed that memory for highly arousing negative words was still enhanced even when a divided attention manipulation was used at study, whereas memory for non-arousing negative words declined when encoding resources were devoted towards a secondary task. By these results

it is supported that memory enhancement for valenced but non-arousing materials relies on controlled and self-generated encoding processes such as elaboration and rehearsal whereas memory enhancement for arousing words occurs automatically. Experiment 2 of the present thesis, using a comparable divided-attention manipulation, confirmed these results as the recognition advantage for positive low arousing pictures was diminished in the divided as compared to the full attention encoding session. In the former, all three classes of stimuli (negative high arousing, neutral, positive low arousing) were recognized to a comparable extent. This further substantiates the interpretation of the present ERP results of a selective anterior slow wave for positive low arousing pictures to reflect activity of the prefrontal cortex and thus being responsible for the engagement of controlled encoding operations. It can thus be argued that the memory enhancement for valenced but non-arousing materials relies on controlled and self-generated encoding processes such as elaboration and rehearsal, whereas memory enhancement for arousing words occurs automatically.

Are there particular subsequent memory effects for emotional stimuli?

To even further test the idea of controlled and top-down driven encoding processes for positive and low arousing pictures, a subsequent memory analysis (for a review see Paller & Wagner, 2002) was conducted in Experiments 1 and 3. There is some consensus that parts of ERP subsequent memory effects reflect top-down driven processing like attentional orienting towards events or elaborated mnemonic strategies in support of episodic encoding, as well as other parts being related to bottom-up processing (Karis et al., 1984; Paller & Wagner, 2002; Mecklinger & Müller, 1996). If controlled and top-down modulated encoding strategies were engaged and are reflected in the anterior slow wave, then this component should be sensitive to the later memory status. To test this assumption a dm analysis was run. This revealed that the anterior positive slow wave (450 to 850 ms) was larger for later remembered positive pictures as compared to later forgotten ones, whereas the posterior positivity (250 to 450 ms) was not modulated by subsequent memory performance. This selective modulation of the anterior positive slow wave by subsequent memory performance confirms the view that it reflects top-down driven encoding processes for positive and low arousing events. In contrast, the posterior positivity may reflect the automatic bottom-up-driven attentional capturing of valent stimuli.

The subsequent memory effects in Experiment 3, obtained for high and low arousing negative pictures in the short and long retention group mirror their recognition memory performance. Whereas the anterior and central parts of the effect were comparable for the two groups and the two classes of negative stimuli, the posterior part showed a dissociation. This is somehow in agreement with the findings of Dolcos and Cabeza (2002) who found an earlier onsetting subsequent memory effect for positive and negative pictures as compared to neutral ones. They conducted the first study of this kind and postulated that the emotional content granted a privileged access to processing resources that resulted in a better encoding of high arousing stimuli. This in turn, resulted in better retrieval of these pictures. Adapted to the present experiment, this could fit the finding of the more widespread and longer lasting dm effect for high arousing negative pictures in the long retention group that also showed the best memory performance. It can only be speculated about the neural generators of this ERP effect, but there is reason to believe that the amygdala, with its connections to several neocortical regions (Amaral et al., 1992) is responsible, together with other regions like the prefrontal cortex and parietal regions associated with emotional processing (LaBar et al., 1999; Lang et al., 1998). The similarity of the subsequent memory effect for high and low arousing pictures at anterior and central sites may suggest that these ERPs reflect comparable involvement of the same neural generators as those associated with successful encoding in fMRI studies examining neutral materials (Brewer et al., 1998; Wagner et al., 1998).

Taken together with the fMRI subsequent memory effects of recent studies (Cahill et al., 1996; Hamann et al., 1999; Dolcos et al., 2003; Kensinger & Corkin, 2004), the present ERP subsequent memory effects are supposed to reflect the activity of the amygdala and hippocampus in their more posterior parts, and the additional engagement of prefrontal regions in more anterior proportions.

The tunnel memory phenomenon

A somewhat different approach was pursued in Experiment 4. To further and more deeply investigate the mechanisms by which emotional arousal affects encoding processes on a behavioral level, the frequently reported phenomenon of tunnel memory was concentrated on. Hereby, it is widely assumed that attention is focused on the emotionally arousing stimuli which are then processed facilitated and prioritized (Dolan & Vuilleumier, 2003).

Therefore individuals are more likely to attend to emotional elements in a scene together with neglecting other neutral ones. This should lead to enhanced memory for the former parts of a picture (see Kensinger et al., 2005). In Experiment 4 this is revealed by the smaller amount of boundary extensions for negative arousing pictures as compared to neutral ones. Subjects less often demonstrate errors (i.e. false alarms to pictures changed in zoom version from smaller to larger) in this direction when encountering a negative than a neutral picture. However, hit rates were comparable for both types of pictures and thus general recognition performance in this study did not seem to be affected by the emotional status of a picture.

Boundary extension seems to be a general phenomenon when remembering scenes (Intraub et al., 1992). According to the authors this effect is due to the fact that pictures are perceived as being part of the real world with space beyond the limits of the picture, also known as the perceptual schema hypothesis (Intraub et al., 1998). To bring this together with the effects of emotion, Safer et al. (1998) argued that selective processing of central emotional details should work against boundary extension (see also Christianson, 1992). The results of Experiment 4 support this claim. The amount of boundary restriction, on the other hand, was not affected by the emotional status of the pictures in the analysis of occurrence of false alarms. However, when performing the extension value analysis (comparable to the one used by Mathews & Mackintosh, 2004) on individually negative rated pictures, a large overall difference between negative and neutral pictures was found (0.10 vs. 0.32). Nevertheless, as no negative values could be obtained, pure boundary restriction was not apparent when all participants were considered. However, the group of subjects with high trait anxiety showed boundary restriction (-0.10) and the negative correlation of the STAI and the extension score for negative pictures underpins this point: the higher trait-anxious the less boundary extension (i.e. restriction). In accordance with the abovementioned possible mechanisms underlying this phenomenon (Kensinger et al., 2007), it seems that attention in these individuals is more likely to be focused at the location of the central threat, in addition with a neglect of processing other more peripheral aspects. Individuals with low anxiety scores, on the other hand, may be better able to shift their attention away from such threat content and toward more peripheral aspects. This fits well to the results of other paradigms that have shown that individuals with high trait anxiety are more likely than others to selectively attend to and encode emotionally threatening stimuli (Mathews & MacLeod, 1994; Derryberry & Reed, 1998; Yiend & Mathews, 2001). Here, this happened while those individuals accept close up versions of

negative arousing pictures as ‘old’ more pronounced than the reverse (accepting a more distant picture) and as compared to neutral pictures. Thus it seems that negative pictures were already encoded in a more focused format, whereas neutral ones with extended boundaries (Intraub, Bender, & Mangels, 1992). The second underlying mechanism considered in the theoretical background chapter is a greater elaboration of the meaning of emotional scenes and a direct enhancement of memory trace encoding as a result of emotional arousal at the time of processing (Cahill & McGaugh, 1995). It however seems to be quite neglectable as this should not have led to encoding failures (what boundary restriction really is). Hereby the results obtained in our study could not be explained via the tendency of emotion to enhance the likelihood that the gist (i.e. general theme) of a scene is remembered, while reducing the probability that specific visual details are remembered (Adolphs et al., 2005). According to this line of argument, it is quite unlikely that high trait-anxious subjects may have elaborated the critical objects in a negative scene more thoroughly (because they were of special importance for them) and therefore at test accepted the close-up version of such pictures.

Section 5.4 will deal with these questions in more detail and in a different respect when discussing the effects of source memory, i.e. the binding of neutral contextual features to emotional items.

At this stage it seems important to mention that there is a current debate on the concept of attentional capturing by emotional stimuli. Explicitly, it remains open if emotional stimuli differently attract attention or if the problem of disengagement is the crucial variable (Fox, Russo, Bowles, & Dutton, 2001; Yiend & Mathews, 2001; Derryberry & Reed, 2002). The latter refers to the inability to redirect attention away from the emotional stimulus. Therefore, it remains unresolved what the underlying mechanism actually is. It is possible that emotional stimuli attracted special attention and were by this means better processed. However, it could also be true that attention remained on these stimuli and was thus not directed to the neutral stimuli, which in the same way resulted in more efficient processing of the former class of stimuli.

5.3 Emotion and consolidation processes

The data of the present experiments suggest that consolidation benefits memory for emotionally arousing stimuli. In Experiment 1 with immediate testing (5 minutes retention interval) no recognition advantage could be obtained for negative high arousing pictures. Instead, positive low arousing pictures were remembered to a greater extent than negative ones with neutral pictures displaying *Pr* values in between the aforementioned two. The special meaning of this effect will be discussed in the following paragraph, but for consolidation processes it nevertheless means that without the initiation of them, high arousing (here negative) pictures do not gain advantageous memory performance. This is consistent with the findings of Experiment 3. Here, negative high and low arousing pictures were equally well remembered as neutral ones in an immediate test (5 minutes retention interval). Importantly, a 24 hour retention interval revealed differences between the three classes of items. *Pr* values of negative high and low arousing pictures were higher than for neutral ones. Taking a sole look at the hits even revealed differences between high and low arousing pictures, the former exhibiting the highest amount of recollected items. These behavioral results provide evidence for the necessity of the initiation of consolidation processes that lead to enhanced performance for negative stimuli. This is consistent with other behavioral studies showing the same pattern of results (LaBar & Phelps, 1998; Sharot & Phelps, 2004; Sharot & Yonelinas, 2008). These studies partially showed no forgetting or even enhancements for arousing stimuli over a 24 hour interval as compared to immediate testing.

On a behavioral level, there are several possible explanations for this effect. The first is along the lines of the action-decrement theory by Walker (1958) claiming that action decrement is a refractory state that follows performance of a response, correlating with the amount of learning that has accumulated at that same response over time. The superior consolidation due to high arousal is advantageous over time, but produces a more intense refractory state in immediate tests. Thus, information learned under high arousal is supposed to be especially pronounced at delayed test. The second explanation is according to Revelle and Loftus's tick-rate hypothesis (Revelle, 1989; Revelle & Loftus, 1990) which suggests that arousal increases the rate at which a scene is sampled, interfering with accessibility in immediate memory. However, an increase in the rate at which the to-be-learned material is linked with internal and external context may thus aid long-term retrieval.

With regard to the quality of remembering, Experiment 3 showed that as compared to neutral and negative low arousing pictures, negative high arousing pictures were remembered with enhanced recollective experience as reflected in the selective late parietal old/new effect for this class of stimuli. In a behavioral study using the remember/know procedure (Yonelinas & Jacoby, 1995), Sharot et al. (2007) could show that recollective experience for negative arousing pictures was even enhanced after delay as compared to immediate testing. Familiarity-based responses were not affected by testing delay which seems to be consistent with our electrophysiological data of Experiment 3. The authors thus concluded that emotion elicits a mechanism that modulates memory retention, resulting in greater vividness and confidence of memories for emotional events after a delay. This is in accordance with the notion that the emotional advantage in the recollective experience is due in part to slower forgetting, and with the suggestion that the sluggish consolidation of memories serves an adaptive function by enabling neurohormonal processes triggered by an arousing stimulus to modulate memory strength over time.

On a neural level this is supposed to happen via stress hormones that influence noradrenergic activation within the basolateral region of the amygdala, and amygdala activity in turn modulates memory processing in other brain regions, e.g. the hippocampus via long-term potentiation (Cahill & McGaugh, 1998). These processes are fairly researched in humans, but there are attempts to even link behavioral experiments with these mechanisms. In a recent study (Anderson et al., 2006) subjects encoded neutral and emotional (both positive and negative) pictures. The former were presented either 4 or 9 seconds before arousing (or neutral) stimuli. During a recognition test administered one week later, remember/know judgment had to be given. Memory performance for the emotional stimuli varied directly as a function of subjectively experienced arousal with more arousing pictures remembered to a greater extent than low arousing ones. Additionally, memory for neutral pictures preceding the emotional ones by 4 seconds (not by 9 seconds) also varied with the emotional intensity of the emotional pictures. Moreover, specific recollection of the pictures, but not judgments of familiarity, was directly related to the degree of arousal of the pictures. The authors pointed out that it is unlikely that adrenal stress hormones played a role in mediating these effects, because stress hormone release is probably too slow to influence amygdala's functioning within the 4 second window of effectiveness. Also, as peripherally released stress hormones remain active for many minutes, they would have been influential during the presentation

of neutral as well as emotional stimuli. However, PET imaging of amygdala activity (assessed following many minutes of arousal) and event-related fMRI of such activation induced by single items both predict long-term memory of the arousing stimuli (Cahill et al., 1996; LaBar & Cabeza, 2006). Importantly, β -adrenergic activation antagonists (e.g. propranolol) block the increase of amygdala activity and enhanced retention induced by emotional stimuli (Strange & Dolan, 2004; Van Stegeren et al., 2005). Thus, β -adrenergic activation of the amygdala appears to be essential for the short-latency modulation induced by brief and mild emotional arousal such as that observed in the Anderson et al. (2006) study.

For the present results this could mean that there are circumstances under which emotionally negative arousing events result in a direct neurobiological enhancement of memory consolidation, which is only beneficial over time (Experiment 3) and probably too slow to be effective at a short delay. Rather, as shown in Experiments 1 and 2, negative emotional arousal can also have a detrimental influence on immediate retrieval. This could be due to non-terminated short-term consolidation processes. In line with the results of Anderson et al. (2006) it is likely that also some neutral stimuli may have been captured by this effect when presented directly before a negative arousing one (which would be just about 2 seconds away and well in the 4 second interval mentioned above), but cannot have led to systematic effects. The memory enhancement for positive low arousing pictures seen in Experiments 1 and 2 are likely to be established by attentional and elaborative processes for these stimulus materials and possibly do not rely on the same mechanisms as negative stimuli do.

5.4 Emotion and retrieval processes

Regarding the modulation of retrieval processes by the valence and arousal of a to-be-remembered stimulus, the abovementioned four studies provided several behavioral and electrophysiological data points which will be discussed with respect to item and source memory testing.

Item memory performance

The use of immediate and delayed testing, as well as the different types of stimulus characteristics led to distinct patterns of results on a behavioral and an electrophysiological level. In Experiment 1 a recognition memory advantage for positive low arousing as compared to negative high arousing pictures was found after a short retention interval. Additionally, positive low arousing pictures elicited an early frontal and a late parietal old/new effect, whereas negative pictures only gave rise to the former. Thus, it seems that in this study positive pictures were remembered on the basis of familiarity and recollection (for a review of the electrophysiological correlates underlying recognition memory aspects see Mecklinger & Jäger, in press), the latter process not being involved for negative materials. It is generally assumed that the magnitude of the late parietal old/new effect is associated with the amount of information of a study episode being retrieved on the basis of recollection (e.g. Wilding & Herron, 2006). The attenuated late parietal old/new effect for negative pictures likely reflects the smaller amount of negatively valenced items retrieved on the basis of recollection. The immediate recognition test in Experiment 3 gave rise to comparable d' values for negative high arousing, negative low arousing, and neutral pictures, as well as early frontal and late parietal old/new effects for all classes of stimuli. This is only partially consistent with the findings from Experiment 1. At this point it seems to be worth mentioning, however, that stimulus sets were not the same in both studies (for negative and neutral stimulus classes), and that this may have contributed to the present pattern of results. Additionally, the presence of positive stimuli may have prevented negative ones being recognized to a better extent in Experiment 1. Possibly more resources of the subjects were subjected to the elaboration of pleasant picture content (as a consequence of their current goals (see Mather & Carstensen, 2006), which together with the problem of disengagement (Fox et al., 2001) left fewer resources for the processing of negative items.

Moreover, the reduction of recognition memory performance for negative as compared to positive pictures was replicated in the full attention session of Experiment 2. This however fits to the early data by Kleinsmith and Kaplan (1963) and recent ones obtained by Sharot and Phelps (2004), who found that arousing words at immediate testing were recognized to even a lesser extent than neutral ones. There are two possible explanations for this effect as already mentioned in the last section. The first is along the lines of the action-decrement theory by Walker (1958) and the second explanation is according to Revelle and Loftus's tick-rate hypothesis (Revelle, 1989; Revelle & Loftus, 1990). In addition to these two accounts, recent studies imply that the lack of memory enhancement by arousal at immediate test may be specific to cued recall and recognition tests (Richardson, Strange, & Dolan, 2004) rather than to free recall (Strange et al., 2000). It is thus hard to say what might have driven the decrement for negative and high arousing pictures in Experiments 1 and 2. Most likely all these factors add to the current pattern of results.

Another source of possible explanation of the results is the characteristics of the memory task used in Experiments 1 and 2. There is increasing evidence for the view that memory enhancement for highly arousing stimuli is especially pronounced in memory tests with a longer retention interval (LaBar & Phelps, 1998; Sharot & Phelps, 2004). As consolidation of memory occurs over a period of time, and in case of emotional materials involves noradrenergic mechanisms (McGaugh, 2006), the effect of arousal on memory consolidation should be apparent especially pronounced following a delay. The exact duration of this consolidation process is uncertain, but behavioral effects may be evident as soon as 1 hour after encoding (LaBar & Phelps, 1998) and are expected to be visible at least 24 hours later (Sharot & Phelps, 2004). This is highly consistent with the results obtained in Experiment 3 where a short and long retention duration were compared with each other. Here, the behavioral advantage for negative high and low arousing pictures as compared to neutral ones only exhibited over time, which is consistent with prior studies comparing two time points at test (LaBar & Phelps, 1998; Sharot & Phelps, 2004; Sharot & Yonelinas, 2008). These studies however did not compare high and low arousing stimuli which here seem to differ with regard to the amount of hits and false alarms. Both were given to a greater extent to high arousing items which is consistent with prior studies on the emotion-induced recognition bias (Windmann & Kutas, 2001; Windmann et al., 2002) that compared neutral with emotional stimulus materials. Moreover, the quality of remembering was modulated by the arousal status of negative pictures as revealed by a selective parietal old/new effect for high arousing stimuli. This is consistent with the boost

in recollective experience for such items in general, i.e. immediate (Kensinger & Corkin, 2003; Sharot et al., 2004) and delayed testing (Ochsner 2000; Sharot & Yonelinas, 2008; Sharot et al., 2007).

Negative low arousing pictures exhibited the same recognition advantage on a behavioral level, but ‘only’ seemed to be remembered familiarity-based (as revealed by the selective early frontal old/new effect). This is remarkable and provides evidence for a distinction between high and low arousing pictures for their mnemonic relevance, which has until now only been observed for encoding effects (Experiment 1; Kensinger & Corkin, 2004). However, there are other reports that it is specifically arousal that is related to the boost in recollection-based remembering (Dolcos et al., 2005) which fits well to our data. Neutral pictures, that were remembered much less well than negative ones, seem to be done so on the basis of familiarity after the 24 hour delay. There are only two ERP studies that have investigated the effect of retention interval on neutral stimulus materials (Curran & Friedman, 2004; Wolk et al., 2006), and reported an early frontal and a late parietal old/new effect for both time points of testing. The discrepancy from our results might stem from the fact that these studies only used neutral materials and no additional emotionally arousing ones that may compete for processing capacities.

The general modulation of event-related potential old/new effects by emotion is consistent with a line of studies using immediate testing procedures (Windmann & Kutas, 2001; Maratos et al., 2001; Johansson et al., 2004), although the exact manner in which this modulation happens is seemingly affected by a multitude of factors. Using facial expressions, Johansson et al. (2004) found a selective parietal old/new effect for negative pictures, and frontal old/new effects for negative, positive and neutral faces, while recognition performance was not affected. The authors interpreted the difference in quality of remembering considering that both positive and negative facial expressions are of high biological relevance, but that there is an apparent difference in the proximity of the predictable consequences. This is not in accordance with the results of Experiments 1, 2, and 3, but possibly is due to the large difference in stimulus materials. Facial expressions may obtain greater biological self-relevance than most pictures of the IAPS and by this be selectively richly remembered as compared to neutral and positive expressions. The electrophysiological results of Windmann and Kutas (2001), however, fit to our data of Experiments 1 and 3 with no difference in the early frontal and parietal old/new effect for neutral compared to negative stimuli. In this study words were used in an intentionally instructed recognition memory paradigm and made an effort to equalize the inter-item

relatedness for the stimulus classes. Still obtaining a more liberal response bias for negative as compared to neutral words, Windmann and Kutas (2001) argued that the difference in response bias rather reflects flexible criterion setting triggered by emotional valence that works to ensure that especially negative stimuli are not missed or taken as irrelevant. This was inferred by the finding that, although ERP old/new effects were not different for negative and neutral words, waveforms for 'old' responses (hits and false alarms) revealed ERP differences in an early time window (300-500 ms) only for neutral items at frontal sites. This was interpreted as a reflection of response bias effects on ERPs linked to recognition memory. The authors proposed that the non-existing difference for negative words reflects a disinhibition of prefrontal control mechanisms which thus leads to an enhanced false alarm rate for these stimuli. Taken together, the current state of research on immediate and delayed testing cannot directly draw conclusions on the critical variables for modulatory effects of emotional arousal. The results of the present studies lend support for the necessity to investigate different kinds of materials and testing procedures carefully.

Source memory performance and binding mechanisms

Emotional memories are said to produce an enhancement of vividness, as well as an increase in confidence, and consist of more detail (Experiments 1, 2, and 3; Ochsner, 2000; Sharot et al., 2004). However, a parallel boost in memory for the task performed, the location of acquisition, and the point of learning time at encoding was not observed in the abovementioned experiments of this thesis. This suggests that emotion does not provide a general enhancement of recollection, but rather acts in a selective manner. Thus, given that the increase in recollective experience is not always accompanied by better recognition accuracy (Ochsner, 2000; Johansson et al., 2004; Sharot et al., 2007) or memory consistency (Talarico & Rubin, 2003), emotional arousal may enhance this experience without necessarily improving memory for contextual features. Comparable results were obtained in a very recent study by Sharot and Yonelinas (2007) who investigated study task as context information.

Additionally, prior studies showed that encoding instructions can be a critical variable for the occurrence of memory enhancements and impairments for emotional materials. In support of this view is a recent study by Kensinger et al. (2005), which revealed that under incidental encoding instructions, where subjects are unaware that their memory will be

tested subsequently, young adults show good memory for arousing central elements of a scene and poor memory for non-arousing peripheral elements. This memory trade-off disappears under intentional encoding instructions, where young adults show same memories for peripheral features of emotional and neutral scenes. In light of these findings, the result that no impairments of source memory for emotional materials was found in Experiment 1 could be accounted for by controlled encoding strategies, set in train by the intentional encoding instructions. Subjects may have associated the emotional stimuli with the features of the source task (where and when was a particular event encountered) and this may have overwritten the attentional capturing effects for emotional events and detrimental effects on source memory performance. However, this interpretation does not hold for the non-existing source memory modulations in Experiment 3, where encoding instructions were incidental.

Therefore, the type of contextual detail seems to be of even equivalent importance. In a series of experiments, Kensinger and Schacter could show that possibly only aspects of a study episode that are of adaptive value (e.g. the ability to distinguish between seen from imagined items) are better bound to emotionally arousing stimuli than those of less significant meaning (e.g. the task performed) (Kensinger & Schacter, 2005a, 2005b, 2006a, 2006b). Another distinction is made by internally and extrinsically linked details. In line with the studies of Adolphs et al. (2000, 2005), it seems that intrinsically to the emotional item itself liked details (e.g. its physical appearance or its gist) are related to amygdala activity (and thus leads to memory enhancements), whereas elements that are more peripheral or extrinsic to the item (e.g. the task performed with an item) are not. In a study on working memory mechanisms, Mather et al. (2006) provided evidence that the neural processes supporting memory for the spatial location are disrupted by high arousal. These mechanisms may also contribute to enhanced or impaired binding of context information to an item. As noted by Kensinger and Schacter (2006a) in their study on the specific visual details of items, this is another means by which emotional arousal can enhance the binding to 'context' features. These include the color of font in which a word was written, the screen color on which a word was viewed (Doerksen & Shimamura, 2001; D'Argembeau & Van der Linden, 2004; MacKay et al., 2004) and the spatial location of a word (D'Argembeau & Van der Linden, 2004; MacKay & Ahmetzanov, 2005). Thus, the use of the task performed, the location of acquisition, and the point of learning time at encoding as context features that are of lesser adaptive value than e.g. the ability to distinguish between seen from imagined items, or their categorization as extrinsically

linked (as compared to intrinsically) seems to be at least in part responsible for the non-existing modulation of their binding to emotional items in Experiments 1 and 3.

Moreover and importantly, there are a number of studies on emotional source memory in which neutral items are presented in either neutral or emotional contexts (Maratos & Rugg, 2001; Smith, Dolan & Rugg, 2004a; Smith, Henson, Dolan, & Rugg, 2004b; Smith et al., 2006). These constitute either presenting a neutral picture in context of an emotional one, or presenting a neutral word in an emotionally valenced sentence. On the one side, these studies reliably demonstrate a positive effect of the emotional content of information on source memory, i.e. when the contexts to be retrieved are themselves emotional (Smith et al., 2006). On the other side, specific ERP effects are observed for correctly retrieved emotional contexts (Maratos & Rugg, 2001; Smith et al. 2004). As these studies consistently used neutral items (presented in either emotional or non-emotional contexts) and the present studies employed emotional items in neutral context, the aforementioned studies and the experiments of this thesis differ in important aspects. By this the latter findings do not speak against the present interpretation of an attentional capturing function of negative and highly arousing events. Rather, the findings of both experimental approaches suggest, that depending on task characteristics and retrieval demands, the emotional content of information exerts differential mnemonic effects.

Electrophysiological correlates of contextual retrieval

A different issue addressed in Experiment 1 was the extent to which the LPN, a posteriorly distributed negative slow wave frequently obtained in the test phases of source memory tasks, is modulated by source retrieval requirements in case of emotional events. Former studies have shown that the LPN has a parieto-occipital maximum, onsets at around the time at which a response is given, and is of equal amplitude for correct and incorrect source judgments (Johansson & Mecklinger, 2003; Friedman et al., 2005; Herron, 2007). It was proposed that the LPN reflects the search for and retrieval of contextual features in tests of source memory, and retrieval processes that may act to reconstruct a prior study episode when item-context features are not sufficiently recovered or need continuous evaluation.

Consistent with prior studies, the present study revealed a pronounced LPN in all source tasks, underlining the high relevance of this component in the search/retrieval of attribute conjunctions. This is supported by the finding of comparable LPNs for retrieving the

correct item-context association, as well as in the case of a wrong source judgment. Interestingly, even though LPN amplitude in Experiment 1 was not affected by the emotional contents to be associated with either time or location characteristics of the study episode, it differed in scalp topography between the two source memory tests. Retrieving/searching conjunctions between pictures and study time elicited a more widespread LPN than between pictures and their study location, suggesting that a wider range of contextual attributes are relevant for reconstructing the point of time when an item occurred as compared to where it occurred. The likely generator of this component is the parietal lobe, which has recently been shown to be critically involved in episodic memory retrieval (Wagner, Shannon, Kahn, & Buckner, 2005). The authors propose three hypotheses concerning how parietal cortex might contribute to memory. In case of the retrieval of item-context bindings the ‘output buffer hypothesis’ seems especially important. It is assumed that regions of the parietal cortex dynamically represent retrieved information in a form accessible to decision-making processes. Although long-term memories are not stored in neuronal firing patterns, to influence decision-making, such memories must be expressed in active neuronal response patterns. The parietal cortex could act as the buffer into which stored information is transferred. Moreover, the phenomenon of reinstatement suggests that at least part of the retrieved information is represented in the corresponding sensory areas. Linking these thoughts to the electrophysiology of source memory retrieval, the LPN seems to be another piece of evidence that traditional cognitive-control-PFC models (e.g. Miller & Cohen, 2001) are not sufficient to explain episodic memory retrieval processes.

The nevertheless high relevance of the PFC in situations in which the retrieval of emotional information is task relevant was recently also demonstrated in a study examining the effective connectivity between brain regions relevant for processing mnemonic and emotional information (Smith et al., 2006). In a condition in which emotional contexts of a study phase had to be discriminated, the authors found enhanced effective bidirectional connectivity between hippocampus and amygdala and enhanced activity in the orbitofrontal cortex which in turn increased the hippocampus-amygdala connectivity. This suggests that the requirement to retrieve emotional information constitutes a cognitive set that modulates retrieval in a top-down manner.

Further studies, capitalizing on the high spatial resolution of fMRI measures will be required to elucidate the neural sources of retrieving the mentioned sorts of item-source conjunctions.

5.5 Conclusion

Taken together, the investigation of emotional arousal on memory processes as examined behaviorally and with the use of event-related potentials revealed new insights into the understanding of our cognitive system. Generally, the results lend support to the evolutionary threat theory and the arousal theory regarding the influence of emotion on attention mechanisms. These mechanisms are further highly relevant for the build up of a stable memory trace and guarantee the detection of threat signals in the future, as well as positive chances. Moreover, evidence was obtained that there is individual reactivity with respect to attentional capturing mechanisms by emotion.

Encoding activity was especially sensitive to the valence and arousal characteristics of the stimuli, with positive and low arousing pictures leading to an early attentional capturing mechanism (reflected in a posterior positivity) and a later elaborative processing (reflected in an anterior slow wave) that is of high mnemonic relevance (Experiment 1). Dividing attention at this stage of processing diminished the recognition memory advantage obtained with full attention conditions, possibly by preventing the engagement of controlled encoding operations (Experiment 2). Negative and high arousing pictures elicited a comparable early posterior positivity (Experiments 1 and 3), but did not produce a memory advantage after immediate testing. In Experiment 3 a positivity for these pictures could be obtained across the whole scalp which likely reflects a generally higher activation of the whole brain system when processing highly arousing stimuli. Negative and low arousing pictures here exhibited comparable but significantly smaller positivities. The mnemonic relevance is additionally captured by the subsequent memory effects that presumably directly reflect successful encoding processes responsible for the better memory performance for negative high arousing pictures in the long retention group. At retrieval, negative high arousing pictures were only distinguishable from neutral and negative low arousing ones when tested after a 24 hour delay, with a selective parietal old/new effect likely reflecting recollection-based remembering as opposed to 'only' familiarity-based recognition for the other types of stimuli (Experiment 3). Consolidation mechanisms proved to be of significant importance to make a recognition memory advantage for negative pictures possible, and additionally modulated the richness of remembering (Experiment 3). This means that both the amount of recollected information,

as well as recollection-based remembering profit from a time-dependent consolidation process.

Thus, the data lend support that memory processes are strongly guided by emotionally significant stimuli and that this is highly adaptive for flexible acting in an environment overloaded by cues. The present results strongly confirm a ‘valence evaluation system’ proposed by several researchers (in the domain of cognitive neuroscience especially LeDoux, 1996; but see also Gray, 1991; Mogg et al., 2000). According to this framework and with respect to the interaction of emotion and episodic memory, this can be exemplified as follows. The reoccurrence of a past perpetrator (or another threatening object like a snake, as well as something positive) would in a first step be identified quickly without the retrieval of any detailed information. This is sufficient to gain the information that this person (or object) has e.g. been dangerous and allows immediate preparedness (low road memories, LeDoux, 1996). By means of high road memories rich and detailed information would be retrieved in order to evaluate details of the episode in which this person (or object) has been met. The higher the experienced arousal at the first encounter, the better and richer this memory can be reexperienced. In addition, this is modulated by the time between the first and next encounter. The detection and encoding of a positive opportunity seems to result in a memory advantage already after some minutes. The same does apparently not hold true for negative (more survival-significant) stimuli. Instead, they first produce some kind of ‘confusion’ (perhaps by still processing possible other threatening stimuli and thus hinder consolidation in a first step), but later on (after intense consolidation processes terminated successfully) are well accessible. As revealed by the source memory results of the current studies, it appears that it is only adaptive to encode contextual details inherent in the emotional stimuli or important for their meaning.

As can be inferred from the electrophysiological correlate results in the current study, all these mechanisms and processes seem to mostly rely on emotion-specific brain regions and neural networks. Their development and existence underlines the adaptive value of our cognitive system.

5.6 Perspectives

To get an even deeper insight into the mechanisms by which emotional arousal modulates encoding, consolidation, and retrieval process further research needs to be pursued in several lines.

First and very generally speaking, it seems to be of great importance to use test stimuli comprising the whole spectrum of valence and arousal, being positive and high arousing, positive and low arousing, neutral and non-arousing, neutral and arousing (if existing), negative and high arousing, negative and low arousing. This would be a helpful means by which effects can more directly be attributed to the special valence and/or arousal characteristics of a stimulus.

Moreover, electrophysiological and fMRI measures should be obtained for the intentional and incidental encoding of the abovementioned stimuli. These should aim at the dissociation of automatic and strategic effects modulated by one the kind of instruction and two the valence and arousal of the materials. Here, it would be of special importance to investigate positive and negative stimuli with comparable arousal characteristics in one experiment.

Future research is also needed to elucidate the involvement of stress hormones in humans. It is still of debate whether the effects of β -adrenergic activation of the amygdala can be observed in a short time interval of stimulus presentation, and how this becomes later memory-relevant. Defining a minimum and maximum of consolidation time could also be aimed at in this respect.

A topic of much controversy concerns the binding mechanisms of emotionally arousing stimuli to neutral context features, as well as the binding of neutral stimuli into an emotional context. Here, different features seem to produce either enhancement or impairment effects with regard to later source memory testing. The concrete circumstances under which these happen are supposed to be researched, especially as the emotional reactivity of the spectator seems to be of great importance.

To fully examine the effects on the quality of remembering emotional events, it would be desirable to test recognition performance via the use of behavioral indicators (e.g. the remember/know procedure or ROC curves) in addition to the recording of event-related potentials. This would produce safer conclusions about the engagement of qualitatively different ways of remembering.

In order to clarify the mechanisms by which the tunnel memory phenomenon is elicited, imaging data (ERPs or fMRI) of a suitable design would be desirable. Hereby, attentional versus elaborative mechanisms could be dissociated and lend to a better understanding of how these effects are modulated in individuals with differing emotional reactivity (e.g. trait anxiety).

6. Zusammenfassung

6.1 Einleitung

Am Morgen beobachten Sie auf dem Weg zur Arbeit einen Autounfall, die Pasta beim Mittagessen schmeckt unerwartet gut, Bilder eines Flugzeugabsturzes in den Abendnachrichten machen Sie betroffen. Das tägliche Leben ist dominiert von Ereignissen, die diverse Nuancen und Plateaus von Gefühlen auslösen. Was passiert, wenn wir versuchen diesen Erinnerungen an die Ereignisse näher zu kommen? Wie verändert sich das spätere Wiedererkennen oder der Abruf des Autounfalls, des Mittagessens, der Fernsehnachrichten, weil diese Erfahrungen emotionale Reaktionen auslösten, als sie zum ersten Mal auftraten?

Viele verschiedene aufeinander bezogene wissenschaftliche Herangehensweisen (kognitive, neurowissenschaftliche) wurden unternommen, um sich diesem Sachverhalt zu widmen. Zumeist betrafen sie die Frage, ob emotionale Erinnerungen besser und lebhafter als neutrale erlebt werden (z.B. Ochsner, 2000); ob zentrale oder periphere Details von Erinnerungen durch Emotionen unterstützt werden (z.B. Christianson, 1992; Safer et al., 1998); und ob es die emotionale Valenz oder der Grad des Arousal (der emotionalen Erregung) ist, der bestimmt wie gut eine emotionale Episode erinnert wird (z.B. Matlin & Stang, 1978). Diese gesammelten behavioralen, und in letzter Zeit auch vorwiegend bildgebenden, Daten beschreiben die Bedingungen, unter denen Erinnerungen für emotionale Ereignisse und Stimuli verzerrt oder zerstört werden (z.B. Schacter, 1996); die Arten und Details von Information, die diesbezüglich besonders resistent sind (z.B. Heuer & Reisberg, 1992); und wie valente Stimuli, Stimmungen oder Grade von Arousal diese Effekte modulieren (z.B. Bradley et al., 1992; Christianson, 1992). Es steht allerdings noch aus, und es ist gleichzeitig von enormem Interesse, was die exakten Umstände sind, die zu Gedächtnisbeeinträchtigungen und Gedächtnisverbesserungen führen.

In anderen Bereichen der kognitiven Neurowissenschaften bieten die Untersuchung von hirnerkrankten Patienten einen zentralen Ausgangspunkt, um Struktur-Funktions-Beziehungen zu entschlüsseln, in diesem Fall zu bestimmen, welche Aspekte von emotionalen Erinnerungen vom Funktionieren der Amygdala (des Mandelkerns) abhängen. Beim Menschen betreffen organische Syndrome die Amygdala selten selektiv. Schlüsseleinsichten haben die Untersuchung von postoperativen Studien bei Temporallobektomie-Patienten mit unilateraler Verletzung des MTLs infolge einer

Epilepsie, sowie von Patienten mit selektiver bilateraler Amygdalopathie aufgrund der Urbach-Wiethe-Krankheit, gebracht.

Ausgehend von den frühen behavioralen Befunden von Kleinsmith und Kaplan (1963) haben Studien an gesunden Erwachsenen gezeigt, dass Gedächtnisverbesserungen für emotionales Material manchmal über die Zeit besser werden. Beispielsweise sind die Retentionsvorteile für emotional erregende Wörter im Vergleich zu neutralen größer, wenn das Gedächtnis für solche nach einem langen (1 Stunde bis 1 Tag) versus ein kurzes (sofort folgendes) Intervall getestet wird (LaBar & Phelps, 1998; Sharot & Phelps, 2004). Solche Beobachtungen leisten Evidenz, dass emotionales Arousal die Erinnerung zu einem Teil aufgrund von erleichterter Konsolidierung, die Zeit braucht um vorstatten zu gehen, verbessert. Temporallobektomie-Patienten zeigen keine verbesserte Arousalgeleitete Gedächtniskonsolidierung, sondern vergleichbare Vergessensraten für neutrale und emotional erregende Wörter bei einem sofortigen Testzeitpunkt bis zu einem Retentionsintervall von einer Stunde (Phelps et al., 1998). Patienten mit Urbach-Wiethe-Krankheit zeigen vergleichbare Beeinträchtigungen beim Abruf oder dem Wiedererkennen von emotionalen Wörtern, Bildern und Geschichten (Markowitsch et al., 1994; Adolphs et al., 1997). Somit hat sich die Amygdala als hochrelevant für Gedächtnisverbesserungseffekte herausgestellt.

Emotionales Arousal hat auch komplementäre, sofortige Effekte während des Enkodierens gezeigt, die zeitinvariant sind, und als attentionale Beeinflussungen auf das Gedächtnis interpretiert wurden (Hamann, 2001). Eine solche weitere Konsequenz emotionalen Arousal ist das Fokussieren von Aufmerksamkeit auf zentrale Information einer Szene auf Kosten von peripheren Details, wie das Beispiel des Waffenfokus (Stebly, 1992) in der Zeugenaussagenforschung veranschaulicht. Attentionales Fokussieren versichert, dass emotional bedeutsame Teile von komplexen Szenen bevorzugt im Gedächtnis abgelegt werden, was evolutionäre Vorteile mit sich bringt. Patienten mit Amygdalaschädigung fokussieren nicht auf diese zentrale Information, wenn die Erinnerung für audiovisuelle Erzählungen, die emotional erregende Ereignisse beschreiben, getestet wird (Adolphs, Tranel, & Buchanan, 2005).

Die große Relevanz der Erforschung von Emotion und Gedächtnis liegt auch in dem erwünschten Verständnis von psychiatrischen Krankheiten, die diese beiden Konzepte betreffen, begründet. Von besonderer Wichtigkeit ist hierbei die Posttraumatische Belastungsstörung (PTBS). Sie entsteht nach Aussetzen eines traumatischen Stressors, der Furcht, Horror oder Hilflosigkeit auslöst, und körperliche Verletzung oder Bedrohung

einer Verletzung, sowie den eigenen Tod oder den einer anderen Person einschließt. Diagnostische Symptome umfassen das persistierende Wiedererleben des traumatischen Ereignisses, die Vermeidung von erinnernden Details, Verarmung von Reaktionen, und erhöhtes Arousal. Neurobiologische Modelle von PTBS fokussieren auf Gehirnregionen und Stresshormonsystemen, die an Furcht, Arousal und emotionalem Gedächtnis beteiligt sind. Chronischer Stress bei PTBS trägt zum einen zu kleinerem Hippocampusvolumen und Defiziten im deklarativen Gedächtnis bei (Bremner et al., 1995); zum anderen präzisieren kleinere Hippocampi die Symptomschwere bei PTBS (Gilbertson et al., 2002). Um zielgerichtete Behandlungen für diese Krankheit zu finden, ist es von großem Interesse das grundlegende Funktionieren des Gedächtnisses in Verbindung mit Emotion tiefer zu verstehen. Nicht zuletzt deswegen versucht diese Dissertation offene Fragen in Bezug auf verschlechternde und verbessernde Effekte von Emotion auf Gedächtnisprozesse zu beantworten. Dabei ist es von besonderem Interesse die genauen Gegebenheiten, d.h. situationalen und persönlichen Faktoren zu greifen, die zu pathologischer Emotionsverarbeitung führen können.

Im Folgenden werden vier Studien (zwei behaviorale und zwei EKP-Studien) beschrieben, die Enkodier-, Konsolidierungs-, und Abrufprozesse mit ihren zugrunde liegenden elektrophysiologischen Korrelaten untersuchen. Ich werde mich den zentralen Fragen widmen, ob und unter welchen Umständen negative und positive Ereignisse auf andere Art und Weise enkodiert werden als neutrale, und ob diese Mechanismen zu dem viel beschriebenen Gedächtnisvorteil führen. Des Weiteren wird es darum gehen, ob der Abruf der Bindung des emotionalen Ereignisses an neutrale Kontextmerkmale aus der Studierepisode infolge eines „attentional capturing“ der emotionalen Reize abgeschwächt wird. Wie machen sich bei all dem Unterschiede in der Valenz und im Grad des Arousals bemerkbar? Und was macht ein verlängertes Retentionsintervall in Bezug auf die Gedächtnisleistung aus? Wie werden die elektrophysiologischen Korrelate des Rekognitionsgedächtnisses (der frühe frontale und der späte parietale alt/neu-Effekt) moduliert? All diese Fragen sollen in den folgenden Experimenten eine Antwort erhalten.

6.2 Experimente

Experiment 1 untersuchte die zentrale Hypothese, ob emotionale Ereignisse (positive und negative Bilder) besser und qualitativ anders erinnert werden als neutrale. Das EEG wurde hierzu bei 20 Probanden in 2 Sitzungen abgeleitet. In der Orts-Sitzung hatten die Probanden die Aufgabe sich fotografische Bilder aus dem IAPS (International Affective Picture System), und den Ort an dem sie sie sehen, einzuprägen. Hierbei befanden sie sich in 2 verschiedenen Räumen. An einem dritten neutralen Ort unterzogen sich die Versuchspersonen ca. 5 Minuten nach der Lernphase einem Rekognitions- und einem Quellengedächtnistest. Dazu wurden ihnen neue und alte Bilder präsentiert, die gemäß diesen Status in einem ersten Schritt klassifiziert werden mussten. Nach jeder „alt“-Antwort war zusätzlich anzugeben, ob das Bild in Raum 1 oder Raum 2 gesehen wurde. In der Zeit-Sitzung, die an einem anderen Tag stattfand, sollte sich als Quellenmerkmal der Enkodierzeitpunkt gemerkt werden, d.h. ob das jeweilige Bild in Liste 1 oder Liste 2 (getrennt durch eine Pause) präsentiert wurde. Es wurde erwartet, dass positive und negative Bilder auf Itembasis besser erinnert werden als neutrale. Gemäß dem Konzept des „attentional capturing“ von emotionalen Reizen wurde zudem die Hypothese formuliert, dass das Quellengedächtnis für diese Reize vermindert sein sollte. Auf elektrophysiologischer Ebene wurde die Hypothese verfolgt, ob die PP (posteriore Positivierung) während des Enkodierens in einem Zusammenhang mit der Gedächtnisabrufleistung steht. Unter der Annahme, dass sie automatische Aufmerksamkeitsprozesse widerspiegelt, und diese für den Gedächtnisvorteil emotionaler Reize verantwortlich ist, sollte sie mit dem Auftreten dessen kovariieren. Des Weiteren sollte herausgefunden werden, ob positive und negative Bilder einen frontalen und parietalen alt/neu-Effekt auslösen, d.h. familiaritäts- und rekolektionsbasiert erinnert werden; und ob sich diese Effekte von denen für neutrale Bilder unterscheiden. Gemäß vorheriger behavioraler (Ochsner, 2000) und elektrophysiologischer Studien (Johansson et al., 2004) wurde angenommen, dass emotionale Reize detailreicher (d.h. zu einem größeren Ausmaß rekolektionsbasiert) erinnert werden. Zuletzt ging es um die LPN (späte posteriore Negativierung) und die Frage, ob sich diese für emotionale Reize und verschiedene Quellengedächtnismerkmale unterscheidet. Einige dieser Hypothesen konnten bestätigt, andere mussten aufgrund der Datenlage verworfen werden. Auf behavioraler Ebene konnte ein Rekognitionsvorteil für positive Bilder verzeichnet werden. Zwischen dem Pr-Maß für negative und neutrale Bilder gab es keinen signifikanten

Unterschied. Die Quellengedächtnisleistung war zudem nicht beeinflusst vom emotionalen Status des Bildes, weder in der Orts- noch der Zeitversion. Während des Enkodierens fand sich für positive und negative Bilder eine frühe PP (250-450 ms) im Vergleich zu neutralen Bildern, sowie eine sich anschließende positive slow wave an posterioren und anterioren Ableiteorten ausschließlich für positive Bilder. Während des Gedächtnisabrufes ergaben sich frühe frontale alt/neu-Effekte für alle Klassen von Bildern. Einen späten parietalen alt/neu-Effekt lösten allerdings nur neutrale und positive Bilder aus. Die LPN konnte für alle Reizgruppen gefunden werden, allerdings war sie in der Orts- und Zeitversion räumlich unterschiedlich verteilt. Zusammenfassend kann man sagen, dass der emotionale Gehalt der Bilder sowohl Enkodier- als auch Abrufprozesse beeinflusste; allerdings in einer nicht unbedingt erwarteten Art und Weise. Ein anschließendes Rating der Stimuli von der Versuchspersonengruppe ergab, dass sich positive und negative Bilder nicht nur in Bezug auf die Valenz, aber auch das Arousal unterschieden (was präexperimentell eigentlich durch das normierte IAPS-Rating gewährleistet worden war). Negative Bilder erhielten ein signifikant höheres Arousal-Rating als positive. Eine ebenfalls post-hoc durchgeführte Dm-Analyse (d.h. subsequent memory-Analyse) ergab zudem, dass lediglich die anteriore slow wave für positive Bilder sensitiv für den späteren Gedächtnisstatus war. Es kann also gefolgert werden, dass der Verarbeitung negativer (stark erregender) und positiver (schwach erregender) Bilder unterschiedliche Prozesse zugrunde liegen. Hinweise darauf gab die fMRI-Studie von Kensinger & Corkin (2004), die für negativ hocherregende und nichterregende Wörter in einer Dm-Analyse herausfanden, dass unterschiedliche neuronale Netzwerke zum erfolgreichen Enkodieren der Reizklassen verantwortlich waren. Der linke Hippocampus und die Amygdala waren zentral an der Verarbeitung hocherregender negativer Wörter beteiligt, demgegenüber der Hippocampus und der linke inferiore PFC für nichterregende. Des Weiteren reduzierte in einer behavioralen Zusatzstudie die Verwendung einer Ressourcenteilenden Manipulation zu einem selektiven Ausbleiben des zuvor für beide Reizklassen gefundenen Gedächtnisvorteils bei den nichterregenden Wörtern. Während in Experiment 1 die negativen Reize scheinbar eher einer automatischen Verarbeitung unterliegen, werden positive wahrscheinlich durch den Einsatz elaborierter Enkodierstrategien eingepreßt; was unter den gegebenen Test Umständen zu einem Gedächtnisvorteil führte. Die Frage welche Variablen dies begünstigt haben (z.B. Enkodierinstruktion, Zeitpunkt der Testadministration), bleibt in den kommenden Experimenten zu klären.

Experiment 2 sollte gemäß der Interpretation der Ergebnisse aus Experiment 1 testen, ob positive und negative Bilder tatsächlich aufgrund ihrer unterschiedlichen Arousal-Werte auf verschiedene Art und Weise enkodiert wurden. Hierzu diene eine geteilte Aufmerksamkeits-Manipulation während des Enkodierens der Bilder. Wenn positive Bilder wirklich aufgrund von strategischen selbstgenerierten Operationen eingepägt wurden, dann sollte eine Verringerung der Ressourcen diese unterbinden. Wenn die Versuchspersonen also während des Enkodierens eine weitere Aufgabe zu bearbeiten haben, dann sollte dies dazu führen, dass der Rekognitionsvorteil für positive Bilder ausbleibt. Dies wurde mit einer behavioralen Studie getestet, in der 20 Probanden in zwei Sitzungen (der full attention-Bedingung (FA) und der divided attention-Bedingung (DA)) das Experiment 1 durchliefen. Hierbei wurde lediglich die Ortsversion verwendet, da sich hier die größten Unterschiede in den Pr-Maßen zeigten. Die Hypothese konnte bestätigt, und somit die Interpretation aus Experiment 1 untermauert werden. In der full attention-Bedingung stellte sich erneut ein selektiver Rekognitionsvorteil für positive Bilder ein. Demgegenüber blieb dieser in der divided attention-Bedingung aus, wo die Pr-Maße für alle Emotionsklassen vergleichbar waren. Negative und neutrale Bilder wurden in dieser Bedingung zwar auch schlechter erinnert als in der ursprünglichen, allerdings war dies nur ein numerischer Unterschied. Experiment 2 konnte nun also eindeutig den wahrscheinlichen Einsatz kontrollierter Enkodierstrategien für positive Bilder stützen, und trägt damit entscheidend zu der angenommenen Dissoziation von unterschiedlich valentem und erregendem Material bei. In dem hier gezeigten Fall wurden negative und stark erregende Bilder scheinbar über einen relativ automatischen Mechanismus enkodiert, der zu keinem Gedächtnisvorteil führte. Positive und schwach erregende Bilder profitierten demgegenüber vom wahrscheinlichen Einsatz selbstgenerierter Enkodieroperationen, und wurden auf diese Weise besser enkodiert und erinnert als negative und neutrale Reize.

In Experiment 3 sollten nun die noch offenen Fragen aus Experiment 1 in einer weiteren EKP-Studie bearbeitet werden. Hierzu wurden zwei elementare Faktoren manipuliert: die Enkodierinstruktion und das Retentionsintervall. Im Vergleich zu Experiment 1 wurden neutrale und zwei Klassen von negativen Bildern verwendet, solche mit hohem und solche mit niedrigem Arousal. Des Weiteren wurden die Bilder nicht intentional, sondern inzidentell enkodiert. Als Quellenmerkmal diene die Enkodieraufgabe, die zu absolvieren war (drinnen/draußen oder größer/kleiner als der Bildschirm). Eine Gruppe von

Versuchspersonen (n=20) unterzogen sich dann nach 5 Minuten dem Quellenrekognitionstest, die andere Gruppe (n=20) einen Tag (im Mittel 24 Stunden) später. Da emotionale Reize von erhöhten Konsolidierungsprozessen profitieren sollen (z.B. Sharot & Phelps, 2004), wurde in der Gruppe mit dem Test nach einem Tag eine verbesserte Gedächtnisleistung im Vergleich zu neutralen Bildern erwartet. In der Tat fanden sich in der Gruppe mit dem direkt folgenden Test keine Unterschiede in den Prämaßen zwischen den drei Reizklassen. Zudem ergab sich elektrophysiologisch keine Differenzierung, alle Bedingungen lösten einen frühen frontalen und einen späten parietalen alt/neu-Effekt aus. Demgegenüber zeigte sich in der anderen Gruppe von Probanden eine deutlich bessere Rekognitionsleistung für negative hoch- und niedrigerregende Bilder im Vergleich zu neutralen. Des Weiteren gab es eine weitere Dissoziation im EKP-Bereich. Während alle Bilder aufgrund von Familiarität (reflektiert durch den frühen frontalen alt/neu-Effekt) wiedererkannt wurden, spielte bei negativen hocheherregenden Bildern zusätzlich die Rekolektion (später parietaler alt/neu-Effekt) eine entscheidende Rolle. Diese Klasse von Bildern wurde also qualitativ und quantitativ besser bzw. hochwertiger erinnert. Während des Enkodierens zeigten sich weitere Unterschiede zwischen den Bilderarten. An nahezu allen Ableiteorten verliefen die von negativ hocheherregenden Bildern ausgelösten EKPs deutlich positiver als solche von negativ niedrigerregenden und neutralen, beginnend um 250 ms. Negativ schwacherregende Bilder demonstrierten aber auch positivere EKPs als neutrale Bilder, an posterioren Elektroden ab 600 ms und an anterioren ab 350 ms. Eine Dm-Analyse bestätigte die vorgezogene Verarbeitung negativer, insbesondere hocheherregender, Reize. Es fanden sich anteriore und posteriore dm-Effekte für diese Stimuli, länger andauernd für hocheherregende Bilder. Diese Prozesse scheinen somit schon die bessere anschließende Gedächtnisleistung vorhersagen.

Experiment 4 widmete sich dann noch dem viel berichteten Tunnelgedächtnisphänomen in besonderem Detail. Dafür wurde ein neues Design entwickelt, das die Schwächen der in der Literatur bereits vorhandenen eindämmen sollte. 36 Versuchspersonen unterzogen sich also einem Gedächtnistest der spezifischen Art. In einer inzidentellen Enkodierphase sahen die Probanden neutrale und negative Bilder aus dem IAPS in 3 verschiedenen Zoom-Varianten, und sollten sie bezüglich ihrer Valenz auf einer 3-Punkt-Skala klassifizieren. Nach einer 15-minütigen Pause war dann ein Gedächtnistest in Bezug auf die Zoom-Variante zu absolvieren. Es wurden zu einem Teil die gleichen Bilder wie in

der Enkodierphase gezeigt, sowie in der Zoom-Variante veränderte. Die Aufgabe der Probanden war dies zu detektieren. Bei gleichen Bildern sollte „alt“, und bei in jegliche Richtung veränderten Bildern „neu“ geantwortet werden. Von besonderem Interesse waren nun „alt“-Antworten auf veränderte Bilder. Wenn die Versuchspersonen ein näher herangezoomtes Bild als „alt“ klassifizierten, wurde der Fehler „boundary restriction“ genannt; wurde ein herausgezoomtes Bild als „alt“ klassifiziert, hieß er „boundary extension“. Es wurde angenommen, dass diese Bilder schon beim Enkodieren als näher heran oder weiter heraus eingepägt wurden. Gemäß der Hypothese in Anlehnung an das Tunnelgedächtnisphänomen sollte bei negativen Bildern der Fehler „boundary restriction“, und bei neutralen Bildern der Fehler „boundary extension“ passieren. Es fand sich allerdings eine Tendenz zu „boundary extension“ für beide Reizklassen, welche für negative Bilder kleiner ausfiel als für neutrale. Betrachtete man nun die Gruppe von Probanden nach einem Mediansplit in Bezug auf ihre Eigenschaftsangst, fand sich in der Tat „boundary restriction“ in der hochängstlichen Gruppe für negative Bilder. Dies legt nahe, dass Aufmerksamkeitsprozesse zu diesem Gedächtnisfehler beitragen, die bei Menschen mit hoher Eigenschaftsangst besonders anfällig für negatives Material zu sein scheinen.

6.3 Diskussion

Die beschriebenen Experimente der vorliegenden Arbeit widmeten sich der Modulation von Gedächtnisprozessen durch emotionales Material. Es ging hierbei um die Frage, welche Testgegebenheiten zu einer Verbesserung und einer Verschlechterung der Gedächtnisleistung führen. Des Weiteren sollten die zugrunde liegenden elektrophysiologischen Prozesse entschlüsselt werden, und einen Beitrag zum Verständnis der Mechanismen auf Enkodier- und Abrufebene beitragen.

Als besonders relevant stellte sich die Dissoziation zwischen dem Grad der Valenz und des Arousal des Testmaterials heraus. Experiment 1 zeigte unter intentionalen Enkodierinstruktionen differentielle EKP-Effekte für negative Bilder mit hohem Arousalgehalt im Vergleich zu positiven mit niedrigem. Eine initiale posteriore Positivierung reflektierte initiale eher aufmerksamkeitsgetriebene Mechanismen für beide Stimulusklassen, für positive Bilder schloss sich dann eine selektive anteriore und posteriore slow wave an. Die anteriore slow wave war zudem moduliert vom späteren Gedächtnisstatus der Stimuli. Diese Stimuli waren es auch, die am besten wiedererkannt wurden. Anteriore EKP-Effekte und der wahrscheinliche Generator PFC stehen mit kontrollierter top-down-Verarbeitung in Verbindung, und legen in diesem Fall den Einsatz elaborierter Enkodierstrategien nahe. Die EKP-alt/neu-Effekte der Abrufphase deuteten zudem darauf hin, dass auch die Qualität des Gedächtnisabrufs moduliert wurde. In Experiment 2 konnte durch Verwendung einer divided attention-Manipulation während des Enkodierens die Interpretation der Verarbeitung positiver Reize untermauert werden. Das Teilen der Ressourcen verhinderte das Ausbilden eines Rekognitionsvorteils positiver Bilder im gleichen Gedächtnisparadigma. In Zusammenschau mit einer fMRI-Studie (Kensinger & Corkin, 2004), die den Einsatz präfrontaler Strukturen und des Hippocampus während des erfolgreichen Enkodierens negativer nichterregender Wörter demonstrierte, liegt die o.g. Interpretation nahe. In dieser Studie zeigte sich hippocampale und amygdaläre Aktivität verantwortlich für die Enkodierung negativer hocherregender Wörter. Diese Befunde könnten auch mit der selektiven posterioren Positivierung für negative Bilder in Experiment 1 in Verbindung gebracht werden. Unter komplett anderen Bedingungen, der inzidentellen Enkodierung in Experiment 3, konnten weitere Aktivitätsmuster gefunden werden, die offenbar spezifisch für diesen Typ von Instruktion sind. Die EKPs niedrig- und hocherregender negativer Bilder verliefen weitaus positiver als die neutraler. Eine in Stimulusklassifikationsparadigmen typischerweise gefundene

LPP (späte posteriore Positivierung) (Schupp et al., 2000, 2006) war somit evident, und vom Ausmaß des Arousal moduliert. Diese soll die hohe motivationale Relevanz dieser Stimuli widerspiegeln.

Für die Gedächtnisabrufprozesse erschien es äußerst relevant das Retentionsintervall zu beachten. Während in Experiment 1 (mit sofortigem Rekognitionstest) der erwartete Vorteil für negative Bilder ausblieb, zeigte sich selbiger in Experiment 3 nach einem nach 24 Stunden applizierten Test. Negative Stimuli scheinen also besonders von andauernden Konsolidierungsprozessen zu profitieren. Die Qualität des Gedächtnisabrufes war, wie die EKP-alt/neu-Effekte nahelegen, zudem auch ausschließlich nach dieser Zeit moduliert. Der zusätzliche Einsatz rekolektionsbasierter Prozesse (später parietaler alt/neu-Effekt) war ausschließlich für hochechregende negative Bilder zu verzeichnen, und deutet darauf hin, dass auch diese von anhaltenden Konsolidierungsprozessen profitieren. Dies konnte bislang nur in einer behavioralen Studien nachgewiesen werden (Sharot et al., 2007), Modulationen von EKP-Effekten sind nur nach kurzem Retentionsintervall bekannt (Windmann & Kutas, 2001; Maratos et al., 2001; Johansson et al., 2004). Die unterschiedlichen Stimuli (Wörter, Bilder, Gesichter) sowie Testbedingungen scheinen hier außerdem großen Einfluss zu nehmen.

In Bezug auf die Verknüpfung von emotionalen Items mit neutralen Kontextmerkmalen ist zu erwähnen, dass in den vorliegenden Experimenten bei der Verwendung von Studieraufgabe (Experiment 3), Studierort und Studierzeitpunkt (Experiment 1) keine Modulationen zu beobachten waren. Gemäß der Annahme, dass emotionale Reize besonders viel Aufmerksamkeit auf sich ziehen, sollte die Bindung an neutrale Kontextmerkmale vermindert werden (Kensinger et al., 2005; Adolphs et al., 2005). Wie sich in einer Reihe von Studien von Kensinger und Schacter herausstellte, ist dies aber scheinbar zu vernachlässigen (Kensinger & Schacter, 2005a, 2005b, 2006a, 2006b). Die Autoren fanden, dass auf der anderen Seite nur Merkmale von adaptiver Validität (z.B. ob ein Item gesehen oder sich nur vorgestellt wurde) besser an emotionale Reize als an neutral gebunden werden, und sich sonst keine Modulation einstellt. In diesem Zusammenhang wird auch diskutiert, dass intrinsische und extrinsische Bindungen Unterschiede machen. Studien von Adolphs et al. (2000, 2005) konnten des Weiteren zeigen, dass nur intrinsisch gebundene Merkmale (z.B. die physikalische Erscheinung oder der Inhalt) mit Amygdalaaktivität in Verbindung gebracht werden (und somit zu Gedächtnisverbesserungen führen können, wohingegen eher periphere oder extrinsische Merkmale (z.B. Studieraufgabe) das nicht werden. Aufgrund dieser Befunde ist die

ausbleibende Modulation der Quellengedächtnisleistung in den Experimenten 1 und 3 auch nicht unbedingt verwunderlich.

Experiment 4 zeigte, dass das besondere Enkodierphänomen "Tunnelgedächtnis" kein stabiler Effekt ist, sondern von verschiedenen Variablen anhängt. Das spezielle Testdesign, die Beschaffenheit der Stimuli, die Auswertemethode, sowie die emotionale Reaktivität der Probanden modulierten das Auftreten des Phänomens. Reduzierte „boundary extension“ konnte für negative Bilder im Vergleich zu neutralen gefunden werden. Des Weiteren stellte sich für diese Stimuli „boundary restriction“ für Probanden mit hoher Eigenschaftsangst ein. Es wird angenommen, dass diese ihre Aufmerksamkeit mehr auf den Ort der Bedrohung legen, und somit andere Teile der Szene vernachlässigt werden. Somit würden die negativen Bilder schon als näher heran eingepägt, und führen so zum späteren Gedächtnisfehler.

Zusammenfassend kann man sagen, dass die Untersuchung von emotionalem Arousal und Gedächtnisprozessen mit behavioralen Paradigmen und EKP-Maßen modulatorische Effekte erzielte. Es scheint besonders wichtig zu sein sich Effekte der Valenz und des Arousal separat anzusehen, da diese scheinbar unterschiedlich verarbeitet werden. Die Enkodieraktivität erwies sich als stark sensitiv für diese Stimuluscharakteristiken. Positive schwacherregende führten unter intentionalen Enkodierbedingungen zu einem frühen "attentional capturing"-Mechanismus (reflektiert in der posterioren Positivierung), sowie späterer elaborierter Verarbeitung (reflektiert in der anterioren slow wave), was von enormer memonischer Relevanz war (Experiment 1). Das Teilen von Aufmerksamkeit (oder Verarbeitungsressourcen) ließ den Rekognitionsvorteil verschwinden, der sich unter voller Aufmerksamkeit fand. Dies war zurückzuführen auf das Verhindern des Einsatzes kontrollierter Enkodieroperationen (Experiment 2). Negative hocherregende Bilder lösten eine vergleichbare frühe posteriore Positivierung aus (Experimente 1 und 3), die allerdings unter intentionalen Enkodierinstruktionen und ohne die Einbeziehung frontaler Ressourcen nicht zu einem Gedächtnisvorteil führten. In Experiment 3 unter inzidentellen Instruktionen und mit einem höheren Ausmaß an Arousal, konnte eine Positivierung an allen Ableiteorten gefunden wurden, die wahrscheinlich eine generell höhere Aktivierung des gesamten Gehirns darstellt. Negative schwacherregende Bilder führten zu ähnlichen, aber deutlich kleineren Positivierungen. Die memonische Relevanz wird hier noch besser durch die subsequent memory-Effekte deutlich, die wahrscheinlich erfolgreiche Enkodierprozesse widerspiegeln, die verantwortlich sind für die bessere Gedächtnisleistung hocherregender Bilder. Während des Gedächtnisabrufs waren die

negativen Bilder allerdings nur unterschiedlich von den neutralen, wenn der Test nach 24 Stunden appliziert wurde (höhere Pr-Maße und ein selektiver parietaler alt/neu-Effekt für hocherregende Bilder). Somit stellten sich Konsolidierungsprozesse als besonders bedeutend heraus, um zu einem Gedächtnisvorteil für negative Stimuli zu führen, und die Qualität des Erinnerns zu beeinflussen (Experiment 3). Das heißt, dass sowohl die Menge an erinnerter Information als auch rekolektionsbasiertes Erinnern von einem zeitabhängigen Konsolidierungsprozess profitieren.

Die vorliegenden Daten legen also nahe, dass unsere Informationsverarbeitung entscheidend von emotionalen Stimuli geleitet wird, und das dies hochadaptiv für ein flexibles Handeln in einer Umwelt voller Reize ist. Die Ergebnisse bestätigen ein 'Valenzevaluationssystem', das von einigen Forschern vorgeschlagen wurde (in den kognitiven Neurowissenschaften vor allem LeDoux, 1996; aber siehe auch Gray, 1991; Mogg et al., 2000). Nach dieser Theorie und mit Bezug auf die Interaktion von Emotion und episodischem Gedächtnis kann man dies wie folgt darstellen. Das Wiedererscheinen eines vergangenen Täters (oder eines bedrohlichen Objekt wie eine Schlange, sowie aber auch etwas Positives) würde in einem ersten Schritt schnell und ohne den Abruf von detaillierten Informationen erfolgen. Dies ist ausreichend, um die Information zu erlangen, dass diese Person (oder dieses Objekt) gefährlich war, and ermöglicht sofortige preparedness ('low road memories'). Via 'high road memories' würde detaillierte Information abgerufen werden, um die Details der vorherigen Episode zu evaluieren. Je höher das erlebte Arousal bei dieser vorherigen Episode, umso besser und detaillierter kann die Erinnerung wiedererlebt werden. Zudem ist dies moduliert durch die Zeit, die zwischen dieser vorherigen Episode und der aktuellen liegt. Das Entdecken und das Enkodieren einer positiven Gelegenheit scheinen bereits nach Minuten zu einem Gedächtnisvorteil zu führen. Das gilt allerdings nicht für negative (eher überlebensbedeutsam) Reize. Stattdessen scheinen sie zunächst eine Art 'Verwirrung' zu stiften, aber dann (nach intensiven Konsolidierungsprozessen) perfekt zugänglich. Wie die Ergebnisse des Quellengedächtnisses zeigen, ist es nur adaptiv kontextuelle Details zu enkodieren, die dem emotionalen Reiz inhärent oder bedeutsam für seine Bedeutung sind. Wie aus den Ergebnissen im EKP-Bereich geschlossen werden kann, scheinen all diese Mechanismen und Prozesse zum größten Teil auf emotionsspezifischen Gehirnregionen und Netzwerken zu beruhen. Ihre Entwicklung und Existenz unterstreicht den adaptiven Wert unseres kognitiven Systems.

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Abbreviations

BOLD Blood Oxygenation Level Dependent

DA Divided Attention

ERP Event-Related Potential

FA Full Attention

fMRI functional Magnetic Resonance Imaging

IAPS International Affective Picture System

ms milliseconds

MTL Medial Temporal Lobe

OFC Orbitofrontal Cortex

PET Positron Emission Tomography

PFC Prefrontal Cortex

RME Retrograde Memory Enhancement

ROI Region of Interest

RT Reaction Time

SAM Self Assessment Manikin

Annotation

The experiments reported in this thesis are also included in the following manuscripts:

Experiment 1:

Koenig, S. & Mecklinger, A. (2008). Electrophysiological correlates of encoding and retrieving emotional events. *Emotion*, 8(2), 162-173.

Experiment 3:

Koenig, S. & Mecklinger, A. (in preparation). The effects of emotional arousal and retention duration on recognition memory and its neural correlates.

Experiment 4:

Koenig, S., Beck, S., & Mecklinger, A. (in preparation). A light at the end of the tunnel: New insights into the tunnel memory phenomenon.

Experiments 1, 2, and 3:

Koenig, S. & Mecklinger, A. (in preparation). A review of binding emotional memories: The influence of valence and arousal in item and source memory tasks.

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