Emotional modulation of memory encoding and performance monitoring

Dissertation
zur Erlangung des akademischen Grades
doctor rerum naturalium (Dr. rer. nat.)

genehmigt durch die Fakultät für Naturwissenschaften
der Otto-von-Guericke-Universität Magdeburg

von Dipl.-Psych. M.Sc. Daniel Wiswede
geb. am 07.März 1978 in Salzwedel

Gutachter:
PD Dr. Jascha Rüsseler
Prof. Dr. Lutz Jäncke

eingereicht am: 19.Dezember 2006
verteidigt am: 01. März 2007

“If we fancy some strong emotion, and then try to abstract from our consciousness of it all the feelings of its characteristic bodily symptoms, we find we have nothing left behind, no "mind-stuff" out of which the emotion can be constituted, and that a cold and neutral state of intellectual perception is all that remains.”

(James, 1884, p. 291)

Contents

Zusammenfassung

Bisherige neuropsychologische Studien trennen oft zwischen kognitiven und emotionalen Prozessen und untersuchen diese unabhängig voneinander. Dieses führt zu einem unvollständigen Verständnis, da Kognition und Emotion hochgradig interagieren. In der vorliegenden Dissertation werden die Einwirkungen von Emotionen auf kognitive Prozesse am Beispiel von Gedächtnisspeicherung und Verhaltensüberwachung untersucht. Dabei kommen als Hauptuntersuchungsmethode ereigniskorrelierte Hirnpotentiale (EKPs) zum Einsatz.

Im ersten Teil der Arbeit werden zwei Experimente vorgestellt, in denen Versuchspersonen Wortlisten lernen, welche gleichzeitig mit neutralen Hintergrundbildern präsentiert wurden. Ein Wort in jeder Liste unterscheidet sich von den anderen, indem entweder die Wortfarbe verändert oder das Hintergrundbild hoch emotional ist. Die erste Studie dient als Pilotstudie. Die Verhaltensdaten zeigen eine bessere Wiedergabeleistung für Wörter mit positivem, nicht jedoch mit negativem Bildhintergrund. Anhand der EKPs kann gezeigt werden, dass das Geschlecht der Versuchsperson eine wichtige Einflussgröße ist. Deshalb untersuchen sämtliche nachfolgenden Studien dieser Dissertation ausschließlich Frauen. Wenn möglich, basiert auch die Auswahl der emotionalen Stimuli auf von Frauen durchgeführte Stimulusevaluation.

Abgeleitet aus den Erkenntnissen des ersten Experiments enthält die zweite Studie eine verbesserte Unterscheidung der Stimuli auf der Grundlage der Dimensionen Ruhe/Aufregung (Arousal) und angenehm/unangenehm (Valence). Unter verbesserten experimentellen Bedingungen ist die Gedächtnisleistung der Versuchspersonen erhöht für farbig markierte Wörter, nicht jedoch für Bilder mit emotionalem Hintergrund. In den EKPs zeigt sich eine verstärkt positive Komponente für erinnerte im Vergleich zu nicht erinnerten Wörtern. Dieses ist nicht der Fall, wenn die Wörter vor emotionalem Hintergrund präsentiert wurden. Es wird gezeigt, dass emotionale Einflussgrößen elementar wichtig sind, wenn die spätere Gedächtnisleistung vorhergesagt werden soll. Hoch emotionale, unangenehme Einflüsse könnten das kognitive System zur Unterbrechung von „Rehearsal “-Prozessen (Aufrechterhaltung von Gedächtnisinformationen durch „inneres Sprechen“) veranlassen. Emotionale Zusatzinformationen könnten andererseits jedoch auch

die Speicherung in langlebigeren Gedächtniskomponenten fördern. Der Einfluss von hoch emotionalen Reizen auf Aufmerksamkeitsprozesse wird ebenfalls diskutiert.

Im zweiten Teil der Dissertation werden vier Experimente vorgestellt, in denen Versuchspersonen auf verschiedene Weise in emotionale Zustände versetzt werden, während sie eine Aufgabe durchführen, die Überwachung des gezeigten Verhaltens erfordert.

Hauptsächlich werden emotionale Beeinflussung zweier EKP-Komponenten untersucht: Die N2 ist ersichtlich, bevor die Versuchsperson eine aufgabengerechte Reaktion gezeigt hat. Diese Komponente könnte unter anderem das Vorhandensein von kognitiven Konflikten, verursacht durch gleichzeitig aktive, gegensätzliche Reaktionsalternativen widerspiegeln. Die ERN (Fehlerinduzierte Negativität) ist nach fehlerhaften Reaktionen in den EKPs ersichtlich. Die genauen Prozesse, welche der ERN zugrunde liegen, werden intensiv in der Wissenschaft diskutiert. Diese Dissertation bietet einen Überblick über die einflussreichsten Theorien der ERN und der N2. Eine dieser Theorien zeigt sich als besonders geeignet, um emotionale Einflüsse, vor allem auf die ERN, vorherzusagen.

Im ersten Experiment betrachten die Versuchspersonen kurzzeitig Gesichter mit glücklichem, ängstlichem oder neutralem Gesichtsausdruck. Unmittelbar nach jedem Bild wird eine Reaktionszeitaufgabe durchgeführt. Sowohl die Verhaltensdaten als auch die EKP-Daten zeigen, dass das experimentelle Design geeignet ist, um altbekannte Effekte zu replizieren. Ein emotionaler Einfluss kann jedoch weder auf der Verhaltens- noch auf der physiologischen Ebene gezeigt werden. Dieses könnte daran liegen, dass die emotionalen Gesichter zu schwach waren, um emotionale Veränderungen der kognitiven Verarbeitung hervorzurufen.

Die zweite Studie verwendet anstelle von Gesichtern sehr angenehme, neutrale und sehr unangenehme Szenendarstellungen, welche einer wissenschaftlichen Bilderserie entnommen sind. In den EKPs kann gezeigt werden, dass unangenehme Bilder die N2-Komponente unverändert lassen, während die ERN verstärkt zum Vorschein kommt. Es wird geschlussfolgert, dass negative, nicht jedoch positive Emotionen experimentell hervorgerufen werden konnten.

Das dritte Experiment beschäftigt sich deshalb mit Veränderungen durch positiven Affekt. Dieser wird durch mechanisches Ansprechen der beim Lachen beteiligten Muskulatur erzeugt. In den EKPs ist ersichtlich, dass die ERN diesmal nicht stärker, sonder schwächer ausgeprägt sind. Die N2 ist wieder unverändert.

Eine vierte Studie zeigt anhand eines Fragebogens, dass negative, nicht jedoch positive Emotionen durch positive und negative Verhaltensrückmeldung erzeugt werden können. In den EKPs zeigt sich ein sehr differenziertes Bild. Sowohl die N2 als auch die ERN kommen stärker zum Vorschein. Es wird vorgeschlagen, dass die ERN auf leichte emotionale Veränderung anspricht, während zur Beeinflussung der N2 stärkere emotionale Reaktionen notwendig sind.

Die Ergebnisse werden in neue Modelle der Verhaltensüberwachung integriert, was zur Erweiterung dieser Modelle dient. Es wird geschlussfolgert, dass Emotionen einen maßgeblichen Einfluss auf die Ausführung von geistigen Leistungen haben, welche bislang vorwiegend unter dem rein kognitiven Aspekt betrachtet wurden.

Abstract

Two cognitive processes, namely memory encoding and performance monitoring, are selected to examine how emotional processes interact with cognition. The main examination tool is event-related brain potentials (ERPs).

The first section presents two experiments which require subjects to recall items from lists consisting of 12 words, which were presented in front of emotional and non-emotional pictures. One word per list is made distinct either by font color or by a highly arousing background picture. The first experiment served as a pilot study, the second experiment implements major improvements suggested by the pilot study. Recall performance was enhanced for color but not for emotional isolates. Event-related brain potentials (ERP) showed a more positive component for recalled non-isolated words and color-isolated words, compared to the respective non-remembered words, but not for words isolated by arousing background. Those findings indicate that it is crucial to take emotional mediator variables into account, when predicting later recall. Highly arousing environments might force the cognitive system to interrupt rehearsal processes in working memory, which might benefit transfer into other, more stable memory systems. The impact of attention-capturing properties of arousing background stimuli is also discussed.

The second section consists of four experiments. Various methods are used to bring subjects into pleasant or unpleasant emotional states while they perform a task that requires continuous monitoring of the ongoing behavior. Event-related potentials indicate that typical markers of performance monitoring, namely the Error related negativity (ERN), are enhanced when subjects perform under negative emotional condition, whereas the ERN is decreased when subjects perform under positive emotional conditions. Results also demonstrate emotional changes in other components engaged in error monitoring. The results are integrated in current models of performance monitoring by extending these by an affective dimension.

Keywords

- Performance monitoring
- ERN
- CRN
- P_e
- Memory
- Llist learning
- Emotion
- IAPS
- N2
- Reinforcement Learning Hypothesis
- Conflict Monitoring Hypothesis

Abbreviations

(in alphabetic order)

ACC	Anterior Cingulate Cortex
ANOVA	Analysis of Variance
ANS	Autonomic nervous system
ASTS	Aktuelle Stimmungsskala (Current feelings)
CRN	Correct response negativity
CNS	Central nervous system
DM-effect	Difference due to subsequent Memory Effect
ERN	Error related Negativity
ERPs	Event-related potentials
IAPS	International Affective Picture System
ICA	Independent Component Analysis
ms	Milliseconds
PCA	Principal Component Analysis
PSW	Positive Slow Wave
RmANOVA	Repeated measurement ANOVA
RT	Reaction time
SE	Standard Error
SOBI	Second-order blind identification correction
SN	Substantia nigra
VRI	Von-Restorff-Index
VTA	Ventral tegmental area

1. General Introduction

1.1. Structure of the present thesis

The dissertation presented here examines how emotions influence cognitive processes. Emotion itself is a topic which fills rows of shelves in libraries. Thus, it is far beyond the scope of this thesis to give a complete account how emotions might interact with all cognitive functions. Instead, I restrict myself to neuropsychological aspects of emotions, and I will choose memory and performance monitoring out of the broad variety of cognitive functions.

The thesis starts with a more general part, introducing basic concepts, classification methods and neuropsychological aspects of emotions, methods to induce emotions. A short overview how cognition interact with emotions is given at the end of the general introduction.

The experimental section consists of two parts. Two experiments examine emotional modulation of memory encoding. Four experiments bring further insight how emotions interact with brain functions concerned about monitoring ongoing behavior. Each experimental part starts with a separate introduction, where current literature is reviewed and hypotheses are derived. A specific discussion is provided for each experimental part. The thesis ends with a general discussion.

1.2. Defining emotions

1.2.1.1. Introductory remarks

Every person has an idea what is meant when talking about emotions, but it is extremely hard, if not impossible, to find a definition that will be accepted by all who experience and investigate emotions.

Because every person experiences emotions, asking for folk concepts might be an appropriate starting point. Emotions are something that is felt, something that is related to subjective experience, something that can be classified as either positive or negative. The word emotion is a composite formed from the Latin words. ex/ (out, outward) and motio (movement action, gesture). However, to understand what an emotion is, it is probably more fruitful to look how the word “emotion” is used in language. Wierzbicka (1999) points out that the most appropriate German word for emotions might be “Gefühle”, which is derived from “fühlen” (feeling) and puts emotions at the same level as feeling. The German language allows to use the word “Gefühl” to describe bodily states like “Hungergefühl” (feeling of hunger), but also to describe mental states without direct link to primary bodily needs like “Schamgefühl” (feeling of shame). In contrast, the French word “sentiment”, does distinguish between bodily and mental states. One can speak of a “sentiment de honte” (feeling of shame), but not of a “sentiment de faim” (feeling of hunger) (Wierzbicka, 1999).

The main shortcoming of folk concepts of emotions is that they are usually pretty vague. In addition, there is good evidence that the concepts people have of emotions differ radically across cultures (Wierzbicka, 1999). What scientist can learn from folk concepts of emotion is that emotion is not one thing; it might contain references to bodily states and to mental states.

A scientific concept has to define what mental stages have to have in common to be regarded as emotion and, after that, how distinctions between emotions can be made. Everyday experience taught us that there are many different mental states that can be felt. Sometimes we are hungry, thirsty, happy, sad or angry. Sometimes we feel pride, shame. Sometimes when we are listening to music we can feel goose pimples all over the body. Sometimes we are in pain. Although all examples are mental states that can be felt, there are still large differences between them. A starting point to distinguish between those states is to group them - but along which criteria? The aforementioned mental states might be grouped into pleasant and unpleasant. Being hungry is unpleasant, being angry or ashamed or feeling pain is unpleasant as well. Alternatively, some of those mental states can be linked to primary bodily needs, feeling hungry or thirsty induces us to get some food. Feeling proud or ashamed does obviously not belong to this group. Emotions might also be grouped according to their timing. Some bodily states can last for long times, hunger can be felt until we get food. Others, like goose pimples while hearing our favorite song, might last for only a few seconds. These examples indicate that states that can be felt are highly diverse. They are elicited by different events, have different timing and they serve different functions. However, is the subjective experience that a mental state can be felt enough to regard a mental state as an emotion? Is an emotion the same as a feeling? What do have all emotions in common? What distinguishes emotions from other mental states? Those questions have to be clarified before the realm of emotions can be examined scientifically.

The present thesis does not attempt to retrace scientific thinking on emotions from the first reasoning about emotions to modern emotion theories. The interested reader might find philosophical and historical reflections elsewhere. I restrict myself to psychological, especially neuropsychological perspectives and start at the point where Psychology differentiated from Philosophy.

Probably the first theory of emotions which included psychological as well as physiological aspects was largely independently proposed by William James and Carl Lange at the end of the 20th century (James, 1890; Lange, 1887). According to the "James-Lange-theory of emotions", the autonomic nervous system reacts to environmental stimulation with physiological events such as changes in heart rate, muscular tension, perspiration etc. We experience those changes in bodily states and deduce our emotions from these. William James summarized it in stating: "My theory, on the contrary, is that the bodily changes follow directly the perception of the exciting fact, and that our feeling of the same changes as they occur IS the emotion". (James, 1890) Thus, we feel afraid because we recognized that our hands are shaking, or we feel sorry because we observe that we cry.

The James-Lange theory was chosen as a starting point that demonstrates aspects of emotion research that are still up-to date: It links environmental events with bodily states and with changes in subjective feelings. The theory assumes that there are changes on multiple levels of the organism, which include reactions seen at effectors as well as directly in the nervous system. The fact that a clear distinction between feeling and emotion is not included in the theory had strong impact on later research, which attempted to draw a clear line between both (LeDoux, 1997; Scherer, 2000, 2005). The next section tries to clarify those aspects and defines how emotion is understood in the thesis presented here.

1.2.2. The purpose of emotions

This section highlights the question “What have all emotions in common”? Since I emphasize the biological view, this cannot be separated from the question “Why do we have emotions”. There are many attempts to explain why organisms have emotions. Instead of summarizing them all and adding an additional view, I restrict myself to some statements given by emotion researchers that they think describe elementary parts of an emotion. Section 1.2.3 collects the essence of those statements and goes into further detail.

- “Emotions evolved for their adaptive value in dealing with fundamental life tasks” (Ekman, 1994, p. 15).

- “Emotion guides action and organizes behavior towards salient goals”(Davidson & Irwin, 1999, p. 11).

- „The affect system has evolved to discriminate hostile from hospitable events and to decide quickly whether approach or withdrawal is adaptive“ (Cacioppo & Berntson, 1999, p. 134).

- “They (emotions) developed from primitive actions that facilitated the survival of species and individuals, and can be broadly characterized in humans as motivationally tuned states of readiness” (Lang, Bradley, & Cuthbert, 1998, p. 397).

- “... Emotions are embodied and manifest in uniquely recognizable, and stereotyped, behavioral patterns of facial expression, comportment, and autonomic arousal” (Dolan, 2002, p. 1191).

- “There must be unique physiological patterns for each emotion, and these CNS patterns should be specific to theses emotions and not found in other mental activity (Ekman, 1994, p. 18)”

- “Emotions allow goal-oriented, that is, flexible behavior instigation by relevant events, instead of mere rigid fixed action patterns” (Frijda, 2000, p. 199).

- “The first function proposed for emotions is the elicitation of autonomic responses (e.g. a change in heart rate) and endocrine responses (e.g. the release of adrenaline)” (Rolls, 1999, p. 67).

- “A (...) function of emotion is that it is motivating” (Rolls, 1999, p. 68).

- “A (...) effect of emotions is that the current mood state can affect the cognitive evaluation of events and memories ... and facilitate the storage of memories ... and trigger recall of memories stored in neocortical representations” (Rolls, 1999, p. 70).

1.2.3. Common features of emotions

As shown above, emotions contain many different aspects. Reviewing the literature, there appears to be a consensus about the following basic features of emotions.

Appraisal: Appraisal can be understood as a complex but rapidly working detection mechanism to distinguish between events of immediate importance from things that are less significant (Ekman, 1999; Robinson, 1998; Scherer, 2005). Emotions result from this appraisal process (Robinson, 1998). As pointed out by Scherer (2005) and Ekman (1999), the appraisal process might work on two distinct levels: a very fast automatic level and a conscious, higher evaluated or extended level (Ekman, 1977, in Ekman, 1999). The latter one accounts for appraisal mechanisms that interact with previously learned information; they reflect the ontogenetic modification of emotional responses. The extended appraisal mechanism is deliberate and conscious and was intensively examined from more sociological backgrounds; it has also been labeled “Top-down appraisal” or “Reappraisal”(Ochsner & Gross, 2005). In this thesis, I focus on the automatic aspect of emotions, which serves immediate concerns of the organism. This appraisal mechanism can be described to be unconscious or preconscious (Lazarus, 1991, in Ekman, 1999).

Onset and duration: Sometimes, environmental events change very rapidly. To be adaptive, emotions must have a very fast onset; they can be present even before one is aware that an emotion has begun (Ekman, 1994, 1999). The duration of this emotional response must be pretty short, because long-term emotions would not allow the organism to show massive response mobilization if the environment changes (Scherer, 2005). This may sound a bit counterintuitive, since every day experience shows that we can be angry or happy for extended periods of time. Ekman (1994, p. 16) argues that an emotion that endures for longer time periods (more than some seconds) is actually a series of briefer emotional episodes. Long-term predominance of certain subjective feelings might be better described as mood and will be discussed below (section 1.2.4). In keeping with the automatic aspect of appraisal, emotions are experienced as involuntary; they happen to us and are not chosen consciously (Ekman, 1994, p. 17).

Universal antecedent events: When assuming that emotions result from an automatic appraisal mechanism, there must be some class of stimuli that initiate automatic appraisal and thus, always co-occur with emotions. Those environmental aspects have been labeled as “universal antecedent event signals” (Ekman, 1994, 1999) or as “event focus” (Scherer, 2005). I see such a high similarity between both labels that I regard the underlying concepts as identical. The eliciting stimulus might be the sudden appearance of a new, possible threatening object or organism. As pointed out by Ekman (1999), there are still not enough data to find specific and universal antecedents for every emotion. An example can be given with regard to fear, which is always associated with the danger of being physically harmed[1]. Scherer (Scherer, 2005) points out that the organism’s own behavior might serve as the emotion-eliciting event, emotions labeled as pride or shame are given as an example. Including an “event focus” in emotions clearly states that emotions do not happen “out of the blue”.

Intensity: Emotions are of direct importance for the well-being of the organism, because they might appear in situations of threat or danger. Thus,

---

[1] Not only physical, but also the danger of psychical harm can induce emotions of fear, but I believe that this does refer to the cognitive appraisal mechanism and will therefore not be further discussed here.

responses are relatively intense, and so is the corresponding emotional experience (Scherer, 2005).

Specific autonomic patterns: Folk concepts would state that emotions can be differentiated, because there is a different subjective feeling for each emotion. Since subjective feelings cannot be accessed directly, scientists refer to changes in physiological states. Ekman (1994, 1999) argues that there are distinctive autonomic patterns for anger, fear and disgust, and there is some evidence that there are also distinctive patterns for sadness. Because Ekman (1994, 1999) also states that there must be a specific pattern also in the CNS for each emotion, this aspect will be worked out in detail in section 1.4.

1.2.4. Emotions versus other affective phenomena

In the previous section, it was argued that a mental state can be regarded to be emotional if it includes automatic and rapid appraisal, a fast onset, response mobilization, short duration, universal antecedent events, and specific physiological states. Those points are now used to draw a line between emotions and other mental processes.

Mood: The concepts of “emotion” and “mood” are highly related, both terms are often used interchangeably. As pointed out by Beedie and colleagues (Beedie, Terry, & Lane, 2005), there have been many attempts to draw a clear line between both; but distinctions were often based on the particular interest of the researcher. For this thesis, the distinction between emotions and mood is based on the properties of emotions introduced in section 1.2.3. In contrast to properties of emotions introduced above, mood can be defined as affective states that are long-lasting, diffuse and lower in intensity. Mood is neither focused on nor about anything in particular (Ekman, 1999; Scherer, 2005). Examples for moods are being cheerful, depressed or listless.

Feelings: A very important issue is the distinction between emotions and feelings. Although often used interchangeably in folk concepts, philosophical and psychological literature, there are important differences between them. Many researchers prefer the term "emotion" over the term feeling, because it seems to be somewhat more objective (Wierzbicka, 1999). This view assumes that emotions have a biological foundation, which enables researchers to study them objectively. Others define clear lines between emotions and feelings, which might be of special importance when defining core components of emotions.

Approaching the problem from the biological and evolutionary perspective, LeDoux . (1997) stated "I think it's safe to say fear behavior preceded fear feelings in evolution. If so, feelings are probably the wrong thing to focus on when we study emotions. In this sense, animals were unconscious, unfeeling, and non-linguistic before they were conscious, feeling, and linguistic". In agreement with previous opinions (Dolan, 2002; LeDoux, 1997; Scherer, 2000, 2005), for the present thesis feelings are regarded as the subjective part of emotion. Thus, feelings are associated with emotions, feelings are caused by emotions, and emotions precede feelings.

Motivation: It is a serious endeavor to draw a clear line between emotions and motivation. Both concepts are intensively discussed within psychology and neuroscience, and there are many different approaches how to disentangle both. I see agreement in the point that emotion and motivation are highly interrelated. There is also the view that both cannot be distinguished at all. Research articles sometimes avoid clear distinctions by using the term “emotion and motivation” and consider also the same or highly similar neural circuits to be involved (Davidson, 2004). Edmund T. Rolls argues that “brains are designed around reward- and punishment evaluation systems, the systems, the brain mechanisms of both emotion and motivation are considered together” (Rolls, 2000, 2004). Emotion is motivating; motivation is a result of emotion. Rolls considers emotions to be the state elicited by rewards or punishers, and this state is motivating. The motivation is to obtain the reward or to avoid the punisher (Rolls, 2000). Emotions serve first as relevance detectors, focusing people’s attention on changed events, then as motivators of action. Buck summarizes his view with the words “I suggest it is not possible to distinguish coherently between motivation and emotion because they are aspects of the same phenomenon, two sides of the same coin, which by definition always occur together. (...) Motivation is not seen but is manifested in emotion: in arousal, expression, experience” (Buck, 2000, p. 196). In a similar vein, Lang and colleagues summarized this issue with the words “Whereas the patterns of emotional expression are highly varied, their motivational basis can be conceived as a simpler, two-factor organization. That is, affects are founded on brain systems that adaptively respond to either appetitive or aversive stimulation” (Lang, Bradley, & Cuthbert, 1998, p. 397).

It is far beyond the scope of this thesis to provide an exhaustive concept of both, emotion and motivation. For now, it should be sufficient to state that both are highly related and might rely on the same more basic mechanisms of the brain.

1.3. Classifying emotions

Classification is essential in human thinking. In language use, for example, people distinguish between plants, animals, tools, furniture and hundreds of other things. This is also true for emotions; language distinguishes them clearly from other events within the body. Within each category, language provides hierarchical organization. In the same way as a chair belongs to the group of furniture, fear belongs to the group of emotions. If language provides words for an emotion, one could assume that this emotion is a basic member of the category emotion. The idea of clearly distinguishable emotions is the essence of theories summarized below as “discrete emotional systems”. The idea of describing emotions to be not discrete, but arranged along a dimension ranging from one extreme to the other, is introduced below as “dimensional systems”. Neuropsychological aspects of discrete and dimensional classifications are considered in section 1.4.

1.3.1. Discrete emotion systems

We consider something to be basic, primary or fundamental if it fulfills an important function. This can also be said for emotions, basic emotions should serve a vital function. But as pointed out in Averill (1994), vital for what? Vital for survival of the species, what emphasizes the biological aspect, vital for the society, what puts the sociological aspect in the center, or vital for the person itself, what focuses on the psychological aspect. Being well aware of the fact that all three points are co-existing in literature and that there are good reasons to examine each on them, in the next section I restrict myself to the biological standpoint (see Ekman, 1999 for other aspects of the term "basic").

Discrete or categorical classification systems are based on the assumption that evolution has equipped us with some emotions which proved to be advantageous in natural selection. If an emotion is regarded as basic, it should therefore be universal among the human species, it should also be observable in nonhuman primates, and it should be heritable. Those basic emotional states are assumed to be clearly separable in terms of their eliciting conditions and by specific physiological, expressive and behavioral pattern.

Basic emotions can be communicated verbally using language or nonverbally using expressive behaviors, among them facial expressions. It has been shown that there are some emotional words that can be non-ambiguously translated into all languages examined; those words were anger, fear, sadness, joy, disgust, shame and guilt (see Scherer, 1994). However, this still does not mean that those emotions are basic in that they are given by natural selection; emotions like guilt or shame might be necessary in every culture and thus, be generated by social interactions.

Research on facial expressions was highly influenced by Paul Ekman and colleagues. In the 1960s and 1970s, he examined facial expressions across many cultures. Ekman demonstrated that some facial expressions are universal in that they are generated by all humans. He also showed that humans can classify facial expressions even when the expression is generated by a person with very distinct cultural background (Ekman, 1993). Expressions he found to be universal were anger, disgust, fear, joy (or happiness), sadness and surprise. Findings on contempt are less clear, though there is at least some preliminary evidence for its being universally recognized.

Ekman (1994, 1999) introduced the concept of “emotional families”, which makes emotions appear less categorical. Emotions of one family differ from another emotional family in some aspects, but there are common mechanisms within one family. A possible example might be an emotional family comprising amusement, contentment, satisfaction and relieve. They share a particular type of smile and are perceived as being positive, but they differ from other families in terms of physiological signals, facial expression and perceived valence. It was suggested that the commonalities within a emotional family are a product of emotion, whereas the differences within one emotional family are produced by learning (Ekman, 1994, 1999). This idea can also explain the existence of emotions beyond the six basic emotions introduced above. In line with this, LeDoux (1997) summarized his view with the words: „I tend to agree with theorists who say there are basic emotions that are hard-wired into the brain's architecture, and that one of the advantages of having an extra big cortex is that we can blend different hard-wired emotions together to create softer emotions, where cognitions come into play in a major way. For example, while detection and responding to danger may be built into the brain, the capacity to be afraid of falling in love is something that requires the cognitive integration of the system for finding mates and the system for defending against predators.“

1.3.2. Dimensional systems

Some of the basic emotions appear to be antagonistic (i.e. happiness and sadness). This suggests that emotions might also be classified along dimensions. In addition, basic emotions can easily be classified to be either positive or negative. Scientists used different dimensions, such as “positive vs. negative”, “pleasant vs. unpleasant”, “appetitive vs. aversive” and “calm vs. excited”. There were also very influential approaches to classify emotions along two or more dimensions, for example valence and arousal. Instead of defining dimensions based on the subjective experience of the emotion, some dimensional theorists described emotions along the action pattern the emotions prepare (action tendencies), such as “approach and withdrawal”.

1.3.2.1. Unidimensional models

Proponents of unidimensional emotional systems hold the view that it is sufficient to describe emotions along the valence dimension with concepts like positive/negative or pleasant/unpleasant being the end points. The main advantage is that such a distinction is highly intuitive; emotions might be easily classified as being positive or negative. This emphasizes the subjective aspects of the emotion, thus, the feeling generated by the emotion.

A somewhat different idea is to organize emotions in terms of the action pattern they prepare. As pointed out by Murphy et al. (Murphy, Nimmo-Smith, & Lawrence, 2003) approach and withdrawal are basic response patterns which are fundamental to all complex behavior. In the context of human emotion, the approach system facilitates appetitive or goal-directed behavior and generates certain forms of positive affect that are approach related (Davidson & Irwin, 1999). Contrary to that, the withdrawal system facilitates the withdrawal from aversive stimuli and generates certain forms of negative affect that are related to withdrawal (Davidson & Irwin, 1999).

Other researchers defined very similar ideas by using the terms “appetitive vs. aversive” or “approach/avoidance” (Cacioppo & Berntson, 1999; Lang, Bradley, & Cuthbert, 1998). As mentioned above, the appetitive/aversive dimension links emotions directly to motivation, since some researchers described emotions to be based on a motivational basis structured along appetitive or aversive stimulation (Lang, Bradley, & Cuthbert, 1998).

Although it might appear that the dimensions approach/withdrawal can be easily transferred into the positive/negative or the pleasant/unpleasant dimension, Ekman (1994) provides examples that this is not always the case. Anger and fear are classified as being negative and unpleasant, but might also involve approach rather than avoidance behavior.

1.3.2.2. Multidimensional models

At around beginning of the last century, the German psychologist Wilhelm Wundt suggested that subjective feelings can be described using three dimensions (Wundt, 1905):

- Valence, which represents the value positive or negative
- Arousal, which spans from calm to excited and represents the degree of alertness, wakefulness, engagement with the emotion-eliciting object
- Tension, which spans from tense to relaxed.

The third dimension (such as tension, control, or potency) has not been consistently identified and distinguished from arousal. Thus, many modern dimensional theorists limit themselves to the valence and arousal dimension (Scherer, 2005). Wilhelm Wundt believed that those three dimensions are accompanied by specific bodily states that can be measured.

Later work by Osgood and his colleagues (Osgood, 1957, in Scherer, 2005) has been strongly influenced by Wundt's dimensional approach. Osgood introduced the semantic differential, a technique that requires subjects to "locate" an object (a particular behavior, a person, a word etc.) on a set of bipolar rating scales. Each scale consists of an adjective at each end which together describe a continuum (e.g. from "large" to “small"). Based on factor analysis, those ratings yielded three dimensions that conform closely to the dimensions suggested by Wundt half a century earlier. However, most variance was explained by a single factor, the affective valence (found in Bradley & Lang, 2000). The fundamental role of valence in describing emotional dimensions gained further support from language categorization studies. There, it has also been shown that the superordinate division is between positivity (pleasure, joy) and negativity (anger, sadness, fear) (Bradley & Lang, 2000).

Dimensional systems using the primary dimensions affective valence and arousal have also been used to classify emotional pictures (for example, the International Affective Picture System, IAPS, (Lang, Bradley, & Cuthbert, 1997, 1999)), sounds (International Affective Digitized Sound System IADS, (Bradley & Lang, 2000)) and affective English words (Bradley & Lang, 1999). The IAPS is of special importance for this dissertation and will be introduced in detail below (section 1.5.1).

Despite the fact that valence and arousal are not completely independent, there is good evidence that variations along both scales result in different physiological reactions. For instance, it has been shown that facial electromyographic activity is selectively modified either by valence or arousal. It has been shown that the Corrugator Supercilii[2] is sensitive to the arousal dimension. It contracts when a picture is rated as unpleasant; there is modest but above-baseline contraction when neutral pictures are presented, and there is below baseline activity following pleasant pictures (Bradley & Lang, 2000; Lang, Greenwald, Bradley, & Hamm, 1993). There are also other facial muscles responsive to arousal, i.e. the Zygomaticus Major[3]. It shows increased activity for very pleasant and unpleasant IAPS stimuli, but it shows almost no activity for stimuli being moderate in valence (Bradley & Lang, 2000). In contrast, electrodermal activity is affected by changes in arousal, but not in valence level. It has been shown that the amount of skin conductance increases linearly with

---

[2] The Corrugator Supercilii is a small muscle placed at the medial end of the eyebrow. It draws the eyebrow downward and medialward, producing the vertical wrinkles of the forehead. It is the “frowning” muscle, and may be regarded as the principal muscle in the expression of suffering (Dimberg & Thunberg, 1998)).

[3] The Zygomaticus Major is a muscle of facial expression draws the angle of the mouth superiorly and posteriorly and is therefore involved in generating a smile.

arousal level. This effect is relatively independent of changes in valence ratings; the same arousal patterns are observed for highly pleasant and unpleasant stimuli (Lang, Greenwald, Bradley, & Hamm, 1993).

However, some researchers assume that a bipolar view of valence and arousal might not be sufficient. For example, it has been argued that positive and negative valence are two separable dimensions, which act independently. According to that, affective behavior can be described to be either low or high on a positivity scale and, at the same time, low or high on a negativity scale (Cacioppo & Berntson, 1999). This idea is the basis of the evaluative space model, which allows the co-existence of approach-and avoidance tendencies at the same time. However, there is relatively less empirical research on this model; future research has to show whether it is better in explaining and predicting behavior than previous models.

1.4. Neuropsychology of emotions

1.4.1. Are there specific emotional brain systems?

Probably the most prominent theory that hardwires emotions to the brain is the limbic system theory of emotions, first introduced by MacLean in 1949 (MacLean, 1949, cited in Murphy, Nimmo-Smith, & Lawrence, 2003). There are some variations in literature which cortical and subcortical brain structures constitute the limbic system. The most consistently found structures are the amygdala (involved in fear and arousal processing, see below), the cingulate gyrus (autonomic functions to regulate heart rate and blood pressure, cognitive and attentional processing; see section 4.1), the hippocampus (major structure in forming new memory), the hypothalamus (hormonal regulation of autonomic nervous system, affects and regulates blood pressure, heart rate, hunger, thirst, sexual arousal, and the sleep/wake cycle), the mammillary body (involved in formation of memory), the nucleus accumbens (involved in reward, pleasure, and addiction), the orbitofrontal cortex (multiple higher cognitive functions, among them decision making) and the parahippocampal gyrus (involved in the formation of spatial memory). For many years, the limbic system was regarded as the general emotional system in the brain which generates every variety of affects. Based on recent research, LeDoux (1997) summarized the current view with the words "I think that the study of the limbic system, or more generally the idea that there is an emotion system in the brain, is misguided. It seemed clear that the limbic system, if it existed at all, was not systematically involved in any clear way." Thus, the limbic system model and the more general idea of one major emotional system in the brain might no longer be sufficient (LeDoux, 1997; Murphy, Nimmo-Smith, & Lawrence, 2003).

But if emotions are not generated by a “single emotional processor”, are there specific regions or functional circuits for generating basic emotions? Or is there evidence that brain structures generate states of activation that can be described along dimensions?

1.4.2. Discrete and dimensional brain systems

As shown above, discrete or dimensional approaches are widely accepted to classify and distinguish between emotions. If one approach is superior, i.e. capturing the real nature of emotion, then this should have neuropsychological underpinnings. Thus, if the “basic emotion” approach is right, neuroimaging studies should find specific brain structures that are always engaged when fear is induced, but not engaged when happiness is induced. Ekman (1999) summarized this view with the words „There must be unique physiological patterns for each emotion, and these CNS patterns should be specific to these emotions not found in other mental activity“ (p. 50). If dimensional approaches are true, there should be brain areas that are consistently involved in processing of arousing stimuli (independently of whether they are classified as pleasant or unpleasant), but they should be less active when processing low arousing stimuli. This double dissociation should be found for all modalities. Research has just begun to examine brain function with modern imaging methods. Since the methods and technologies are still far from being perfect, one can not draw comprehensive conclusions from a single study. However, literature provides some meta-analytic summaries that might help to decide on that topic (Murphy, Nimmo-Smith, & Lawrence, 2003; Phan, Wager, Taylor, & Liberzon, 2002; Wager, Phan, Liberzon, & Taylor, 2003).

1.4.3. Evidence for discrete emotional systems

Fear: Fear is the most widely studied emotion in neuroscience. I assume that the immense interest on fear emerges, because early studies reported changes in fear perception and fear responses after lesions of a specific brain structure, namely the amygdala. The amygdalae are almond-shaped groups of neurons located deep in both medial temporal lobes of the brain. It is relatively small in volume; it possesses an average width of only 15 mm, with being slightly longer in length (Talairach & Tournoux, 1988; Zald, 2003).

The amygdala plays a crucial role in processing of fearful face stimuli (Adolphs, Tranel, Damasio, & Damasio, 1994; Adolphs et al., 1999). However, in a study based on nine participants with bilateral amygdala damage, Adolphs and colleagues (1999) showed that most patients were also impaired in recognition of other negative emotions (especially anger), whereas perception of positive emotions remained unaffected. They concluded that the amygdala shows not clear fear-related response, but that the amygdala is crucial in the detection of potentially harmful or threatening situations.

Although the most consistent finding across two meta-analyses (Murphy, Nimmo-Smith, & Lawrence, 2003; Phan, Wager, Taylor, & Liberzon, 2002) was that the amygdala is involved in fear processing, both reported also a considerable amount of studies without fear-specific amygdala activation. Apparently, there are additional issues besides fearful stimulus properties that have to be considered. The amygdala seems to be especially responsive for visual presentation of fearful stimuli; this is notably true for fearful faces (Phan, Wager, Taylor, & Liberzon, 2002). However, results are far from being conclusive; there is research reporting that (left) amygdala response is very robust across three time-separated scan sessions (Johnstone et al., 2005), whereas others report fast habituation of amygdala responsiveness to fearful faces (Breiter, 1996) and other fearful stimuli (see Phelps et al., 2001, for overview).

Contrary results might also emerge because many studies do not clearly distinguish between fear perception and experiencing fear. As pointed out by Phan et al, (Phan, Wager, Taylor, & Liberzon, 2004), subjects do not report to be afraid of fearful faces. Instead, fearful faces may serve as a threat indicating signal, which alerts the organism towards salient cues. In line with this are findings which report increased amygdala activation to novel compared to repeated faces (Dubois et al., 1999; Wright et al., 2003) and to positive and negative emotional verbal stimuli (Hamann & Mao, 2002). Thus, fearful or threatening stimuli are also more salient than neutral stimuli and have a higher biological significance. To summarize, the view that the amygdala represents the core of the “fear system” is probably too simplistic.

Disgust: Disgust was frequently associated with activation in the basal ganglia, mainly in the globus pallidus. In addition to that, Murphy and colleagues (2003) reported activation in the insula, which is right adjacent to the prefrontal cortex and strongly associated with processing of taste, smell, somatic and visceral activity (Barrett & Wager, 2006). In line with this, selective impairment in disgust perception was reported in a patient with damage to the insula and putamen (Calder, Keane, Manes, Antoun, & Young, 2000). The patient incorrectly labeled disgust among various face sets, among them the Ekman and Friesen face set employed in the present thesis (experiment 4.2). In addition, the patient showed large deficits in recognizing disgust-related information from verbal emotional sounds, emotional prosody, and by disgust-provoking scenarios, which shows that the impairment was independent of stimulus modality. Selective impairments in disgust and sadness recognition was also reported in abstinent ecstasy users (Yip & Lee, 2006). Ecstasy causes damage to the serotonin system of the brain, but Yip and colleagues (2006) pointed out that this might contribute to secondary dopaminergic system damage. However, Phan and colleagues (2002) described the insula to be responsive to negative emotions in general.

Anger: Anger was associated with activity in the lateral orbitofrontal cortex (Murphy, Nimmo-Smith, & Lawrence, 2003), a region that has also been linked to aggressive behavior (Blair & Cipolotti, 2000). However, there are only few data available examining regions associated with anger; which requires some care with interpretation of the results.

Sadness and Happiness: Somewhat surprisingly, activations found for sadness are not separable from those found for happiness (Murphy, Nimmo-Smith, & Lawrence, 2003). This is especially true for the rostral portion of the anterior cingulate cortex (ACC). This indicates that happiness and sadness are not as easily explained in the framework of basis emotions as fear, disgust and anger. In clear contrast to the meta-analysis presented by Murphy and colleagues (2003), Phan et al. (Phan, Wager, Taylor, & Liberzon, 2002) and Wager et al. (Wager, Phan, Liberzon, & Taylor, 2003) associated happiness (or positive emotions) with basal ganglia activation. This region has been shown to be involved in reward prediction (Hamann & Mao, 2002; Holroyd & Coles, 2002).

1.4.4. Evidence for dimensional emotional systems

Although dimensions defined by end points like approach/withdrawal, appetitive/aversive or positive/negative are distinguishable to some extent, there is always a high degree of overlap. Thus, when reviewing the literature, one might not expect to get an answer on the question “What are the right dimensions”, but merely on the question “Is there evidence that emotions are structured along dimensions”.

The most parsimonious view would assume that there is a single system that evaluates stimuli to be either positive or negative and guides the cognitive system to show either approach- or withdrawal related behavior (see section 1.3.2.1). However, recent research shows that the assumption of a single bipolar emotion evaluator is not sufficient (see Cacioppo & Berntson, 1999, for review.). For example, sadness and anger are classified as negative emotions, but they elicit either withdrawal or approach behavior, respectively (Murphy, Nimmo-Smith, & Lawrence, 2003). Thus, action tendencies (approach vs. withdrawal) and valence (positive/negative or pleasant/unpleasant) are considered separately in the next section.

Action tendencies: Withdrawal is more related to left-lateralized activation, whereas approach results more often in right-site-activation (Murphy, Nimmo-Smith, & Lawrence, 2003; Wager, Phan, Liberzon, & Taylor, 2003). More specific, withdrawal-related activity was found in the amygdala, the left medial prefrontal cortex, the ACC and in the basal ganglia (Wager, Phan, Liberzon, & Taylor, 2003). A clear distinction between approach and withdrawal was found in the medial prefrontal cortex.

Valence: The idea that the brain organizes emotions around the dimension ranging from positive to negative is relatively widespread. An early example is the valence asymmetry model (Davidson, 1984, in Murphy, Nimmo-Smith, & Lawrence, 2003) claims that the left site is more involved for positive emotions, whereas the right hemisphere is involved in negative emotions. However, a clear valence-asymmetry hypothesis is not supported by recent meta-analysis (Murphy, Nimmo-Smith, & Lawrence, 2003) or finds only little support (Wager, Phan, Liberzon, & Taylor, 2003).

Arousal: As introduced above, anger and fear activate distinct brain regions. Both emotions have a high arousal level. As pointed out by Murphy and colleagues (2003), this argues against a specialized system for processing of highly arousing, unpleasant emotions. However, there is the idea that high arousing stimuli increase the overall activity of the neural system. This can also be observed on very early processing stages; there is increased activity in the primary and secondary visual areas (Lang et al., 1998; Murphy, Nimmo-Smith, & Lawrence, 2003). Whether this activation pattern reflects a competitive advantage in information processing for arousing stimuli or merely reflects differences in stimulus properties (arousing stimuli are often more colorful, complex and interesting) remains to be investigated.

Valence and arousal: Researchers often structure emotions along a two-dimensional system defined by valence and arousal (see section 1.3.2.2). Lang and colleagues (Lang, Greenwald, Bradley, & Hamm, 1993) proposed that variations along those dimensions should correlate with brain states. A recent study found that responses along the valence dimension correlated with activity in the amygdala and the insular cortex, whereas arousal responses were associated with thalamic and frontomedial activity (Anders, Lotze, Erb, Grodd, & Birbaumer, 2004).

However, the concepts of valence and arousal are not entirely independent, which is also reflected in the neuroanatomical underpinnings. Again, the amygdala provides an example: it has been shown to be activated by stimuli described as highly salient (Hamann & Mao, 2002; Phan, Wager, Taylor, & Liberzon, 2004). However, it is hard, if not impossible, to draw a clear line between valence, arousal and salience. Accordingly, amygdala activation found for salient stimuli might also be described in terms of valence and arousal. Another idea was added by LaBar and colleagues (LaBar, Gatenby, Gore, & Phelps, 1998). They reported amygdala activation when subjects passively viewed negative or positive IAPS pictures which were high on the arousal scale. The authors concluded that the amygdala is involved in the evaluation of arousing scenes, including positive ones, but may play a special role in processing negative valence.

The prefrontal cortex (PFC), which is involved in higher-order emotional evaluation processes and operates in close interaction with other cognitive functions and with behavioral goals (Davidson & Irwin, 1999), has also been shown to be differentially activated by valence and arousal properties of incoming stimuli. Whereas positive pictures activate the left prefrontal cortex (dorsolateral PFC), pictures with negative valence are associated with right side prefrontal activation (ventrolateral PFC) (Dolcos, LaBar, & Cabeza, 2004).

1.4.5. Beyond mapping

The previous section has shown that it is not possible to link every emotion clearly to a brain structure. Instead, emotional processing engages highly connected systems, which interact with other cognitive functions. Again, the amygdala provides an example: It can by activated by all sensory modalities, which characterizes the amygdala as a central point where information converges and gets prepared for fast reactions or subsequent cognitive processing (Zald, 2003). The precise nature of those functions is still not fully understood.

The amygdala holds extensive connections to the frontal lobe. It can be said that the frontal lobe processes emotional stimuli on a general level. A clear mapping of emotions is not possible. Frontal lobe damage often cause massive, often less specific emotional changes. It has been shown that the frontal lobe implements both, positive and negative affects (Davidson & Irwin, 1999). As mentioned above, a meta-analysis found no differences between happiness and sadness in rostral supracallosal ACC and dorsomedial prefrontal cortex (Murphy, Nimmo-Smith, & Lawrence, 2003).

To conclude, the previous sections have shown that both, discrete and dimensional emotional systems find some support in the functional structure of the brain, but none of the views explains the whole picture. The amygdala provides an example how the neuroscientific view has changed from core structures responsible for one aspect of emotion to a more systematic view which allows a structure to be involved in many aspects of emotional processing. However, whenever research reports amygdala activation, one should keep in mind that the amygdala is not a single structure. Instead, it consists of various nuclei, which might serve different functions (Davidson &

Irwin, 1999). Future research using methods with increased spatial resolution and improved methods for comparing different brains should clarify this issue.

There are further challenges for future emotional research. Most things we know about emotions is derived from research working with stimuli that are somewhat artificial; for example the stimulus sets consist of posed emotions or still pictures. In line with this, most research does not draw a clear line between experiencing an emotion and perceiving an emotion (Davidson & Irwin, 1999; Davidson, Maxwell, & Shackman, 2004; Reisberg & Hertel, 2004). Those aspects have to be considered to gain further insight into the realm of the emotional brain.

1.5. Methods to induce emotions

Studying emotions in controlled laboratory settings requires stimuli that reliably evoke cognitive, emotional and physiological reactions. Those reactions have to vary systematically over the range of expressed emotions (Bradley & Lang, 2000). Research provides different sets of emotion-inducing stimuli, a subset of them which are important for the present dissertation are introduced in this section[4].

1.5.1. Observing emotional scenes

One widely used method to manipulate affective states in experimental settings is to present participants with visual or pictorial stimuli. The advantage of those stimuli is that the characteristics (picture content, physical properties, stimulus onset and duration) can be controlled. One of the most often used picture stimulus sets is the International Affective Picture System IAPS (Lang, Bradley, & Cuthbert, 1997, 1999). This set comprises more than 600 colored pictures, which depict scenes of people, insects, snakes, spiders, attacks, diseases, tumors, mutilations, male and female nudes, erotic couples and many others. Lang and Greenwald (1988) developed and extended (Lang, Bradley, &

---

[4] There are many other ways to induce emotions beyond those mentioned in the next section. An example might be the shiver elicited by a person’s favorite music. Those emotional states have been summarized as "aesthetic emotions" (Scherer, 2005). In contrast to emotions considered in the present thesis ("utilitarian emotions", (Scherer, 2005)), "...the functionality for an immediate adaptation to an event that requires the appraisal of goal relevance and coping potential is absent or much less pronounced" (Scherer, 2005, p. 706). Those emotional states will not be further discussed in the present thesis.

Cuthbert, 1997, 1999) a methodology to describe the IAPS slides based on a dimensional model of emotion (see section 1.3.2.2). The two primary dimensions of the IAPS are valence and arousal. The arousal scale has 9 levels, with 1 depicting the lowest (calm), 5 a medium and 9 the highest arousal level (excitement). The valence scale ranges from 1 (unpleasant) to 9 (pleasant).

The IAPS is standardized in that it provides valence and arousal norms for both male and female subjects (Lang, Bradley, & Cuthbert, 1997, 1999). Valence and arousal are not completely independent of each other and the pictures are not equally distributed across the space spanned by valence and arousal. Thus, pictures that are high in arousal are often high or low in valence. And there are no pictures which are very low on the arousal scale and concomitantly low or high on the valence scale. In other words, exciting pictures are either very pleasant or unpleasant, calm pictures are never very pleasant or unpleasant.[5]

As shown in section 1.3.2.2, variations along the valence and arousal dimensions lead to specific changes in physiological responses. Whether this goes along with changes in perceived emotions (feelings) can be examined when subjects are requested to rate IAPS pictures along scales of a widely used instrument to measure current affective states. This was done by Patrick & Lavoro (1997). They asked students to rate IAPS pictures along the scales of the PANAS (Positive and Negative Affect Schedule). The PANAS (Watson, Clark, & Tellegen, 1988) is a well-validated and widely used self-report index of positive and negative mood dimensions. It requires rating of 10 adjectives related to pleasurable engagement and 10 relating to unpleasant activation or distress. Results showed in general that pleasant pictures load high on the positive affect scale and unpleasant pictures loaded high on the negative affect scale. Since the PANAS does not clearly distinguish between valence and arousal, unpleasant pictures loaded also high on some scales claiming to measure positive affect (for example adjectives like attentive or alert). The study

---

[5] Some literature describes also a third dimension, dominance. But it emerges less consistently across factor analytic studies. It was argued that dominance deals with antecedents or consequences of emotion rather than current experience. (Patrick & Lavoro, 1997). In addition, dominance has been shown to correlate very high with valence ratings (Lang & Greenwald, 1988). For these reasons, the present thesis considers only the valence and arousal dimensions.

shows that a two-dimensional description of affect is superior over rating scales used to measure affect in clinical settings. Using the PANAS, Simon-Thomas and colleagues (Simon-Thomas & Knight, 2005) showed that presentation of aversive IAPS pictures (low in valence and high in arousal) during a cognitive task elicits negative feelings. However, PANAS ratings showed a strong increase in negative affect only for the beginning of the experiment. After the first few blocks, emotional reactions to the pictures decreased. This shows that the IAPS pictures, mainly those loading high on the arousal and low on the valence scale, are suitable to elicit changes in affective state. Those changes are short, and, as pointed out by Patrick and Lavoro (1997) might be confounded by attention-capturing properties of emotional stimuli (see section 1.6).

How IAPS picture presentations affect brain responses was extensively examined. Because the present thesis employs ERPs, the following section is restricted to electrophysiological findings only. In general, emotional compared to neutral stimuli have been associated with more positive ERP components. Beyond emotionality, those positive components have been related to stimulus evaluation, target detection, attention and stimulus probability (Kok, 1997; Polich & Kok, 1995). Cuthbert and colleagues (Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000) conducted a study in which subjects were required to view IAPS pictures for six seconds. Subjects rated each picture directly after presentation along the original valence and arousal scales (Lang, Bradley, & Cuthbert, 1997, 1999). ERPs showed a late positive potential (LPP) for arousing IAPS pictures (positive and negative in valence), which emerged beyond 200 ms. The LPP was most pronounced at parietal electrode Pz. A possible explanation of positive waveforms as being a variant of the oddball phenomenon (P300 for rare compared to often presented stimuli) was ruled out by presenting the same amount of neutral, positive and negative IAPS pictures[6].

Using high density EEG recording, more positive ERPs to affective stimuli have been replicated (Schupp, Junghöfer, Weike, & Hamm, 2003). In addition, Schupp and colleagues (2003) reported an early posterior negativity, starting around 150 ms, which was also modulated by arousal and did not

---

[6] However, an oddball-effect cannot completely be ruled out, because in every day experience, highly emotional stimuli are less frequently experienced than neutral stimuli. Emotional stimuli might therefore work as a “natural” oddball, even when presented with the same frequency.

distinguish between valence. They interpreted the early posterior negativity as early facilitation of visual processing for emotional cues, which guides attentional processes. Recent research has shown that it is sufficient to present IAPS pictures for only short time periods to elicit very similar ERP responses as seen for longer presentation times (Schupp, Junghöfer, Weike, & Hamm, 2004).

However, studies considered so far did not describe pronounced differences between positive and negative IAPS stimuli in late positive potentials (Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000; Schupp, Junghöfer, Weike, & Hamm, 2003, 2004). Those findings are challenged by research reporting an earlier emerging and more positive ERP wave (Ito, Larsen, Smith, & Cacioppo, 1998) for negative compared to positive IAPS pictures. This picture fits well in the idea that negative emotional stimuli require a faster and more intense response, since they might indicate harmful or threatening events (negativity bias, see section 4.3.3).

Shortly presented pleasant and unpleasant IAPS pictures were used in experiment 4.3 to induce short-time affective modulations in the context of a performance monitoring task.

1.5.2. Perceiving emotions of others

“Smile – and the world smiles with you”
(English proverb)

Humans react to emotional expressions of other humans. Seeing somebody being very happy brings us in a pleasant state; seeing somebody suffering makes us feel unpleasant. There is some research providing deeper insight into the underlying processes. Although emotions can be communicated via different channels (for example, laughing and crying for the auditory channel), here I will restrict to emotions communicated by facial expressions.

Perception of human emotion was examined using different picture sets, among them the Ekman and Friesen face picture set (Ekman & Friesen, 1976; Young, Perrett, Calder, Sprengelmeyer, & Ekman, 2002). Research revealed that people react with specific facial expressions when perceiving emotional expressions of others. For example, when humans perceive happy faces, they react spontaneously with increased activation of the Zygomaticus Major[3]. On the other hand, when subjects are exposed to angry faces, there is increased Corrugator supercilii[2] activation.

Dimberg and Thunberg (1998) measured the electromyogram while subjects were presented with happy and angry faces from the Ekman and Friesen face series (Ekman & Friesen, 1976). They found the above-described Zygomaticus Major[3] and Corrugator Supercilii[2] activation. Most interestingly, the muscle reactions occurred as early as 300 ms after stimulus onset.

It was shown that perception of emotional face expressions elicits distinct ERP components. When subjects are required to view neutral and fearful faces while doing a repetition detection task, fearful faces elicit a more positive waveform beyond 300 ms which is similar to late components described for IAPS pictures (Eimer & Holmes, 2002) (see section 1.5.1). More interestingly, there was also a frontocentral positivity for fearful faces, which emerges within the first 120 ms after face onset. This indicates that fear is processed very rapidly. Since the N170, a temporo-occipital component related to structural encoding of faces (Bentin & Deouell, 2000; Eimer, 2000), emerged after the frontocentral positivity and did not show any modulations due to face expressions, it was concluded that face emotions are processed independently of face identification processes. Eimer and Holmes (2002) suggested that “the early emotional positivity might reflect the rapid activation of prefrontal areas involved in the detection of emotionally significant events” (p. 431).

Schupp and colleagues (Schupp et al., 2004) included friendly, angry and neutral faces taken from the Karolinska Directed Emotional Faces series (Lundqvist, Flykt, & Öhman, 1998). While friendly faces showed no clear differences relative to neutral faces, angry faces elicited an early posterior negativity and a late posterior potential very similar as described for arousing IAPS pictures (Schupp, Junghöfer, Weike, & Hamm, 2003, 2004). Since subjects described angry faces to be more arousing, this finding can be explained based on the arousing picture properties. Unlike others (Eimer & Holmes, 2002), Schupp et al. (2003; Schupp, Junghöfer, Weike, & Hamm, 2004) did not report a positive ERP component related to unpleasant stimuli. However, differences in face picture selection (Ekman face sets vs. Karolinska Directed Emotional Faces series), face emotions (fearful vs. angry faces), and reference method (linked earlobe vs. average reference) might contribute to those differences.

There is evidence that even extremely short, subliminal presentation of facial emotions is sufficient to elicit emotion-specific responses. Whalen and colleagues (Whalen et al., 1998) found amygdala activation for masked fearful faces (33 ms, offset coincident with onset of a neutral face shown for 167 ms) despite the fact that subjects did not report perception of fearful face expression. There was no amygdala activation when subjects viewed masked happy faces.

Taken together, these results support the hypothesis that brain responses to facial reactions are elicited automatically and controlled by rapidly operating facial affect programs. The experiment presented in section 4.2 uses shortly presented neutral, happy and fearful faces to induce emotions while subjects conduct a performance monitoring task.

1.5.3. Facial feedback

Улыбнись и ты почувствуешь себя лучше!
(*Smile, and you'll feel better)*
Russian Proverb

As mentioned above, the onset of facial muscle activation associated with emotions is very rapid (Dimberg & Thunberg, 1998). Thus, it is conceivable that the facial expression anticipates the emotion. Integrating this reasoning in the James-Lange theory (see section 1.2.1.1), facial expressions might not only precede the emotion. Instead, efference from facial muscles might play a causal role in regulating emotional experience and behavior. This "facial feedback hypothesis" finds experimental support in recent research.

Research to prove this hypothesis seems appropriately comical. In a famous study, participants were instructed to watch cartoons while holding a pencil either between their lips or between their teeth. The pencil between the teeth was to contract the Zygomaticus Major[3], whereas the pencil between the lips was to prevent subjects from smiling. Participants with the pencil between their teeth rated cartoons funnier than those who were prevented from smiling (Strack, Martin, & Stepper, 1988). The most elegant point in this stimulation procedure is that people do not have to be aware that they are smiling. This excludes alternative explanations based on people's self-perception, for example that people perceive themselves to be smiling and infer that they are probably happy (Laird, 1974, in Strack, Martin, & Stepper, 1988). In addition, one might argue that people are set in an emotional state because they feel silly or funny when holding a pen in the mouth during an experiment. Strack and colleagues (1988) excluded this alternative by introducing the “hold the pen with the lips” condition: People were prevented from smiling, but there is no reason to assume that they feel less silly or funny compared to the “pencil between the teeth” condition. This passive paradigm allows also to direct attention toward another task; a sham story can be used to explain the necessity to hold a pen in the mouth.

However, whereas the James-Lange theory assumes that facial expressions are causal for the emotions, Strack and colleagues (1988) provided evidence that emotions are merely modulated by facial feedback. Literature refers to this distinction using the terms “modulation hypothesis” and “initiation hypothesis” (Soussignan, 2002). The initiation hypothesis is of special importance for the present dissertation. It states that affective experience can be generated by facial expressions even in the absence of an emotional stimulus (Soussignan, 2002). The initiation hypothesis is supported by reports of physiological changes in heart rate, electrodermal activity and peripheral temperature due to muscle-by muscle-manipulation of emotion-relevant facial muscles (see McIntosh, 1996 and Soussignan, 2002, for overview).

There were also alternative explanations how face actions interfere with emotions, for example by vascular changes, which alters the thermoregulation of the brain. See McIntosh (1996) for overview.

Experiments using facial feedback to initiate or to modulate emotions are limited because not all basic emotions can be initiated with the same simple procedure. For example, it is easier to initiate a smile, because people can smile using one muscle only (Zygomaticus Major[3]), whereas negative patterns needs more than one muscle (McIntosh, 1996). In addition, it might be argued that a real smile (“Duchenne smile”) is much more than just contraction of the Zygomaticus major, because it involves the orbicularis oculi muscle near the eyes as well (Soussignan, 2002).

To summarize, there is good evidence that feedback from the facial muscles modulates or even initiates emotions, but those effects are relatively small. The experiment presented in section 4.4 uses a facial feedback paradigm to set the brain into a state of positive emotions while subjects perform a performance monitoring task. To my knowledge, it is the first experiment examining the physiological changes induced by facial feedback with event-related potentials.

1.5.4. Positive or negative feedback

It is pleasant to receive positive feedback in a given task, whereas negative feedback induces feelings of unpleasantness. Thus, feedback to task performance can be used to induce positive or negative emotions. However, this is hardly done in neuroscience. This is somewhat surprising, given that the effort in understanding the neurological underpinnings of emotions is immense. I see the advantage in inducing emotions via performance feedback in the personal involvement of the subject. As pointed out elsewhere (Davidson & Irwin, 1999; Davidson, Maxwell, & Shackman, 2004; Reisberg & Hertel, 2004), it makes a major difference whether a subject merely perceives or experiences an emotion.

One study provided subjects with positive or negative feedback (“Win” or “Loose” on a screen) in a simple reaction time task (Zalla et al., 2000). Unbeknownst to the subjects, this feedback was independent from the subject’s actual performance. Positive feedback was associated with left amygdala activation, whereas loosing activated the right hemisphere amygdala. However, this study did not focus on the subjective part of the task; feelings of pleasantness during winning or unpleasantness during loosing were not assessed. An example how arbitrary positive or negative feedback for the performance on a cognitive task can change emotional states is given in a study published by Krohne and colleagues (Krohne, Pieper, Knoll, & Breimer, 2002). Subjects conducted the “Positive and Negative Affect Schedule” (PANAS) prior and after the experiment. The scale “Joviality” increased after success and decreased after failure, whereas “anxiety”, “hostility” and “shame” showed the opposite pattern. Thus, providing either positive or negative feedback appears to be a feasible method to induce emotions.

The present thesis uses performance feedback for induction of emotions while subjects conduct a performance monitoring task (experiment 4.5).

1.6. Interactions of emotions and cognition

"... Emotions are less encapsulated than other
psychological states as evident in their
global effects on virtually all aspects of cognition."
(Dolan, 2002, p. 1191)

The term “Cognition” is central in cognitive neuroscience and cognitive psychology. A comprehensive definition is hard to provide. In the broadest sense, cognition describes high level functions carried out by the human brain. This includes reasoning, comprehension and use of speech, attention, memory, and executive functions such as planning, problem-solving, and self-monitoring. To denote "higher"-level abstractions, the term cognition is occasionally distinguished from perception.

As pointed out by Gray, “Emotion has also been left out in the cold by cognitive psychology” (Gray, 1999, p. 84). After cognitive psychology could not deny the importance of emotions for the understanding of cognition, there has been an long and intense debate regarding their relationship (see Lazarus, 1999 for detailed discussion on this debate). A core part of this discussion was the question "What comes first - cognition or emotion"? Izard (1984; p. 24, found in Wierzbicka, 1999) explicitly states that "emotion has no cognitive component”. This does not mean that there are no interactions between emotions and cognitions; it is merely assumed that emotions precede and determine cognition, and not the other way around. Although there are alternative views (Lazarus, 1999), there is emerging evidence that emotional stimuli can act at such a speed that they outperform other cognitive functions. A good example is provided by the way how emotions interact with attentional processes.

Emotional stimuli capture attention. It takes less time to detect an emotional stimulus among other stimuli. This is especially true for fear-relevant stimuli (Ohman, Flykt, & Esteves, 2001). Emotional processing occurs even before the operation of selective attention on a pre-attentive base (Dolan, 2002; Dolan & Vuilleumier, 2003). For example, it has been shown that even a patient with damage to the primary visual cortex can distinguish between facial expressions without being aware of them (de Gelder, Vroomen, Pourtois, & Weiskrantz, 1999). Again, the amygdala was the crucial structure in eliciting those extremely fast and pre-attentive mechanisms that guide later cognitive processes. In line with this, it has been shown that an angry face picture, previously coupled with an aversive stimulus, elicits activation in the right amygdala even when subjects do not perceive the angry face consciously (Morris, Ohman, & Dolan, 1998). Similar results have been presented by Whalen and colleagues (Whalen et al., 1998). It is conceivable that those amygdala-circuits constitute the neurological underpinning of what have previously proposed as "appraisal mechanisms" (Ekman, 1999; Robinson, 1998; Scherer, 2005), see section 1.2.3.

On the other hand, cognitive processes can also have a major impact on emotions. For example, thinking of something else diminished the aversive properties of a painful heat stimulus (Tracey et al., 2002). There is emerging evidence that anticipation of an emotional event, for example a painful shock, is sufficient to activate the amygdala. Phelps and colleagues told their subjects that they might receive a painful electric shock when one of two neutral stimuli (blue or yellow squares) appears on the screen (Phelps et al., 2001). Although subjects did never receive any aversive stimulation, the amygdala (mainly the left site) showed increased activity to the stimulus which was verbally linked to the painful event. Amygdala activation have previously been reported during fear conditioning with real aversive stimuli, although the laterality issues are still not finally clear (LaBar, Gatenby, Gore, LeDoux, & Phelps, 1998; Morris, Ohman, & Dolan, 1998; Phelps et al., 2001). It was also shown that expectation of pain enhances perceived unpleasantness of a non-painful stimulus. Those changes in pain perception were correlated with increased activation in the anterior cingulate cortex (Sawamoto et al., 2000). Another example how cognition interferes with emotional responses can be given by the placebo effect: Placebos given to relieve pain reduced activation in pain-relevant brain areas, among them the thalamus, the insula and the anterior cingulate cortex (Wager et al., 2004).

Those examples demonstrate that emotion and cognition interact. Lazarus (1999) emphasized the principle of reciprocal causality. Depending on the starting point, which is arbitrary, emotion can influence cognition or the other way around. The present thesis examines how emotions interact with cognitive processes like memory and performance monitoring. More detailed information to those specific cognitive functions is provided in section 3.1 and 4.1.

2. General methodological issues

2.1. Overview of studies and participants

All participants who contributed to the data of the present study were right-handed and had normal or corrected to normal vision. They received course credits or € 6.50 per hour after completion of the experiment. All participants gave written informed consent prior to the experimental session. All study protocols had been approved by the ethics committee of Magdeburg University.

2.2. Overview of software used

Experiment 3.2 was programmed by Jascha Rüsseler and Daniel Wiswede, all other experiments were programmed by Daniel Wiswede using Presentation software package (Neurobehavioral Systems Inc., http://www.neuro-bs.com/).

Statistical analysis was conducted using SPSS statistical package, version 11 and 12 (http://www.spss.com). ERP data were analyzed and plotted using ERPSS software package and special purpose programs. Preprocessing of behavior data and modification of ERP conditions was made using the free text pattern manipulation software tool AWK (Aho, Kernighan, & Weinberger, 1988). All graphics were made using Corel Draw (http://www.corel.com/). Sound files for experiment 3.3 were recorded, transformed and analyzed using Adobe Audition software (http://www.adobe.com/de/products/audition/).

2.3. Overview of statistical analysis

Statistical analysis: All df-values are given uncorrected. Whenever necessary, Greenhouse-Geisser corrected p-values und F-values are provided.

2.4. Overview of ERP settings

2.4.1. General recording issues

Recording environment: All measurements were conducted in the ERP lab of the Neuropsychology Unit at the University of Magdeburg. Recordings were conducted in an electrically shielded, but not sound proofed recording chamber with a Neuroscan EEG amplifier. Participants were seated in a comfortable chair with a distance of 1 m (experiments 3.2 and 3.3) or 80 cm (experiments 4.2, 4.3, 4.4 and 4.5) to the screen. Stimuli were presented on a 19 inch analog monitor. Chamber illumination was slightly dimmed.

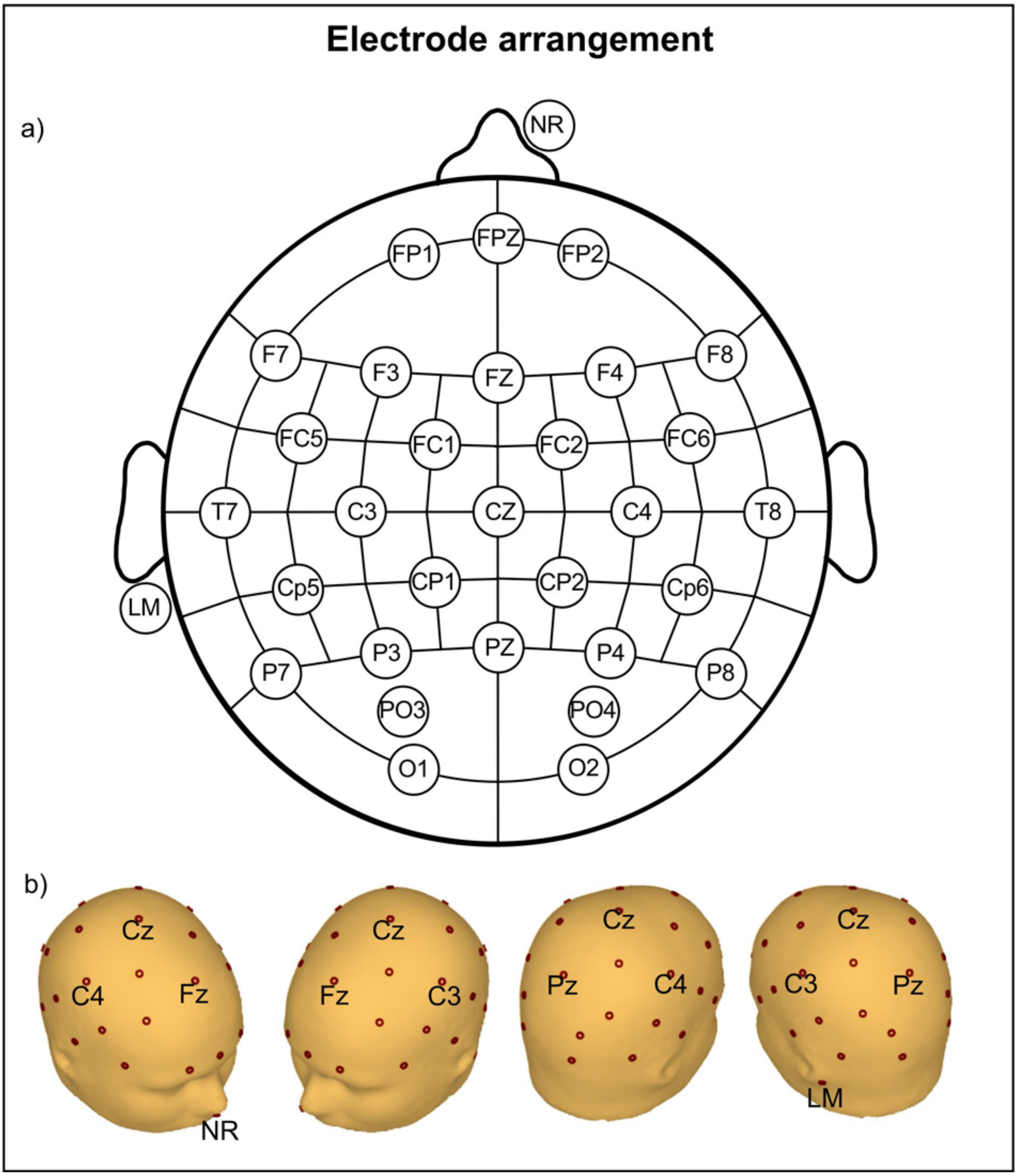


Figure 1: Electrode arrangement. Experiments in section 3 were referenced to the left mastoid electrode (LM), experiments in section 4 were referenced to a electrode placed on the tip of the nose (NR).

Recording settings: The electroencephalogram (EEG) was recorded from 29 electrodes including all 19 standard locations of the 10/20 system (Jasper, 1958) with tin electrodes mounted in an elastic cap relative to a reference electrode placed either on the left mastoid electrode (experiments 3.2 and 3.3) or on the top of the nose (experiments 4.2, 4.3, 4.4, 4.4.1.1). If other reference methods are used, this will be explicitly stated in the data analysis section of the particular experiment. Eye-movements were recorded with electrodes affixed to the right and left external canthi (horizontal electrooculogram (hEOG), bipolar recording) and at the left and right orbital ridges (vertical electrooculogram (vEOG), bipolar recording). Impedances of all electrodes were kept below 10 kΩ. Biosignals were amplified with a band-pass from 0.05 to 30 Hz and stored with a digitization rate of 250 Hz. Due to the limited number of physical recording channels available on the amplifier, either left mastoid electrode (experiment 3.2 and 3.3) or electrode Fpz (experiments 4.2, 4.3, 4.4, 4.4.1.1)were excluded as recording electrode. See Figure 1 for electrode arrangements.

Artifacts: Prior to ERP data analysis, all trials containing eye artifacts were either discarded using a special purpose program with individualized peak-to-peak-amplitude criteria on vEOG, hEOG (experiment 3.3) or corrected (experiments 3.2, 4.2, 4.3, 4.4, and 4.5) using a blind component separation (Joyce, Gorodnitsky, & Kutas, 2004). See section 2.4.2. for additional information on eye artifact correction. Head artifacts were rejected based on individual peak-to peak amplitude criteria using the same special purpose program as for artifact rejection. Artifact correction was always applied when there were conditions containing low number of trials.

Averaging: Stimulus-locked ERPs were averaged for epochs of 1024 ms starting 100 ms prior to stimulus onset for stimulus-locked data analysis and 200 ms prior to response for response-locked analysis. Detailed analysis of ERP conditions is given separately in the “Data analysis” sections for each experiment.

Filtering: Unless not explicitly stated (see experiment 3.2), all ERP figures and all ERP statistics are based on unfiltered data (except band-pass from 0.05 to 30 during recording).

2.4.2. Dealing with eye artifacts

Eye artifacts can have a major impact on the electroencephalogram due to two reasons: First, with the cornea (front of the eye) being electrically positively charged and the retina (back of the eye) being negative, the eye bulb can be regarded as a dipole. Movements of this dipole (movement artifacts) change the electrical field in the surrounding of the eye. Second, eye blinking also causes artifacts, because the moving eye lid changes the electric field around the eye bulb[7]. Relative to eye movement artifacts, eye blink activity decreases more rapidly with distance to the eyes, but is higher in amplitude (Joyce, Gorodnitsky, & Kutas, 2004). Potentials generated by blinks and eye movements can be orders of magnitudes larger (more than ten times) than the brain activity, thus, it overlays and dilutes the brain signal even on electrodes which are relatively far from the eyes. The electrical activity attained at the head electrodes is therefore assembled by a relatively small “real” brain signal, eye movement and blink artifact and overall brain activity which is not associated with the current task (noise). The noise is controlled by generating ERPs out of the EEG signal; this procedure will not be further discussed here. The next section gives a short overview how to deal with eye artifacts and derives an appropriate correction method for the present thesis.

A well-established method to handle eye artifacts is to detect movements and blinks with electrodes placed close to the eyes (see section 2.4.1) and remove artifact-containing EEG sections prior to creation of ERPs. However, artifact rejection causes substantial data loss. It is therefore inapplicable for ERP conditions based on low trial numbers, as it is the case in the present dissertation. Thus, an algorithm which removes the artifacts from the brain signal without distorting the brain signals provides the best solution.

Eye artifact correction mechanisms can be subdivided based on the statistical and mathematical algorithms. There are regression-based approaches, methods based on principal component analysis (PCA) and on independent component analysis (ICA). Regression-based methods perform correction for one electrode at one time. That means they do not use data of all electrodes simultaneously. PCA- and ICA-based methods use data from EEG and EOG

---

[7] Researchers do not agree whether movement artifacts and blink artifacts should be treated as the same, see (Croft, 2000; Verleger, 2000) on this topic.

simultaneously to perform the correction. ICA based methods decompose data into statistically independent components utilizing higher-order statistical measures, which extend over the second-order statistics used in PCA. Those methods represent a subclass of the more general group of blind source separation algorithms (Joyce, Gorodnitsky, & Kutas, 2004). A recent study concluded to prefer regression-based or PCA-based over ICA-based correction algorithms (Wallstrom, Kass, Miller, Cohn, & Fox, 2004), but new developments in ICA-based methods challenge this conclusion. A new and very promising ICA-based algorithm was introduced by Joyce, Gorodnitsky, and Kutas (2004) and was labeled SOBI (second-order blind identification correction). In contrast to earlier methods, SOBI is highly automatic and therefore not susceptible to subjectivity. Although SOBI performs especially well on eye movement artifacts, it also outperforms other algorithms in correcting eye blinks. A recent study compared six artifact correction algorithms (Kierkels, van Boxtel, & Vogten, 2006). They report that differences between algorithms are large, but “for almost every EEG configuration the SOBI algorithm shows the best correction” (Kierkels, van Boxtel, & Vogten, 2006, p. 251). Thus, the SOBI algorithm was seen to be most appropriate to correct for eye artifacts and therefore employed in experiments 3.2, 4.2, 4.3, 4.4, and 4.5.

3. Part 1: Emotional modulation of memory encoding.

3.1. Background

Distinctiveness affects memory performance. Subjects are better in recalling items from a list that are distinct in at least one dimension. This phenomenon is called the von-Restorff or VR-effect (von Restorff, 1933). Distinctiveness of an item can be created by changing the color, the size, the meaningfulness, the background color or many other aspects of a stimulus (see Cimbalo, 1978 for techniques to isolate items). As an example, Fabiani & Donchin (1995) visually presented lists of 20 words which included one physical (different font size) or semantic isolate (different semantic category). Memory for the isolated items was better than for standard items in free recall as well as recognition tests.

There are different approaches to explain the superior memory performance for isolated items. According to the total-time hypothesis, isolated items are rehearsed for a longer time in working memory, leading to a relative increase in rehearsal compared to non-isolated items (Cooper & Pantle, 1967). Alternatively, subjects could consider isolated items as a special category in a free recall task (Fabiani & Donchin, 1995; Hunt & Lamb, 2001). This is supported by the finding that the reproduction of isolated items tends to be organized: In the word list produced in the recall phase, subjects recall physically isolated items more often at the end, whereas they produce semantic isolates more often at the beginning (Fabiani & Donchin, 1995).

The studies 3.2 and 3.3 were conducted to further delineate the relationship between item distinctiveness and recall performance by introducing arousing or physical attributes to the words to be learned. In particular, the experiments aimed at the description of the neural correlates of distinctiveness effects through the recording of event-related brain potentials (ERPs). To put the observed brain potential modulations into perspective, I will provide a short review on how distinctiveness, memory performance and emotional information affect ERP components.

3.1.1. Novelty

Research has shown that novel (as well as isolated, distinct) events trigger a variety of neural processes which are related to attention, perception, learning and memory. Stimulus novelty can be examined by comparing the behavioral and neural responses elicited by the first and repeated presentation of a stimulus. However, the present set of two experiments focuses on another form of distinctiveness, namely contextual novelty, which is given when a stimulus occurs in an unexpected context (Ranganath & Rainer, 2003).

In ERPs, novel or distinct stimuli elicit an increased positive waveform between 250 and 400 ms (Simons, Graham, Miles, & Chen, 2001). This ERP component is regarded as a member of the "P300 family" and labeled novelty P3 or P3a. (Polich & Kok, 1995; Ranganath & Rainer, 2003). The P3a is not tied to any particular modality, it can be elicited even when a stimulus is not task-relevant or if it is ignored (Ranganath & Rainer, 2003). It has been argued that the P3a reflects mechanisms engaged in preparing the organism for speeded responses to biologically significant stimulus changes.

Event-related fMRI studies showed that contextually novel stimuli elicited increased BOLD responses in the ventrolateral prefrontal cortex, the insula, and the cingulate gyrus (see Ranganath & Rainer, 2003 for overview). Strange and colleagues (Strange, Henson, Friston, & Dolan, 2000) postulated a generic "deviance detection system", which is activated by different kinds of deviance attributes (semantic, perceptual or emotional deviants). It involves right inferior prefrontal and bilateral posterior fusiform cortex. Most importantly, it has been shown that contextually novel events elicit initial activation in the hippocampus, which links processing of novel stimuli to structures directly involved in generating memory (Strange & Dolan, 2001).

3.1.2. Difference due to subsequent memory

ERPs have also been used to predict later recall in list learning tasks. A consistent finding has been a greater positive ERP deflection during encoding for those items that are subsequently recalled compared to items that cannot be recalled. This effect has been labeled "difference due to subsequent memory" or DM-effect (Paller, Kutas, & Mayes, 1987).

The DM effect has been found in a variety of experimental settings (see Wagner, Koutstaal, & Schacter, 1999 , for overview): for nouns in free recall or recognition tasks (Fabiani & Donchin, 1995; Neville, Kutas, Chesney, & Schmidt, 1986; Paller, Kutas, & Mayes, 1987) , for high and low frequency words (Fernandez et al., 1998), for physically and semantically isolated words (Fabiani & Donchin, 1995), and for picture stimuli in a recognition task (Friedman & Sutton, 1987). Some researchers have explained this effect within a P300 framework. However, the DM-effect (Paller, Kutas, & Mayes, 1987; see Wagner, Koutstaal, & Schacter, 1999, for overview) extends over several hundred milliseconds and, thus, has a different timing than the P300 component. Friedman, Ritter and Snodgrass (1996, p. 11) suggested that the DM effect "… could be a unitary ERP activity with a unique functional role that overlaps several ERP deflections, or it could reflect the contribution of several overlapping components, each reflecting a different process."

Functional imaging studies have repeatedly shown the involvement of the inferior frontal cortex and the medial temporal lobe (MTL) including the hippocampus in the generation of the DM-effect (Erk et al., 2003; Wagner, Koutstaal, & Schacter, 1999). Importantly, the same prefrontal, medial temporal and lateral temporal regions (i.e. hippocampus) that generate the DM-effect are also active during detection of stimulus novelty (Kirchhoff, Wagner, Maril, & Stern, 2000).

3.1.3. Novelty and Memory

To detect novelty, it is required to compare incoming information with content stored in memory. Therefore, it is reasonable to assume that structures involved in novelty detection are also crucial in encoding and retrieval. Recent work supports this idea: Contextually novel events elicit initial activation in the hippocampus, a brain structure directly involved in encoding and recall of memory content (Lisman & Grace, 2005; Strange & Dolan, 2001). Lisman and Grace (Lisman & Grace, 2005) proposed a functional loop comprising the hippocampus and the ventral tegmental area, linking both, novelty detection and memory. The hippocampus detects rapidly incoming information that is not stored in long term memory. Then it generates a novelty signal, which is conveyed through various structures (subiculum, nucleus accumbens) to the ventral tegmental area. The upward arm of this loop increases dopamine in the hippocampus, which facilitates long-term potentiation and learning.

3.1.4. ERPs and the von-Restorff effect

If a stimulus differs from other stimuli in a series by a distinct feature, this feature will be encoded in working memory in addition to the item-specific semantic information. According to the context updating hypothesis of the P300 (Donchin & Coles, 1988), additional encoding should be reflected in an increased P300 amplitude. In an early study (Karis, Fabiani, & Donchin, 1984), subjects were presented with series of 20 words that had to be recalled after every series. Most of the word lists contained a distinct word (different font size). An increased P300 and better memory performance for the isolated items was observed for subjects that reported using primarily a rote rehearsal strategy (based on silent repetition of the word list). In contrast, subjects using an elaborative strategy (making up sentences or stories) did not show increased performance for the isolated words and no P300-recall-relationship, but an increased overall recall rate. Instead, they showed a 'frontal positive slow wave', which was enhanced for subsequently recalled items (Karis, Fabiani, & Donchin, 1984). In a subsequent study, subjects were instructed to use an elaborative strategy in one, and a rote strategy in the other of two recording sessions. A larger P300 was found for recalled compared to non-recalled items in the rote rehearsal strategy (Fabiani, Karis, & Donchin, 1990). This effect was seen for the isolated as well as for all other words. However, no differences in the P300 between recalled and non-recalled items were found for the elaborative strategy. Instead, a 'frontal positive slow wave' starting at 800 ms was more pronounced for the elaborative strategy, with subsequently recalled words being more positive. Apparently, different encoding strategies are reflected in separate ERP components (see also Otten & Donchin, 2000).

In the studies discussed above, distinctiveness could not be separated from the item that had to be learned, the distinct information was "integral". Integral dimensions cannot be separated from the stimulus to be encoded because they (a) define the relevant aspects of the items or (b) occupy the same spatial location (Otten & Donchin, 2000, p. 645). Even when the semantic category is changed, the distinctiveness attribute is still integral to the word. In addition to an integral isolate word (increased font size), Otten and Donchin (2000) used frames at a close or at a far distance to make a word distinct in a non-integral manner. For non-isolated items, they found a larger P300 for recalled than for non-recalled items. Changing the size of the word (integral attribute change) also resulted in an increased P300 for subsequently recalled items. In the non-integral condition (isolated by a frame in far distance), the P300 was smaller than in the integral condition and there was no relationship between P300 amplitude and subsequent recall. Instead, a larger frontal slow wave was seen for subsequently recalled framed words (non-integral isolates). Free recall performance was increased for isolated items, regardless of whether distinctiveness was integral or not. Those findings imply that it is crucial how distinctiveness is created. Integral distinctiveness attributes had to be fully processed because "processing the size of the characters may be a necessary step towards processing the orthographical, phonological and / or semantic attributes relevant for memorization" (Otten & Donchin, 2000, p. 658). This resulted in more context updating and a larger P300 component. Other organizational processes might be reflected in the frontal positive slow wave, since the recall performance was also increased for non-integral distinct items. The context updating hypothesis thus might be suitable for explaining the standard DM effect for integral isolates, but not for the frontal DM-effect seen for non-integral items.

3.1.5. Memory and emotions

Emotionally arousing events are more likely to be recalled later than more neutral events. A well-known example is the flashbulb phenomenon: it describes that memory consolidated during high arousal will be stored for a long time. From the evolutionary perspective, it can be argued that highly emotional events have direct consequences for the well being of an organism. Storing these events in memory is therefore highly adaptive to cope with future situations that might be related to the organism’s well-being.

Amygdala activation has been shown to be crucial in predicting later recall. For example, Canli and colleagues (Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000) presented their subjects with neutral and negative scenes. Subjects indicated how emotionally intense they found each scene. The amygdala had the greatest response to scenes rated as most emotionally intense. Activity in the left amygdala predicted recall performance in an unexpected delayed recall task (three weeks later) for scenes rated to be most emotionally intense (see Hamann, 2001, for review).

However, as mentioned in section 1.4 , recent research has shown that the amygdala is not only responsive to fearful, but also to highly salient, attention drawing stimuli (Hamann & Mao, 2002; Phan, Wager, Taylor, & Liberzon, 2004). In line with this, it can be argued that emotional arousal leads to a narrowing of attention, in which information in the periphery is less likely to be attended to and therefore less likely to be later remembered. This phenomenon has been labeled “weapon focus”, as it refers to the fact that the witnesses to crimes often seem to “lock” their attention onto the weapon and ignore all other parts of the scene, among them crucial details of the criminal (Reisberg & Hertel, 2004). Somewhat similar to that, a decline in memory performance has been described for stimuli that directly precede or succeed emotional events (Strange, Hurlemann, & Dolan, 2003).

Independent of subsequent recall, emotional pictures as those taken from the IAPS (Lang, Bradley, & Cuthbert, 1997, 1999) have been shown to modulate the P300 component (Keil et al., 2002), or late positive potential (LPP) (Ito, Larsen, Smith, & Cacioppo, 1998; Schupp et al., 2000) and the positive slow wave (PSW) (Amrhein, Muhlberger, Pauli, & Wiedemann, 2004). Those components are more positive going for pleasant and unpleasant compared to neutral pictures (Cuthbert, Schupp, Bradley, Birbaumer, & Lang, 2000; see section 1.5.1). Some research found a stronger positivity for negative IAPS pictures, (Ito, Larsen, Smith, & Cacioppo, 1998). Dolcos and Cabeza (Dolcos & Cabeza, 2002) reported that the emotion effect on parietal scalp regions is more sensitive to arousal, whereas it is more sensitive to valence on frontocentral electrodes. The neural origin of the emotion effect is not entirely known, but it is assumed that the arousal effect is generated by interactions between the amygdala and cortical regions, whereas valence-related activity reflects prefrontal cortex involvement (Dolcos & Cabeza, 2002).

I see at least three different ways in which affective stimuli might contribute to changes in recall performance. First, affective stimulus material might elicit physiological and evaluative processes that are not evoked by non-emotional stimuli. Second, affective stimuli capture attention, which might lead to speeded processing and / or increased rehearsal (Ochsner, 2000). For example, subjects are faster and more accurate in detecting emotional stimuli compared to neutral stimuli (Ohman, Flykt, & Esteves, 2001). Third, there is a general recall advantage for items belonging to a common category compared to uncategorized items. One might argue that emotional items are semantically coherent (Maratos, Allan, & Rugg, 2000); that is they are more similar to each other than non-emotional items. Taken together, those additional attributes may increase the distinctiveness or add additional retrieval cues during encoding and, thus, support later recall.

How non-integral emotional information affects memory processes has been the subject of recent research. A word can be made emotionally distinct in a non-integral manner by presenting a highly emotional but task-irrelevant picture prior to the neutral item (Erk et al., 2003) or in the background of the neutral word (studies presented in section 3.2 and 3.3). Encoding processes for non-integral emotional information was examined in a fMRI study conducted by Erk and colleagues (2003). They used IAPS pictures to induce positive or negative emotions prior to the presentation of the word. Recall performance was better for words preceded by positive but not for words preceded by negative pictures. Successful recall for positive encoding trials was predicted by activation of the right anterior parahippocampal and fusiform gyrus, whereas recalled items from negative encoding conditions were associated with amygdala activation. This supports the view that different pathways are involved when a person encodes words in a neutral, positive or negative context.

3.1.6. The current studies

The experiments presented in section 3.2 and 3.3 use a von Restorff paradigm comprising the presentation of word lists, in which one word was made distinct by either changing an integral attribute (font color of one of the words) or by changing a non-integral attribute (highly arousing instead of low arousing background pictures). While experiment 3.2 does only manipulate the arousal level without controlling for valence of the background picture, experiment 3.3 controls for both, valence and arousal. For the sake of simplicity, the arousing background condition will be referred to as “arousing background condition" in both experiments. Both experiments use a free recall rather than a recognition paradigm because it has been shown that emotional effects on emotion are generally stronger when active retrieval is required (Erk, Martin, & Walter, 2005; Fiedler, 2001).

The following predictions are made:

- First, it is assumed that there is an increased memory performance combined with an increased ERP positivity (P300-recall-relationship) when changing an integral stimulus attribute. In contrast to earlier studies (Fabiani, Karis, & Donchin, 1990; Otten & Donchin, 2000), the changed integral item was font color rather than font size and subjects were not instructed to use a specific encoding strategy.
- Second, it is predicted that a P300-Recall-relationship might also be seen for words isolated by a task-irrelevant, but highly arousing background picture. In contrast to changes of an emotionally neutral, non-integral item attribute (Otten & Donchin, 2000), emotionally arousing background information should facilitate rehearsal processes in working memory and result in an even stronger P300-recall relationship.

3.2. Experiment 1a: Memory recall in arousing situations – a pilot study

3.2.1. Methods

3.2.1.1. Participants

Data were acquired from22 subjects (14 women). Data from one subject had to be removed due to extensive recording artifacts. Thus, analysis is based on data from 21 subjects (13 women, mean age all subjects: 22.5 years, range 19 to 29). All of them were students at the Otto-von Guericke University, all were German native speakers. See section 2.1 for additional information.

3.2.1.2. Stimuli and procedure

A trial consisted of an IAPS picture, superimposed by a German noun. The noun was presented in white capital letters with ARIAL font in front of a black filled frame presented in the lowest part of the IAPS picture. The words covered between 5.1° and 7.4°, and the pictures covered horizontally 8.5° of visual angle.

During the experiment, subjects were presented with 1200 trials. The trials were made up of 600 nouns and 300 IAPS pictures (International Affective Picture System; see “Picture selection” below). Thus, each noun was presented twice, each IAPS picture was presented four times. Words and IAPS pictures were allocated randomly and it was checked whether there is no obvious link between word and background picture. All subjects were presented with the same trial sequence and, thus, saw the same word-picture combinations. The experiment was conducted in 2 sessions, which contained the same selection of IAPS pictures and nouns, but at different sequences and with a different IAPS-noun allocation. Both sessions were separated by at least one week.

Each session consisted of 40 lists; each list consisted of 15 trials. Each trial was presented for 1500 ms. Trials were separated by a fixation cross shown at variable length between 1500 and 2000 ms (mean 1750 ms).

Deviant stimuli: Each list contained two deviant trials, which were either deviant by word font color (red instead of white; “color isolated” condition) or by valence of the background picture (arousing background isolate condition).

To achieve emotional modification of the background picture, one word per trial was presented in front of a highly arousing IAPS picture See "picture selection" below for detailed background picture information.

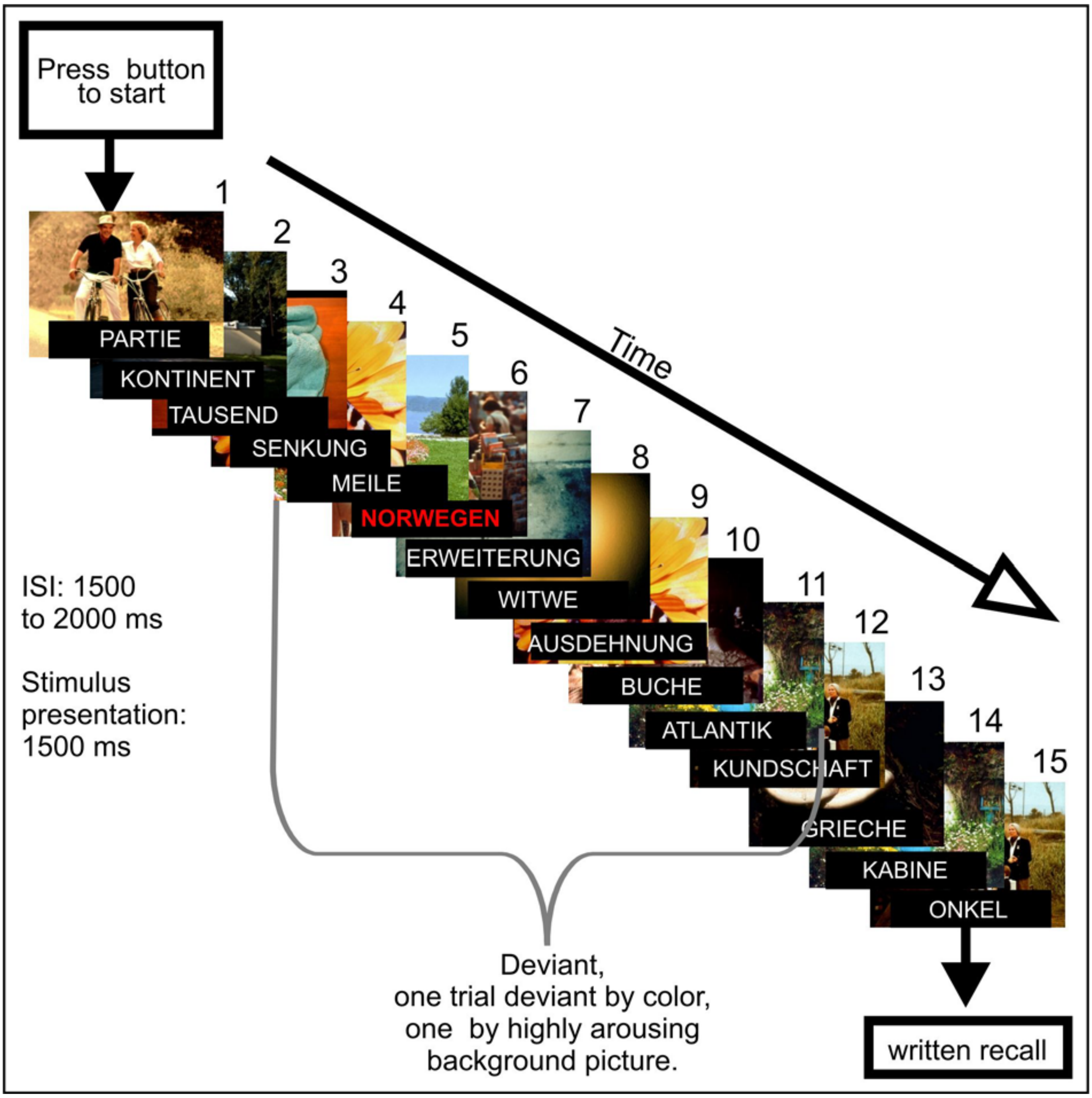


Figure 2: Experimental setup of study 3.2. A sequence of 15 trials constituted one list. Isolation was achieved either by changing the font color (color isolate) to red or by changing the emotional background picture from neutral to highly arousing (arousing background isolate). There was a color and an emotional background isolate in each list. All pictures selected as arousing background isolates are shown in Figure 3.

To avoid interactions with the well known superior performance for first list and last list items (primacy and recency effect), color deviant and arousing background deviants were presented with the same probability on list positions 5 to 11 only, but never on list position 1 to 4 or 12 to 15. Both deviant conditions were never presented in successive trials. After each list, there was a screen indicating the beginning of the recall phase. After finishing recalling the last list, the next list was initiated by a button press. An example of a 15-word-list is provided in Figure 2.

Instruction: Participants were instructed to write down as many words as they could remember from the previous list. They were not required to recall the words in the same sequence as previously shown and there was no instruction regarding the encoding strategy.

In contrast to the subsequent study provided in section 3.3, subjects were informed that word stimuli are superimposed by pictures and that it is important to pay attention to the pictures as well.

Word selection: The 600 words were German nouns selected from the CELEX data base (Baayen, Piepenbrock, & Gulikers, 1995). The nouns had a mean Mannheim Word frequency of 22 per million; word length ranged from 4 to 11 letters. All words were emotionally neutral. Emotional neutrality was assured by a pre-study, in which 15 subjects were asked to mark every word they considered as not being emotionally neutral. The original list comprised of 800 words. Words rated by more than two people as not being emotionally neutral were excluded.

Picture selection: The background pictures were taken from the International Affective Picture System IAPS (Lang, Bradley, & Cuthbert, 1997, 1999) based on their mean arousal level without distinguishing between women and men. As introduced in section 1.5.1, high positive and negative valence both involve high levels of arousal. In contrast to the study provided in section 3.3, arousal was the only selection criterion for picture selection. Thus, emotional deviant pictures were always high on the arousal scale. However, there were some emotional deviant pictures loading high on both, the arousal and the valence scale (exciting and pleasant pictures), whereas others were high on the arousal and low on the valence scale (exciting and unpleasant pictures). Emotional pictures included scenes of mutilations, injuries, attacks (low valence), but also pictures of erotic scenes (high valence). See Appendix 1 for arousal and valence ratings and Figure 3 b for all arousing pictures.

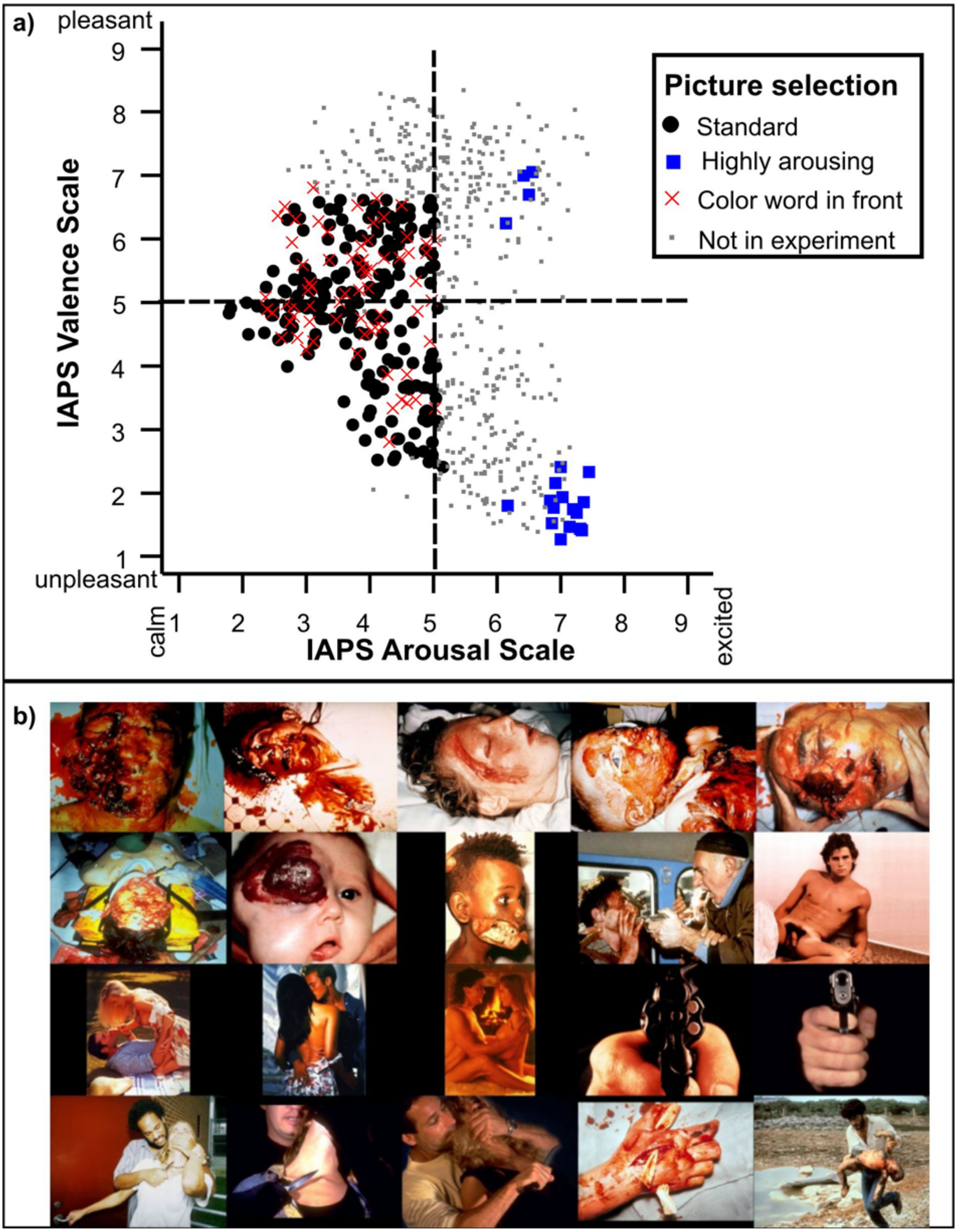


Figure 3: a) Pictures selected to provide either neutral or emotional background, arranged along the IAPS dimensions valence and arousal. Picture selection was based on IAPS ratings for men and women. b) All pictures taken for the emotional background condition. IAPS picture numbers in reading direction: 3000, 3010, 3030, 3053, 3060, 3080, 3170, 3266, 3530, 4490, 4607, 4608, 4656, 6230, 6260, 6313, 6350, 6540, 9405, 9410. See Appendix 1 for ratings.

All other pictures, taken as neutral background for color deviant words or for the not deviant condition, were low or medium on the arousal scale and ranged from pleasant to unpleasant on the valence scale. See Figure 3 a for a graphical illustration for picture selection based on valence and arousal.

Mean arousal and mean valence ratings for selected IAPS pictures are listed below, standard deviations are given in brackets:

Neutral IAPS pictures	arousal: 3.8 (0.8)	valence: 4.9 (1.1)
Neutral IAPS with color Words	arousal: 3.7 (0.8)	valence: 5.2 (0.9)
Emotional IAPS pictures	arousal: 6.9 (0.4)	valence: 2.8 (2.1)

Arousing pictures differed from neutral pictures and neutral pictures with colored words in both, arousal and valence values (ANOVA, F (2,297) < 34.1; p < .001, post hoc comparisons, p < .001).

3.2.1.3. Data recording and preprocessing

See section 2.4.1 for general recording issues. Normal artifact rejection procedure (see section 2.4.1) was not appropriate for this study because recall performance was pretty low on middle list positions (see section 3.2.2.1). Artifact rejection would decrease the amount of trials to a degree that reliable ERPs could no longer be generated. This is especially true for recalled items on midline positions. Thus, eye artifacts were corrected using blind component separation as described in section 2.4, head artifacts were rejected as described in section 2.4.1. To reduce muscle artifacts, data were filtered using a 10 Hz low pass filter.

3.2.1.4. Data analysis

ERPs were averaged relative to a 100 ms pre-trial baseline for the conditions “Standard-not isolated”, “Arousing background isolated” and “Color isolated”. Trials presented on primacy position (list position 1 to 4) or on recency position (list position 12 to 15) were not further analyzed (see Wiswede, Rüsseler, & Münte, 2007, for analysis of serial position effects). Thus, ERPs for all three conditions were based on list positions 5 to 11 only. A distinction between recalled and not recalled items was made for analyzing the DM-effect (difference due to subsequent memory), but not for analyzing the deviance effect. The total number of trials included in the conditions is listed in Table 1.

CONDITION	RECALL	Mean trial number	SD	Range
Standard	**Recalled**	103.1	38.1	59-199
	Not recalled	277.3	36	187-327
Arousing	**Recalled**	24.7	8.9	9-45
	Not recalled	51.9	9.2	34-70
Color	**Recalled**	20.1	8.2	10-43
	Not recalled	55.9	8.0	33-67

Table 1: The number of trials included to generate the ERP conditions in study 3.2.

Time windows for mean amplitude analysis were based on visual inspection. The deviance effect was examined in a 400 ms to 900 ms time window. Due to differences in latency onset and less clear pronounced differences, the DM effect was examined in the following time windows: 200 to 300 ms; 200 to 450 ms; 300 to 400 ms; 300 to 600 ms; 400 to 900 ms; 500 to 900 ms; 600 to 900 ms; 700 to 900 ms.

Repeated measurement ANOVAs were based on mean amplitude on midline electrodes Fpz (frontopolar), Fz (frontal), Cz (central) and Pz (parietal, see Figure 1 for electrode location). To examine the DM-effect, separate ANOVAs (Factors ELECTRODE and RECALL) were conducted for all three conditions. The deviance effect was based on the factors CONDITON and ELECTRODE.

3.2.2. Results

3.2.2.1. Behavioral data – recall performance

Visual inspection: As depicted in Figure 4 a, recall performance shows the normal U-shape with superior recall performance for items on first and last positions. This refers to the well-known Primacy/Recency effect and will not be further discussed. Within the plateau position, there was an increased recall performance for words shown in front of an arousing background picture. However, this effect seems not to be very consistent; it is not seen for emotional words shown on position 8 and 9. Color isolated items did not differ from non-isolated items.

However, as mentioned above (section 3.2.1.2), emotional background pictures were selected based on their arousal level only and were either high (pleasant) or low (unpleasant) in their valence level (see Figure 3 a). Therefore, it is conceivable that the superior performance for highly arousing background trials could be subdivided into a high valence and a low valence effect. As shown in Figure 4 b and c, this is clearly the case. Participants were better in recalling words when shown in front of arousing pictures which were high in valence (exciting and pleasant), but not when words were shown in front of arousing pictures which were low in valence (exciting and unpleasant). This explains also that there was no superior performance for arousing items shown on list positions 8 and 9, where the emotional trials contained either no high valence picture (list position 8) or only 1 high valence picture (list position 9).

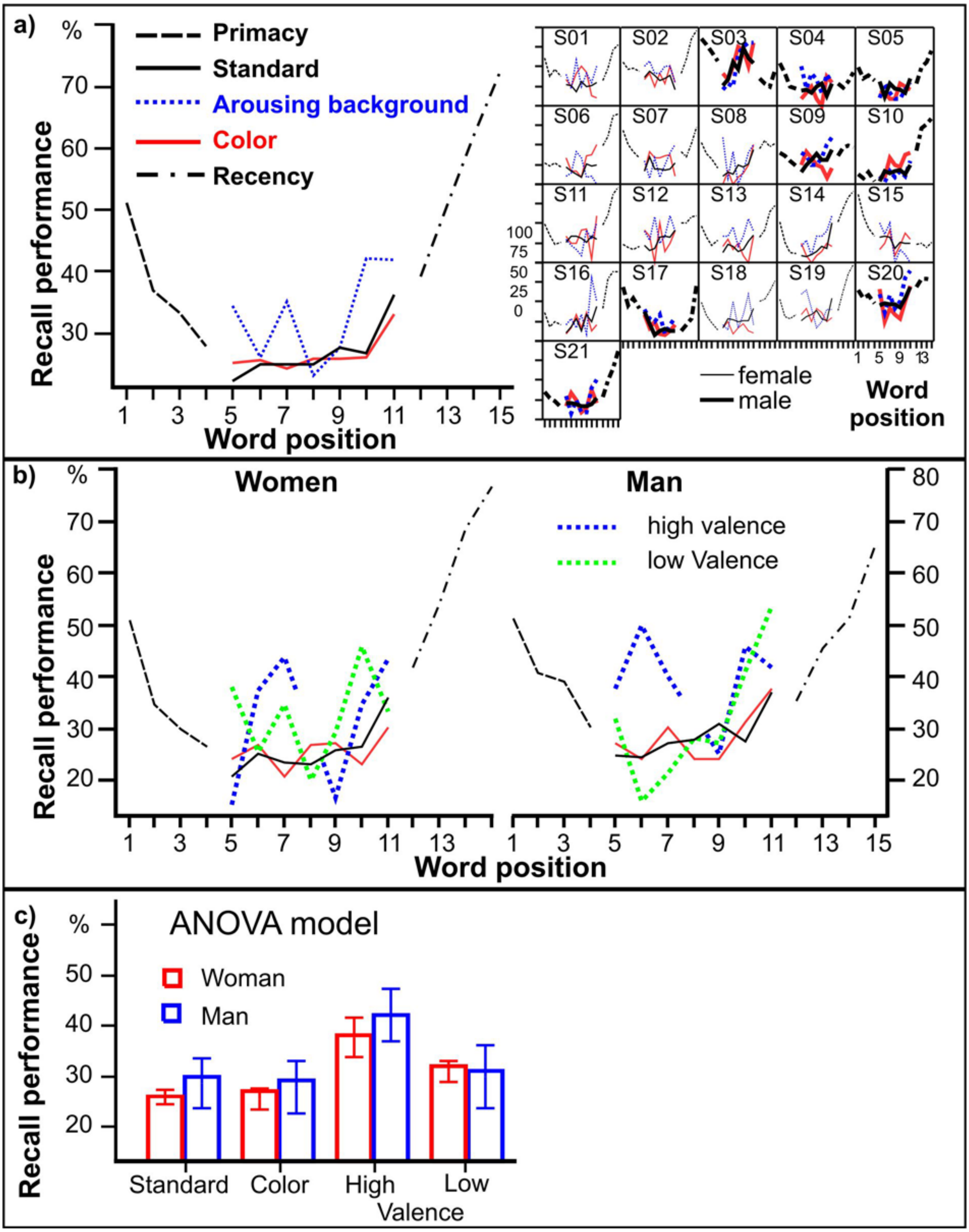


Figure 4: Behavior data for experiment 3.2. a) Recall performance across all 15 serial positions, divided by isolation attribute. right panel: recall performance for single subjects. b) recall performance, separately for men and women. The arousing background condition is divided into high and low valence (pleasant or unpleasant) c) Data as used for statistical analysis. Middle serial positions were merged, highly arousing was divided into high and low valence. Error bars indicate +/- 1 SE.

Statistical analysis: As for the ERP data analysis, the 15 serial positions were summarized as follows: Standard (all not isolated items on position 5 to 11), Color deviant (all color word items on positions 5 to 11), Arousing background deviant (all arousing deviants on positions 5 to 11). Differences in recall performance were found for highly arousing stimuli, gender differences were not emergent on middle positions (rmANOVA, factors CONDITION (3 levels) and GENDER (between factor, 2 levels); F (2, 38) = 7.06; p < .002; GENDER or CONDITION x GENDER n.s., pairwise comparisons: Arousing background differed from both other conditions, p < .016).

However, as indicated by visual impression, differences in valence level might explain superior performance for arousing items. To test this, the same analysis as described above was conducted except that the factor CONDITION had four levels (arousing background divided into “High Valence” and “Low Valence”; Color deviants, Standard). This revealed that the superior recall performance for arousing background pictures was caused only by arousing pictures with high valence level (exciting and pleasant) and not by arousing pictures with low valence rating (exciting and unpleasant). As above, subject’s gender did not have a major impact on recall performance (Main effect of CONDITION, F (3,57) = 12.45; p < .001; pairwise comparisons: High valence trials differed from all other conditions, p < .017 (Bonferroni-corrected); no significant main effect of GENDER or interaction). See Figure 4 c and Table 2

CONDITION	**Standard Pos 5-8**	**Color**	**Arousing Background**	
			High valence	**Low valence**
Recall	26.9 (9.4)	26.4 (10.7)	39.4 (14)	30.5 (11.9)
VRI		-.53 (5.7)	12.5 (12.7)	3.6 (6.2)

Table 2: Recall performance in percent for the *Standard*, the *Color and the Arousing Backgroun*d (subdivided into high and low valence) condition. Values are means across all 21 subjects, SDs are given in brackets. VRI indexes the Von-Restorff-index, computed by subtracting the recall percentage for *Standard* words from the arousing or color recall percentage.

3.2.2.2. ERP data

ERPs modulated by deviance

To test whether deviance was detected for color isolates as well as for emotional background isolates, ERPs were averaged for all three conditions independent of recall performance (see Figure 5 left panel).

Visual inspection: There was an increased positive ERP component, strongest on parietal scalp portions, seen for color isolates and even more pronounced for emotional background isolates. This component emerged around 400 ms and lasted until the end of the averaging period. See Figure 5, left panel.

Statistical analysis: Differences between the 3 conditions were seen on parietal, but not on frontal electrode sites (rmANOVA based on mean amplitudes, 400 to 900 ms time window, factors CONDITION (3 levels), ELECTRODE (4 levels), between group GENDER (women, men): significant CONDITION x ELECTRODE interaction, $F(6, 114) = 6.73$, $p < .001$). The emotional deviant condition elicited the strongest, the standard condition the weakest positive component. The gender or the subjects did not influence the amplitude (rmANOVA on Pz, Factor CONDITION, GENDER; Main effect CONDITION: $F(2,38) = 11.77$, $p < .001$; no other significant effects. Mean amplitudes on Pz: standard 3.3 µV, emotional isolate 6.0 µV, color isolate 4.1 µV, all conditions differed; $p < .031$.). See Figure 5, left panel.

ERPs modulated by deviance and recall performance

Visual inspection: Visual inspection showed that there was a long-lasting more positive ERP wave found for recalled compared to not recalled items (DM-effect). Although also seen for not isolated items, this effect was strongest for color isolates and for emotional isolates. However, the DM effect was quite variable across subjects, what might be at least partly caused by limited number of trials, especially in the “recalled” conditions.

Statistical analysis: Statistical analysis as described above (section 3.2.1.4) revealed no reliable DM-effects in any of the three conditions. This was unexpected, since visual inspection indicated clear differences and the DM-effect is often described in literature.

Failure to validate the effect statistically might be due to differences between subjects. One possible factor could be the gender of the subject, since it was shown that woman react differently on arousing IAPS stimuli (Kemp, Silberstein, Armstrong, & Nathan, 2004; Wrase et al., 2003). Thus, the same analysis was conducted for the 13 women. Due to the limited number of male subjects measured, this subgroup was not further analyzed. See Figure 6 b and c for grand averages separately for man and women.

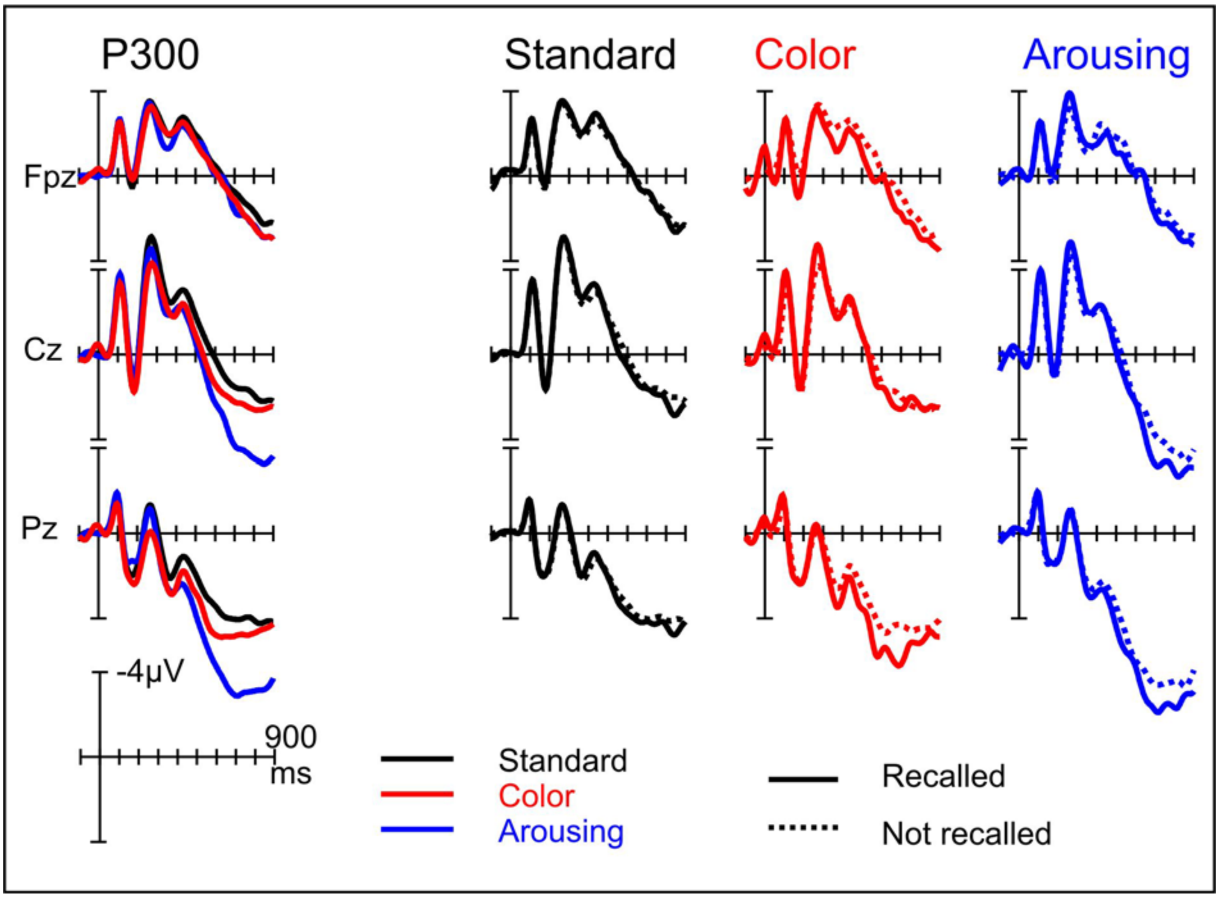


Figure 5: ERP waves for standard (no isolation), color isolated and emotional background isolated items on midline electrodes Fpz, Cz and Pz for all subjects.

Visual inspection, ERPs of women: shows that women showed a DM effect for all three conditions. The DM effect was strongest on frontal sites for color deviant trials and strongest on parietal sites for emotional deviant trials. The DM-effect for not isolated trials was seen on frontal, central and parietal electrode sites.

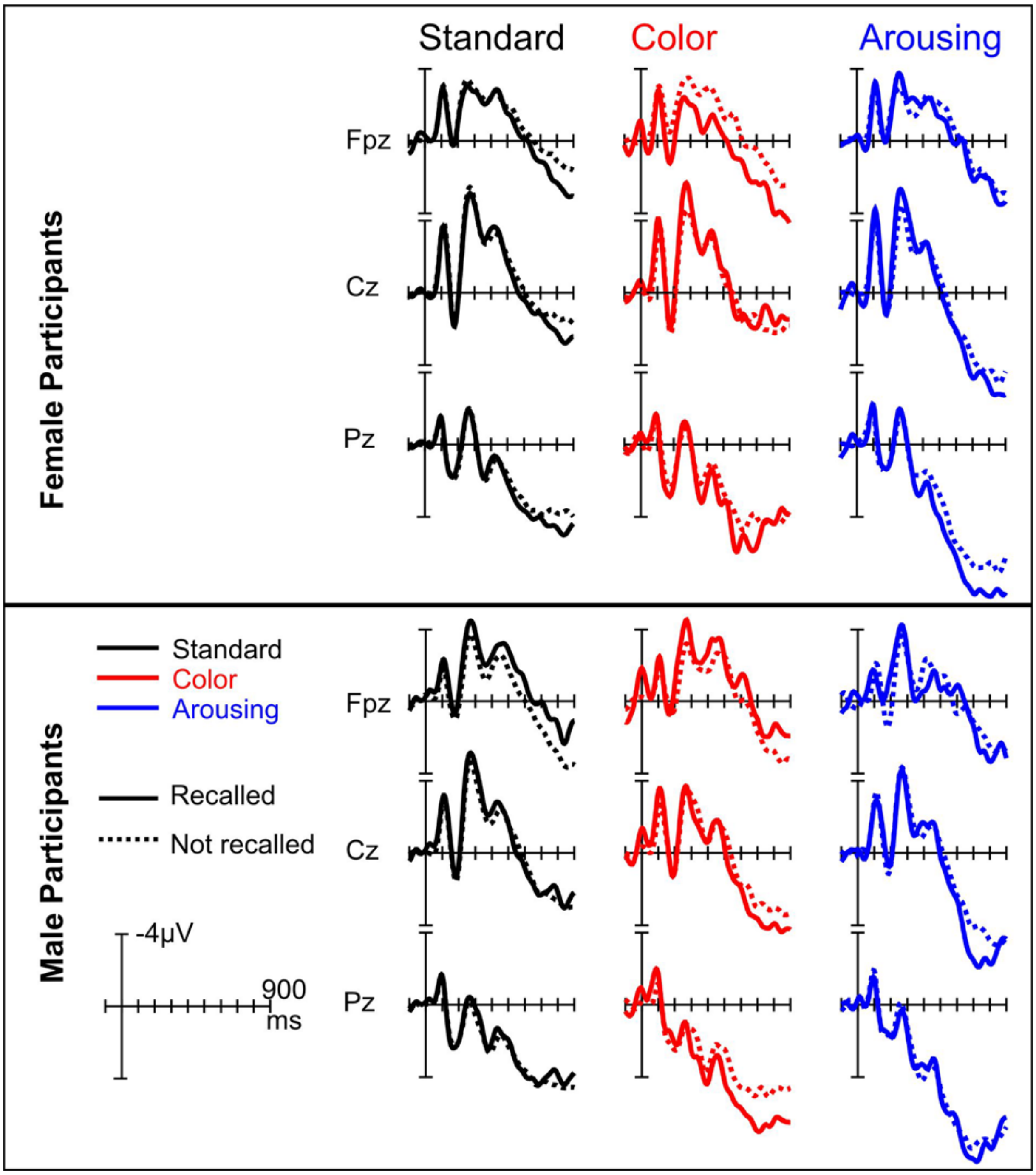


Figure 6: ERP waves for standard (no isolation), color isolated and emotional background isolated items on midline electrodes Fpz, Cz and Pz separately for woman and men.

Statistical analysis, data of women: The DM effect was significant for non-isolated items in the 700 to 900 ms time window (RECALL, F (1, 36) = 5.34, $p < .039$). Color deviant trials showed an widespread DM-effect on frontal, but not on parietal electrode sites, which was earlier in onset compared to the non-isolation condition (RECALL x ELECTRODE, F (1,36) > 2.88; p < .09 on all examined time windows, e.g. time window 200 to 450 ms: F = 4.94; p < .024; time window 400 to 900 ms: F = 4.35; p < .023;). Most interestingly, there was no reliable DM-effect found for emotional isolated trials (no significant main effect of RECALL or significant RECALL x ELECTRODE interactions in any of the examined time windows (see 3.2.1.4)).

As reported in section 3.2.2.1, valence might be an important issue in explaining arousal effects. However, due to the relatively low number of trials for recalled arousing items, a further distinction between “arousing-high valence” and “arousing – low valence” as done for behavioral data, was not possible for the ERPs in this experiment. To avoid intermixture between valence and arousal, the study in section 3.3 includes only highly arousing pictures that are low in valence.

3.2.3. Summary and perspective

Summary: Study 3.2 presented subjects with neutral or highly arousing IAPS pictures superimposed by German nouns. The subjects were required to recall the nouns only in the recall phase. Behavioral data show that words are better recalled when presented in front of arousing pictures. However, detailed analysis revealed that increased recall performance was only seen when words were presented in front of arousing high valence (pleasant) pictures, but not when words were presented in front of arousing low valence pictures (unpleasant). In line with this, a recent theory (Ashby, Isen, & Turken, 1999) has shown that positive affect facilitates various aspects of cognitive performance (see section 4.1), among them free recall performance. A superior performance was not seen for colored word trials.

ERPs were more positive for color deviant trials and, especially, for arousing background trials. This indicates that subjects followed the instruction to pay attention to the background pictures, which might have reduced attentional resources allocated to foreground words and to color words (integral isolation attribute, see 3.1). A DM-effect was seen for women for non-isolated items (frontal, central and parietal) and for color isolated items on frontal sites. No reliable DM-effect was found for the emotional condition.

Perspective: Based on the experience gained from study 3.2, there is some room for improvement regarding stimulus selection and experimental design. All improvements listed below were implemented in the next experiment described in section 3.3:

- DM-effects were shown for women, but not for a group of mixed subjects. Thus, agreeing with previous literature (Kemp, Silberstein, Armstrong, & Nathan, 2004; Wrase et al., 2003), gender might be a major issue when working with emotional stimuli. This is especially true when stimuli include erotic scenes (Bradley & Lang, 2000; Costa, Braun, & Birbaumer, 2003; Karama et al., 2002). Thus, study 3.3 includes only women and no erotic pictures.
- IAPS ratings are different for men and women (Lang, Bradley, & Cuthbert, 1997, 1999). For example, when only unpleasant pictures are considered, rating of women shows a high correlation between valence and arousal; this correlation is less pronounced in men (Bradley & Lang, 2000). Consequently, picture selection for study 3.3 was based on IAPS ratings for women only.
- As shown in study 3.2, it is important to select emotional stimuli carefully based on both, arousal and valence ratings. Thus, study 3.3 includes only IAPS pictures which are high on arousal and low in valence (exciting and unpleasant). In addition, in study 3.2, there is less variance on the arousal scale among neutral pictures.
- Although study 3.2 attempted to avoid any relationship between background pictures and superimposed words, it cannot be excluded that at least some subjects had specific picture-word associations. This might confound memory effects caused by words and by background information. To exclude this possibility in study 3.3, word/list allocations were randomized across all subjects.
- Recall performance on middle positions was relatively low. Thus, ERPs for recalled items for some subjects were based on a relatively low trial number (see 3.2.1.4). A general increase of middle position recall performance can be achieved by reducing the number of words to be encoded per list. Thus, in experiment 3.3, subjects were presented with 12 item-lists instead of 15 item lists.

- Participants were required to pay attention to both, background pictures and pictures to be learned. However, one could argue that a background picture is not regarded as background information if the task requires to pay attention to it. That subjects paid much attention especially to the arousing background information is reflected in the increased positive ERP component. To keep the background picture on the level of additional, but not task-relevant information, subjects in study 3.3 were instructed to encode the words only. Any explicit reference to the background pictures was avoided.
- Study 3.2 contained a color and an emotional isolate item in each list. However, although they were never presented directly adjacent, it cannot be excluded that there are interactions between both isolates. An isolated item is defined in the framework of other items. If one of the non-isolated items is distinct in any dimension, the isolating property of the “oddball” is weakened. To get clearer isolation attributes, study 3.3 includes only one isolated item per list, which, again, was either isolated by color or by background arousal level.

3.3. Experiment 1b: Memory recall in arousing situations

3.3.1. Methods

3.3.1.1. Participants

Data were acquired from 23 right-handed women from different faculties at the Otto-von Guericke-University Magdeburg (age range 20 to 35, mean age: 24, SD 3.9). All subjects were native speakers of German. Data from 5 subjects had to be discarded due to excessive artifacts in the EEG-tracings. Thus, data of 18 subjects were analyzed. See section 2.1 for additional information.

3.3.1.2. Stimuli and procedure

The experiment was based on the study described in section 3.2. There were several improvements regarding stimulus selection and experimental design (see section 3.2.3).

Each subject participated in 2 sessions, separated by at least one week. Both sessions consisted of a *Color* deviant and an *Arousing background* deviant block. The sequence of the blocks was counterbalanced across subjects and sessions.

All parameters except the distinctiveness manipulation were identical for the blocks. There were 40 lists per block, yielding 480 words per block, 960 words per session and 1920 words for the entire experiment (12 words x 40 lists x 2 blocks (arousing vs. color deviant) x 2 sessions). The same 480 words were used in all blocks, but the position of the words and the accompanying background pictures were allocated randomly. Thus, in contrast to experiment 3.2, there was a new and unique picture-word sequence for every subject, block and session.

Each list consisted of 12 trials (compared to 15 in experiment 3.2). A trial consisted of an IAPS picture background and a superimposed German noun. Trial properties (frame, font, size, visual angle and word position) were the same as in experiment 3.2. Each trial was presented for 1500 ms. Prior to each trial, a fixation cross with a varying duration between 600 and 1000 ms was shown. A screen at the end of the list indicated the beginning of the recall phase. The next list was started by a button press.

Instruction: Participants were instructed to recall all words shown in the previous block verbally (rather than written as in experiment 3.2). Recalled words were recorded with a computer microphone for later analysis. Participants were not required to recall the words in the same sequence as previously shown, and there was no instruction regarding the encoding strategy. Unlike instruction in experiment 3.2, subjects were not informed that word stimuli are presented in front of pictures. The task was simply to recall as many words as possible.

Deviant stimuli: Distinctiveness was created by changing either the word's color from white to colored (*Color deviant* condition, see below for color selection) or the word's background picture from low on the arousal scale to high on the arousing/low on the valence scale (unpleasant) (*Arousing background* condition, see below for picture selection). In contrast to experiment 3.2, there was only one distinctiveness manipulation in each list, color isolate in the *Color* blocks, arousing background in the *Arousing background* blocks. Trials with a low arousing IAPS picture background (see below for picture selection) and white font words in the foreground constituted the *Standard* condition. To avoid confounds with the primacy and recency effect, the distinctiveness attribute was only changed on word positions from 5 to 8, and also behavioral and ERP data for the *Standard* condition were only generated from list position 5 to 8. The distinctiveness attribute appeared with the same frequency on each of the 4 middle positions. An example of a single list is depicted in Figure 7.

Word selection: 480 German nouns were selected from the CELEX Lexical Database (Baayen, Piepenbrock, & Gulikers, 1995). Four to 11 letter words were included and all words were emotionally neutral. Emotional neutrality of words was assured using the same procedure as described in section 3.2.1.2. The 480 words were randomly selected from the remaining word set.

Picture selection: Words were presented in front of colored pictures taken from the IAPS (Lang, Bradley, & Cuthbert, 1997, 1999) (see section 3.2.1.2 for additional information). In contrast to the experiment described in 3.2, background pictures were selected based on their arousing values for women and only high arousing pictures with low valence level were selected. A picture was defined to be low arousing when the mean value of the arousing scale plus 0.5 SD did not exceed the value 5 on the IAPS arousal scale. Pictures with portrait alignment were excluded, 120 of the remaining pictures were selected on a random basis (mean arousal value = 3.2; minimum = 1.9; max = 4.4) for the neutral background condition. A picture was considered to be arousing when the mean arousal value minus 1 SD was above 5 and the valence was lower than 5. Pictures with portrait alignment and extremely intrusive pictures were excluded. Ten pictures were chosen from the remaining set (mean arousal level 7.3; minimum 6.9; maximum 7.4). Pictures contained i.e. mutilations, dead bodies, snakes, threatening situations. See Appendix 2 for arousal and valence ratings for arousing pictures and Figure 8 for the selected pictures in the IAPS valence arousal space.

Color selection: Since the *Arousing Background* condition was made distinct by 10 different emotional backgrounds, 10 different colors from the 256 RGB color scale were selected for the color word condition. Only colors that are easy to discriminate were included.

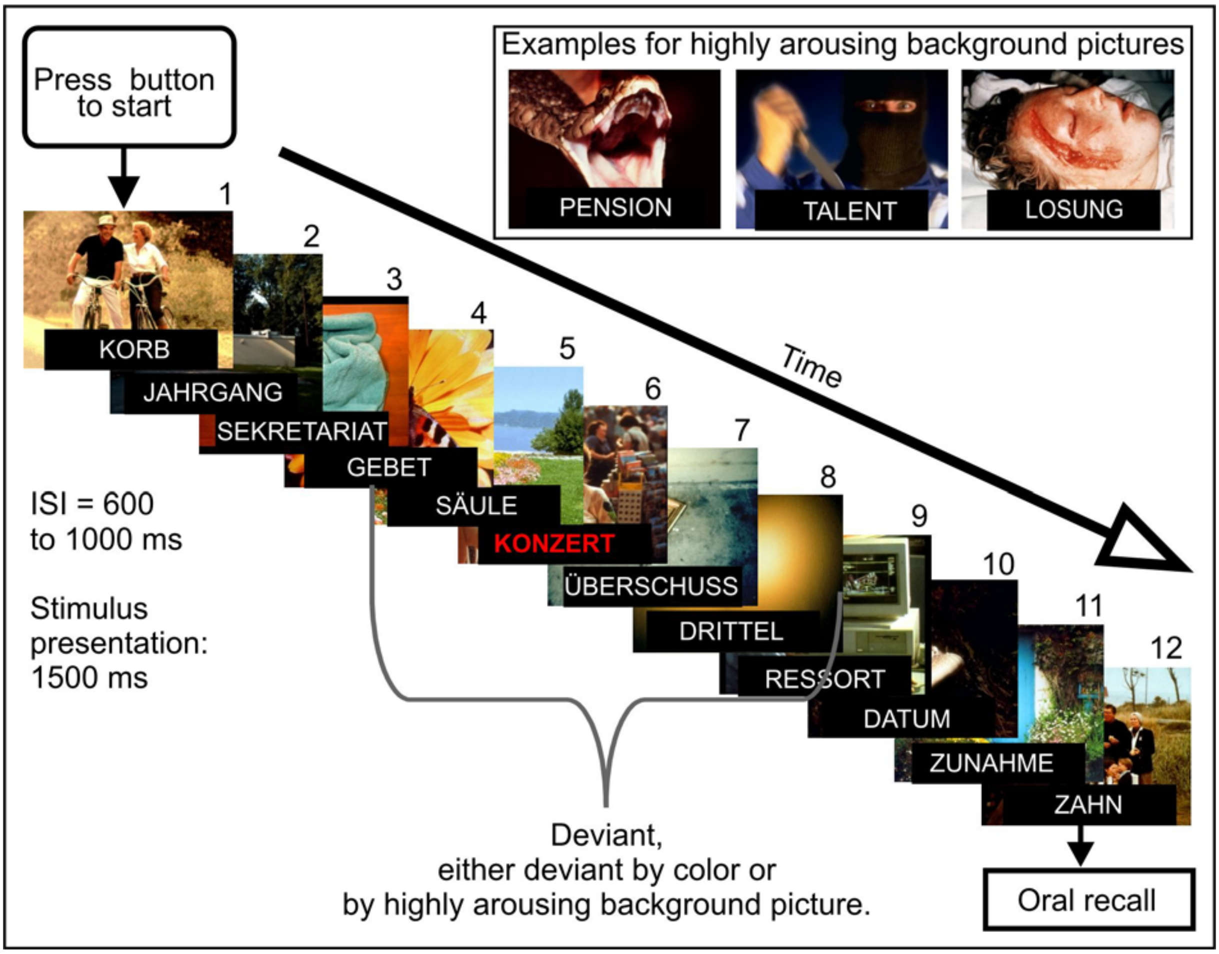


Figure 7: Experimental setup for experiment 3.3 . A sequence of 12 trials constituted one list. Isolation was achieved either by changing the font color (color isolate) to one of 10 colors or by changing the emotional background picture from neutral to highly arousing (arousing background isolate). There was either a color or an emotional background isolate in each list.

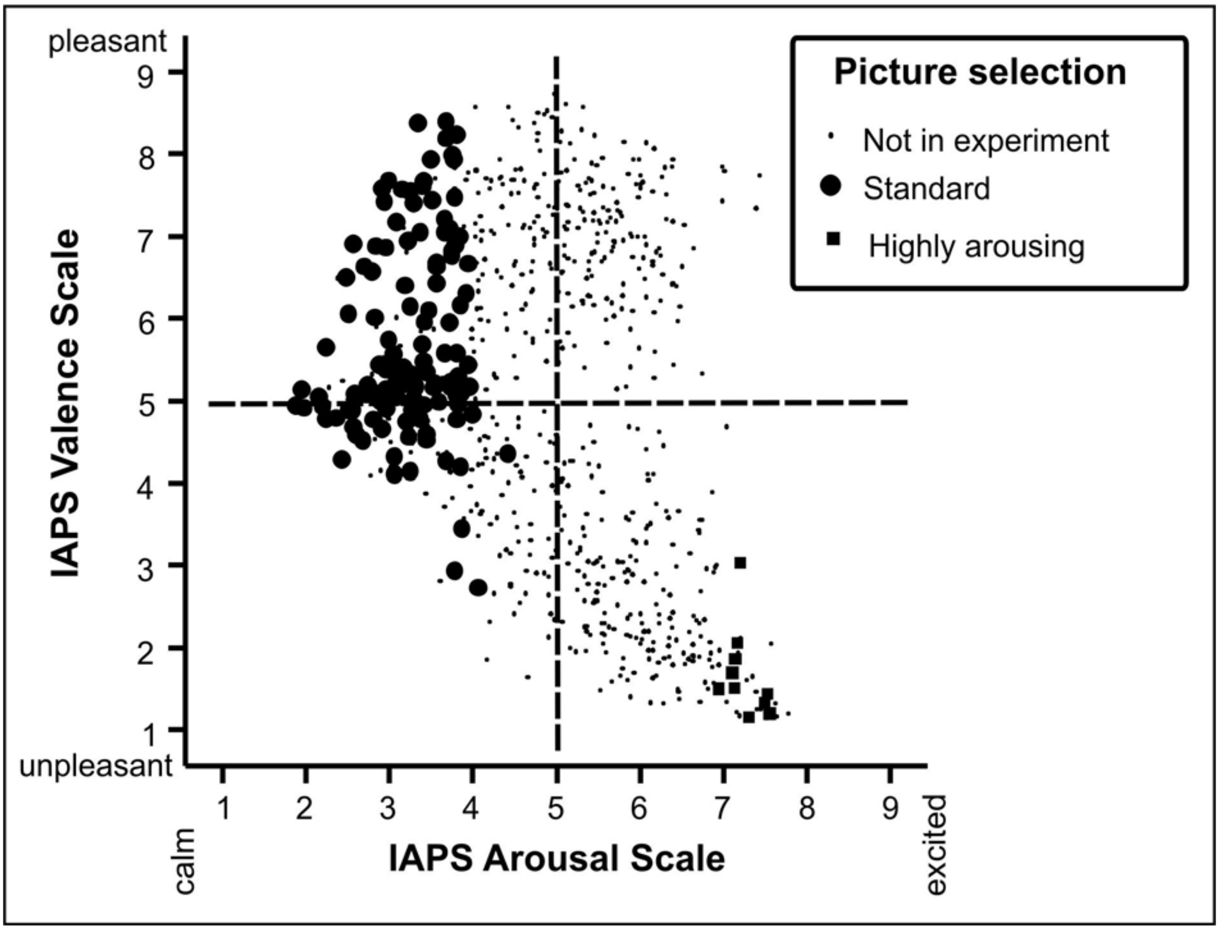


Figure 8: IAPS stimuli selected for the neutral and the arousing background condition in experiment 3.3, ratings are for women only. Picture details for the arousing background pictures are given in Appendix 2.

3.3.1.3. Data recording and preprocessing

See section 2.4.1 for general recording issues. Eye artifacts were rejected as described in section 2.4.1 and 2.4.2, head artifacts were rejected as described in section 2.4.1. Due to more recalled trials on middle positions, it was not necessary to conduct any artifact correction or filtering.

3.3.1.4. Data analysis

The same conditions as described in section 3.2.1.4 were generated relative to a 100 ms pre-trial baseline. Midline positions were ranging from list positions 5 to 8, trials presented on positions 1 to 4 and 9 to 12 were not further analyzed here. Detailed analysis of Primacy and Recency effects based on the same data will be available elsewhere (Wiswede, Rüsseler, & Münte, 2007).

The mean number of trials included in each of the six conditions is listed in Table 3.

CONDITION	RECALL	Mean trial number	SD	Range
Standard	**Recalled**	127	44	80-236
	Not recalled	197	54	81-309
Arousing	**Recalled**	22	6	14-34
	Not recalled	34	11	10-55
Color	**Recalled**	25	7	11-42
	Not recalled	32	12	15-56

Table 3: The number of trials included to generate the ERP conditions in study 3.3.

Although, after artifact correction, there were a few subjects with a low number of trials included in some of the averages (lowest trial number: 10), all averages provided clear signals.

Time windows for statistical analysis were based on visual inspection. The deviance effect was examined in time windows 180-250ms, 250-350 ms, 450-700 ms and 700-900 ms. The DM-effect was examined in time windows 200-450 ms and 450-800 ms. Statistical analysis was the same as described in section 3.2.1.4.

3.3.2. Results

3.3.2.1. Behavioral data – recall performance

Overall, participants recalled 46.5 percent of the words. Words at the beginning of the list (position 1 to 4, Primacy effect) were recalled in 41.1 percent, at the end of the list (position 9 to 12, Recency effect) in 67.7 percent of the cases (Fig. 1). The Primacy and Recency effect will not be further discussed in this paper (see Wiswede, Rüsseler, & Münte, 2007).In the following, trials that occurred at positions 5 to 8 of each list are considered only.

There was better recall performance for the *Color* condition compared to *Arousing background* and *Standard* conditions (F (2,34) = 5.78, P < .007; see Table 4 for recall performance). Paired t-tests revealed significant differences between *Standard* and *Color* (T (17) = -3.39; P< .003), *Color* and *Arousing*

Background (T (17) = -2.43; P< .026), but no differences between *Standard* and *Arousing Background* (T (17) = -.71). See Figure 9 and Table 4.

		Condition	
	Standard Pos 5-8	**Arousing Background**	**Color**
Recall	38.4 (10.1)	39.9 (11.0)	45.3 (11.6)
VRI		1.5 (9.2)	6.9 (8.7)

Table 4: Recall performance in percent for the Standard, the Arousing Background and the Color condition. Values are means across all 18 subjects, SDs are given in brackets. VRI indexes the Von-Restorff-index, computed by subtracting the recall percentage for Standard words from the arousing or color recall percentage.

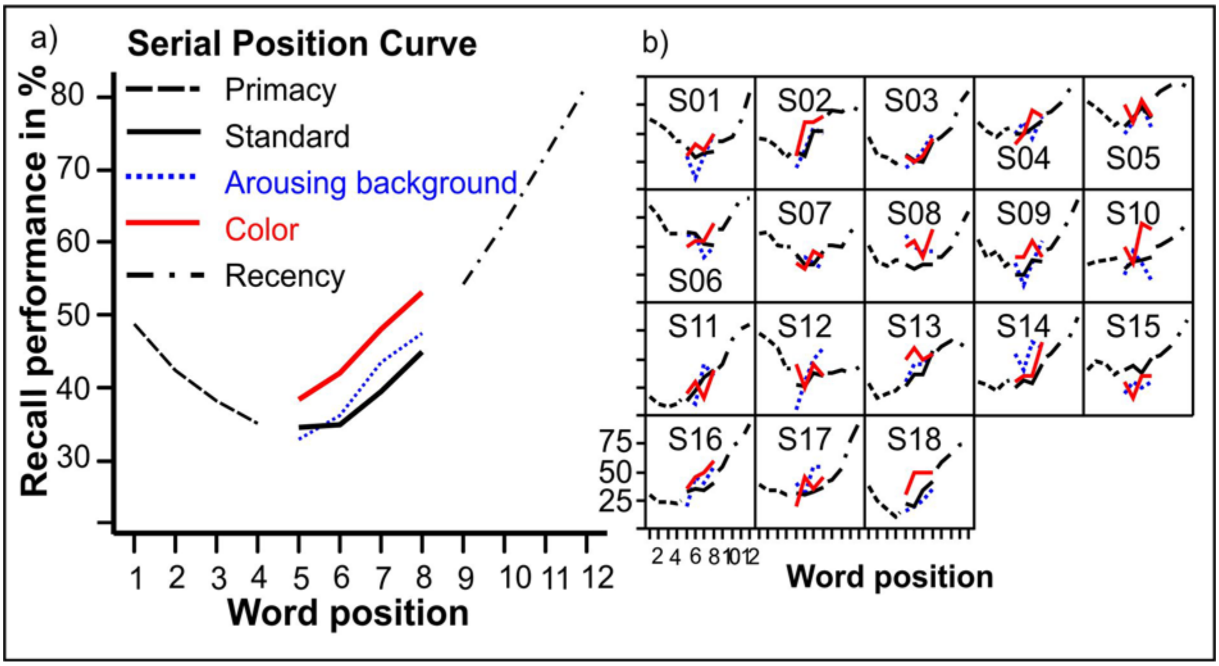


Figure 9: Behavior data for experiment 3.3. a) Recall performance across all 12 serial positions, divided by isolation attribute. Right panel: recall performance for single subjects.

3.3.2.2. ERP data

ERPs modulated by deviance

Visual inspection: Grand average ERPs averaged across recalled and non-recalled words are shown in Figure 10 a. The first clearly distinguishable component is the N100-P200 complex, which is typically seen for visually presented words.

Color isolates elicited a more positive ERP deflection around 180 ms, which was most pronounced at electrode-sites Fz and Cz (see Figure 10). A strong positivity was seen for *Color* as well as for *Arousing Background* isolates emerging around 300 ms. This component was parietally distributed for *Arousing Background* and seen on parietal and in attenuated manner on more anterior electrodes.

Statistical analysis: The *Color word condition* differed from the *Neutral* and the *Arousing* condition within the 180-250 ms time window (rmANOVA, factors CONDITION (*Standard, Color*, *Arousing Background*) and SITE (Fpz, Fz, Cz, Pz) based on mean amplitude in the 180-250 ms time window; CONDITION (F (2,34) = 6.69; p < .004, CONDITION x SITE n.s., pairwise comparisons: *Color word condition* differed from both others, p < .033). Three further time intervals based on visual inspection of the grand average waveforms were assessed, 250 to 350 ms; 450 to 700 ms and 700 to 900 ms. In the 250 to 350 ms interval, mean amplitude for *Color* words was more positive compared to *Standard* words. Amplitude differences between standard and *Arousing Background* words did not reach statistical significance (significant effect of CONDITION (F (2,34) = 4.09; p < .03). The same pattern was found in the 450 to 700 ms time window (CONDITION (F (2,34) = 5.02; p < .03; *Color* words more positive than *Standard* words).

Within the 700 to 900 ms time window, both classes of isolates differed from the *Standard*, whereas there are no significant differences between both types of isolates (CONDITION (F (2,34) = 4.92; p < .015).

ERPs modulated by deviance and recall performance

Visual inspection: There was a more positive going waveform for recalled compared to non-recalled items, starting at 250 ms for the *Standard* and at 450 ms for the *Color* condition. Importantly, this clear and long-lasting DM effect was not seen for the *Arousing Background* condition (see Fig. 3a and 3b).

Statistical analysis: In the 200 to 450 ms time window, there was a significant effect of RECALL in the *Standard* (F (1, 17) = 12.17, p < .003), but not in the *Color* (F (1,17) = .11; p < .74) or *Arousing Background* condition (F (1,17) = .93; p < .35) . In the 450 to 800 ms time window, there was a significant main effect of RECALL for the *Standard* (F (1,17) = 13.17, p < .003) and the *Color* (F (1,17 = 5.17, P <.04), but not for the *Arousing Background* condition (F (1,17) = .40; p < .53).

While visual inspection hinted at a small DM-effect in the *Arousing Background* condition between 300 and 400 ms, statistical analysis did not confirm this (ANOVA on the mean amplitude 300 to 400 ms, RECALL: (F (1,17) = 1.21; p < .29). Visual inspection might imply that there is an inverse DM-effect for the *Color* condition in the 200 to 300 ms time range. However, statistics conducted as described above revealed that the more negative waveform for recalled color isolates was not significant (F (1,17) = .87; p < .37; n.s.).

The scalp distribution of the DM-effect in the 450-800 ms time window is depicted in Figure 10 d. For the *Standard* condition, the difference between recalled and non-recalled words had a frontoparietal distribution. In contrast, the DM-effect for the *Color* condition has a clear frontal maximum.

Figure 10: a) to c): ERP waves on midline electrodes Fpz, Fz, Cz and Pz. a) Grand average for the Standard, the Color and the Arousing background condition without considering recall performance. b) DM-effect for the three conditions. c) Difference waves (recalled minus non-recalled) for the three conditions. A clear DM-effect is only seen for the Standard and the Color word condition. d) Scalp distribution for the 450-800 ms time window.

3.3.3. Summary

Words that are isolated by a different color are remembered better than non-isolated words. This isolation advantage is not seen for words that are presented in front of a highly arousing picture. ERPs show that there is an increased P300 effect for words isolated by color and a delayed P300 for words isolated by a highly arousing background. An ERP modulation due to subsequent memory, a DM-effect, is seen for *Standard* and *Color* isolates, but not for *Arousing Background* words. This DM-effect starts later for colored words than for standard words.

In contrast to study 3.2, the *Arousing Background* stimuli elicited a P300 that was enhanced relative to *Standard*, but not larger in amplitude than the P300 elicited by *Color* isolates. This might reflect differences in the instruction; the explicit instruction in study 3.2 to pay attention also to the background pictures might result in an additional P300 enhancement. Thus, the P300 is seen as evidence that arousing background pictures were salient enough to catch attentional resources, while remaining nonintegral information.

3.4. Discussion – Part 1

3.4.1. Behavioral data

The finding that words isolated by color are recalled better replicates earlier results (Fabiani & Donchin, 1995; von Restorff, 1933; Wallace, 1965). Failure to find enhanced memory effects for color isolated items in experiment 3.2 are attributed to the instruction (subjects were required to pay attention to the emotional background stimuli) and to the presence of two distinctiveness attributes per list, which might diminish the distinctiveness of the color attribute.

Study 3.3 has shown that there was no memory enhancement when words were presented exclusively in front of arousing unpleasant stimuli. This was unexpected when having only the non-integral background picture properties and not the emotional properties in mind, because previous research has shown that changing a non-integral item attribute results also in a VR-effect (Otten & Donchin, 2000). Consequently, the absence of the VR-effect in the *Arousing Background* condition in study 3.3 can not merely be attributed to the non-integral nature of the isolation. Higher coherence among emotional stimuli

(Maratos, Allan, & Rugg, 2000) is also no major issue in the present study, since this would be expected to result in better than normal recall performance for the arousing background condition.

Adolphs, Tranel and Buchanan (2005) presented neutral pictures embedded either in a neutral or in an emotionally highly arousing story to amygdala-damaged subjects, brain-damaged controls (unimpaired amygdala) and healthy controls. They found that under the emotionally arousing condition, recall performance was increased for gist, but not for peripheral information of the neutral pictures in healthy and amygdala-unimpaired subjects. This pattern was reversed in amygdala-impaired subjects. At first glance, those data appear to contradict the present finding; recall was not enhanced for word stimuli with arousing background. However, it is crucial how to distinguish between gist and irrelevant information: Adolphs and colleagues defined (2005) gist information as information essential to the meaning of the picture (for example, who were the main characters in the picture) and background information to be irrelevant (for example, what the clouds looked like) for the meaning of the picture. A distinction between gist and irrelevant information cannot be made for the words in experiment 3.3. A gist/irrelevant distinction for background pictures was not conducted in the present studies, because background pictures were not task-relevant and recall performance was not assessed. Thus, instead of distinguishing between gist and irrelevant information, the relationship between task-relevant word and task-irrelevant, but highly arousing background picture, will be considered in more detail.

While it has been shown previously that emotionally enriched stimuli enhance memory performance (Bradley, Greenwald, Petry, & Lang, 1992; Dolcos & Cabeza, 2002; Palomba, Angrilli, & Mini, 1997), there is evidence that under some circumstances, memory performance can also be decreased in highly arousing situations. For example, Erk et al. (Erk et al., 2003) found no increased memory performance for words in negative compared to non-emotional encoding trials. They (Erk et al., 2003) pointed out that negative emotion might improve memory performance when it is part of the item to be encoded, but that it does not improve performance when it is part of the learning environment, as it was the case in the present study. Thus, similar to the integral vs. non-integral distinction introduced in section 3.1.4, the emotional content might be a central or a peripheral aspect of the encoding material (see Reisberg & Hertel, 2004 for overview). This idea is derived from an old hypothesis introduced by Easterbrook in 1959 (Easterbrook, 1959): Arousal causes a narrowing of attention, which makes the aroused organism more sensitive to central information, but less sensitive to encoding material presented at the periphery. More recent research with human subjects supports this idea; central details were recalled more frequently than peripheral details in memories of shocking events (Berntsen, 2002; Reisberg & Hertel, 2004). Following this argumentation, the *Arousing background* condition in study 3.3 can be regarded as a stimulus set consisting of an attention-capturing highly arousing, unpleasant element underlying an unemotional, less attention-attracting word. This puts the arousing background information rather than the word in the center of attention. This pattern is reversed in all other conditions, since the non-emotional background pictures do not act as an "attention-magnet" (Reisberg & Hertel, 2004) and, thus, remains background information overlaid by a central, task-relevant word. That means that only in the *Arousing background* condition the background information could interact with memory processes. It is conceivable that the arousing information interrupted encoding processes, and, thus, decreases recall performance back to normal level.

In study 3.2, also no enhanced memory effect for words presented in front of arousing unpleasant pictures was obtained. However, increased memory performance for words presented in front of arousing pleasant IAPS pictures was clearly seen. Although this finding replicates earlier results (Erk et al., 2003), this finding requires a more detailed differentiation of the "attention magnet" explanation introduced above. This can be done by taking not only the arousal, but also the valence level into account: While negative context enhance memory performance only for the negative item and withdrawing attentional resources from other items (weapon focus, see section 3.1.5), study 3.2 provides evidence that positive context cues enhance memory performance also for non-emotional information. Thus, positive context might not possess the same "attentional magnet" properties than negative context stimuli; attention is not withdrawn from the task-relevant, but emotionally neutral item. Instead, the neutral item is enhanced with pleasant information and, thus, more likely to be recalled.

Recent research suggests that changes in affective state interact with a broad variety of cognitive functions (see section 4.1). For example, there is emerging evidence that positive affects facilitates creative problem solving, decision making and flexibility (Ashby, Isen, & Turken, 1999; Dreisbach & Goschke, 2004). For memory encoding, it has been argued that positive affect increases memory for task that require active recall rather than recognition (Erk, Martin, & Walter, 2005). This is in line with the presented findings; experiment 3.2 shows increased memory performance when pictures in front of positive pictures.

One could argue that the behavior effects described in both studies are not caused by emotion, but merely by attention directed toward or away from the stimulus to be encoded.

- Memory performance was increased for pleasant arousing background pictures in experiment 3.2 because the pleasant background enhances all, central and peripheral details and does not withdraw attention from the word to be learned.
- Memory performance was not enhanced for words presented in front of unpleasant arousing stimuli (experiment 3.2 and 3.3), since unpleasant pictures withdraw attention from the non-emotional item.
- Memory performance was enhanced for the color condition in experiment 3.3 because additional attentional resources were allocated to the central color attribute in the *Color* condition

However, I do not think that this is a feasible alternative explanation, because other research (Christianson & Loftus, 1991; Reisberg & Hertel, 2004) demonstrated a clear distinction between emotion-induced and attention-induced effects on memory performance: emotional contents increases memory selectively for central information, whereas attention-capturing, but unemotional stimuli do not selectively increase recall performance for central as well as peripheral information.

3.4.2. Brain Potentials

Behavioral data clearly indicate that it is of major importance to clearly distinguish between pleasant and unpleasant valence when working with emotional pictures. A valence-based distinction was not possible for study 3.2, see section 3.2.3. Thus, the following section discusses ERP findings from study 3.3 only.

The most important ERP findings were a) a P300 effect, seen for the *Color* as well as *Arousing background* isolates, b) a DM-effect for the *Standard* and the *Color* condition, but not for the *Arousing background* condition, c) no positive slow wave in the *Arousing background* condition. These findings will now be discussed in detail.

The P300 for *Color* isolates as well as for *Arousing Background* isolates clearly indicates that subjects did process the arousing background information. Unlike previous research (Otten & Donchin, 2000), which included also a non-integral, but non-emotional isolation attribute (frame around the word), the P300 in the *Arousing background* condition was not markedly reduced in amplitude compared to the integral isolation condition. This might reflect emotional processing which adds to the P300 amplitude elicited by pure non-integral properties. The large P300 for the *Arousing background* condition might be the neuropsychological correlate of the attention-capturing properties of emotional stimuli discussed above. The delayed peak latency for *Arousing backgrounds* might reflect increased stimulus complexity.

The DM-effect for the *Color Isolate* condition consists of a frontal and a parietal part: the latter likely represents a modulation of the P300, while the former is not easily explained in a P300 framework. The parietal DM-effect has often been discussed based on the context updating hypothesis developed to account for P300 modulations (Donchin & Coles, 1988; Fabiani & Donchin, 1995; Fabiani, Karis, & Donchin, 1990; Otten & Donchin, 2000). More intense context updating leads to a better memory trace, which increases the likelihood of successful recall. Words isolated by color contain additional information, which elicits more updating in working memory and leads to an improved memory trace during encoding and therefore to an increased VR-effect and P300-enhancement. As pointed out by Otten and colleagues (Otten & Donchin, 2000), an integral part of the word (color in the current study, word size in

(Otten & Donchin, 2000)) cannot be separated from the words’ informational content at an early processing stage; enhanced context updating might therefore be an obligatory processing step. The earlier onset of the DM-effect for the *Standard* compared to the *Color* condition might be due to the additional information content of the words isolated by color.

Otten and Donchin (Otten & Donchin, 2000) pointed out “that some of the non-isolated words were distinctive in some sense, for semantic or contextual reasons. Specific words may appear to the subject to deviate from the general vocabulary used in the study. Or they may have personal associations that make some words distinct” (p.659). This might explain the DM-effect for non-isolated words (*Standard* words).

The generally increased P300 amplitude for *Arousing Background* stimuli was not associated with increased recall performance. Although unexpected and not supported by studies using IAPS pictures only (Dolcos & Cabeza, 2002), this finding is nevertheless in line with earlier observations (Fabiani, Karis, & Donchin, 1990; Otten & Donchin, 2000) showing that the P300 amplitude is not necessarily a valid predictor for recall performance. Consequently, distinctiveness alone is not sufficient to elicit an enhanced P300 component for recalled items. Thus, having in mind that the *Arousing background* condition elicited a strong P300 independent of recall performance, I conclude that a P300-recall-relationship does not merely arise because a distinctiveness attribute triggers deeper and more extensive processing. It also matters how distinctiveness is achieved.

I see three ways to explain the missing P300-recall-relationship for the *Arousing Background* condition: First, the highly arousing pictures draw attention from the words toward the arousing background pictures. Unlike in the study conducted by Otten and Donchin (Otten & Donchin, 2000), who concluded that the cognitive system could redirect the attentional resources away from a non-integral, but unemotional distinctiveness attribute, such an attentional redirection was not possible for our non-integral, but highly arousing isolation attribute. This resulted in an increased P300 for the *Arousing background* condition. It seems unlikely that recall performance for the words could benefit from the increased overall arousal level induced by the background picture, because arousing information increases memory performance for gist, but not for peripheral information (Reisberg & Hertel, 2004). Thus, the P300 is solely caused by the background pictures; there is no contribution of context updating elicited by the words. Consequently, there is also no P300-recall relationship for the recalled words. It appears that the recall-predicting part of the P300 can only be added by integral items. It is conceivable that a P300-recall-relationship would be seen if subjects were required to recall the content of the emotional background task. In this way, the emotional content would be an integral part *and* a gist of the encoding material. However, this assumption cannot be tested by the present study, because recall performance to the emotional background pictures was not acquired. Second, words with *Arousing Background* might be transferred into working memory, but are instantly overwritten by the arousing picture content. This would predict a memory performance for the *Arousing Background* condition that is even lower than for non-isolated words which was not the case. The third explanation is based on the earlier finding that subjects do not show a VR-effect in behavioral data and no P300-recall relationship in the ERPs when they were instructed to use an elaborative rather than a rote rehearsal strategy to encode word stimuli (Fabiani, Karis, & Donchin, 1990; Karis, Fabiani, & Donchin, 1984). To some extent, this finding is similar to the results presented here. Since a P300-recall-relationship is not seen when subjects refrain from rote strategies, I assume that arousing context could interrupt the rehearsal strategy normally used in simple memory tasks.

In contrast to Donchin and Fabiani (Fabiani, Karis, & Donchin, 1990), the present experiment did not yield a positive slow wave for the *Arousing background* condition, which needs some further explanation. There are important differences between this putative "enforced strategy change" and the instructed strategy changes used elsewhere (Fabiani, Karis, & Donchin, 1990): Instructing a subject to use a specific encoding strategy triggers top-down processes, which might influence memory performance and ERP components. There was no strategic instruction in the present study, the proposed strategy change was stimulus driven. These differences might contribute to the emergence of the recall sensitive frontal positive slow wave in Fabiani et al. (Fabiani, Karis, & Donchin, 1990).

On the other hand, a positive slow wave was also found when subjects used a rote encoding strategy (Otten & Donchin, 2000). Otten and Donchin (Otten & Donchin, 2000) attributed the positive slow wave to “the retrieval of preexisting knowledge about the word or to connecting the words with episodic information” (p. 658). Apparently, depending on task requirements and stimulus properties, successful encoding processes might be reflected in an increased P300 or an increased positive slow wave. I add another aspect, namely that recall performance and ERPs might be decoupled as seen in the *Arousing background* condition. It has to be kept in mind that fMRI revealed a number of deep brain structures who display strong DM-type effects. Especially the amygdala has been shown to be involved in processing of arousing information (Adolphs, Tranel, & Buchanan, 2005; Dolcos & Cabeza, 2002; Erk et al., 2003). However, those structures are not directly accessible by ERP technique, and thus, their “DM-activity” can not be demonstrated by ERPs. Thus, the following conclusions have to be considered as tentative. As mentioned above, emotional information enhances recall performance for the gist, but not for peripheral information. Adolph and colleagues (Adolphs, Tranel, & Buchanan, 2005) linked this finding directly to amygdala functions: they found that patients with unilateral amygdala damage do not show enhanced memory for gist information when encoding in emotional situations. Thus, the amygdala, possibly in cooperation with the hippocampus, might be involved in recalling words from the emotional background condition.

A possible limitation of the current study is the fact that highly arousing but pleasant emotional background pictures (upper right quadrant of Figure 8) were not used. Thus, future studies should examine, whether positive affective information might lead to a von Restorff effect in the ERP.

Experiment 3.3 was recently published in a peer-reviewed international journal (Wiswede, Rüsseler, Hasselbach, & Münte, 2006). Analysis of Serial Postion effects based on data described in experiment 3.3 are published as well (Wiswede, Rüsseler, & Münte, 2007).

4. Part 2: Emotional modulation of performance monitoring.

4.1. Background

Everyday experience teaches us that the way we perceive and act upon our environment is influenced by our current affective state. Research has shown that changes in affective state modify many aspects of our cognitive performance. For example, it is well documented that positive affect facilitates creative problem solving, decision making and flexibility (Dreisbach & Goschke, 2004; Isen, 2001; Isen, Daubman, & Nowicki, 1987).

There is increasing evidence that the anterior cingulate cortex (ACC) and its afferent and efferent connections are crucial in generating complex behavior and in mediating affective influences on behavior. The ACC is a part of the medial frontal cortex; functionally it is a part of the brain's limbic system. Previous research indicated that the ACC can be subdivided into a dorsal cognitive and a rostral affective subdivision (Allman, Hakeem, Erwin, Nimchinsky, & Hof, 2001; Ashby, Isen, & Turken, 1999; Bush, Luu, & Posner, 2000). The cognitive subdivision holds strong reciprocal interconnections with lateral prefrontal regions, parietal cortex and many other structures. It has been shown to be activated in cognitively demanding tasks, among them stimulus-response-selection, stroop-like tasks and performance monitoring tasks. As a part of the anterior attention system (Posner & Petersen, 1990), it is engaged in the conscious direction of executive attention. The rostral affective ACC subdivision holds strong connections to the amygdala, nucleus accumbens, hypothalamus, ventral striatum, hippocampus and orbitofrontal cortex subdivision (Ashby, Isen, & Turken, 1999; Bush, Luu, & Posner, 2000). It is involved in assessing the salience of emotional and motivational information, the mediation of arousal and in the regulation of emotional responses (Bush, Luu, & Posner, 2000; Phan, Wager, Taylor, & Liberzon, 2004).

The ACC has been extensively examined in the last years, since there is good evidence that it is a key structure linking cognitive and emotional processes. One of the most intensively addressed functional properties is performance monitoring. The second section of this thesis examines the interactions between cognitive and emotional processes exemplified by emotional modulation of performance monitoring. An introduction to recent research is provided focusing on behavioral and electrophysiological correlates of choice-reaction tasks. The main hypotheses which provide the theoretical framework for performance monitoring processes are introduced and linked to modern theories of positive and negative affect. Specific hypothesis are derived and tested in four ERP studies.

4.1.1. The Flanker task in performance monitoring

Anticipation, detection, correction and avoidance of errors are major parts of goal-directed behavior. These processes are summarized by the term performance monitoring (or action monitoring); they are fundamental in understanding how organisms flexibly adjust to fast changes in the environment. Performance monitoring can be understood as the process of monitoring the appropriateness of an action in a given context. Inappropriateness of a response, defined as errors, is evaluated relative to the context of the action (Luu & Pederson, 2004).

An often used paradigm to induce a reasonable amount of errors is based on a choice response time (RT) task introduced by Eriksen and Eriksen (1974). In this task, a centrally presented target letter is surrounded by distracting letters, which are either equivalent to the target letter (congruent) or different from the target (incongruent). Subjects are required to respond as fast and as accurate as possible to the central letter. For example, a letter string might consist of either a central S or a central H surrounded by peripheral SS or HH. S requires a button press with the left, H with the right hand. Thus, there are two conditions with the target and the flanker being congruent (SSSSS and HHHHH) and two conditions with the target and flanker being incongruent (SSHSS and HHSHH). It has been consistently shown that RTs are faster and error rates are lower in congruent trials (HHHHH, SSSSS) compared to incongruent trials (HHSHH, SSHSS). Eriksen and colleagues suggested that delayed RTs and higher error rates for incongruent flanker trials might result from competition at the motor response level, since incongruent flankers might invoke a conflict between flanker and target based motor responses. This effect has been replicated using a broad variety of non-letter flanker stimuli (i. e. arrow heads in Kopp, Rist, & Mattler, 1996).

Behavioral studies have consistently shown that erroneous responses are given faster than correct responses. Subjects are usually aware of committing an error (Rabbitt, 2002). They adapt their performance after the erroneous response was given. One behavioral consequence of an error is that subjects tend to rapidly correct for their errors by providing the correct button press directly after the erroneous response, irrespective of whether they are instructed to do so or not. The response time for the corrective response is usually faster than for normal correct responses.

A change in response strategy after error commission is indicated by the finding that subjects show a strong increase in reaction time for the next correct response following an error. This effect was first described by Rabbit (Rabbitt, 1981) and is referred to as "post-error slowing" or “Rabbitt-effect” (Falkenstein, 2004). Post-error slowing indicates a change in response strategy in favor to more cautious responses. As pointed out in recent research, post error slowing has to be carefully discriminated from regression to the mean effects (Hajcak, McDonald, & Simons, 2003b, 2004). This issue will be further discussed below (section 4.3.2.1).

4.1.2. Neural correlates of performance monitoring

In ERPs, there are two main components that are consistently found when subjects perform a Flanker task, depending on whether examining cognitive processes prior to the response or processes after the response to the central letter. When examining processes elicited by properties of the flanker-stimuli, the ERPs are generated stimulus-locked with the presentation of the flanker stimulus providing the zero point for averaging. A flanker-typical activity is an ERP deflection which is more negative for incongruent compared to congruent flanker stimuli and has been labeled N2. The N2 emerges beyond 200 ms after stimulus onset; it is largest at frontal to central areas Fz to Cz (Kopp, Rist, & Mattler, 1996; Rüsseler, Hennighausen, Münte, & Rösler, 2003; Rüsseler & Rösler, 2000; Van 't Ent, 2002).

When ERPs are generated with the subject’s response being the zero point (response-locked ERPs), a more negative component is seen for erroneous compared to correct responses. This negative component has been labeled as ERN (Error related negativity, (Gehring, Goss, Coles, Meyer, & Donchin, 1993)) or N_e (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991). It is observed for frontal to central scalp regions within 0 to 100 ms after the erroneous response. The present thesis uses the label ERN. Within the same time range, there is a smaller negative deflection following correct responses; which has been labeled CRN (Correct response negativity (Hajcak, Moser, Yeung, & Simons, 2005) or conflict related negativity (Simon-Thomas & Knight, 2005)). The N2 and the ERN/CRN will now be introduced in detail.

Another, but far less examined component emerges after the ERN/CRN in response-locked data around 200 ms. This component is a positive deflection for errors, which has been labeled P_e (Error Positivity). It emerges around 200 ms after error commission with a parietal maximum. It has been hypothesized to reflect conscious error processing (Falkenstein, 2004), but has also been associated with affective processes. Thus, the P_e might be of special importance for the present thesis; it will be further introduced in section 4.1.2.3.

4.1.2.1. The stimulus-locked N2 and the response-locked ERN/CRN

In the flanker task, the N2 emerges beyond 200 ms after the presentation of the stimulus and shows increased amplitude for incongruent compared to congruent trials. It is reasonable to assume that the N2 seen after incongruent flankers corresponds to the negativity described in Go/NoGo reaction time tasks. In Go/NoGo tasks, subjects are required to withhold a reaction. Similar to that, in a flanker task, subjects are required to withhold action tendencies induced by the flanker which surround the target. Thus, the N2 might be related to motor inhibition processes (Falkenstein, Hoormann, & Hohnsbein, 1999; Kopp, Rist, & Mattler, 1996; Van 't Ent, 2002) and is thought to represent pre-response conflict.

Whenever an erroneous response is given, a more negative deflection is seen in response-locked ERPs. This Error-related negativity (ERN) emerges around the time of an erroneous response, and peaks 50-100 ms later. The very fast onset after the response indicates that the underlying generator must have had access to an efference copy of the initiated incorrect response (Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). The ERN is best seen on frontocentral scalp portions and is symmetrical to the midline (Yeung, Cohen, & Botvinick, 2004). A similar, but much smaller negativity is often seen after correct responses and labeled as "CRN" (conflict-related negativity) or "Nc" (Falkenstein, 2004). The CRN has been described to reflect a general, non-error specific, response-related process (Falkenstein et al., 2001). Literature provides conflicting results about the distribution of the CRN. There is the view that the CRN has a different topography than the ERN, with the reference method being a major criterion: The CRN has been shown to be most pronounced somewhat more posterior than the ERN on centroparietal scalp portions when a linked mastoid reference is used. The topographical difference disappears when employing a spatial reference (current source density, CSD) (Falkenstein, 2004). However, others report no differences in CRN/ERN distribution when using linked mastoid reference (Hajcak, McDonald, & Simons, 2004; Simon-Thomas & Knight, 2005).

The ERN/CRN and the N2 dipole sources have been shown to be consistent with a neural generator in various subregions of the anterior cingulate cortex (ACC). Van Veen and Carter (Van Veen & Carter, 2002b) have also reported a dorsal ACC source for both ERN and N2 components. However, due to limited spatial resolution of ERP data, fMRI results might provide further insight. A meta-analysis of 38 fMRI studies published between 1997 and 2004 revealed a very consistent finding: Regardless of whether studies examined response errors, response conflict, decision uncertainties or undesired outcomes, increased brain activation was found in the posterior medial prefrontal cortex, more specifically in the anterior cingulate cortex (ACC). Within this region, there is still debate whether exactly the same regions are activated when the conflict occurs prior to or after the response. Although both sorts of conflict show high overlap in areas activated. Pre-response conflict activates regions of the posterior medial frontal cortex that are slightly more dorsally than regions activated by error monitoring (Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). However, those authors point out that a clear distinction between regions for conflict and error monitoring cannot be ubiquitously confirmed by their meta-analysis.

4.1.2.2. Mismatch, conflict or bad outcome?

There is debate about whether the ERN/CRN and the N2 reflect different or similar mechanisms. The following sections review the most common theories in explaining the underlying mechanisms of the ERN and, if possible, integrate the ERN/CRN and the N2 into one theoretical framework.

There are four major hypotheses describing the functional significance of the ERN/CRN, namely the mismatch hypothesis, the conflict monitoring hypothesis, the inhibition hypothesis and the reinforcement learning hypothesis (Falkenstein, 2004). Those theories are best regarded as being not fundamentally conflicting, but, instead, they do emphasize different aspects of performance monitoring. All of them have in common that the ERN/CRN (and in some of them the N2) signals that an internal or external goal or a reward might not be achieved and that there is need to increase cognitive control (Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). All four theories will be shortly introduced, with special focus on the conflict monitoring hypothesis and the reinforcement learning theory, since they are of special theoretical importance for the present experiments.

Mismatch: The mismatch hypothesis states that the ERN reflects a monitoring process that signals errors whenever it detects that the neural representation of a given response does not match the neural representation of the intended (correct) response. There are some data which support the mismatch hypothesis. For example, the ERN has been shown to be larger under moderate compared to severe time pressure. A possible explanation for this is that the response determination process is not conducted as thoroughly as under high time pressure, because the representation for the correct response might be impaired (Falkenstein, 2004).

Inhibition: The Inhibition Hypothesis provides a theoretical framework that unifies pre-and post-response conflicts in one theory. It assumes that the ERN reflects the attempt to inhibit an ongoing error (Falkenstein, 2004; Falkenstein, Hoormann, & Hohnsbein, 1999). It is well known that subjects show an increased mediofrontal component after successful withholding a response (NoGo-N2) (Eimer, 1993). However, it can be reasoned that the ERN reflects the final (but unsuccessful) attempt to prevent the error. This hypothesis was challenged by studies that found different distributions of the N2 and the

ERN (N2 largest at Fz to Cz, ERN largest on Cz, linked earlobes reference) (Van 't Ent, 2002). In addition, the N2 amplitude is more pronounced in subjects with a high error rate, while the ERN was reported to be not responsive to overall error rate (Falkenstein, Hoormann, & Hohnsbein, 1999). However, I regard the last-mentioned point as not very strong, since there is also literature reporting a stronger (more negative) ERN in subjects with a low error rate compared to subjects with a high error rate (Gehring, Goss, Coles, Meyer, & Donchin, 1993; Hajcak, McDonald, & Simons, 2003b) and there is also literature reporting identical distribution of the N2 and the ERN (Van Veen & Carter, 2002b).

Conflict monitoring: In contrast to the mismatch hypothesis, the conflict monitoring hypothesis assumes that the ERN does not reflect the mismatch between the representation of a given and an intended response, but the conflict between response representations (Carter et al., 1998; Falkenstein, 2004; van Veen & Carter, 2002a, 2002b). An error might occasionally occur due to premature responding. The correct response tendency, activated by continued stimulus processing, conflicts with the already executed incorrect response. This conflict is reflected in the ERN (Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). Most importantly, the conflict hypothesis makes only predictions about the amount of conflict; an ERN-like component would therefore also be expected when conflict is induced without having committed an error. This means that the conflict hypothesis is feasible to explain not only conflicts between given and intended response, but also between conflicts established prior to the response. In a flanker task, only the incongruent stimuli elicit conflict, because partial analysis of the stimulus material might activate correct response preparation based on middle items and incorrect response preparation based on flanker stimuli. Thus, the conflict hypothesis allows to explain the ERN/CRN and the N2 in one theoretical framework (van Veen & Carter, 2002a; Yeung, Cohen, & Botvinick, 2004). As mentioned above, there are ERP studies reporting the same distribution for the ERN and the N2, which supports the idea of a common underlying mechanism (Van Veen & Carter, 2002b). On the other hand, a recent study has convincingly shown that the ERN is increased after administration of Yohimbine (a selective alpha2-adrenergic receptor antagonist), whereas the N2 remains unaffected (Riba, Rodriguez-

Fornells, Morte, Münte, & Barbanoj, 2005). This might imply that at least partially distinct neural processes underlie the ERN and the N2. However, there is accumulating evidence that conflicts and errors do not engage exactly the same brain regions. There is research using a Go/NoGo-paradigm which showed that conflict activate dorsal aspects of the ACC, whereas errors activate more rostral ACC regions (Kiehl, Liddle, & Hopfinger, 2000; Menon, Adleman, White, Glover, & Reiss, 2001).

Reinforcement learning: In the “reinforcement learning hypothesis”, Holroyd and Coles (Holroyd & Coles, 2002) propose that an ERN is generated whenever an event is worse than expected. This is somewhat similar to the mismatch hypothesis, with the mismatch not being between given and intended response, but between expected and actual outcome.

More specifically, the reinforcement learning hypothesis proposes that a motor control system involving the anterior cingulate cortex generates behavior appropriate to the current external context. Simultaneously, a monitoring system located in the basal ganglia predicts the outcome (good or bad) of the response, based on information received from the external environment and an ‘efference copy’ of the response. When the basal ganglia estimate that the outcome of the response is better than predicted, they induce a phasic increase in mesencephalic dopaminergic brain structures activity. In contrast, when the outcome is worse than expected, the basal ganglia induce a phasic decrease in midbrain dopaminergic structure activity. The error signals are carried by the mesencephalic dopamine system to the anterior cingulate cortex, where they reinforce performance on the current task, and back to the basal ganglia, where they are used to improve the predictions of the monitor. The theory holds that the ERN is produced when a phasic decrease in activity of mesencephalic dopaminergic neurons following error commission disinhibits the apical dendrites of motor neurons in the anterior cingulate cortex. No ERN is produced when these dendrites are inhibited by a phasic increase in activity of mesencephalic dopaminergic neurons following correct responses (Holroyd & Coles, 2002; Holroyd & Yeung, 2003).

One of the biggest advantages of the Reinforcement Learning hypothesis is that it specifies exactly the functional circuits involved, which makes it possible to integrate the hypothesis with other theories of specific brain functions (see below). In contrast to the conflict monitoring hypothesis, the Reinforcement Learning hypothesis does not make any specific predictions regarding the N2 component (Holroyd & Yeung, 2003).

4.1.2.3. The error positivity P_e.

A further component associated with action monitoring and error processing in response-locked ERPs is the error positivity P_e. In contrast to the N2 and ERN/CRN, there is relatively little research on the P_e.

Falkenstein (2004) lists two theories which are supported by some data: The “conscious error recognition” hypothesis is mainly based on the finding that an error has to be fully perceived and thus, be conscious, to invoke an P_e. This hypothesis is supported by research using an antisaccade paradigm, in which subjects are instructed to respond with an opposite side saccade to a peripheral abrupt onset cue (Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001). Antisaccade data contain a fairly amount of unperceived, incorrect reflex-like saccades. This makes this task feasible to distinguish between perceived and unperceived errors. Whereas the ERN was consistently found for both, perceived and unperceived erroneous saccades, the P_e was much more pronounced for perceived compared to unperceived errors (Nieuwenhuis, Ridderinkhof, Blom, Band, & Kok, 2001). A second theory relates the ERN to emotional error processing. Errors are perceived by the subjects to create unease. Taking this into account, the P_e has also been described to reflect an “Oh shit!”-response (Falkenstein, 2004). In fact, it is not unusual to hear this expressive word directly after the subject committed an error. There is also some evidence from source localization that the P_e is generated in the rostral part of the ACC (Van Veen & Carter, 2002b). As mentioned above, the rostral ACC has been associated with affective processing (Bush, Luu, & Posner, 2000).

4.1.3. Emotional modulation of performance monitoring

Research on whether the ERN/CRN, the N2, and the P_e are sensitive to affective changes has just begun to emerge. This is surprising, because people usually report that unease, disappointment and frustration arises when committing an error or when an outcome that is worse than expected. The following section reviews current studies of affective modulation in performance monitoring. A comprehensive model of positive affect is introduced and integrates it into the reinforcement learning theory introduced above.

There is emerging evidence that the ERN/CRN reflects, at least to some extent, the emotional response to an error. This idea is not very surprising, since the anterior cingulate cortex is part of the limbic system, which has been extensively shown to be involved in affective responses (see section 1.4). A higher than normal performance monitoring rate, indicated by an increased ERN, has been observed in a variety of studies using subjects with high anxiety level or with psychiatric disorders characterized by high anxiety levels. Increased ERN amplitude was also reported for patients suffering from obsessive compulsive disorder (OCD) (Gehring, Himle, & Nisenson, 2000), an anxiety disorder characterized by intense, recurrent, unwanted thoughts and rituals that are beyond the person's control and high level of negative affect (Brown, Chorpita, & Barlow, 1998). Fitzgerald et al. (2005) found that both, patients with OCD and healthy subjects, showed increased activation in the dorsal cognitive division of the ACC during error commission, whereas OCD patients only showed increased activation in the rostral emotional ACC section.

Medication has also been shown to affect the ERN. Johannes and colleagues (Johannes, Wieringa, Nager, Dengler, & Münte, 2001) administered Oxazepam to a group of subjects and compared the ERN relative to a placebo group. Oxazepam is a benzodiazepine derivative and possesses anxiolytic properties. They found that the ERN is reduced in the Oxazepam group and interpreted this finding “...as support for a link between affective distress, associated behavior patterns, and frontal lobe executive functions” (Johannes, Wieringa, Nager, Dengler, & Münte, 2001, p. 104). Thus, reduced anxiety leads to reduced action monitoring. Interestingly, Johannes and colleagues (2001) report no behavior effects caused by medication.

ERN modulations due to negative affect were also shown in non-psychiatric subjects: Hajcak and colleagues (Hajcak, McDonald, & Simons, 2004) conducted a stroop-like experiment employing students which scored either high or low on a negative affect scale. There were no performance differences between both affect groups, neither in reaction time nor in post error slowing. However, within the ERN time window, there was an enhanced negative deflection for the negative affective group. This was seen for error as well as for correct trials. The P_e was smaller in the high negative affect group. Again, this effect was seen for erroneous as well as for correct trials. A similar ERN increase for college students with high negative affect was also reported by Luu, Collins and Tucker (Luu & Pederson, 2004). Simon-Thomas and Knight (2005) used a working memory delay task with numeric Stroop-like stimuli in a within-group design on healthy subjects to investigate how the CRN and the P_e might be modulated by cognitive demands and negative affect. They induced emotions by presenting highly negative or neutral IAPS picture stimuli prior to a response-requiring stimuli. They found that the CRN and the P_e were selectively increased for initial blocks under negative affective state condition. Affective modulation of the ERN was not examined by Simon-Thomas and Knight (2005). As mentioned in section 4.1.2.2, Riba and colleagues (Riba, Rodriguez-Fornells, Morte, Münte, & Barbanoj, 2005) showed that the ERN in an Eriksen-flanker task is selectively enhanced when subjects take Yohimbine. However, this drug is known to produce states of high arousal and anxiety. Thus, this effect might also be explained in the framework of affective modulation.

4.1.3.1. Affect and performance monitoring – a common framework?

Ashby and colleagues (1999) proposed a comprehensive model of how positive affect might impact cognitive performance. The key issue is that positive affect is associated with an increased dopamine level in various brain areas, among them the prefrontal cortex and the anterior cingulate cortex (ACC). Rewarding stimuli are associated with dopamine release and, at least in humans, with positive affect. A dopaminergic system heavily involved in reward processing is the mesocorticolimbic system, which consists of dopamine producing neurons in the ventral tegmental area (VTA) and projects to different limbic and cortical areas. There are two dopaminergic VTA connections which might be of particular interest in understanding how positive affect modulates cognition: The VTA-prefrontal connection, which has been shown to interact with working memory processes, and the VTA-ACC connection, which facilitates executive attention and the selection of cognitive perspective (Ashby, Isen, & Turken, 1999).

A comprehensive proposal which links mesencephalic dopaminergic structures with the ACC was provided by Holroyd and Coles (2002). The reinforcement theory has been introduced above as a general indicator that signals bad outcomes. As introduced above (section 4.1.2.2), the mesencephalic structures, among them the VTA and the substantia nigra (SN), forward the error signal generated by the basal ganglia to the ACC, where the signal is used to adaptive behavior modification. A strong mesencephalic signal results in strong inhibition of the ACC error monitoring system, whereas a weaker signal causes the ACC to be more active. The theories proposed by Ashby, Isen, and Turken (1999) and by Holroyd and Coles (2002) overlap in that they describe mesencephalic changes in dopamine level which lead to cognitive modifications mediated by the ACC. Both place interactions between midbrain dopaminergic structures and the ACC in the center of a complex system that mediates and adapts behavior. I see good reason that both theories describe different aspects of the same (or, at least, highly overlapping) behavior regulation system and might be brought together: An unexpected reward or the absence of any threat or danger in the environment is associated with increased dopamine level and positive affect. This, in turn, might facilitate the switching among alternative cognitive perspectives and behavior alternatives (Ashby, Isen, & Turken, 1999; Dreisbach & Goschke, 2004). Thus, the organism starts to explore the environment less cautiously, which increases the probability of a rewarding outcome. However, to maintain this behavior, the ACC performance monitoring system must adapt in that it evaluates the consequences in a less rigid way than it does in the wake of threat, i.e. in a state of negative affect. Integrating the reinforcement learning theory (Holroyd & Coles, 2002), it is conceivable that the increase in dopaminergic midbrain activity caused by the reward predicting signal from the basal ganglia accumulates with the midbrain activity caused by positive affect. Consequently, the midbrain signal to the ACC should be stronger than under neutral affect conditions, which increases inhibition of the ACC performance monitoring system. This should result in a diminished ERN.

Brain structures involved in generating affect are highly connected to the ACC performance monitoring system. Thus, in threatening situations, which might be associated with negative affect and go along with rapid amygdala activation, an organism has good reasons to avoid any behavior that might lead to an unpredictable and potentially threatening outcome. To avoid any aberration from established behavior, the ACC performance monitoring system should be activated in a higher than normal manner, which should be reflected in an increased ERN.

A similar idea was proposed by Wager, Phan, Liberzon, and Taylor (2003). They linked positive affect to the basal ganglia: “In positive emotions, basal ganglia may play a pivotal role in broadening the repertoire of accessible thoughts and actions that leads to exploratory behavior and skill-building, leading to activation of a number of functional loops in the basal ganglia that implement a wide range of thoughts and behaviors. In aversive situations, the basal ganglia may play a role in developing a specific action plan to deal with threat, leading to focal activation of circuits implementing more stereotyped responses “(p. 526). Here, the same idea is extended beyond the basal ganglia by integrating the anterior cingulate cortex.

4.1.4. The current studies

The four studies presented in section 4 examine how mild changes in affective state interfere with processes involved in supervising ongoing behavior. Especially experiments 4.2 and 4.3 were inspired by recent research published by Dreisbach and Goschke (Dreisbach & Goschke, 2004). They demonstrated that, when appropriate paradigms are used, shortly presented positive IAPS pictures can have clear effects on behavior: Dreisbach and Goschke (2004) instructed their participants to detect a target of a certain color, while they had to ignore a distracter presented in what had previously been the target color. Normally, those task settings lead to “perseveration costs” on the first few trials following the task switch, because the old target color is difficult to ignore. However, perseveration costs were reduced when the trials were preceded by shortly presented (250 ms) high-valence (positive) IAPS pictures relative to neutral and negative pictures. They concluded that positive affect enhances cognitive flexibility, which facilitates orientation of attentional resources towards the new requirements. In line with Ashby’s theory of positive affect introduced above (Ashby, Isen, & Turken, 1999), Dreisbach and Goschke speculated “that positive affect serves as an appraisal signal indicating the absence of danger or obstacles in the pursuit of current goals, thereby promoting less focused, explorative modes of thought and behavior" (p. 351).

The experiments presented in section 4 extend those findings to the cognitive domain of performance monitoring and make specific predictions about the modulations induced by unpleasant emotions. In addition, the following experiments do allow more direct conclusions regarding the neural mechanisms, because physiological measures (ERPs) are also applied. Four experiments were conducted, in which subjects performed a flanker task while emotions are induced via different techniques.

In experiments 4.2 and 4.3, emotional pictures are rapidly presented directly prior to the presentation of each flanker task trial. Experiment 4.2 uses facial expressions, experiment 4.3 highly arousing pictures taken from the IAPS (Lang, Bradley, & Cuthbert, 1999).

In contrast to most previous studies, the present thesis underscores the distinction between "seeing emotions or emotional situations" and "producing emotions by being personally involved"(Davidson & Irwin, 1999). Thus, experiment 4.4 uses facial feedback to induce emotions, experiment 4.5 provides subjects with either positive or negative feedback to make them either feel good or bad.

The predictions are based on the theoretical framework introduced in section 4.1.3.1 and are summarized as followed:

- The ERN is increased under negative affective conditions
- The ERN is decreased under positive affective conditions.

Since the reinforcement learning theory does not make explicit statements about the N2 and the conflict monitoring hypothesis has not yet been linked to emotional processing, specific N2 modulations cannot be predicted.

4.2. Experiment 2a: Emotions induced by observing facial expressions

4.2.1. Methods

4.2.1.1. Participants

Data were acquired from 9 women. See section 2.1 for additional information. One subject had to be excluded due to extensive head artifacts. Thus, analysis was based on data from 8 subjects (mean age 22.3 years, range 18 to 33 years).

4.2.1.2. Stimuli and procedure

A trial consisted of the following sequence: fixation cross – emotional face picture – fixation cross – flanker stimulus with the following timing:

- First fixation cross, varying duration 600 to 1000 ms, mean 800 ms
- Emotional face picture (80 ms)
- Second fixation cross, varying duration 600 to 800 ms, mean 700 ms
- Flanker stimuli until response, but no longer than 800 ms.

See below for exact description of flanker and face stimuli. Faces subtended a visual angle of 4° horizontally and 6° vertically. See Figure 11 for an example of a trial. The experiment consisted of 2100 trials. A feedback screen was presented after every 30 trials, informing the subjects whether they were faster or slower than in the previous 30 trials. This procedure was introduced to keep subjects attending and to maintain fast responses. Participants terminated the feedback screen by button press. After 210 trials, there was a break for 15 seconds. Participants could request longer breaks if necessary.

Instruction: Participants were instructed to respond as fast and correct as possible on the middle letter in the flanker stimulus. H was mapped the left hand button and S required a right hand button press. Subjects were not instructed that an emotional face expression was presented prior to the flanker stimulus.

Emotional stimuli: Emotions were induced by presenting emotional face pictures taken from the Ekman and Friesen Face stimuli set(Ekman & Friesen, 1976; Young, Perrett, Calder, Sprengelmeyer, & Ekman, 2002); see section 1.5.2. Stimuli depicted neutral, happy and fearful face expressions of 10 different people. See Appendix 3 for a list of all face stimuli used.

Face pictures were grayscale and depicted four male and six female faces without any artificial features (glasses, necklace, piercing etc.). The picture set was provided in a preprocessed manner depicting the face only; peripheral face features (hair, ears) were replaced by gray color. Examples of face pictures are given in Figure 11 .

In agreement with Whalen et al. (1998), fearful faces rather than angry faces were selected to represent negative valence stimuli. This was done because it is well known that an angry face represents a direct threat. In contrast, the relation between a fearful face and a threat is more ambiguous. It signals the presence of a danger, but not the source of a danger. Thus, a fearful face can be conceptualized as a contextual stimulus, whereas an angry face can be conceptualized as a specific cue.

Research has shown that emotional (or affective) responses to facial stimuli can be activated after only a minimal duration of stimulus exposure or even when subjects do not perceive face expressions consciously (see section 1.5.2). Thus, the very short presentation of emotional face stimuli for only 80 ms was regarded as sufficient to elicit reactions specific to perceiving emotional expressions.

Flanker stimuli: Flanker stimuli consisted of black capital letters (“Courier new” font) H or S presented in front of a gray background (128, 128, 128 in RGB color space). A congruent flanker string was either HHHHH or SSSSS; incongruent flanker strings were SSHSS or HHSHH. Flankers were presented in random order, there were 60 % congruent and 40 % incongruent trials. They covered 2.1 ° of visual angle.

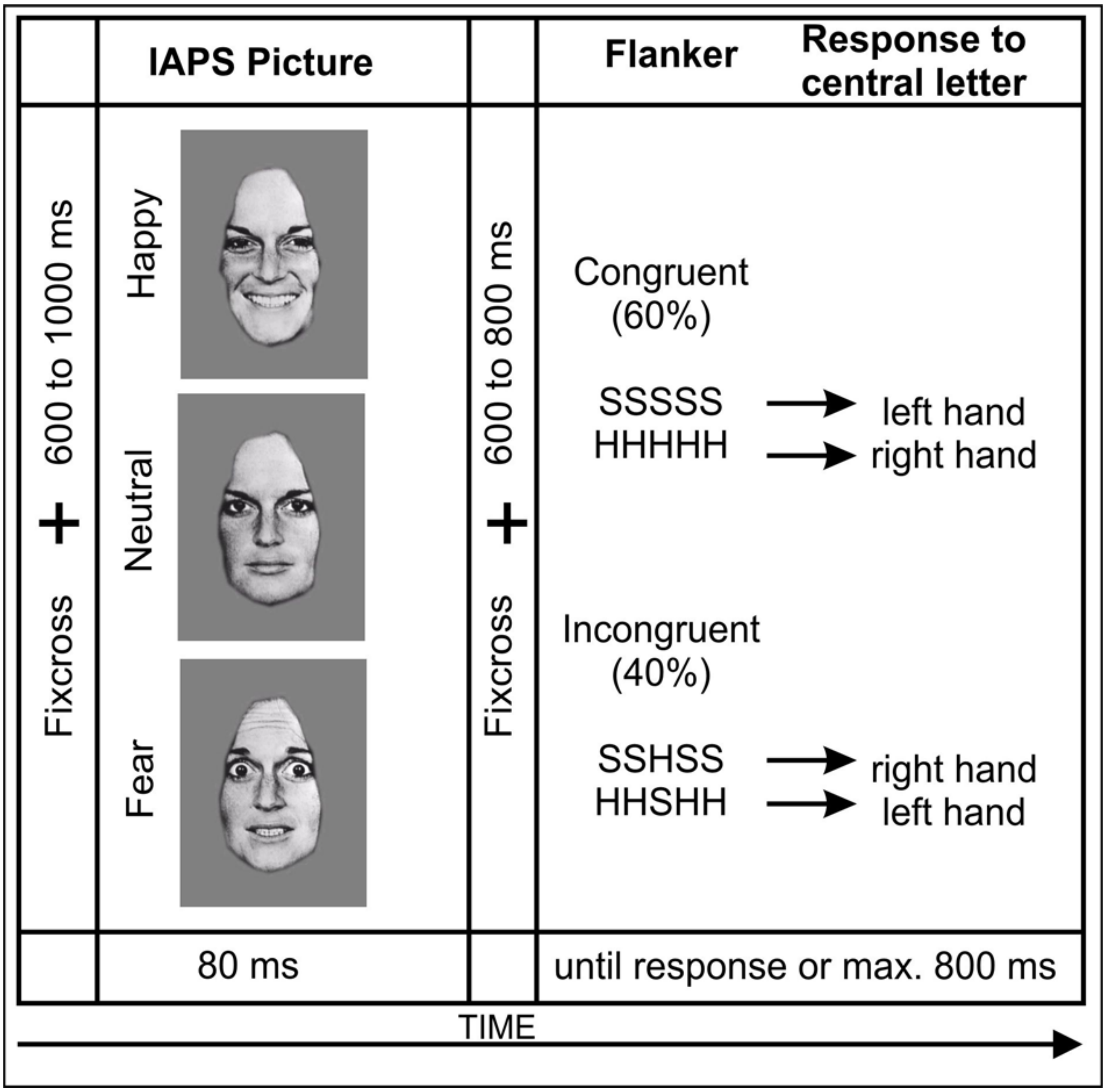


Figure 11: Experimental design for experiment 4.2. Emotional modulation was induced by presenting a neutral, a happy or a fearful face prior to the flanker stimulus.

4.2.1.3. Data recording and preprocessing

See section 2.4.1 for general recording issues. Eye artifacts were corrected using blind component separation described in section 2.4.2., head artifacts were rejected as described in section 2.4.1.

4.2.1.4. Data analysis

Trials with RTs lower than 200 ms or higher than 800 ms were excluded from behavioral data analysis. Behavior data and ERP data were analyzed using repeated measurement ANOVAs. Depending on the question, some or all of the following factors were included in the rmANOVAs: CORRECTNESS (2 levels, Correct or erroneous response to flanker stimulus), FACEEMOTION (3 levels, neutral, happy, fear face). It was assumed that the emotional impact on behavioral data and ERPs change over time (Simon-Thomas & Knight, 2005). Thus, the experiment was divided into two sections. Unlike previous research (Simon-Thomas & Knight, 2005), the present study examines emotional effects not only on correct trials, but also on erroneous trials. Dividing the experiment after half of the trials (Simon-Thomas & Knight, 2005) could result in an unequal number of erroneous trials per experimental half, since errors are often not equally distributed across the entire experiment. To avoid this, the experiment was divided after commission of 50 percent of the errors (Factor ERRORHALVES, levels “first half” and “second half”). However, subjects do not show the same performance across the entire experiment; some subjects have an increased error rate during the beginning of the experiment, whereas others become less accurate later on. Appendix 7 a) provides estimation for each subject whether the same performance (error rate) was maintained during the entire experiment. A value lower than 50 % indicates that less than half of the correct responses were given at the point where 50 % of the errors were committed. In this case, subjects had an increased error rate at the beginning of the experiment.

Post-error slowing: Post error slowing refers to the consistent finding that that trials directly following an error (post-error trials) are slower compared to trials that follow correct responses (post-correct trials) (Hajcak, McDonald, & Simons, 2003b, 2004; Rabbitt, 1981, 2002). However, since erroneous trials are usually faster than correct trials, this effect could be caused by regression toward the mean: Fast responses are relatively rare. Thus, it is more likely that a fast response is succeeded by a more slowly response. Since errors are usually faster than correct responses, it is more likely that a relatively slow correct response follows. To distinguish between post-error effects caused by regression towards the mean from “pure” error-induced RT slowing, a subset of correct trials was selected that matches the erroneous trials in terms of reaction time and total number. Thus, the selected correct trials belong to the faster responses among all of the correct trials. Reaction times of correct trials given directly after those response-matched correct trials (post-correct trials) and response times of correct responses given directly after an erroneous response (post-error trials) provide the basis for post-error slowing analysis.

Face-locked ERP analysis: Face-locked ERPs were analyzed relative to a 100 ms baseline; exact description and selection criteria for the time windows are given in section 4.2.2.2.

Flanker-locked ERP analysis: Flanker-locked ERPs were analyzed relative to a 100 ms baseline in a time window from 300 to 400 ms after flanker stimulus onset. The time window was defined by visual inspection. To be consistent with the analyses of subsequent experiments, statistics were also conducted in a 200 to 400 ms time window. RmANOVA included the factors CONGRUENCY (congruent vs. incongruent flanker) and FACEEMOTION on a parietal patch of electrodes (averaged across CP1, CP2, Cz and Pz).

Response-locked ERP analysis: Statistics were conducted relative to a 200 ms pre response baseline. Consistent with behavioral data analysis and previous ERP research (Hajcak, Moser, Yeung, & Simons, 2005), trials with reaction times faster than 200 ms or slower than 800 ms were excluded from analysis. The ERN was examined on a frontocentral electrode patch (averaged across electrodes FC1, FC2, Fz, Cz); the CRN and the P_e were analyzed somewhat more posterior on a centroparietal electrode patch (averaged across CP1, CP2, Cz and Pz).

It is an established finding that participants display shorter reaction times to erroneous compared to correct responses. Because uniformly fast reaction times can give rise to stimulus-related activity in the response-locked ERN, and because correct trials vastly outnumber incorrect trials, CRN analysis was based on a subset of correct trials which matched the incorrect trials in number and reaction times. This response-matching procedure has been shown to be appropriate in analyzing the ERN (Hajcak, McDonald, & Simons, 2004). The response matching procedure for correct responses was adjusted so that the same amount of correct trials were included in both error halves. ERP conditions for response-locked data and the number of trials[8] included in each condition are listed in Table 5.

Time windows for ERN/CRN peak amplitude analysis were determined based on a time window +/- 30 ms around the ERN and CRN grand average peak; exact time ranges are provided in Table 8. The ERN was defined as the most negative peak, the CRN as the most positive peak. The P_e was analyzed based on man amplitudes from 200 to 400 ms.

FACE EMOTION	**CORRECTNESS**	**ERROR HALF**	**Mean trial number**	**SD**	**Range**
Neutral	**Correct**	**1st**	40.0	15.7	11-65
		2nd	39.1	16.9	14-70
	Error	**1st**	38.4	16.0	13-64
		2nd	38.1	15.6	10-66
Pleasant	**Correct**	**1st**	40.3	16.3	14-66
		2nd	40.8	14.3	14-63
	Error	**1st**	40.0	14.3	15-65
		2nd	39.3	14.3	18-65
Fear	**Correct**	**1st**	39.8	16.4	15-70
		2nd	41.5	17.3	10-67
	Error	**1st**	39.9	17.6	12-72
		2nd	38.4	16.4	13-71

Table 5: The number of trials included to generate the response-locked ERP conditions in study 4.2.

4.2.2. Results

4.2.2.1. Behavioral data

Reaction times and error rates

Erroneous responses were faster than correct responses. Also, responses were faster in the second compared to the first error half. There was no effect of face emotions on reaction times (CORRECTNESS: F (1,7) = 253.52; p < .001;

---

[8] One might expect that the sum of all correct and the sum of all error trials in the first half matches exactly the sum of all correct and the sum of all error trials in the second half. However, small differences in sum of error and correct trials between halves might occur due to head artifact correction, which excluded some trials.

ERRORHALVE[9]: F (1,7) = 20.32; p < .003, FACEEMOTION, CORRECTNESS x FACEEMOTION and ERRORHALVE x FACEEMOTION n.s.). See Table 6. Face emotions did also not affect error rates (percentage of errors: neutral: 12.5; happy: 12.9; fear: 12.6).

CORRECT-NESS	ERROR-HALVE	FACE-EMOTION	Mean RT	SD
Correct	**First**	**Neutral**	395	87
		Happy	396	88
		Fear	393	85
	Second	**Neutral**	377	86
		Happy	378	86
		Fear	376	85
Error	**First**	**Neutral**	338	71
		Happy	344	67
		Fear	338	67
	Second	**Neutral**	323	66
		Happy	323	64
		Fear	317	57

Table 6: Reaction times (mean RT) and standard deviations (SD) for correct and erroneous responses following faces with neutral, happy or fearful face expressions. RTs are in ms.

Congruency effect

To examine the impact of flanker congruency, response times (correct responses only) of congruent (HHHHH or SSSSS) and incongruent (HHSHH or SSHSS) flanker stimuli were compared. Subjects were faster in responding to congruent compared to incongruent flanker stimuli. This effect was consistently found in both error halves (rmANOVA; CONGRUENCY (congruent vs. incongruent flanker): F (1,7) = 162.9, p < .001; ERRORHALVES: F (1, 7) = 28.2, p < .001; no significant effect of FACEEMOTION or interactions). See Table 7 for detailed behavior data.

---

[9] See Appendix 7 a for distribution of errors across the experiment.

Analysis of error rates revealed a similar pattern. Subjects committed more errors following incongruent compared to congruent flanker stimuli; the emotional face presented prior to the flanker did not affect error rates (ANOVA on error rates (percentages); CONGRUENCY: F (1, 7) = 67.2; p < .001; mean error rates: congruent flanker: 6.3%; incongruent flanker: 22.4 %; no significant effects of FACEEMOTION or interactions).

CONGRUENCY	ERROR-HALVE	FACE-EMOTION	Mean	SD
Congruent Flanker	**First**	**Neutral**	377	80
		Happy	375	79
		Fear	374	77
	Second	**Neutral**	359	76
		Happy	359	77
		Fear	359	77
Incongruent Flanker	**First**	**Neutral**	428	88
		Happy	432	91
		Fear	428	88
	Second	**Neutral**	410	94
		Happy	412	93
		Fear	408	91

Table 7: Reaction times (mean RT) and standard deviations (SD) for congruent and incongruent flanker stimuli following faces with neutral, happy or fearful face expressions. RTs are in ms.

Post error slowing

Post error slowing was present in this study; see section 4.2.1.4 for details on post error slowing analysis. Subjects showed delayed reaction times when the previous response was erroneous. The face picture preceding the post-correct or post-error response did not influence reaction times (rmANOVA, Factors POSTRESPONSE (post-correct vs. post-error), FACEEMOTION, POSTRESPONSE: F (1,7) = 5.8, p < .047; mean correct following error: 395 ms; mean correct following correct: 379 ms; no other significant effects or interactions)

4.2.2.2. ERP data

Face locked ERPs

Visual inspection: Facial stimuli elicited a face-typical N170 (Bentin, Allison, Puce, Perez, & McCarthy, 1996) on parieto-occipital sites and a VPP (vertex positive peak) (Jeffreys & Tukmachi, 1992). Differences between emotional face expressions as reported elsewhere (Eimer & Holmes, 2002) were not detected on any electrode site. See Figure 12.

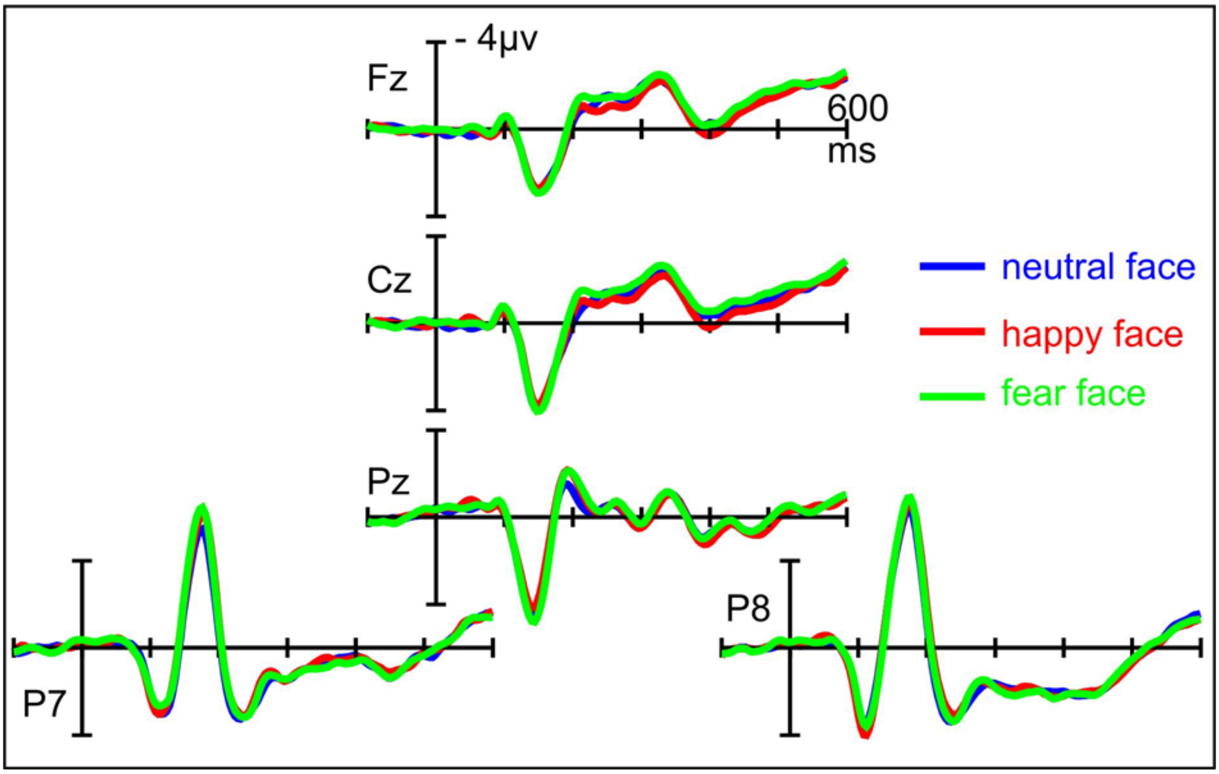


Figure 12: ERPs locked to face stimuli onset. The components typically found for face stimuli (N170 on parieto-occipital sites and vertex positive peak) are clearly found, emotional face content did not influence ERP waves. See Figure 1 for exact electrode locations.

Statistical analysis: Previous research (Eimer & Holmes, 2002) reported first differences between fearful and neutral faces in the following time windows and scalp locations:

- 110 to 150 ms on frontocentral electrodes
- 155 to 200 ms on frontocentral and parietal electrodes
- 250 to 1000 ms on frontocentral electrodes
- 455 to 1000 ms on posterior electrodes.

Due to the fact that visual inspection of the present data did not yield any differences between emotional face conditions, the same time windows as reported by Eimer and Holmes (2002) were examined[10] on a subset of frontal, central and parietal electrodes (Fz, Cz, Pz). There were no differences between emotional face conditions. To test whether emotional effects declined over time, the experiment was split into half, but this did also not reveal any emotional face effects (rmANOVA, no significant effects of FACEEMOTION or significant FACEEMOTION x ERRORHALVES or FACEEMOTION x ANTERIORITY interactions in any of the time windows examined).

Although it was shown that the N170 is not affected by emotional face expressions (Eimer & Holmes, 2002), this component was also examined for emotional effects on electrodes P7 and P8. There were also no emotional effects found.

Flanker locked ERPs

Visual inspection: Around 300 ms, the incongruent stimuli were markedly more negative than the congruent stimuli. This N2 effect did not differ in respect to the face stimulus previously shown. See Figure 13.

Statistical analysis: The visual impression was confirmed statistically (rmANOVA, 300 to 400 ms: CONGRUENCY: $F(1,7) = 61.4$; $p < .001$; no significant effect of FACE or interactions. rmANOVA, 200 t0 400 ms: CONGRUENCY: $F(1,7) = 40.52$; $p < .001$; no significant effect of FACE or interactions).

---

[10] The ERP software used in this experiment does only allow time windows of 1024 ms, baseline inclusive (256 samples at 250 Hz). Thus, ERP averages were no longer than 924 ms. Time windows 250 to 1000 ms and 455 to 1000 ms did therefore end at 924 ms.

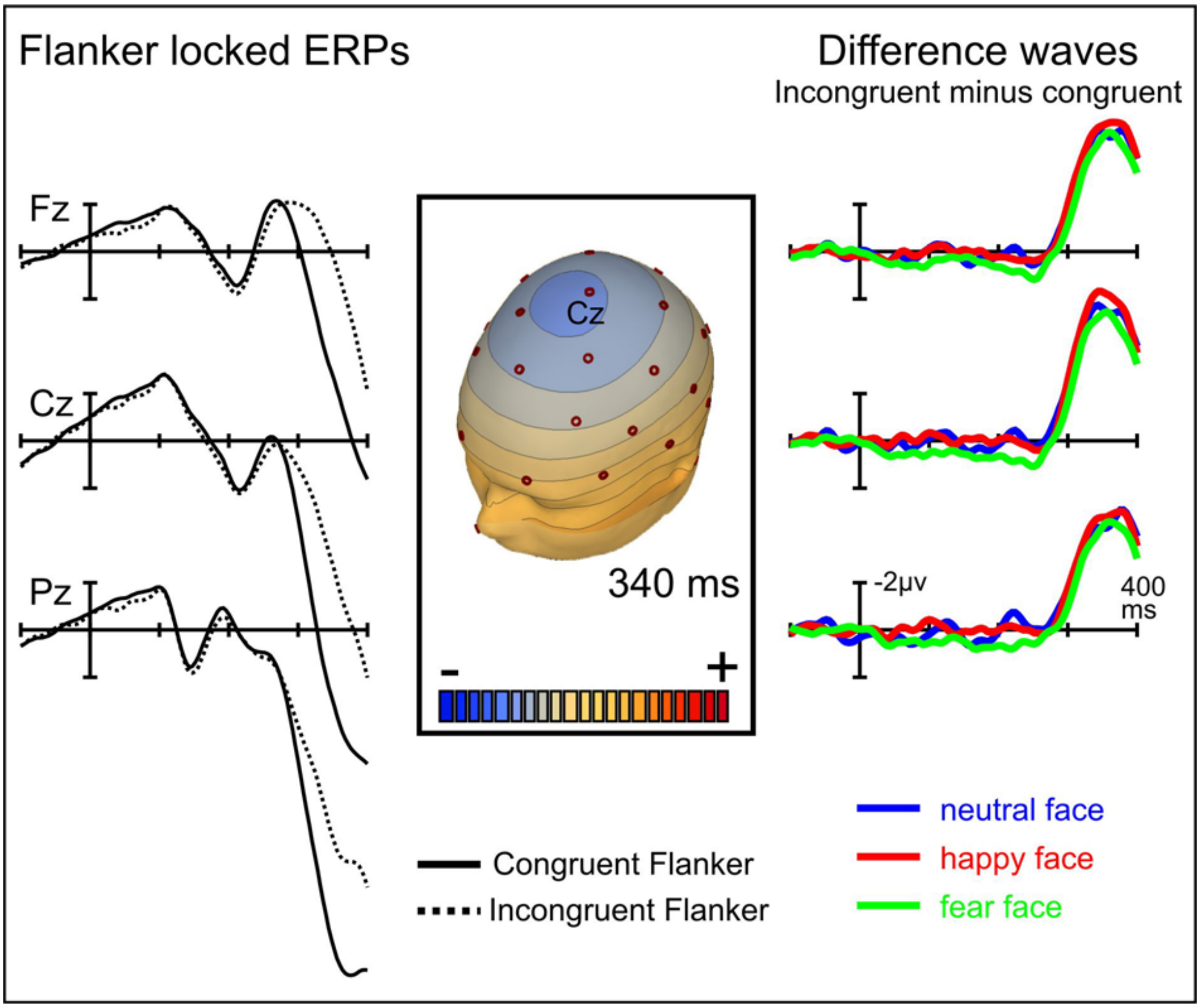


Figure 13: ERPs locked to flanker stimuli. Left panel: N2-effect without regarding preceding face picture. Middle: scalp distribution at 340 ms based on difference waves incongruent minus congruent. Right: Difference waves based on incongruent minus congruent flanker stimuli, separately for all three face conditions preceding the flanker.

Response-locked ERPs-the ERN/CRN

Visual inspection: Erroneous responses elicited a negative component, between 40 and 100 ms, correct responses elicited a more positive ERP component (ERN and CRN). The ERN is seen best on midline central scalp areas. Thus, statistics were conducted on a patch of electrodes consisting of Fz, Fc1, FC2 and Cz. See Figure 14.

Peak latency analysis: Peak latencies of the ERN and the CRN were determined in a time window from 0 to 150 ms. Errors responses peaked earlier than correct responses, especially in the second error half (ERRORHALVES x CORRECTNESS, F (1,7) = 6.09, p < .043). There was no effect of face pictures.

Mean amplitude analysis: Due to different peak latencies for correct and erroneous responses, time windows for mean amplitudes were defined around the peak as depicted in Table 8.

CORRECTNESS	ERROR HALVES	Mean peak latency	Time window for peak amplitude analysis
Correct	1st	83	40 to 120
	2nd	104	60 to 140
Error	1st	78	40 to 120
	2nd	68	30 to 110

Table 8: mean peak latencies and time windows for ERN/CRN peak amplitude analysis. Values are in ms.

Not surprisingly, ERN amplitude was more negative than CRN amplitudes. Emotional faces did neither influence ERN nor CRN amplitudes (CORRECTNESS, F (1,7) = 94.49, $p < .001$, no main effects or interactions of ERRORHALVES or FACEEMOTION).

Response-locked ERPs-the P_e

The P_e was most pronounced on parieto-central electrodes and will be examined on an electrode patch consisting of Pz, Cz, CP1, CP2. See Figure 1 for electrode locations. Mean amplitudes of correct responses were more negative compared to erroneous responses, there were no differences due to face emotions in the P_e (CORRECTNESS, F (1,7) = 86.62, $p < .001$, no significant ERRORHALVES or FACEEMOTION main effects or interactions).

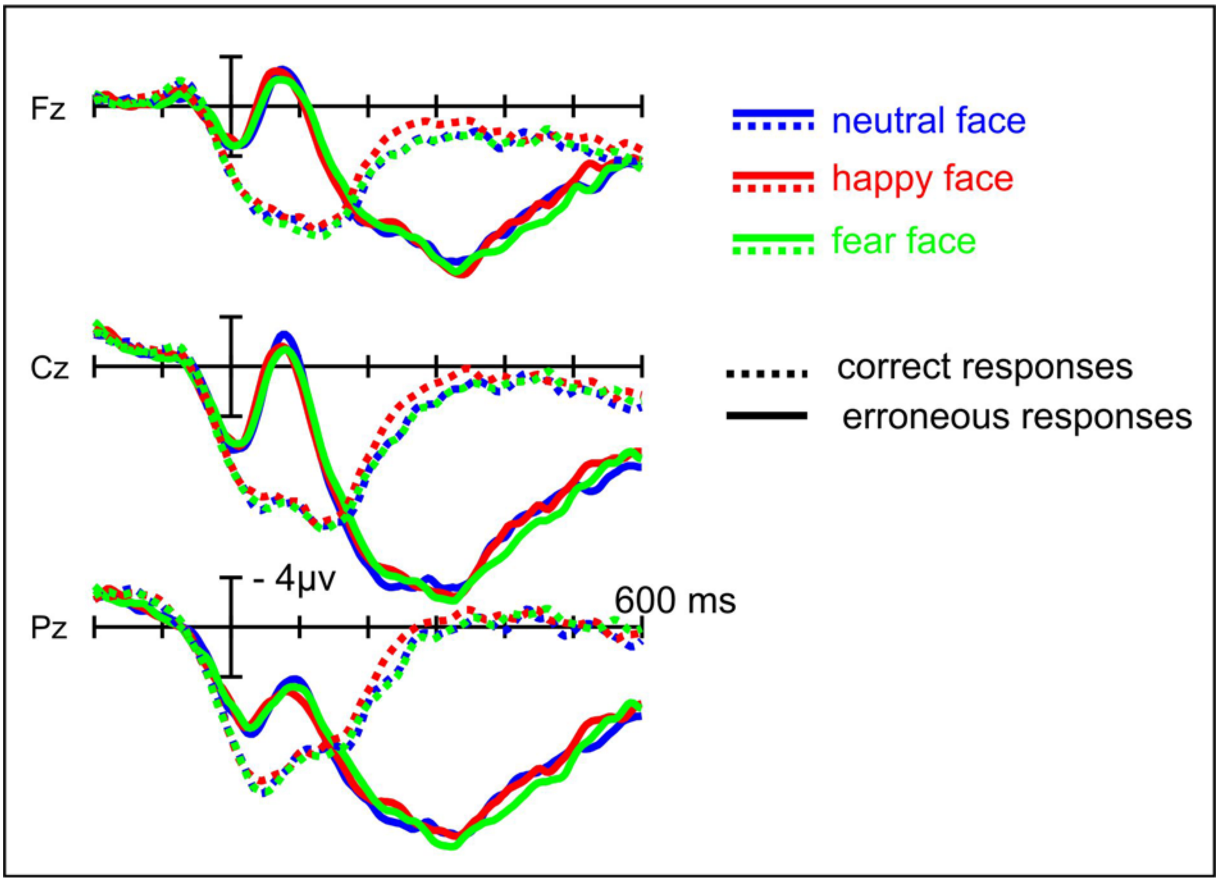


Figure 14: ERPs locked to responses. Correct responses are coded by a dotted line, erroneous responses are solid. Facial emotions preceding the Flanker and the response are color-coded. ERPs for correct responses are based on trials that match incorrect trials in reaction time and total number (response matching).

4.2.3. Summary and perspective

Summary: The study presented in section 4.2 shows well known effects on the behavioral level with correct responses given faster than incorrect answers (Hajcak, McDonald, & Simons, 2004; Hajcak, Moser, Yeung, & Simons, 2005; Riba, Rodriguez-Fornells, Morte, Münte, & Barbanoj, 2005) and faster responses given to congruent compared to incongruent flanker stimuli (Eriksen & Eriksen, 1974; Riba, Rodriguez-Fornells, Morte, Münte, & Barbanoj, 2005).

ERPs also replicated earlier studies with showing the “classical” components: The face-specific N170 (Bentin, Allison, Puce, Perez, & McCarthy, 1996) and a VPP (Jeffreys & Tukmachi, 1992) in face-locked ERPs indicates that the Ekman-faces were presented long enough to be processed . ERPs locked to flanker stimuli (N2) were more negative to incongruent compared to congruent flanker stimuli (Kopp, Rist, & Mattler, 1996). Response-locked ERPs were more negative to errors (ERN) compared to correct responses (CRN) (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991; Gehring, Goss, Coles, Meyer, & Donchin, 1993), and there was a later positive component seen after errors (Falkenstein, 2004).

Most important, the emotional face expressions presented prior to the flanker stimulus did not influence face-locked, flanker-locked or response-locked ERPs. This was surprising and unexpected, since previous research has shown that a short-time presentation of emotional stimuli is sufficient to modify cognitive functions (Schupp, Junghöfer, Weike, & Hamm, 2004; Whalen et al., 1998); see also section 1.5.2.

Perspective: The lack of an emotional effect in any of the examined ERP components could be due to several reasons: Although one might argue that emotional face processing might be rapid and automatic, it is conceivable that this effect habituates very fast, since subjects learn that faces do not really indicate the presence of a threat or danger. In contrast to our passive task, where subjects were not instructed to pay attention to the face pictures, Eimer and Holmes (2002) instructed the subjects to detect immediate repetition, which requires identification of the stimulus category and the stimulus emotion. Habituation to the face stimuli might be prevented or attenuated by this active task. It is conceivable that habituation to face stimuli occurred rapidly in the present experiment because facial emotion pictures were based on 10 different individuals only. Including more individual face pictures would make the experiment less susceptible to become boring, but this would require to use a different, more comprehensive face picture set.

Eimer and Holmes (2002) presented face stimuli for as long as 300 ms, which was considerably longer than the 80 ms presentation rate in the present experiment. Evidence that very short presentation of emotional pictures elicit emotional responses comes mainly from research using the IAPS picture set (Schupp, Junghöfer, Weike, & Hamm, 2004). They presented neutral, pleasant and unpleasant IAPS pictures for 120 ms (See sections 1.5.1 and 4.3.1.4 for more details on this study). Schupp and colleagues concluded that brain activity due to short presentation of affective faces is highly similar to longer presentation. Thus, while it seems feasible to present pictures very short to induce emotional responses, this might work for IAPS pictures, but not for Ekman face pictures (Ekman & Friesen, 1976; Young, Perrett, Calder, Sprengelmeyer, & Ekman, 2002). In addition, the Ekman face set used in this study was generated in the 1970s; pictures are only in grayscale, and people do look a little bit "old fashioned". This might contribute to the finding that emotional expression was not feasible to elicit specific brain response.

To overcome the shortcomings of the previous experiment, the next experiment uses the same basic design with the face pictures being exchanged by pictures taken from the IAPS. The short presentation duration is kept, since there is good evidence that short presentation is sufficient for IAPS pictures (Schupp, Junghöfer, Weike, & Hamm, 2004).

4.3. Experiment 2b: Emotions induced by observing IAPS pictures

4.3.1.1. Participants

Data were acquired from 28 right-handed women. See section 2.1 for additional information. ERP data were analyzed from 22 subjects (mean age 24 years, range from 19 to 36.), two subjects were excluded because the committed less than 60 errors throughout the experiment, which does not allow reliable ERPs for all IAPS-related sub-conditions. Four subjects were excluded due to high and uncorrectable artifact levels.

4.3.1.2. Stimuli and procedure

The experimental design was exactly the same as described in section 4.2.1.2 except that emotional variations were induced by IAPS pictures. Previous research has shown that short presentation of pleasant and unpleasant IAPS pictures is suitable to tune the brain for selective perceptual processing (Schupp, Junghöfer, Weike, & Hamm, 2004).

Emotional stimuli: 30 IAPS pictures (Lang, Bradley, & Cuthbert, 1997) were selected based on their valence rating for women. There were 10 pictures with medium, high and low valence ratings, which provided the neutral, pleasant and unpleasant affective state condition, respectively. Mean valence and arousal ratings are listed below; Standard deviations are given in brackets.

Neutral IAPS pictures	valence: 5.0 (0.1)	arousal: 2.5 (0.4)
Pleasant IAPS pictures	valence: 8.5 (0.1	arousal: 4.5 (0.6)
Unpleasant IAPS pictures	valence: 1.6 (0.3)	arousal: 6.9 (0.6)

The experimental design is visualized in Figure 15. A list of all IAPS pictures used is provided in Appendix 4, all pictures selected among all available pictures in the IAPS valence/arousal space is shown in Figure 16.

Flanker stimuli: Flanker stimuli were the same as described in section 4.2.1.2.

Instruction: The instruction was the same as in section 4.2.1.2.

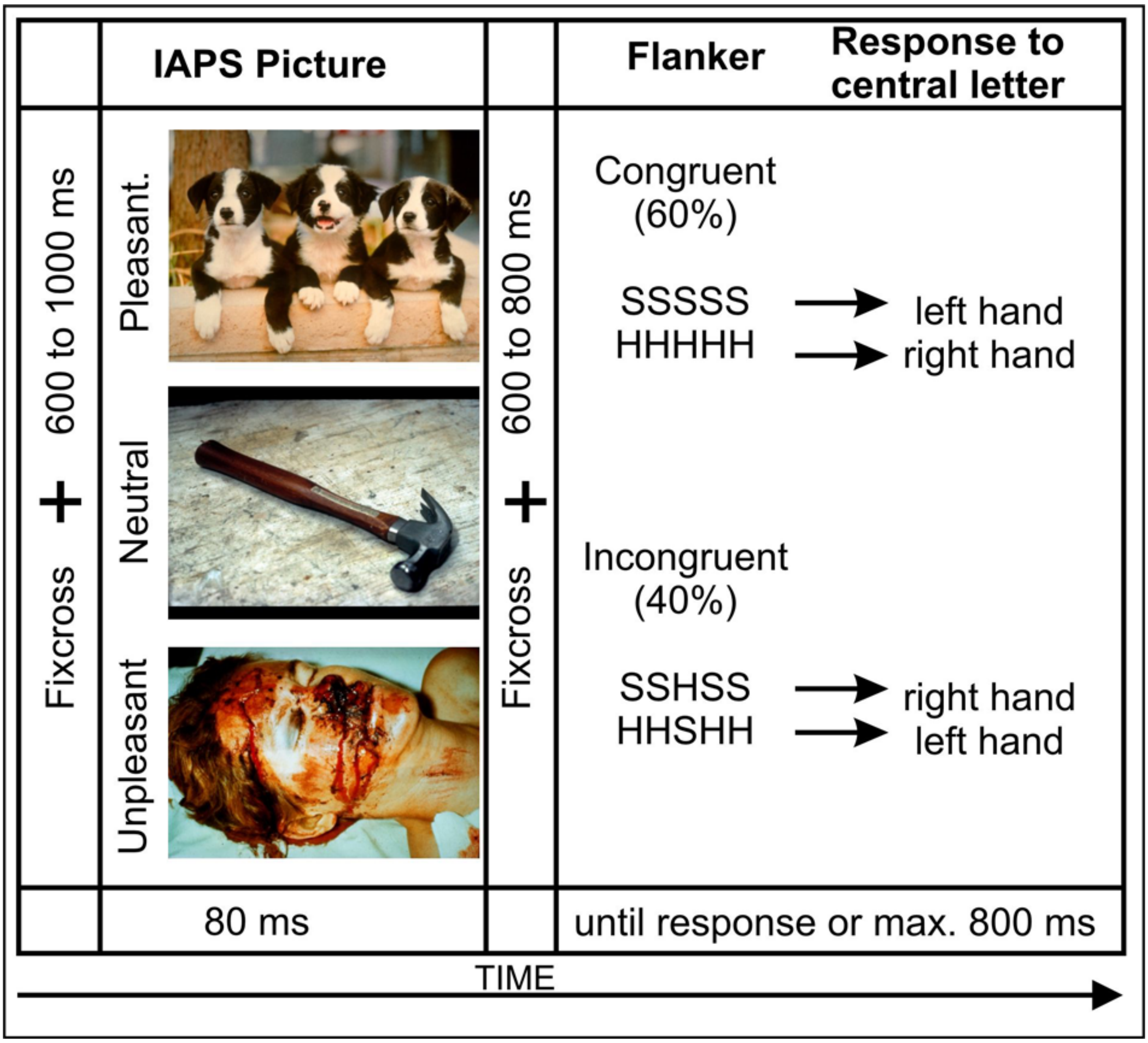


Figure 15: Design for experiment 4.3. Emotional modulation was induced by presenting a neutral, a pleasant, a unpleasant IAPS picture prior to the flanker stimulus. See Appendix 4 for valence and arousal values for each picture.

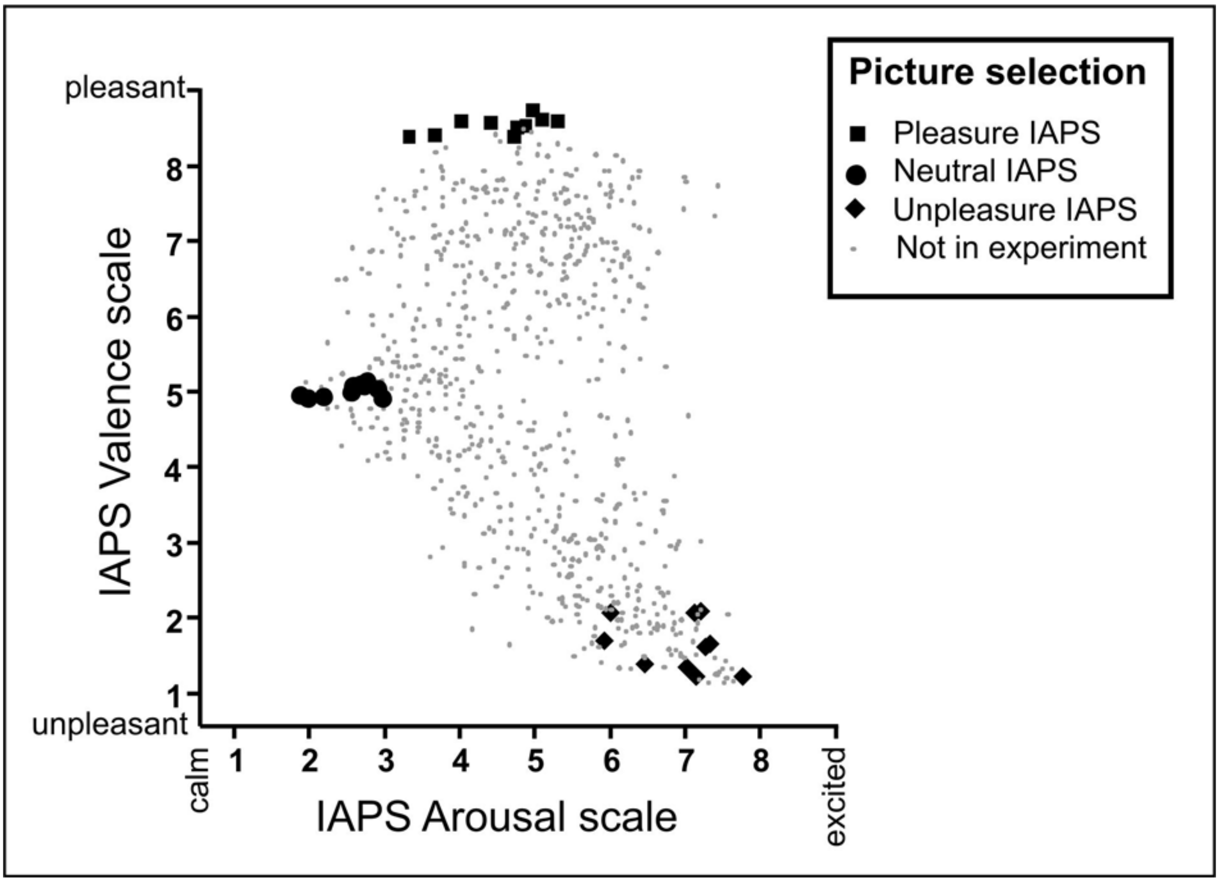


Figure 16: IAPS stimuli selected to provide the neutral, pleasant and unpleasant pictures; ratings are for women only. See Appendix 4 for valence and arousal values for each picture.

4.3.1.3. Data recording and preprocessing

See section 2.4.1 for general recording issues. Eye artifacts were corrected using blind component separation described in section 2.4.2., head artifacts were rejected as described in section 2.4.1.

4.3.1.4. Data analysis

Behavior data: Trials with reaction times lower than 200 ms and higher than 800 ms were excluded behavioral data analysis.

Post error slowing: Response-matching was conducted prior to analysis of post error slowing. See section 4.2.1.4 for details.

IAPS-locked ERPs: The previous experiment described in section 4.2 did not find any modulation due to emotional picture presentation. Thus, the present study pays special attention to demonstrate and analyze ERP effects due to emotional stimuli. Previous research has described an early temporo-occipital negativity, an early centro-medial positivity and a later centroparietal positivity for emotional compared to neutral IAPS pictures (Schupp, Junghöfer, Weike, & Hamm, 2003), even when presented for very short intervals (Schupp, Junghöfer, Weike, & Hamm, 2004). To maintain comparability to this previous research, analysis of IAPS-locked data was conducted using the average reference[11] (100 ms baseline prior to IAPS picture onset). However, because Schupp and colleagues used a 129-electrode array and grouped electrodes to widespread electrode patches, it is not possible to conduct exactly the same analysis. Thus, early effects will be examined based on mean amplitudes in a 200 to 300 ms time window with electrodes P7 and P8 representing the parieto-occipital cluster, and electrode Cz representing centromedial activation. Later effects will be examined based on mean amplitudes in a 400 to 600 ms time window on electrodes Cz and Pz, which represent the centroparietal activity. See Figure 1 for electrode locations. Statistical analysis contained the factor IAPS (3 levels, pleasant, neutral, unpleasant).

Flanker-locked ERPs: To investigate emotional modulations on components following the flanker stimuli, ERPs were averaged with the flanker stimulus onset being the zero point (100 ms baseline, only flankers with a subsequent correct response were included). Statistical analysis was based on mean amplitudes in a 200 to 400 ms time window and contained the factors CONGRUENCY (congruent vs. incongruent flanker), IAPS (neutral, pleasant or unpleasant IAPS picture prior to flanker stimulus). To keep consistency with analysis of response-locked ERPS, the factors ERRORHALVES (first and second error halve) and the between-group factor ERRORGROUP (High and low error group) were included, both factors are explained below.

Response-locked ERPs: To analyze response-locked ERP components (CRN/ERN and P_e), the same data analysis settings as described in section

---

[11] Common references (nose, mastoid etc.) are electrically active. Defining them to be “electrically neutral” might distort the ERP components of interest. Instead, it was suggested to use the average reference (Dien, 1998; Tucker, Liotti, Potts, Russell, & Posner, 1994). It combines all active electrodes and subtracts the activity common to all of them. However, the average reference requires equally distributed electrodes across the entire head and a high number of electrodes (> 64). Thus, it is a suboptimal reference for the present study and will be only used here to maintain comparability with earlier research (Schupp, Junghöfer, Weike, & Hamm, 2003, 2004).

4.2.1.4 were used. Thus, the ERN/CRN were examined relative to a 200 ms pre-response baseline, ERPs for correct responses were based on response-matched trials, and only trials within a time range from 200 to 800 ms were included.

As mentioned earlier (section 4.1.2.2), ERN amplitude is decreased when subjects commit more errors (Hajcak, McDonald, & Simons, 2003b). To take this into account, participants were subdivided based on the median of the overall error rate into a “high error rate group” and a “low error rate group”, both containing 11 subjects (Factor ERRORGROUP). Specific information regarding the number of trials[8] included in each condition is listed in Table 9.

Statistics were conducted on a frontocentral electrode patch or a parietal patch, (see section 4.2.1.4), exact details are given in the result section. To define time windows for statistical analysis, peak latencies were obtained for correct and erroneous responses and for both error halves in a 0 to 150 ms time post-response time window. Latency differences due to CORRECTNESS or ERRORHALVES were considered for defining time windows of CRN and ERN mean amplitude analysis. See Table 10 for selected time windows.

The P_e was analyzed in a 200 to 400 ms time window. To make sure that differences found in the P_e do not merely reflect activity which were already picked up in the ERN/CRN time window, the baseline for correct and erroneous responses and for both error halves was set to the time windows of ERN/CRN analysis (see Table 10). Thus, activation of the ERN\CRN time window was subtracted from activity in the P_e range. See below for further details.

ERROR GROUP	IAPS	CORRECTNESS	ERROR HALVE	Mean trial number	SD	Range
High error group	Neutral	Correct	1st	47.5	15.9	32-76
			2nd	45.7	14.6	28-70
		Error	1st	45.5	14.7	26-78
			2nd	48.2	14.9	30-76
	Pleasant	Correct	1st	45.1	16.5	26-80
			2nd	46.7	15.1	28-78
		Error	1st	42.9	16.3	20-74
			2nd	44.5	17.0	25-73
	Unpleasant	Correct	1st	44.5	12.7	27-67
			2nd	44.3	15.1	25-71
		Error	1st	48.7	16.4	27-76
			2nd	44.8	14.6	23-77
Low error group	Neutral	Correct	1st	20.2	7.3	8-29
			2nd	21.0	5.4	12-29
		Error	1st	20.3	6.8	7-29
			2nd	21.3	6.5	6-31
	Pleasant	Correct	1st	19.5	6.1	8-27
			2nd	22.3	4.8	12-29
		Error	1st	21.4	7.2	12-33
			2nd	21.9	6.7	13-37
	Unpleasant	Correct	1st	21.7	6.1	10-32
			2nd	21.0	5.7	8-28
		Error	1st	20.5	5.3	10-27
			2nd	19.9	5.4	10-27

Table 9: The number of trials included to generate the response-locked ERP conditions in study 4.3

4.3.2. Results

4.3.2.1. Behavioral data

Reaction times and error rates

Reaction times were analyzed for both groups and both error halves. Erroneous responses were faster than correct responses; this finding is consistent over both experimental halves and seen in both error groups (rmANOVA, Factors ERRORHALVES[12], CORRECTNESS, IAPS, ERRORGROUP, Main effect CORRECTNESS: F (1,20) = 90.05, $p < .001$; no significant interactions with ERRORHALVES or ERRORGROUP). Subjects were faster in the first compared the second error half (F (1,20) = 32,18, $p > .001$; no main effect of ERRORGROUP).

RT differences due to preceding IAPS pictures were very small. However, there was a significant CORRECTNESS x IAPS X ERRORGROUP interaction (F (2,40) = 3.66; $p < .035$), which indicates that RTs were somewhat slower for unpleasant compared to pleasant IAPS trials in the second half of the low error group (348 vs. 333 ms). See Figure 17.

Error rates: Since both experimental halves contained the same amount of errors, there was no need to include the factor ERRORHALVE in error rate analysis. Not surprisingly, the “High error group” differed from the low error group (error rate, “High error rate group: mean 275 errors, SD 88.4; “low error group”: mean 133 error, SD 29.5). There was no IAPS effect and no significant ERRORGROUP x IAPS interaction.

---

[12] See Appendix 7 b for distribution of errors across the experiment.

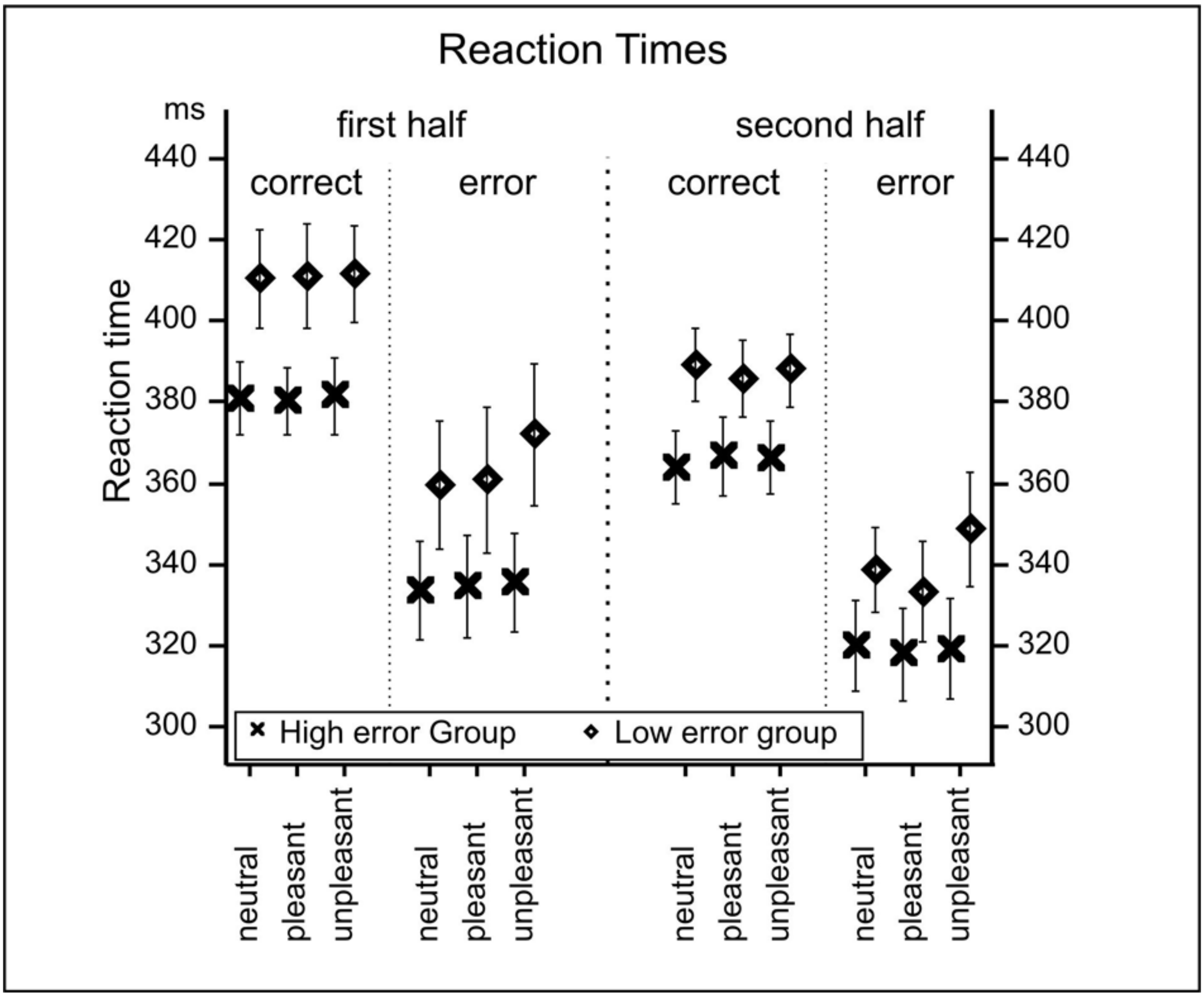


Figure 17: Reaction times to flanker stimuli, divided by error group, error halves, response correctness and IAPS picture preceding the flanker stimuli. Error bars indicate +/- 1 SE.

Congruency effect

The congruency effect (RTs following congruent vs. incongruent flanker stimuli) was analyzed as described in section 4.2.2.1. To keep consistency with prior analysis, error group and error halves were considered as well. Behavioral data showed shorter response times for congruent flanker stimuli compared to incongruent flanker stimuli. As reported in the section above, the high error group was somewhat faster than the low error group and subjects were faster in the first compared to the second error half. However, changes in affective states did not affect response times (rmANOVA; CONGRUENCY (congruent vs. incongruent flanker): F (1, 20) = 236.7, $p < .001$; ERRORHALVES:

F (1, 20) = 40.0, p < .001; ERRORGROUP: F (1, 20) = 3.48; p < .077; no significant effect of IAPS or interactions). See Figure 18 a for reaction times.

A highly similar pattern was observed for error rates: There were more errors following incongruent compared to congruent flankers, this effect was seen independently of error group allocation and in both error halves (ANOVA on error rates (percentages); CONGRUENCY: F (1, 20) = 180.48; p < .001; mean error rates: congruent flanker: 5.3%; incongruent flanker: 17.7 %; no significant effects of ERRORHALVES, IAPS. Of course, there was a significant main effect of ERRORGROUP. No further significant interactions).

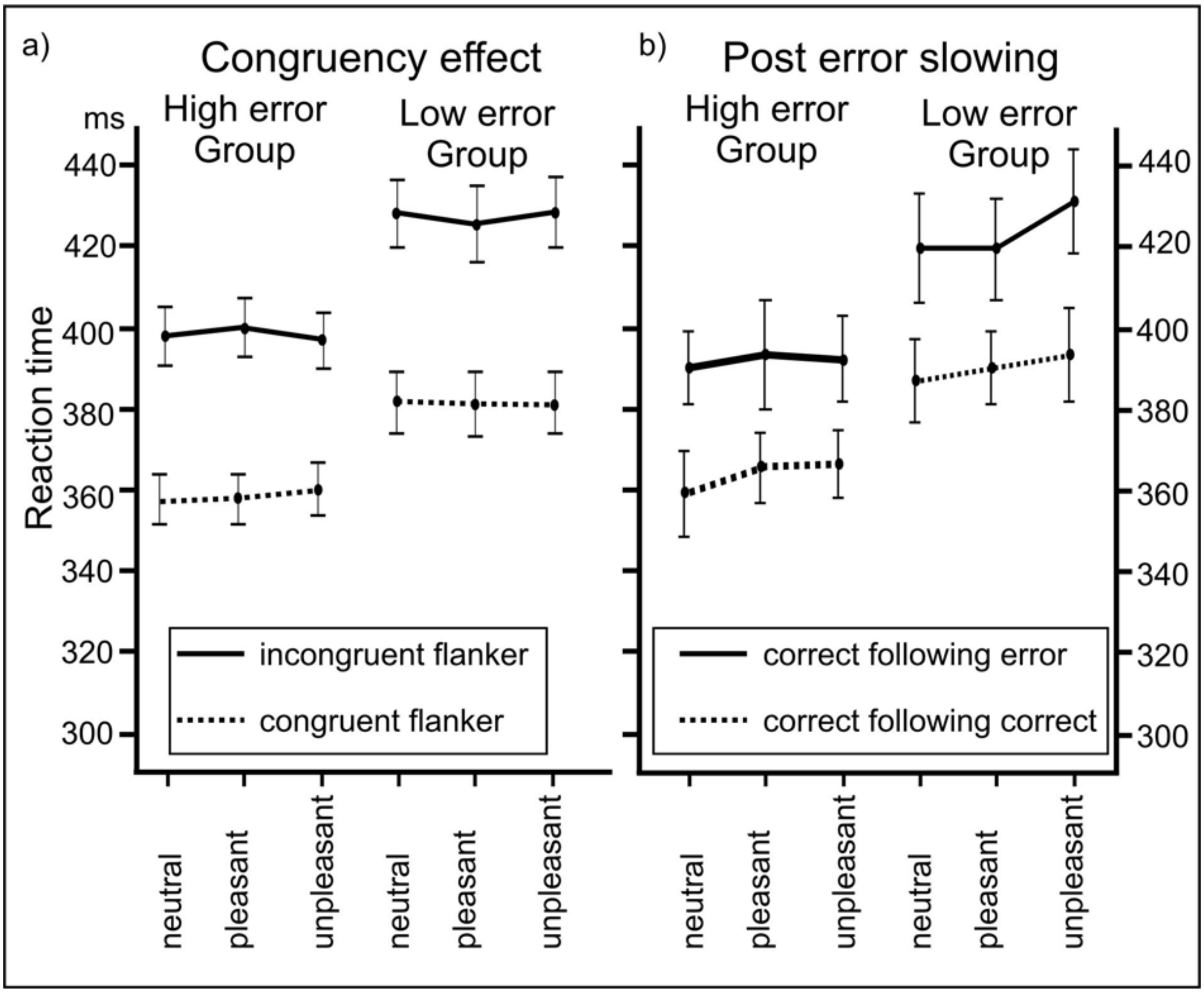


Figure 18: a) Reaction times following congruent and incongruent flanker stimuli, divided by error group. b) Post error slowing data, divided by error group and IAPS picture preceding the subsequent correct response. Error bars indicate +/- 1 SE.

Post error slowing

The same response matching procedure as described in section 4.2.2.1 was conducted to analyze post error slowing. Again, post error slowing was reliably found in the present study. Both groups reacted more slowly in correct trials following an error compared to correct trials that follow response-matched correct trials. The IAPS preceding the post-correct or post-error response did not influence post error slowing (rmANOVA, Factors POSTRESPONSE (post-correct vs. post-error), IAPS, ERRORGROUP; POSTRESPONSE: F (1,20) = 68.68, p < .001; mean correct following error: 408 ms; mean correct following correct: 377 ms; no other significant effects or interactions). See Figure 18 b.

Error correction rate

Although not instructed to do so, participants sometimes gave a subsequent correct response after they have committed an error (see section 4.1.1). It was examined whether error correction was more frequent when an emotional IAPS picture was previously seen. This was not the case (rmANOVA based on error correction rate following neutral, pleasant and unpleasant IAPS, ERRORGROUP: F (1,20) = 4.5; p < .046; no significant effect of IAPS; error correction rate for low error group: 11.2 corrected errors, low error group: 3.5 corrected errors). However, the previous analysis indicated that subjects with more errors (high error group) corrected also more errors. It was tested whether this finding persists when the error correction rate is set in relation to the total amount of errors. This analysis showed that error correction rate did not differ between error groups (rmANOVA based on percentage of corrected errors relative to all errors committed, IAPS, ERRORGROUP and interactions n.s.; error correction rate: high error group: 12.3%; low error group: 7.6%).

4.3.2.2. ERP data

IAPS-locked ERPs

Early effects: There was a clear emotional effect, best seen on occipito-parietal electrodes (P7 and P8) with pleasant and unpleasant IAPS pictures being more negative. On central sites (CZ), differences are emergent between all three emotional conditions, with unpleasant IAPS pictures being most positive and neutral pictures being most negative in amplitude (early effects, mean amplitudes 200 to 300 ms, parietal effect: IAPS F (2,42) = 33.69, p < .001. mean amplitudes in µV: neutral 5.93, pleasant 4.54, unpleasant 4.53; neutral pictures differed from pleasant and unpleasant pictures, p < .001. Central effect: F (2,42) = 31.89, p < .001, all conditions differed, with unpleasant IAPS pictures being relatively most positive, p <.001. Mean amplitudes in µV: neutral -4.24, pleasant -3.76, unpleasant -3.38). The effect was also examined including the factor ERRORHALVES, which showed that IAPS effects were the same in both experimental halves. See Figure 19.

Late effects: On centroparietal sites, the pleasant IAPS pictures elicited most negative amplitudes and the unpleasant IAPS pictures elicited most positive amplitudes. Splitting the experiment in two halves did not change this pattern (late effects, mean amplitudes on a patch consisting of Cz and Pz; 400 to 600 ms, F (2,42) = 10.69; p < .001; all conditions differed; p < .027; mean amplitudes in µV: neutral -.60, pleasant -.79, unpleasant -.38). See Figure 19.

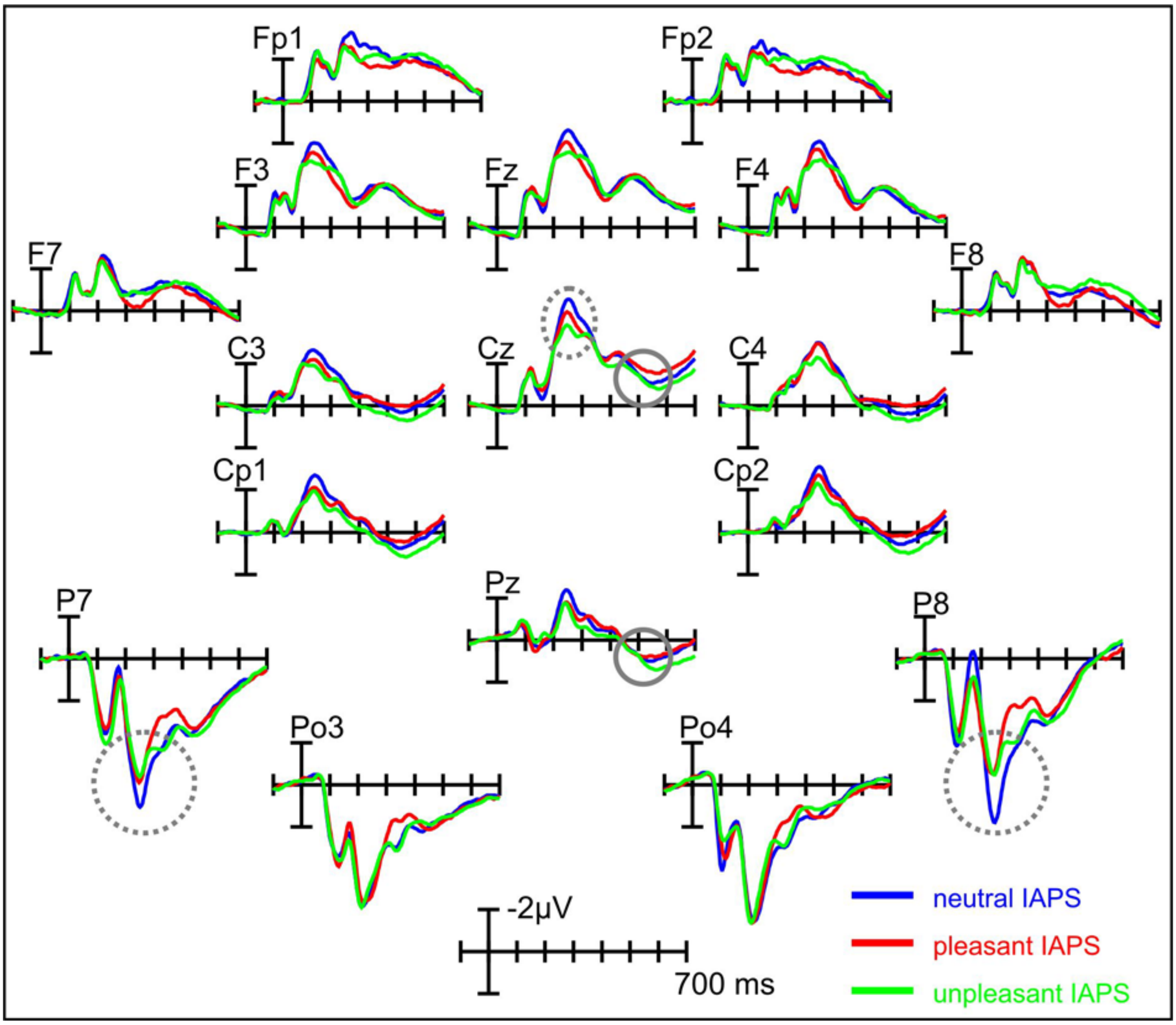


Figure 19: ERPs locked to IAPS stimuli. To make data comparable with prior research (Schupp, Junghöfer, Weike, & Hamm, 2003, 2004), ERPs were re-referenced to the average reference[11]. See Figure 1 for exact electrode location. Dotted circles indicate the early effect, solid circle depict the late effect.

Flanker-locked ERPs

Visual inspection: As depicted in Figure 20, the congruency effect (incongruent flanker minus congruent flanker) was best seen on centroparietal electrodes and will be examined on a electrode patch consisting of Cz, Cp1, CP2 and Pz.

Congruency effect: Incongruent stimuli elicited a stronger negative component compared to congruent stimuli (N2). This effect was seen for subjects with a high as well as with a low error rate. The N2 was clearly seen in both error halves and for subjects with a high and a low error rate.

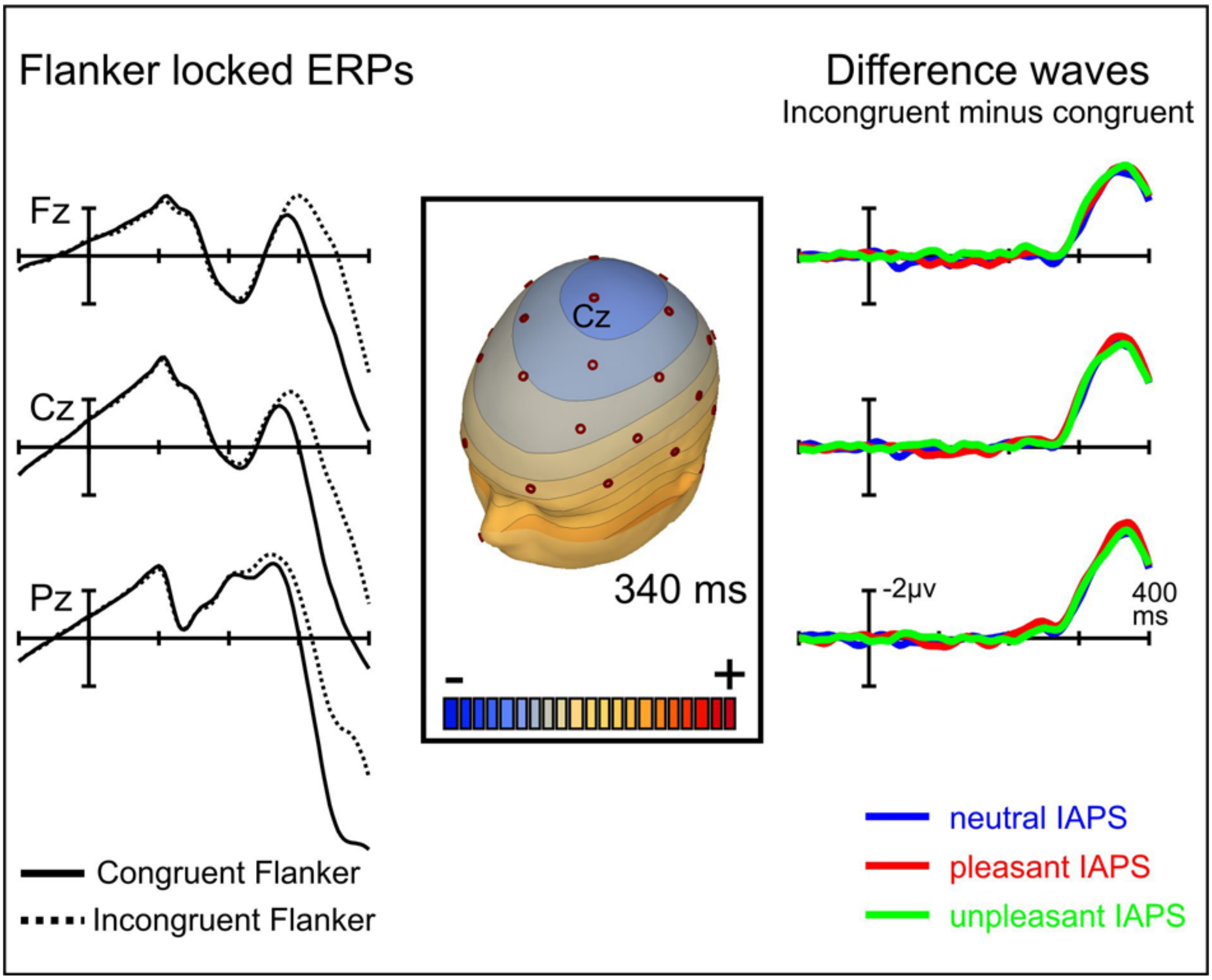


Figure 20: ERPs locked to flanker stimuli. Left panel: N2-effect without regarding preceding IAPS picture. Middle: scalp distribution at 340 ms based on difference waves incongruent minus congruent. Right: Difference waves based on incongruent minus congruent flanker stimuli, separately for all three IAPS conditions preceding the flanker.

Emotional effect: Flanker following unpleasant IAPS items were most negative, flankers following pleasant IAPS items were most positive. This was true in both error halves and in both error groups. Most interestingly, there was no interaction between the factors CONGRUENCY and IAPS; thus, the N2 was not affected by the previous IAPS picture (rmANOVA, mean amplitude in a 200 to 400 ms time window, on centroparietal electrode patch, factors ERRORHALVES; CONGRUENCY, IAPS, ERRORGROUP as between factor, all within factors significant, CONGRUENCY; F (1, 20) = 108.68, p < .001; IAPS: F (1,20)= 20.19, p < .001; CONGRUENCY x IAPS n.s.; ERRORGROUP n.s. (Mean amplitudes for congruent and incongruent flankers: High error group: 2.2 and 0.3 µV; low error group: 2.4 and 0.2µV).

Response-locked ERPs - the ERN/CRN

Visual inspection: The ERN is seen best on midline central scalp areas. Thus, statistics were conducted on a patch of electrodes consisting of Fz, Fc1, FC2 and Cz. Response-locked ERPs of midline electrodes for both subgroups ("high error rate" and "low error rate" group) and both error halves are depicted in Figure 21.

Peak latency analysis: The ERN peaks earlier than the CRN. This was especially true in the second half of the experiment. There was no effect of IAPS on peak latencies. (rmANOVA based on peak latencies determined in a 0 to 150 ms post response time window, most positive peak latency for correct responses, most negative peak latency for erroneous responses, factors ERRORHALVES, CORRECTNESS, IAPS, GROUP; interaction CORRECTNESS x ERRORHALVES: F (1,20) = 7.64, p < .012). Peak latencies are provided in Table 10.

CORRECTNESS	ERRORHALVES	Mean peak latency	Time window for peak amplitude analysis
Correct	1^{st}	89	50 to130
	2nd	94	50 to130
Error	1st	81	40 to120
	2nd	61	20 to 100

Table 10: mean peak latencies and time windows for ERN/CRN peak amplitude analysis for response-locked ERPs in experiment 4.3. Values are in ms.

Mean amplitude analysis with response-matched data: Amplitudes were determined separately for correct and erroneous reactions for both error halves. Time windows were adjusted according to different peak latencies for those subgroups; see Table 10**Fehler! Verweisquelle konnte nicht gefunden werden.**. ANOVA on mean amplitudes was based on the same factors as described for peak latencies. Errors elicited a strong ERN, which was significantly more negative than the CRN following correct responses

(CORRECTNESS: F (1, 20) = 211.23; p < .001). There was a significant CORRECTNESS x ERRORHALVES X IAPS interaction (F (2, 40) = 17.42, p < .013). Thus, IAPS effects were examined separately for correct and erroneous responses, and for both error halves with ERRORGROUP as between-group-factor. Unpleasant IAPS pictures prior to a response caused ERN to be more negative in the first error half of the low error group (IAPS X ERRORGROUP, F (2, 40) = 8.57, p < .003). This effect was also seen in attenuated manner for the CRN; the effect was statistically significant in the second error half (IAPS: F (2,40) = 3.71; p < .033). Visual inspection revealed that the voltage scalp distribution of the CRN is somewhat more posterior than the ERN, which in turn means that the CRN might be better analyzed by a slightly more posterior electrode patch. Examined on a patch consisting of Cz, Pz, CP1 and CP2, separate ANOVAs as described above found a significant IAPS effect for correct responses, for both, the first and the second error half. As for the ERN, the CRN was more negative following unpleasant IAPS pictures (IAPS, both halves, correct responses: F (2, 40) > 5.2, p < .01).

Mean amplitude-no response match: As mentioned above, analysis of the CRN was based on a subset of correct responses which were matched to erroneous responses in terms of reaction times and amount of trials. However, as shown in behavioral data, there was a speed advantage for responses following congruent compared to incongruent flankers. Thus, when selecting a subset of fast correct responses based on their reaction time only, most of them will be preceded by congruent flanker trials. An optimal matching procedure would control for this by considering both, the response speed and the amount of congruent and incongruent flanker trials. This was not possible here because in some subjects, there were not enough fast correct responses following incongruent flanker stimuli. To exclude the possibility that emotional effects seen in the CRN is only emergent when a subset of correct trials is selected (fast responses with a lower proportion of incongruent trials), the same statistics as described for CRN on parietal patch was conducted with the complete set of correct trials. This did not change data interpretation at all; CRN remained most negative following correct responses with preceding unpleasant IAPS pictures in both error halves; correct responses following pleasant and neutral IAPS pictures did not differ (rmANOVA on CRN, parietal patch, separately for both error halves F (2,40) < 4.7; p < .015; pairwise comparisons: unpleasant IAPS differs from all other conditions, p < .02). Thus, the emotional effect is robust enough to be shown without sophisticated response matching algorithms.

Response-locked ERPs - the P_e

The P_e was analyzed based on mean amplitudes in a 200 to 400 ms time window on a centroparietal patch of electrodes (Cz, Pz, CP1 and CP2). Since affective pictures modulated the ERN component, it is reasonable to assume that those effects are still seen in the CRN time window. To clearly distinguish emotional modulation of the P_e from earlier modulations, baseline was set to the time windows where the ERN/CRN was most pronounced (50 to 130 ms for correct responses, 40 to 120 ms for error responses, first half, 20 to 100 ms for errors, second half, see Table 10. Statistics were conducted as described above and revealed a more positive component for correct compared to incorrect responses (CORRECTNESS, F (1,20) = 184.57, p < .001). This very conservative approach did not reveal an effect of IAPS nor any significant interactions.

Correlation between ERPs and Error Rates

Peak amplitudes within the ERN time window and mean amplitudes within the P_e time windows for erroneous responses were correlated with error rates. There was a positive correlation between ERN amplitude and erroneous responses in the ERN time window, indicating that subjects with more errors had a decreased (less negative) ERN amplitude (r = .43. p < .049). Dividing the data set by ERRORHALVE revealed that the amplitude-error rate-relationship is best seen in the first ERRORHALVE for erroneous responses (r = .47, p < .026). There was no relationship between error rate and CRN. Also the P_e time window did not show significant correlations between P_e amplitude and error rate.

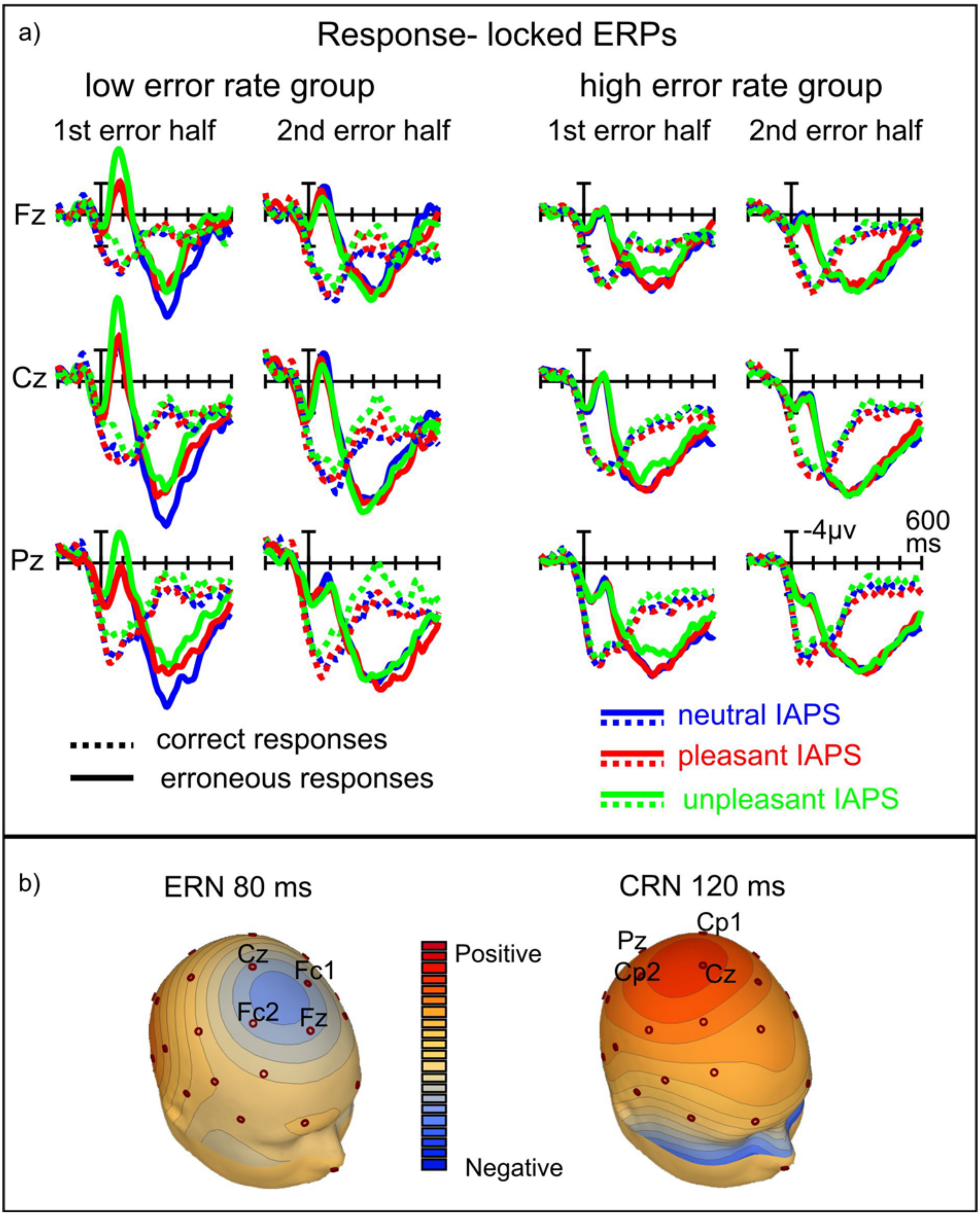


Figure 21: a) Response-locked ERPs on midline electrodes. Correctness is coded by line style, preceding IAPS picture is color-coded. ERPs are divided by error group and error halves. ERPs for correct responses are based on response-matched trials. b) Scalp distribution of the ERN and the CRN. Since the distribution between CRN and ERN differs, scalp distribution was not based on difference waves error minus correct responses.

4.3.3. Summary and perspective

Summary: The experiment presented in section 4.3 displays the classical effects in behavioral and ERP data (see section 4.2): Incorrect responses were given faster than correct responses (Falkenstein, Hoormann, & Hohnsbein, 1999), and subjects responded faster to congruent compared to incongruent flanker trials (Eriksen & Eriksen, 1974). Error rates were higher for incongruent flanker trials. Subjects with a high error rate (high error group) and subjects with a low error rate (low error group) did not differ in speed-accuracy-tradeoff, but only in the absolute error rate. Post error slowing was reliably shown; correct responses were given faster when they succeed correct compared to incorrect responses (Hajcak, McDonald, & Simons, 2003b, 2004; Rabbitt, 1981, 2002). Subjects of both groups tended to correct the same amount of errors. Most importantly, the IAPS picture presented prior to the flanker stimuli did not influence the behavioral data[13].

It was assumed that the overall error rate can be used as a measure for task engagement; subjects with a low error rate were more engaged in the task.

IAPS-locked ERP data showed emotional effects already described in the literature (Schupp, Junghöfer, Weike, & Hamm, 2003, 2004). The N2 was not affected by IAPS stimuli.

The distinction between high and low error rate is of special importance for ERN/CRN analysis, because previous research described an enlarged ERN when subjects commit less errors (Gehring, Goss, Coles, Meyer, & Donchin, 1993; Hajcak, McDonald, & Simons, 2003b). This was also the case in the present study. The most interesting finding is that the ERN and the CRN were more negative in unpleasant IAPS trials at the beginning of the experiment (first error half) in the low error group. Thus, experiment 4.3 shows that unpleasant IAPS pictures are feasible to induce emotion-specific processing. The brain’s action monitoring system was set in a state that it is more active when action follows unpleasant, but not when action follows pleasant or neutral IAPS pictures.

---

[13] The finding that responses were somewhat slower (15 ms) in subjects with a low error rate in the second half of the experiment is interpreted as not very robust and might be caused by type 1 error.

Perspective: The behavioral data are highly similar to those reported in the other experiments of section 4 and will be discussed in 4.6 “Discussion – Part 2”.

Because emotional stimuli were presented on a trial-by-trial-basis, it was not possible to measure effects on subjective emotions with a questionnaire. However, previous research, comparable in that emotions were modified by short-term IAPS picture presentation, showed that trial-by trial based presentation of IAPS pictures does not change subjective mood over the course of the experiment (Dreisbach & Goschke, 2004) or only at the beginning of the experiment when only negative IAPS pictures are presented (Simon-Thomas & Knight, 2005). However, experiment 4.5 allows access to changes in affective state by using a pre-and post-experimental questionnaire in a between-group-design.

IAPS-locked ERP data show remarkable similarity to previous research (Schupp, Junghöfer, Weike, & Hamm, 2003, 2004) and provide further evidence that short presentation of IAPS pictures is a feasible procedure to induce short-term brain modulations. There was an early emotional effect with pleasant and unpleasant IAPS pictures being more negative on posterior sites. I agree with Schupp and colleagues (2003, 2004) that this early posterior negativity reflects a selection negativity caused by intrinsic relevance of emotional stimuli. This effect is fast and automatic and can be observed even when emotional pictures are not task relevant. Thus, even when IAPS pictures presented as short as 80 ms, their intrinsic relevance can be detected so that they draw attentional resources. However, it is reasonable to assume that unpleasant IAPS pictures, which display potentially threatening situations (mutilations, blood, weapons), should also be distinguished from pleasant IAPS pictures at an early stage. Thus, both, pleasant and unpleasant emotional pictures should differ in the same direction from neutral pictures due to detection of salient picture context. Additionally, absolute differences between neutral and unpleasant IAPS stimuli should be larger than absolute differences between neutral and pleasant IAPS pictures due to hyper-salience of unpleasant stimuli (see section 1.5.1). This is exactly the case on central sites in my experiment (see Ito, Larsen, Smith, & Cacioppo, 1998, for similar results). Thus, here it is concluded that the selection negativity on posterior sites reflects emotion-relevant attention drawn towards salient stimuli, whereas central differences reflect the onset of evaluation processes distinguishing between salient and hyper-salient stimuli. It is unclear why Schupp and colleagues (2004) failed to show graded differences in a neutral – positive – negative sequence. Varieties in experimental setup might be an issue. Schupp and colleagues showed sequences of IAPS pictures, which were not interrupted by non-emotional tasks. Even if early affective modulations are automatic, it cannot be excluded that the cognitive system shows some kind of saturation when emotional pictures are presented in sequence.

As in the previous experiment (section 4.2) flanker-locked ERPs (N2) were not affected by preceding emotional IAPS stimuli. This effect is discussed in section 4.6.

The present study confirmed my prediction that the ERN is more pronounced when subjects were presented with negative stimuli prior to the response. This extends previous research, which restricted IAPS-induced performance monitoring examination on the CRN without including ERN modulations (Simon-Thomas & Knight, 2005). Thus, here it was shown that the ERN as well as the CRN is modulated towards greater negativity following unpleasant IAPS pictures. As previously shown, emotions induced by negative IAPS pictures are mild and decrease during the course of the experiment (Simon-Thomas & Knight, 2005). This explains why the ERN increase due to unpleasant IAPS pictures is only seen at the beginning of the experiment. In addition, it is reasonable to assume that subjects with an lower error rate were more engaged in the experiment. Thus, they paid more attention to the flanker stimuli, and, probably also to the emotional stimuli prior to the flanker. An emotional modulation was only achieved in them. Thus, to achieve an effect seen in all subjects and across the entire experiment, it is advisable to conduct the same flanker task with a more powerful method to induce emotions. This is done in experiment 4.5. An integration of the emotional ERN increase in the framework of existing performance monitoring theories (see section 4.1.2.2) is conducted in 4.6 “Discussion – Part 2”.

The absence of an ERN modulation following pleasant IAPS pictures might be due to several reasons: Easiest of all, it could be concluded that the ERN is not susceptible to positive emotions. However, I regard this conclusion as premature, since there are other explanations that have to be ruled out.

Alternatively, it is conceivable that the ERN is susceptible to pleasant stimuli, but the paradigm was not feasible to set the brain into a state of positive emotions. The paradigm could be suboptimal because pleasant IAPS pictures are not powerful enough to induce positive emotions with the same intensity as elicited by unpleasant stimuli. This argument gets support from the biological perspective: unpleasant pictures are perceived as unpleasant because they signal harm or threat, thus, they are of immediate importance for the well-being of the organism. Speeded and intense adaptation of the cognitive system might therefore only be adaptive for unpleasant, but not for pleasant stimuli. This propensity to react more strongly to negative stimuli has been termed the negativity bias has been often described in literature (see Cacioppo & Berntson, 1999, for overview.; Ito, Larsen, Smith, & Cacioppo, 1998). To conclude, I see good evidence that it is not enough to present the subject with pleasant pictures to set the performance monitoring system into a state of less cautious and less restrictive processing, which would be indicated by lower ERN amplitude for positive pictures.

The experiments presented in section 4.2 and 4.3 are limited in a few aspects, which will be discussed in the next paragraphs. Starting with general properties of the IAPS picture set used for stimulation in experiment 4.3, one might argue that pictures differ not only in valence, but also in arousal. As shown in Figure 16, unpleasant pictures (low valence) are more exciting (high arousal) than positive and neutral pictures. Due to IAPS rating properties, it was not possible to select a subset that differs in valence, but not in arousal. In addition to that, it can be argued that unpleasant pictures differ in physical properties. For example, they contain more often pictures of people, the depicted situations might be more complex, or it could easily be that they contained another spectrum of colors (for example the higher red contend in pictures of mutilations).

There is also a more basic shortcoming of experiments presented in section 4.2 and 4.3. Until now, subjects perceived emotions of other people (4.2) or perceived pleasant or unpleasant scenes (4.3). Thus, it might be argued that there is a basic difference between perceiving emotions and experiencing emotions (Davidson & Irwin, 1999). To experience emotions, it is necessary to bring the subjects in direct contact to emotion-eliciting stimuli. Reisberg and Hertel (2004) summarized this important and in most research neglected distinction with the words "We become emotional, in other words, when we encounter issues and information that are pertinent to our lives, goals, and values (or, perhaps, the lives and values of people we care about). We refer to this more common kind of emotion as thematically induced, in contrast to the visually induced reactions involved in most previous studies, produced by the presentation of a specifically defined emotional visual stimulus" (p.14).

The introduction of personal involvement instead of merely observing emotional faces or scenes is the basic change in the next two experiments presented in section 4.4 and 4.5. Experiment 4.4 uses facial feedback as an environmental stimulation that is in direct contact to the subject. Experiment 4.5 goes one step further-by providing either positive or negative feedback based on the subject's performance, it is attempted to bring subjects in a situation where positive or negative emotions are self-relevant.

4.4. Experiment 2c: Emotions induced by facial feedback

4.4.1.1. Participants

Data were acquired from 25 right-handed women. See section 2.1 for additional information. ERP data were analyzed from 22 subjects (mean age 22 years, range 17 to 28), two subjects were excluded due to high and uncorrectable artifact levels, and one subject was excluded because she mixed up stick-positions during the experiment.

4.4.1.2. Stimuli and procedure

The experimental design was similar to experiments in section 4.2 and 4.3 in terms of flanker tasks. There were no emotional pictures presented prior to the flanker. Thus, a trial consisted of a fixation cross with varying duration 600 to 800 ms, (mean 700 ms), followed by a flanker stimulus with the same properties as described in section 4.2.1.2.

The experiment consisted of 2100 trials. A feedback screen was presented after a sequence of 30 trials, informing the subjects whether they are faster or slower than in the mean reaction time of the previous 30 trials. Participants terminated the feedback screen by button press. After seven 30-trial sequences, there was a 15 sec. break, indicating the end of a block. Subjects were able to request for longer breaks if necessary. Thus, the experiment was subdivided into 10 blocks, each block consisted of 7 sequences of 30 trials each. Flanker trials were randomized within each sequence with the restriction that there were 40 % of consistent (HHHHH and SSSSS, 20 % each) and 60 % of inconsistent flankers (HHSHH or SSHSS, 30 % each). See Figure 22.

Emotional modulation: Experimental emotional modulation was introduced on a block-wise basis: Subjects were asked to hold a stick (Chinese disposable chopstick) either

- Horizontally between the teeth (“Smile”-condition, see Figure 22)
- Vertically with the upper lip only (“No-smile”-condition, see Figure 22)
- Or have no stick in the mouth (“No stick”-condition).

There were three Smile-condition blocks, three no-smile-condition blocks and four no-stick blocks. The sequence of blocks was randomized with the restriction that two of the same conditions were never directly adjacent and the last block was always the “no-stick”-condition. To equalize the number of trials for each condition, the last 210 trials (always no-stick condition) were excluded from behavioral and ERP data analysis. Thus, each condition contained finally 3 x 210 = 820 trials. See Figure 22.

Flanker stimuli: Flanker stimuli were exactly the same as described in section 4.2.1.2.

Instruction: As in previous experiments, participants were asked to respond as fast and as correct as possible to the central letter of the flanker string. They responded with a left-hand key to the H and with a right-hand key to the S.

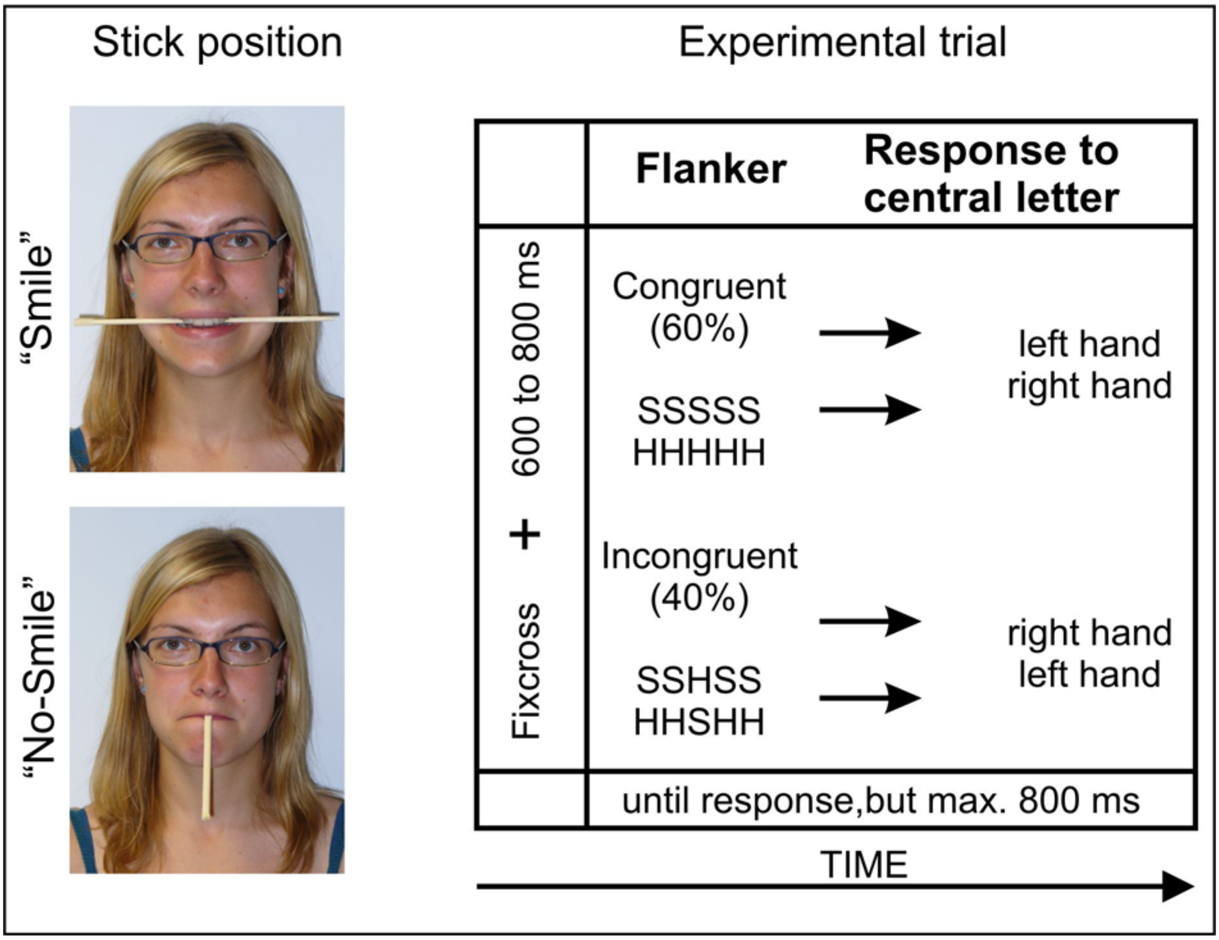


Figure 22: Setup for experiment 4.4. Emotional modulation was induced by feedback received from facial muscles. A "Smile" was induced by holding a wooden chopstick horizontally in the mouth, a smile was prevented ("no-Smile") by holding the stick vertically with the lips. In a third condition, subjects had no chopstick in the mouth ("no stick"). A trial is visualized in the right panel.

Sham story: Participants were not informed about the intended emotional modulations. Thus, to explain why they were required to hold a chopstick with either the lips or between the teeth, a sham story was introduced: Participants were told that the present ERP study examines how facial muscle artifacts influence ERP recordings. To demonstrate muscle artifacts, the experimenter presented the subjects with their own EEG on the presentation computer prior to the beginning of the experiment. Subjects were asked to blink and to move the eyes, what resulted in high and clearly detectable artifacts on the EEG. Now that subjects knew that eye artifact severely impacts ERP recordings, they were told that researchers know how to handle eye artifacts, but little is known about how to handle muscle artifacts generated by the mouth and by the cheek muscles. Thus, to examine this in detail, mouth and cheek muscles will be innervated by different chop stick positions. To make sure that subjects believed the story, most of the subjects were not studying psychology, and none of them was enrolled in higher than 2nd year psychology courses. At the end of the experiment, a questionnaire asked the participants to explain the purpose of the experiment. None of them was suspicious about the cover story.

4.4.1.3. Data recording and preprocessing

See section 2.4.1 for general recording issues. Eye artifacts were corrected using blind component separation described in section 2.4.2. Head artifacts were rejected as described in section 2.4.1.

4.4.1.4. Data analysis

Behavior data: Trials with reaction times lower than 200 ms and higher than 800 ms were excluded from behavioral data analysis.

Post error slowing: Response-matching was implemented to analyze post-error slowing, because it allows a comparison of post-error slowing with potential RT-slowing after equally fast correct trials. See section 4.2.1.4 for details on response matching.

Flanker-locked ERPs: To examine emotional modulations on components following the flanker stimuli, ERPs were averaged with the flanker stimulus onset being the zero point (100 ms baseline, only flankers with a subsequent correct response were included). Consistent with analysis described in 4.3.2.2, the N2 effect will be examined on an electrode patch consisting of Cz, Cp1, CP2 and Pz. Statistical analysis contained the factors CONGRUENCY (congruent vs. incongruent flanker) and STICKPOSITION (“No-stick” “No-Smile” and “Smile”).

Response-locked ERPs: ERPs were generated relative to a 200 ms pre-response baseline, only responses given within 200 to 800 ms after flanker stimulus onset were included.

Response matching of correct trials was not performed, because it was shown that emotional effects on correct trials can also be displayed including all correct responses (see 4.3.2.2). Statistical analysis was based on the factors “CORRECTNESS” (correct vs. erroneous responses) and STICKPOSITION. Visual inspection of data showed that emotional effects were seen in both ERRORHALVES and for subjects with a low and a high error rate. Thus, to keep analysis simple, Factors “ERRORHALVE” and “ERRORGROUP” (see section 4.2.1.4) were not further regarded. See Table 11 for details on trials included in ERPs.

STICK POSITION	CORRECT NESS	Mean trial number	SD	Range
“No stick”	Correct	554.1	27.1	500-600
	Error	64.0	23.7	30-119
“Smile”	Correct	546.0	32.3	486-594
	Error	70.8	28.5	30-131
“No-smile”	Correct	551.5	26.0	496-587
	Error	67.0	25.4	14-126

Table 11: The number of trials included to generate the response-locked ERPs in study 4.4.

Time windows for statistical analysis were defined based on peak latencies for correct and erroneous responses in a 0 to 150 ms post-response time window. Latency differences due to CORRECTNESS were considered for defining time windows of CRN and ERN mean amplitude analysis. See Table 14 for selected time windows. Consistent with analysis reported in section 4.2.1.4 and 4.3.1.3, the ERN was examined on a frontocentral electrode patch, the CRN and the P_e on a parietal electrode patch.

The P_e was analyzed in a 200 to 400 ms time window. Consistent with analysis described in 4.3.1.3, the baseline for correct and erroneous responses was set to the time windows of ERN/CRN analysis (see Table 14). Thus, activation of the ERN\CRN time window was subtracted from activity in the P_e range.

4.4.2. Results

4.4.2.1. Sham story

After completion of the experiment, subjects were asked to write down why it was required to hold the stick between the teeth. The answers were given in an open manner. None of the subjects was suspicious that the stick was to induce emotions. On a second sheet of paper given after completion of the first, subjects were prompted to find alternative explanations for the stick by asking them whether they could think of any other reasons for holding the stick. Again, none of the subjects mentioned that the stick was administered to evoke a smile or prevent from smiling. On a third sheet of paper, subjects were asked how they felt when holding the stick. There was one woman who reported to feel “somewhat happier in the teeth condition”. Beside that, there were no clear emotional modulations reported due to stick position.

4.4.2.2. Behavioral data

Reaction times and error rates:

Reaction times showed a very similar pattern as described in section 4.3.2.1 in that erroneous responses were faster than correct responses. The three facial feedback conditions did not influence reaction times (ANOVA, CORRECTNESS: F (1,21) = 339.4, p < .001; STICKPOSITION or interactions n.s.). See Table 12 for RTs.

STICKPOSITION	Correct	Error
“No stick”	397 (26)	338 (25)
“Smile”	394 (30)	333 (24)
“No-smile”	395 (29)	337 (24)

Table 12: Reaction times for correct and erroneous responses in study 4.4; values are in ms, standard deviations are given in brackets.

Congruency effect

The congruency effect was examined similar as described in section 4.3.2.1: Reaction time analysis included correct trials only following congruent and incongruent flankers for all three facial feedback conditions. As expected, RTs were faster following congruent flankers. Again, emotional modulation did not interfere with the congruency effect (rmANOVA, Factor CONGRUENCY: F (1, 21) = 265.14; p < .001; mean reaction times: congruent flanker: 380 ms; incongruent flanker: 424 ms. No significant effect of STICKPOSITION or interactions).

A highly similar pattern was found for error rates; error rates were higher for incongruent trials, facial feedback modulation did not impact error rates (rmANOVA on error rates (percentages); CONGRUENCY: F (1, 21) = 251.95; p < .001; mean error rates: congruent flanker: 5.6%; incongruent flanker: 18.9 %; no significant effects of STICKPOSITION or interactions).

Post error slowing

Similar post error slowing effects as described in section 4.3.2.1 were found. Correct trials following erroneous responses were faster than correct trials following response matched correct trials (response-matching procedure selected a subset of correct trials that matches erroneous trials in terms of total number and reaction time). The stick position did not influence post-error slowing, neither for correct nor for erroneous trials (rmANOVA, POSTRESPONSE (correct responses following correct responses vs. correct responses following erroneous responses), STICKPOSITION. POSTRESPONSE: F (1,21) = 28.99, p < .001); no further main effects or interactions). Reaction times for trials following correct and erroneous responses are provided in Table 13.

STICKPOSITION	Correct responses following correct responses	Correct response following erroneous responses
“No stick”	389 (25)	421 (33)
“Smile”	393 (34)	417 (34)
“No-smile”	392 (37)	416 (37)

Table 13: Reaction times for post-correct and post-error responses in study 4.4; Values are in ms, standard deviations are given in brackets.

4.4.2.3. ERP data

Flanker locked ERPs

Visual inspection: The congruency effect (Incongruent flanker minus congruent flanker) was best seen on centroparietal electrodes. Visual inspection of the difference waves separately plotted for the three facial feedback conditions indicates that the N2 effect is somewhat smaller when there is a stick in the mouth. This effect is not very consistent, since it is seen for the “Smile” and the “No smile” condition. See Figure 23.

Congruency effect: The same pattern as described in section 4.3.2.2 was observed: ERPs following incongruent stimuli were more negative compared to congruent stimuli.

Emotional effect: facial feedback condition did not influence the N2 (ANOVA, mean amplitude 200 to 400 ms, CONGRUENCY: $F(1, 21) = 79.49$; $p < .001$; mean amplitudes: congruent flanker: 4.5 µV; incongruent flanker: 2.3 µV, no significant effect of STICKPOSITION or interactions) Thus, small differences seen in visual data inspection were not confirmed statistically.

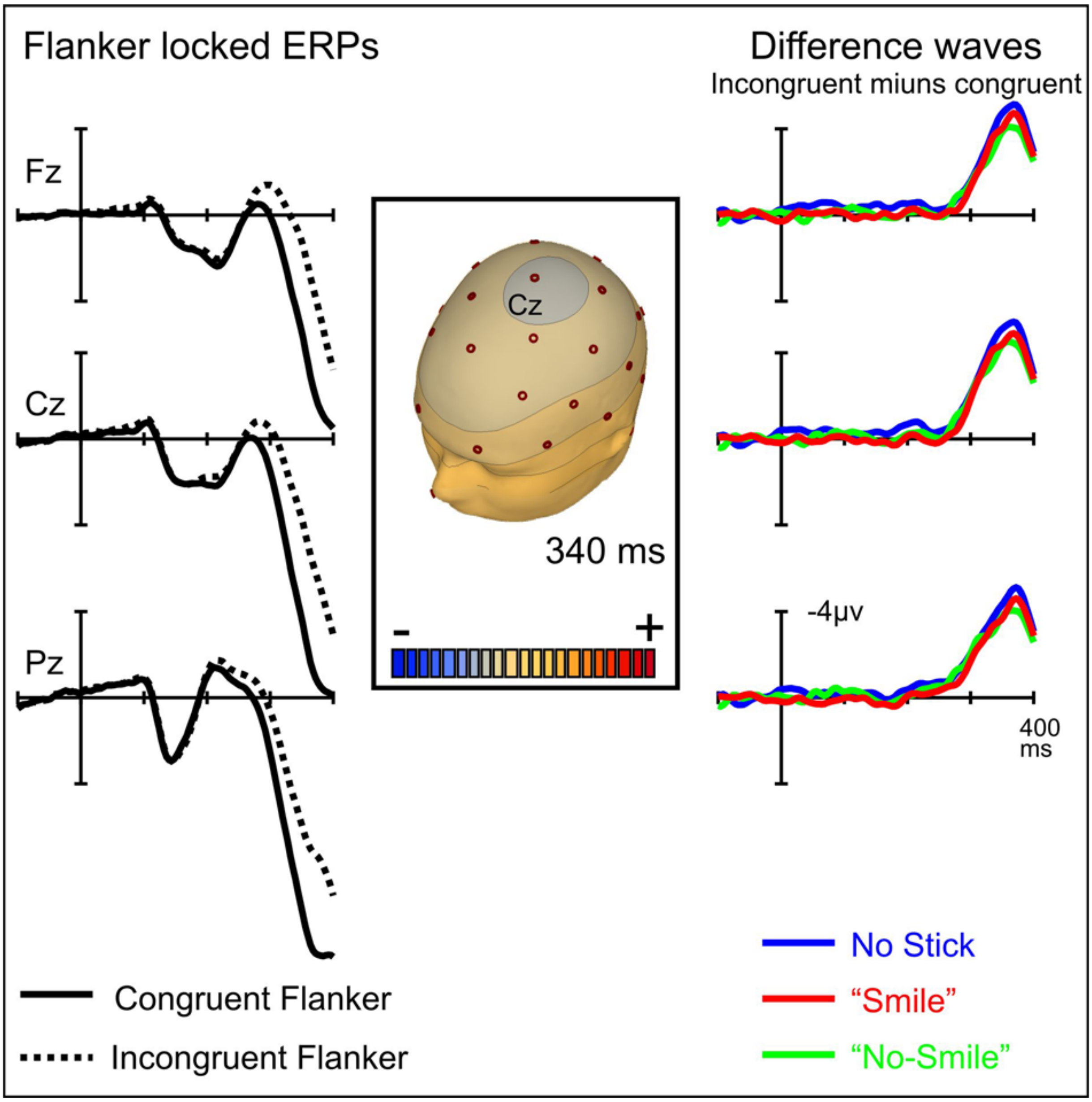


Figure 23: ERPs locked to flanker stimuli. Left panel: N2-effect without regarding Stick-position. Middle: scalp distribution at 340 ms based on difference waves incongruent minus congruent. Right: Difference waves based on incongruent minus congruent flanker stimuli, separately for "Smile", "No-Smile" and "No stick condition.

Response-locked ERPs - the ERN/CRN

Visual inspection: A typical ERN was seen following errors, a CRN was seen following correct responses. The ERN was most pronounced on a frontocentral patch of electrodes, the CRN was best seen somewhat more posterior. As predicted, the ERN and the CRN were less negative when facial muscles generating a smile (especially the zygomaticus major) were innervated during the “Smile” condition. Both other conditions were not distinguishable in

ERN or CRN amplitude. As in previous experiments, the ERN peaked earlier than the CRN; experimental manipulation did not influence ERN or CRN peak latencies. See Figure 24.

Peak latency analysis: Visual impression was confirmed; the ERN peaked earlier than the CRN, experimental manipulation did not impact peak latencies (rmANOVA, factors CORRECT, STICKPOSITION; CORRECT: F (1,21) = 7.2; p < .014; STICKPOSITION or interactions n.s.). See Table 14 for peak latencies.

CORRECTNESS	Mean peak latency	Time window for peak amplitude analysis
Correct	79	40 to120
Error	57	20 to 100

Table 14: mean peak latencies and time windows for ERN/CRN peak amplitude analysis for response-locked ERPs in experiment 4.4. Values are in ms.

Mean amplitude analysis: As expected, erroneous responses elicited a more negative ERP component compared to correct responses. Analysis of emotional modulation yielded a less negative wave for the “Smile” condition only. This was true for correct as well as for erroneous responses (rmANOVA based on mean amplitudes in time windows listed in Table 14, CORRECTNESS: F (1,21) = 77.96; p < .001; STICKPOSITION: F (2,42) = 5.92; p < .007; no significant interactions. Individual comparisons: "Smile" was less negative than both other conditions, p < .016).

Response-locked ERPs - the P_e

To adjust for differences seen in the ERN time window, amplitudes in time windows listed in Table 14 were subtracted prior to statistical analysis (see section 4.3.1.3 for further explanation). As in experiment 4.3, the P_e distinguished clearly between correct and erroneous responses; it was more positive following errors. There were no differences due to emotional modulation (rmANOVA, Factors CORRECTNESS, STICKPOSITION, CORRECTNESS: F (1,21) = 146.66, p < .001; STICKPOSITION or interactions n.s.).

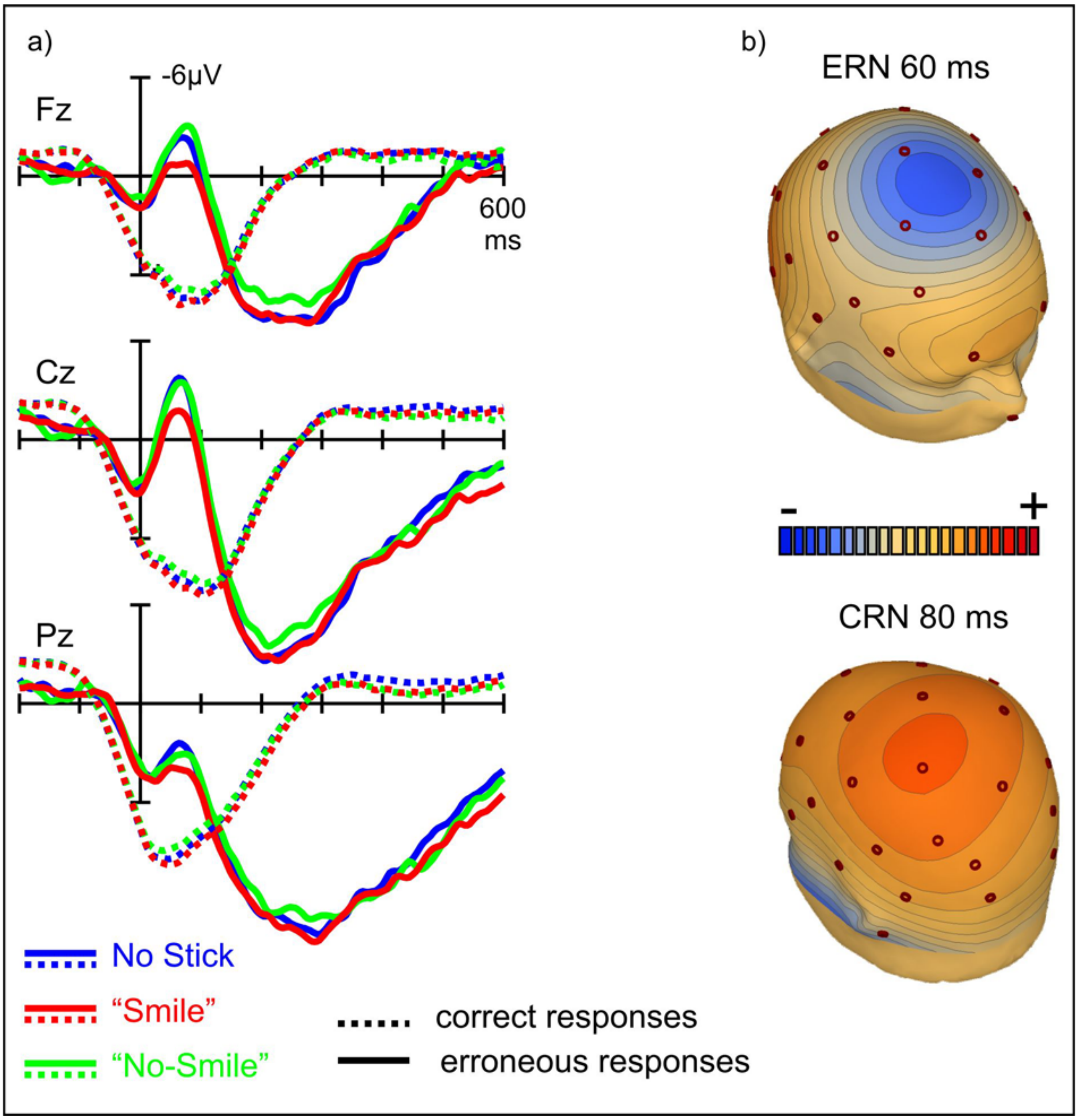


Figure 24: a) Response-locked ERPs. Correctness is coded by line style, stick position is color-coded. b) Distribution of the ERN and the CRN.

4.4.3. Summary and perspective

Summary: As the previous experiments in section 4, subjects were faster in committing erroneous responses and RTs were lower following congruent flanker trials. There was the usual post-error-slowing effect. Again, affective modulation did not impact behavioral data.

Furthermore, the N2 and the ERN/CRN were reliably seen. ERPs locked to the onset of the flanker stimuli were more negative after incongruent flankers

(N2); ERPs locked to responses were more negative when an erroneous response was given (ERN). The most important finding is that the ERN and the CRN were less negative when subjects were required to hold a chop stick between the teeth to innervate facial muscles involved in smiling. The N2 was not modulated by stick position.

Perspective:

The experiment clearly shows that facial feedback exerts a modulation effect on error monitoring. Alternative explanations for the facial feedback effects as introduced in section 1.5.3 have been carefully excluded: The written interview after the experiment indicates that subjects did not perceive themselves to be smiling, which excludes an effect based on self-perception. There is also no reason to assume that the effect was caused because subjects felt silly or funny, because this would predict an ERN effect for the vertical stick position (“no-stick”) as well.

However, the experiments reported up to now did not allow direct access to changes in subject’s affective state, because distinct emotional modulations were induced several times within one subject. Measuring changes in affective state after the experiment were therefore not considered to yield reliable results. This is different in the experiment reported in the next section: Subjects were allocated to either a “negative affect” or a “positive affect” group. Thus, measurements of changes in affective state were possible not only by changes in ERPs, but also by using a mood questionnaire prior and after conduction of the experiment.

It is predicted that subjects show an increased negative ERN and CRN amplitude when receiving negative feedback compared to positive feedback (see section 1.5.4). Feedback was provided based on response times only. Thus, in the next experiment, I expect a speed-accuracy-tradeoff that differs in both groups. The group with negative feedback should show faster reaction times and higher error rates, whereas the positive feedback group should show the opposite pattern. However, as shown in section 4.3.2.2, a higher error rate decreases the ERN amplitude. Thus, the effect caused by increased error rates counteracts the effect predicted by negative feedback. Here I predict that the emotional ERN increase due to negative feedback is strong enough to superimpose the amplitude-decreasing ERN effects due to higher error rates.

4.5. Experiment 2d: Emotions induced by performance feedback

4.5.1.1. Participants

Data were acquired from 25 right-handed women. See section 2.1 for additional information. ERP data were analyzed from 24 subjects (mean age 23.75 years, range 19 to 30 years), one subjects was excluded because she were diagnosed to be epileptic and, therefore, was not free of medication. Subjects were allocated randomly to receive either positive or negative feedback on their reaction times. There were 12 subjects in each feedback group.

4.5.1.2. Stimuli and procedure

A trial consisted of a flanker stimulus, which required either a right- or left hand response. There were 10 blocks with 210 trials each. A feedback screen was presented after every 30 trials. A set of 30 trials will be referred to as sub-block. Thus, there were 7 sub-blocks with feedback screens per block and 70 feedback screens during the entire experiment. Timing of trials and blocks was exactly the same as described in section 4.4.1.2.

Emotional modulation: the only difference to the previous experiment (section 4.4.1.2) was the way how emotional modulation was induced. Subjects were no longer required to hold a chopstick in the mouth. Instead, they received feedback based on the mean reaction time in the last-performed sub-block. Subjects were allocated randomly to receive either only positive or only negative feedback. If the mean RT of the last-performed sub-block N was faster than the mean RT of sub-block N minus 1, subjects in the positive feedback group received positive feedback on the screen, whereas subjects in the negative feedback group received no feedback. If mean RT of the current block was slower than mean RTs in the sub-block N minus 1, subjects in the positive feedback group received no feedback, whereas subjects in the negative feedback group received negative feedback on the screen. There were thee levels of positive and negative feedback, the feedback algorithm is described in Table 15.

Feedback level	**Algorithm**	**Feedback group**	
		Positive	**Negative**
Level 1	RT_N up to 20 ms faster than RT_{N-1}:	“gut”	“no feedback”
Level 2	RT_N up to 40 ms faster than RT_{N-1}:	“sehr gut”	“no feedback”
Level 3	RT_N more than 40 ms faster than RT_{N-1}:	“hervorragend”	“no feedback”
Level 1	RT_N up to 20 ms slower than RT_{N-1}:	“no feedback”	“nicht gut”
Level 2	RT_N up to 40 ms slower than RT_{N-1}:	“no feedback”	“schlecht”
Level 3	RT_N more than 40 ms slower than RT_{N-1}:	“no feedback”	“sehr schlecht”

Table 15: Feedback given for the positive and negative feedback group. RT = mean reaction time for a sub-block; N = last-performed sub-block. German feedback words are translated as: “gut” = “good”; “sehr gut” = “very good”; “hervorragend” = “brilliant”; “nicht gut” = “not good”; “schlecht” = “bad”; “sehr schlecht” = “very bad”.

Feedback words were provided in a sentence; a possible feedback text was “Ihre Reaktionszeit im letzen Durchgang war schlecht” (Your reaction time in the last sub-block was bad”). If no feedback was given, the sentence “weiter mit Mausklick” (press mouse button to continue) was shown. Each feedback screen was terminated by a button press. Thus, subjects could have a break whenever they omitted a button press after each screen.

Flanker stimuli: Flanker stimuli were exactly the same as described in section 4.2.1.2.

Instruction: The instruction was to respond as fast and as correct as possible to the central letter either with the left hand (central H) or with the right hand (central S).

Questionnaire: Changes in “current feeling” (German: “Momentanes Befinden”) were assessed with a questionnaire “Aktuelle Stimmungsskala” (ASTS) directly prior and after the experiment. The ASTS (Dalbert, 1992) is a short and very economic version of the “profile and mood state” scale (McNair, Lorr, & Doppleman, 1971). The ASTS consists of 19 German adjectives; subjects are required to estimate how well those adjective represent their current feelings on a scale ranging from 7 (very strong) to 1 (not at all). The whole questionnaire is provided in Appendix 5. Acknowledging the difficulties of transferring emotion-relevant adjectives into another language, all the labels of the adjectives will be given in German. Translations of the ASTS adjectives are provided in Appendix 6.

4.5.1.3. Data recording and preprocessing

See section 2.4.1 for general recording issues. Eye artifacts were corrected using blind component separation described in section 2.4.2; head artifacts were rejected as described in section 2.4.1.

4.5.1.4. Data analysis

Questionnaire: To analyze data from the ASTS questionnaire, independent t-tests were conducted on each adjective rating on pre-experimental and post-experimental questionnaire with groups defined by obtained feedback (factor FEEDBACK, positive or negative). Since sample size was pretty low for a between-group comparison, p-values were interpreted to indicate differences when being smaller than 0.1. It was expected that groups do not differ in “current feeling” prior to the experiment in ratings for any of the 19 adjectives. After the experiment, it was expected that subjects with negative feedback score higher on scales related to anger and sadness (zornig, unglücklich, traurig, betrübt, verärgert, entmutigt, wütend) and lower on scales related to happiness and well-being (freudig, frohgemut, fröhlich, heiter). Differences between both groups in the post-test were not expected on scales referring to “being tired and exhausted” (abgeschlafft, müde, erschöpft, entkräftet), since the experiment was exhausting independently of the given feedback.

Behavior data: Trials with reaction times lower than 200 ms and higher than 800 ms were excluded from behavioral data analysis.

Post error slowing: Response matching was conducted for the correct responses in response-locked ERP data. Thus, correct responses were equal to erroneous responses in terms of number and reaction time. See section 4.2.1.4 for details on response matching.

Flanker-locked ERPs: To analyze the N2 effect, ERPs were averaged with the flanker stimulus onset being the zero point relative to a 100 ms pre-flanker baseline. Statistical analysis was conducted on a frontal electrode patch consisting of Cz, Fz, FC1 and FC2 in a time window from 200 to 400 ms. Information regarding the number of trials included in each condition is provided in Table 16.

ERROR – GROUP	CONGRUENCY	Mean trial number	SD	Range
Positive feedback group	**congruent**	1115.6	75	921-1214
	incongruent	649.1	73.8	516-758
Negative feedback group	**congruent**	1121	64.2	991-1203
	incongruent	640.1	78.4	480-738

Table 16: The number of trials included to generate the flanker-locked ERP conditions in study 4.5

Response-locked ERPs: Highly similar data analysis settings as described in section 4.2.1.4 were used to analyze response-locked ERPs. Thus, the experiment was divided in two error halves (Factor ERRORHALVES, levels “first half” and “second half), and it was distinguished between correct and incorrect trials (Factor CORRECTNESS, levels correct or erroneous response). Analysis of correct trials was based on a subset of response-matched correct trials; see section 4.2.1.4 for details on response matching for correct trials. Emotional modulation was accessed by the feedback group (Between group factor FEEDBACK, positive vs. negative feedback group). See Table 17 for information regarding the number of trials included in the ERP conditions.

ERROR GROUP	CORRECT-NESS	ERROR HALVES	Mean trial number	SD	Range
Positive feedback group	**correct**	1st	109.7	58.3	45-225
		2nd	108.3	59.3	46-227
	error	1st	107.8	60.0	45-226
		2nd	107.7	59.2	46-228
Negative feedback group	**correct**	1st	127.8	61.0	42-226
		2nd	128.4	60.2	47-226
	error	1st	125.9	60.1	43-218
		2nd	127.8	60.1	45-226

Table 17: The number of trials included to generate the response-locked ERP conditions in study 4.5

Baseline, and electrode patches for the ERN/CRN were the same as described in section 4.2.1.4 ; time windows for ERN/CRN analysis were based on peak latencies and are provided in Table 21.

4.5.2. Results

4.5.2.1. Behavior data

Questionnaire

Prior to conduction of the experiment, the negative and the positive feedback group did not differ in their response to any of the 19 ASTS items (independent sample t-tests for each rated adjective, with FEEDBACK as between group factor, p > .10). This picture changed completely when the questionnaire was conducted after the experiment. The negative feedback group showed higher scores on the scales “zornig”, “unglücklich”, “betrübt”, “verärgert”, “entmutigt” and “wütend”, whereas they showed lower scores on the scales “freudig”, “frohgemut”, “fröhlich” and “heiter” (see Appendix 6 for possible English translations) (independent sample t-tests for each item, with FEEDBACK as between group factor, t- and p-values for each scale are given in Table 18).

Figure 25 depicts differences between pre-experimental and post-experimental questionnaire, based on subtracting the post-experimental ASTS-scores from the pre-experimental ASTS-scores. It is clearly visible that both groups differ on the above-mentioned scales. Scales referring to being exhausted and tired differed between pre- and posttest, but did not differ between groups (rmANOVA with factor PREorPOS (pre- or post-experiment); for the scales “abgeschlafft”, “müde”, “erschöpft”, “entkräftet”, between group factor FEEDBACK, PREorPOS: F (1,22) > 3.58 ; p < .07: FEEDBACK n.s.)

Rated adjective	T	p (2-tailed)
zornig	-4.18	0.00**
abgeschlafft	-0.45	0.66
unglücklich	-1.79	0.09*
traurig	-0.87	0.39
angenehm	0.62	0.54
betrübt	-1.80	0.09*
freudig	3.12	0.01**
hoffnungslos	0.00	1.00
müde	-0.37	0.72
verärgert	-1.79	0.09*
frohgemut	2.14	0.04**
entmutigt	-2.02	0.06*
fröhlich	1.79	0.09*
erschöpft	-0.33	0.74
heiter	2.31	0.03**
verzweifelt	0.60	0.56
wütend	-1.88	0.07*
entkräftet	-0.75	0.46
lustig	0.79	0.44

Table 18: T- and p-values for the post-experimental ASTS questionnaire. The negative feedback group was compared with the positive feedback group on each of the 19 scales. P-values lower than .1 are indicated by a *; p-values lower than .05 are indicated by **.

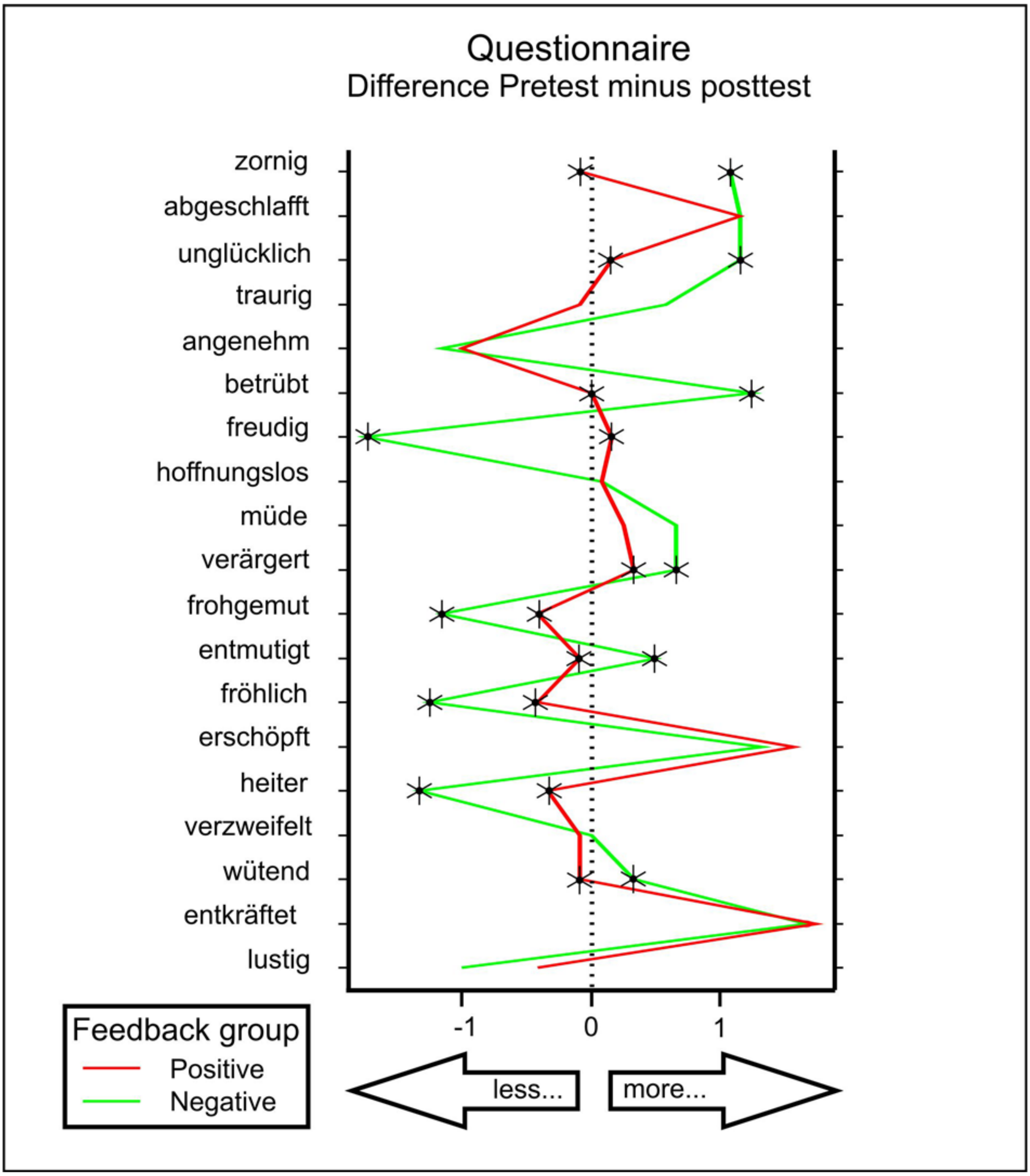


Figure 25: Comparison of the pre- and posttest results of the ASTS questionnaire. Lines are based by subtracting the post-experimental from the pre-experimental ASTS scores. A value close to zero indicates no change between pre- and posttest; negative values indicate that subjects rates loaded higher on the adjective after experiment conduction. Feedback groups are color-coded. Significant differences (p < .01) between groups are indicated by an asterisk.

Reaction times and error rates

Subjects were faster in giving erroneous responses compared to correct responses. This was especially true in the first error half. Subjects responded faster in the second part of the experiment (second error half). Although subjects with negative feedback responded somewhat faster, the response time difference were not confirmed statistically (rmANOVA, Factors CORRECTNESS X ERRORHALVES[14]: F (1,22) = 15.66; p < .001; FEEDBACK n.s.; separate rmANOVAs for both error halves; CORRECTNESS: F (1,22) > 479.7; p < .001, no main effect of FEEDBACK or interactions).

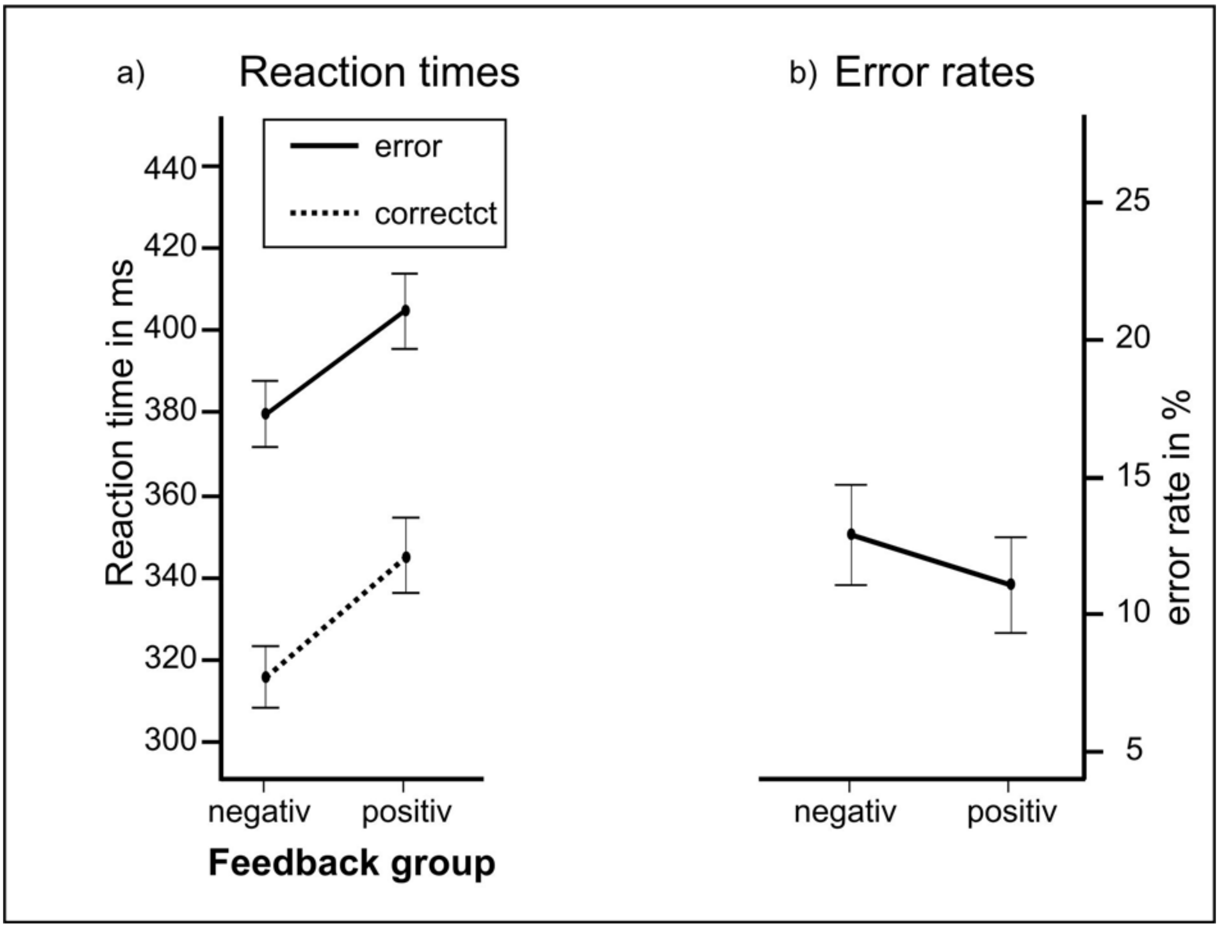


Figure 26: a) Reaction times for correct and erroneous responses separated by feedback group. b) Error rates. Error bars indicate +\- 1 SE.

Error rates did not differ between both feedback conditions (independent t-test on error rates (percentage), between factor FEEDBACK n.s.). Thus,

---

[14] See Appendix 7 c for distribution of errors across the experiment.

behavioral data show that feedback had little impact on behavior data. See Figure 26 for reaction times and error rates.

Congruency effect

Subjects reacted faster to congruent compared to incongruent trials; this effect was seen for booth error halves. The feedback groups did not differ significantly. The speed advantage for congruent flanker trials was seen in both error groups (rmANOVA based on correct responses; CONGRUENCY (congruent vs. incongruent flanker): F (1,22) = 214.07, p < .001; ERRORHALVES: F (1, 22) = 12.02, p < .002; FEEDBACK: F (1,22) = 2.29, n.s.; incorrect trials in the second halve were given faster than correct trials in the first half, indicated by CONGRUENCY x ERRORHALVES interaction, F (1,22) = 7.28, p < .01; no further significant interactions) See Figure 27.

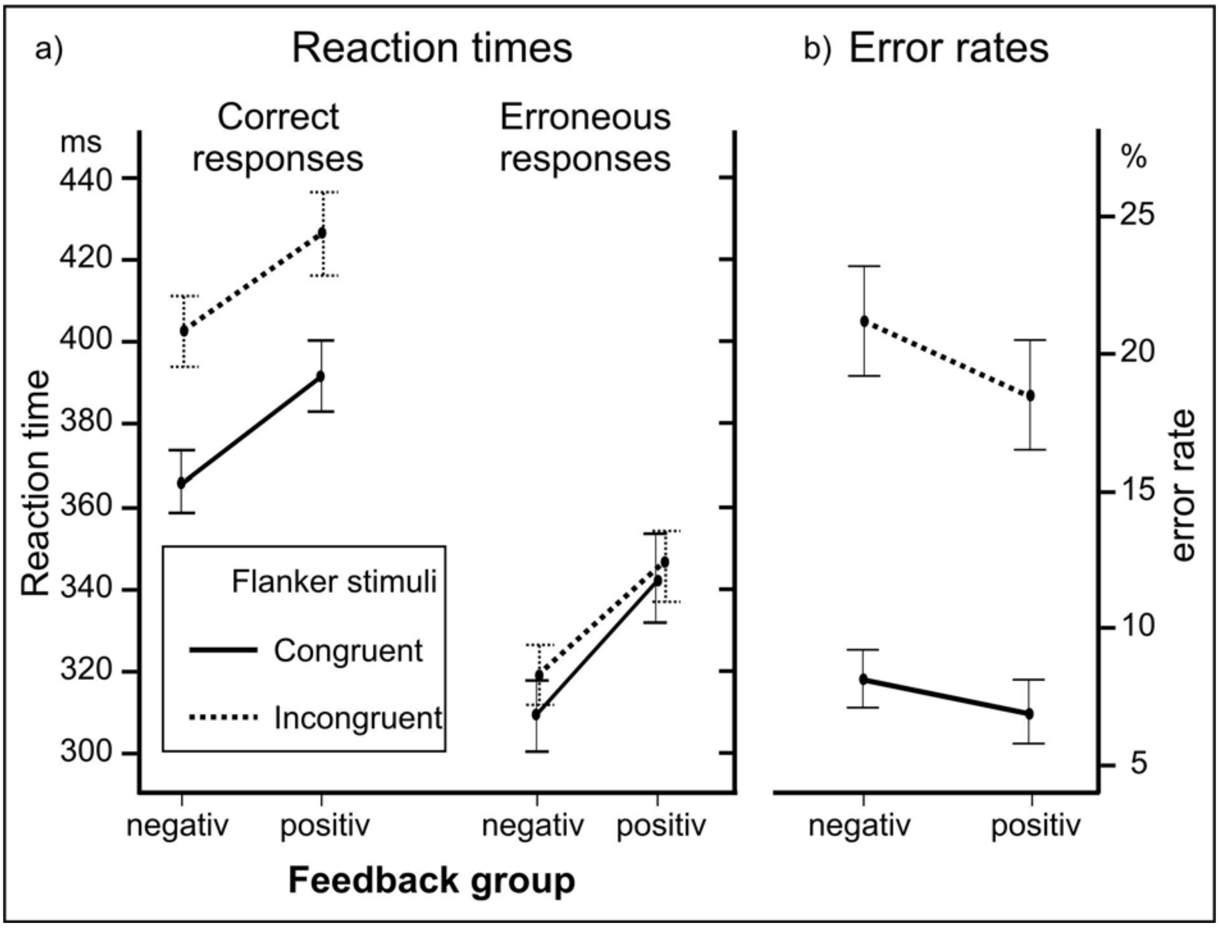


Figure 27: a) Reaction times for congruent and incongruent flankers for both feedback groups, separately for correct and erroneous responses. b) Error rates for congruent and incongruent flankers. Error bars indicate +\- 1 SE.

The same analysis as above was conducted on erroneous responses. As described in the analysis of reaction times above, erroneous responses were given faster than correct responses. Subjects did not show reaction time differences for congruent or incongruent erroneous responses, nor were there RT differences between both error halves or feedback groups (rmANOVA on erroneous responses. Factors CONGRUENCY, ERRORHALVES and FEEDBACK n.s.). See Figure 27.

Subjects committed more errors when responding to incongruent flankers, this effect was consistently shown for both error halves and for both feedback groups. Subjects committed more errors in the second error half. (ANOVA on error rates (percentages); CONGRUENCY: $F(1, 22) = 102.32$; $p < .001$; ERRORHALVES: $F(1, 22) = 4.86$; $p < .038$; no significant effects of FEEDBACK and no significant interactions.) See Figure 27.

Post error slowing

Correct responses were faster when given after a correct trial than given after an erroneous trial. Analysis was based on response-matched correct responses using the same algorithm as described in section 4.3.2.1. This effect was consistently seen in both groups (rmANOVA, Factors POSTRESPONSE (post-correct vs. post-error), FEEDBACKGROUP; POSTRESPONSE: $F(1,22) = 76.42$, $p < .001$; FEEDBACK GROUP and interaction POSTRESPONSE x FEEDBACK GROUP n.s.). See Table 19 for post error slowing data.

	correct responses following correct responses	**correct responses following erroneous responses**
Positive feedback	392 (43)	431 (47)
Negative feedback	371 (40)	407 (53)

Table 19: Reaction times for post-correct and post-error responses in study 4.5; Values are in ms, standard deviations are given in brackets.

Error correction rate

Subjects tended to correct for some of their errors without being instructed to do so (see section 4.1.1). This tendency was found in both feedback groups, groups did not differ (mean error correction rate, relative to error rate, values are in percent, SD is given in brackets: positive: 15.8 (10.8) negative: 15.1 (9.6). independent t-test, between group factor FEEDBACK n.s.).

4.5.2.2. ERP data

Flanker locked ERPs

Visual inspection: As in the experiments reported above, incongruent stimuli elicited an increased negative component, which emerged around 250 ms. Emotional effects indicated by differences between the positive and negative feedback group show two aspects: First, there are differences between positive and negative feedback group emerging around 150 ms without differences between congruent and incongruent flanker trials. Congruency effects emerge around 250 ms with the incongruent stimuli being more negative in both groups (N2). See Figure 28 left panel. However, the N2 effect is larger when subjects receive negative feedback, which is best seen in the difference waves based on subtracting the congruent from the incongruent condition.

Early effect: Tested within a 150 to 250 ms, the visual impression of an feedback group effect prior to an congruency effect did not confirm, neither on the parietal electrode patch nor on the frontal electrode patch nor on electrode Cz (rmANOVA, Factors CONGRUENCY and FEEDBACK; FEEDBACK or FEEDBACK x CONGRUENCY n.s.). Instead, the congruency effect examined in the later time window started to emerge (for example, rmANOVA on frontal patch: CONGRUENCY: F (1,22) = 8.28; p < .009). This effect will be discussed in detail in the next paragraph.

Congruency effect: Incongruent stimuli elicited a more negative ERP than congruent stimuli, this was especially true for the group receiving negative feedback (rmANOVA, Factors CONGRUENCY and FEEDBACK; significant interaction CONGRUENCY X FEEDBACK, F (1,22) = 6.09; p < .022, separate rmANOVAs for both groups: Positive Feedback group, CONGRUENCY:F (1,11) = 37.51; p < .001, Negative Feedback; CONGRUENCY: F (1,11) = 35.07; p < .001; interaction indicated that the congruency effect was larger when subjects received negative feedback). See Figure 28 and Table 20.

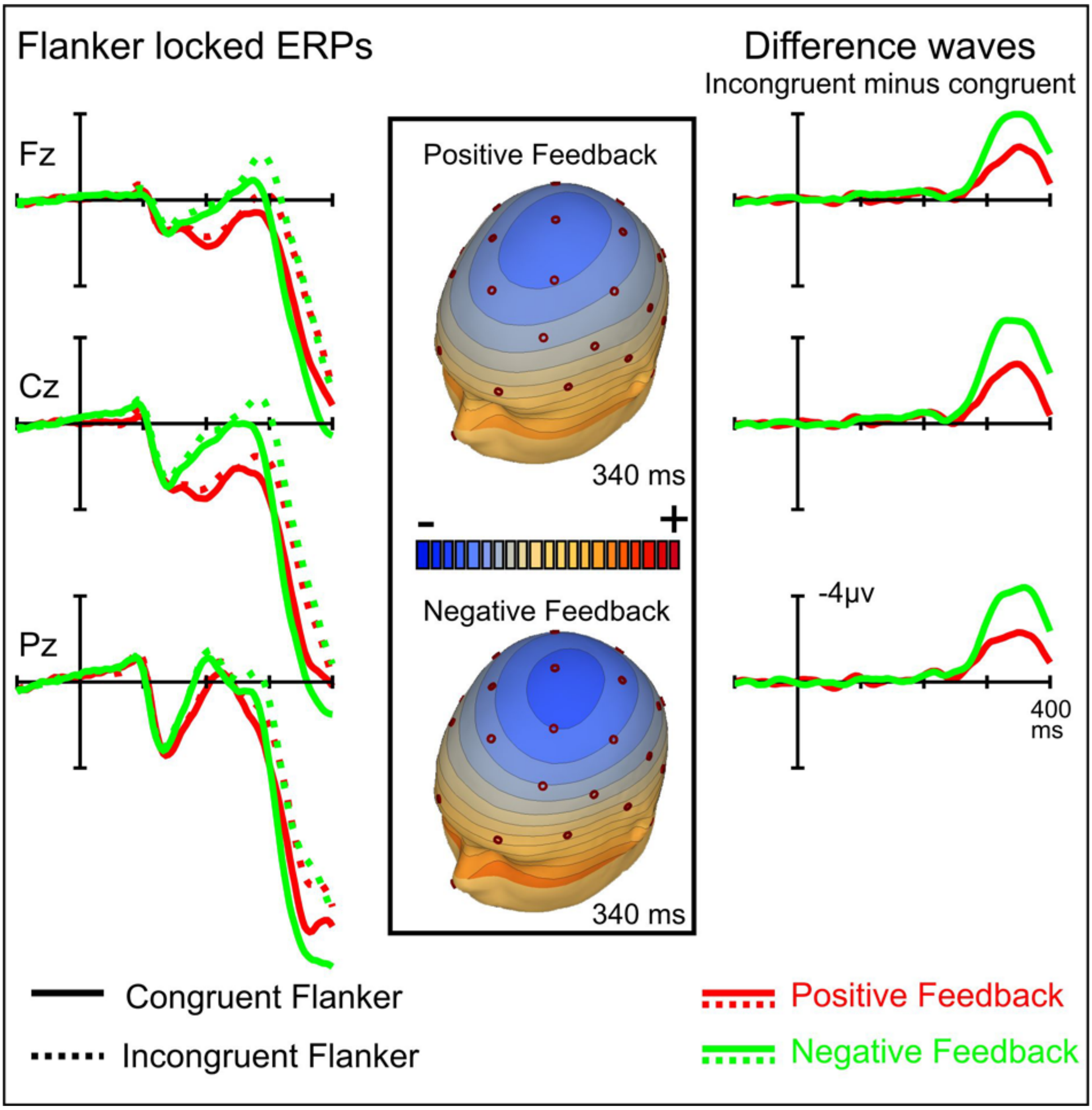


Figure 28: ERPs locked to flanker stimuli. Left panel: N2-effect for both feedback groups. Feedback group is color-coded; flanker congruency is coded by line style. Middle: scalp distribution at 340 ms based on difference waves incongruent minus congruent for both feedback groups. Right: Difference waves based on incongruent minus congruent flanker stimuli, separately for both feedback groups.

Feedback group	Flanker congruency	Mean amplitude in µV
Positive	**congruent**	5.6
	incongruent	4.3
Negative	**congruent**	5.7
	incongruent	3.3

Table 20: mean amplitude for ERPs following congruent and incongruent flanker stimuli on a parietal patch of electrodes.

Response-locked ERPs - the ERN/CRN

Visual inspection: As in previous experiments, a negative-going ERP deflection (ERN) was observed after erroneous responses, which was followed by a positive component (P_e). There was also a less negative component (CRN) following response-matched correct responses. As in the studies reported above, the ERN peaked somewhat earlier than the CRN. The most obvious difference between the negative and positive feedback group was that there are greater absolute differences between the ERN and the CRN display when negative feedback was given. Greater absolute differences between ERPs for correct and erroneous responses were not seen within the P_e time range. In other words, relative to the CRN, the ERN is much stronger activated in the negative feedback group. See Figure 29; differences between erroneous and correct responses (error minus correct) are displayed in the right panel.

Peak latency analysis: Erroneous responses were given faster than correct responses. This was independent of feedback given and seen in both error halves (rmANOVA, Factors ERRORHALVE, CORRECT, Between-group factor FEEDBACK; CORRECTNESS: $F(1,22) = 8.27$; $p < .009$, no further significant main effects or interactions). Thus, for subsequent mean analysis, time windows were only distinguished between correct and erroneous responses, but not between the feedback groups or the error halves. The mean peak latencies are given in Table 21.

CORRECTNESS	mean peak latency	Time window for peak amplitude analysis
Correct	76	36 to 116
Error	49	10 to 90

Table 21: mean peak latencies and time windows for ERN/CRN peak amplitude analysis for response-locked ERPs in experiment 4.5. Values are in ms.

Absolute differences between correct and erroneous response ERPs: Visual inspection indicated that differences between the ERN and the CRN are more pronounced when subjects received negative feedback. To test for this, ERPs for correct responses were subtracted from ERPs for erroneous responses. Statistical analysis confirmed visual inspection within the ERN/CRN time window (rmANOVA on difference waves erroneous minus correct responses (response matched); peak amplitude within 0 to 150 ms post-response; factors ERRORHALVE, between factor FEEDBACK, FEEDBACK: F (1,22) = 7.01; p < .015; no further main effects or interactions).

P_e: The difference between erroneous and correct responses was not replicated in the P_e time window (rmANOVA, mean amplitude 200 to 400 ms, Factors FEEDBACK and ERRORHALVES, no significant effects).

Peak amplitude analysis with response-matched data: The pattern described above with greater differences between ERN and CRN in the negative feedback group was reflected in an FEEDBACK x CORRECTNESS interaction (rmANOVA, FEEDBACK x CORRECTNESS: F (1,22) = 6.62; p < .017). Differences due to FEEDBACK and CORRECTNESS did not differ across both error halves (interaction ERRORHALVES x CORRECT x FEEDBACK n.s.). Separate analysis for the ERN and the CRN revealed group differences for the ERN, but not for the CRN (independent sample t-tests, groups defined by FEEDBACK; ERN: t (22) = 2.11; p < .046; CRN: n.s.). As shown in Figure 29; the CRN is somewhat more posterior distributed than the ERN. However, there were also no group differences in CRN amplitude when tested on a parietal electrode patch (Cz, Pz, CP1, CP2).

One could argue that failure to find group differences for the CRN might be caused by response-matching, since the variance in mean amplitude might be higher in a subset of correct trials compared to all correct trials. To test for this, the CRN for not response matched data was examined as well, but there were still no group differences (independent sample t-tests, groups defined by FEEDBACK; ERN: t (22) = 2.11; p < .046; CRN: n.s.). See Figure 29 c.

Response-locked ERPs - the P_e

To clearly distinguish emotional modulations already picked up in the ERN/CRN domain from “pure” P_e effects, the same procedure as described in section 4.3.2.2 was conducted. Thus, baselines were set to time windows listed in Table 21. This conservative method confirmed differences between correct and erroneous responses. Both feedback groups differed in ERPs following errors, but not in ERPs following correct responses (t-tests on mean amplitudes; between group factor FEEDBACK, error responses: T = 2.46; p < .022: correct responses: t = .15; n.s.).

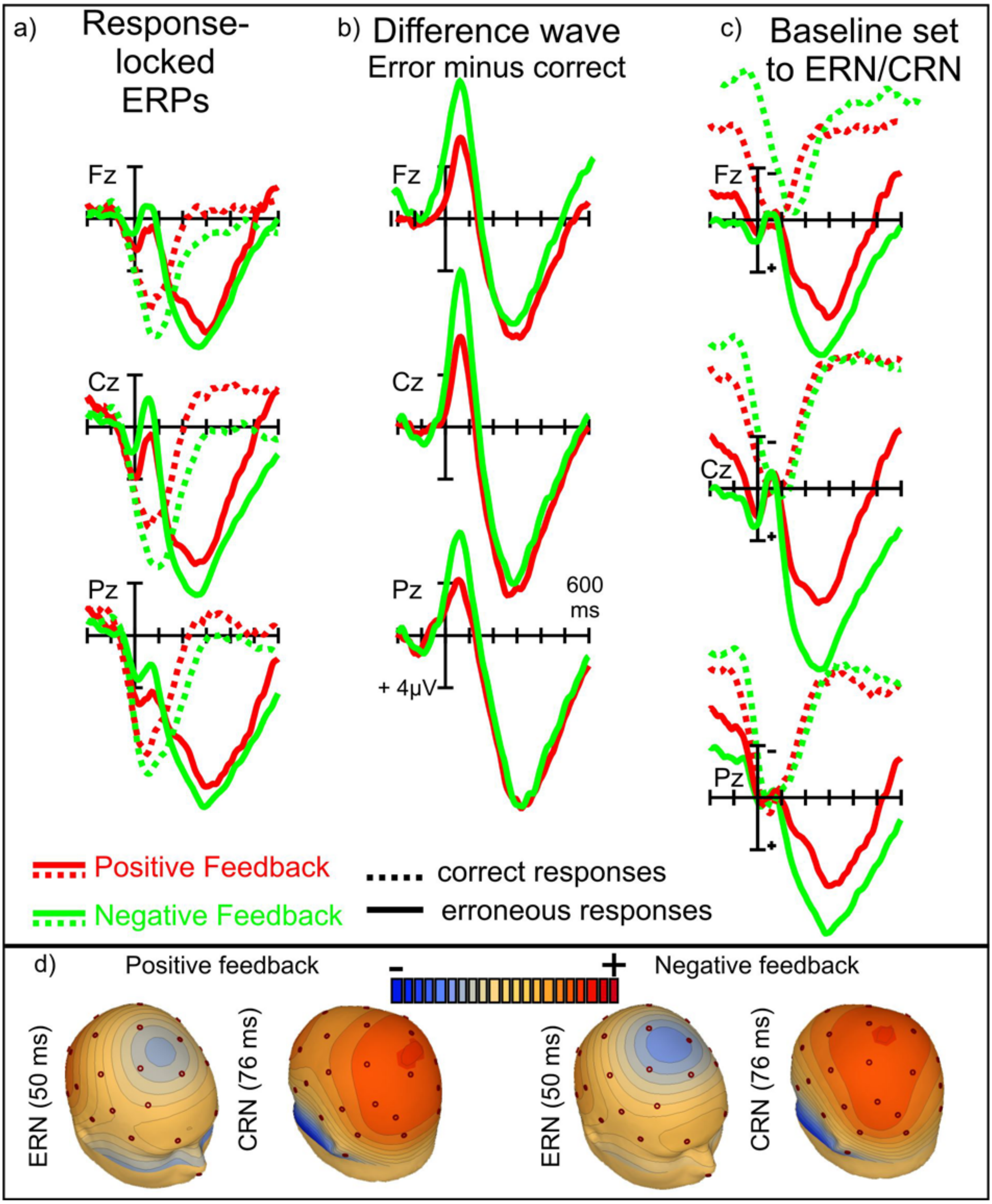


Figure 29: response-locked ERP data for both feedback groups, experiment 4.5. a) Correct (dotted lines) and erroneous responses (solid lines). Difference waves indicate larger absolute differences between the ERN and the CRN when subjects received negative feedback. c) Analysis of the Pe. To adjust for differences emerged in the ERN/CRN time window, the baseline was set to the ERN/CRN time window prior to statistical analysis of the Pe. Differences between both groups are only found for erroneous responses. d) Scalp distribution for the ERN and the CRNfor both groups.

4.5.3. Summary and discussion

Summary: The questionnaire clearly indicates that the paradigm was feasible to induce negative feelings. In contrast, the questionnaire did not indicate changes in affective state when subjects received positive feedback. Thus, the results are interpreted that changes in negative affect were induced, whereas there were no changes in positive affect.

Reaction times display the usual speed advantage for erroneous responses and for congruent flankers observed in the previous experiments in section 4. There was no clear shift from being faster for the cost of committing fewer errors when subjects received negative feedback. The congruency effect, post-error slowing and error correction rate were also not affected by feedback. Feedback had a large impact on all examined ERP components: The N2 was more pronounced when subjects received negative feedback. In addition, there was an enlarged absolute difference between the ERN and the CRN for negative feedback. This effect was mainly caused by the ERN; group differences within the CRN were not confirmed statistically. Later in time, the P_e was more positive for erroneous responses in the negative feedback group. This group difference was not found for correct responses.

Discussion: The discussion in this section refers only to findings exclusively related to experiment 4.5. Issues regarding performance monitoring are discussed in section 4.6.

No performance differences between both feedback groups were found, which is in line with previous research reporting no performance differences between subjects high and low in negative affect (Hajcak, McDonald, & Simons, 2004) and between high-and low-motivating trials (Hajcak, Moser, Yeung, & Simons, 2005).

Feedback was based on subject’s reaction time only. Alternatively, it would be possible to base feedback on the accuracy rate. Reaction time was chosen because previous research (Falkenstein, Hoormann, Christ, & Hohnsbein, 2000; Gehring, Goss, Coles, Meyer, & Donchin, 1993) indicates that emphasizing speed over accuracy leads to an decreased (less negative) ERN amplitude than emphasizing accuracy over speed. There is a slightly tendency in behavioral data (not significant) that subjects were somewhat faster and less accurate when negative feedback was given. Thus, speed was emphasizes over accuracy, which should diminish the ERN. This effect works against the prediction that negative affect enlarges the ERN. However, the increased ERN described here provides a strong point that the effect is not due to speed-accuracy-issues, but caused by the intended emotional modulation.

Hajcak and colleagues (Hajcak, Moser, Yeung, & Simons, 2005) conducted a flanker task in which motivational factors were manipulated by indicating that the next trial was either high or low in value. Subjects were told that performance would result in monetary gain after the experiment; performing especially good on high value trials increases monetary gain. They found no motivational differences on the behavioral level. As in the present study, they showed that the ERN, but not the CRN was more negative for high value compared to low value trials. However, as introduced in section 1.2.4, there is no clear line between emotion and motivation; a motivational state is an result of an emotion. Keeping this in mind, high value trials might be accompanied by an increased arousal level, because there is the danger of loosing. Thus, the increased ERN found by Hajcak et al. (2005) can also be indicative for ERN increase following negative emotions or the expectation of negative emotions. On the other hand, one could argue that a high value trial indicates the chance of a reward, and is therefore related to positive affect. However, which of both alternatives is feasible might depend on many things, among them personal traits and attitudes. Those conceptual difficulties can be avoided when not the motivational state, but the emotional state of the subject is manipulated experimentally, as done in the experiment presented here.

One could argue that the increased N2 and the increased ERN/CRN difference in the negative affect group merely indicate a general increase for all ERP components. This could be caused by increased alertness rather than by affective modulation. However, I do not regard this alternative as feasible, because flanker-locked ERPs between both groups do not differ prior to 150 ms (statistical examination found no significant group differences prior to 250 ms). In addition, group differences within the P_e time window have only been found following erroneous, but not following correct responses; a general increase in overall activity would suggest differences following correct responses as well.

4.6. Discussion – Part 2

Summary: Four experiments were presented in the second part of the thesis to examine emotional influences under positive and negative (experiment 4.2 and 4.3), positive (experiment 4.4) or negative emotions (experiment 4.5). While behavioral measures were not indicative of changes in emotional states, the ERN was enlarged following negative emotions (experiment 4.3 and 4.5) and reduced following positive emotions (experiment 4.4). The N2 and the P_e were enlarged following relatively large negative emotions only (experiment 4.4). The next section discusses the emotion-related findings in detail and integrates them into recent theories of affect and performance monitoring.

4.6.1. Behavioral data

Beyond the classical effects typically seen for flanker tasks (see "Summary and Perspectives" for each experiment in section 4), there were no effects due to affective manipulation. This is true for the congruency effect, for error rates, reaction times, post-error slowing as well as for error correction rate. At a first glance, this might appear somewhat surprising, since the experiments were inspired by Dreisbach's and Goschke's (2004) research (see section 4.1.4), which showed behavioral effects: Pleasant IAPS pictures presented directly prior to a trial eliminate switching costs in a task switching paradigm (Dreisbach & Goschke, 2004). On the other hand, affect-related changes in the ERN without changes on the behavior level were repeatedly described (Gehring, Himle, & Nisenson, 2000; Hajcak, McDonald, & Simons, 2003a, 2004; Johannes, Wieringa, Nager, Dengler, & Münte, 2001; Riba, Rodriguez-Fornells, Morte, Münte, & Barbanoj, 2005; Simon-Thomas & Knight, 2005). Thus, it seems to be the rule rather than the exception to find no emotional effects in typical ERN experiments. The experiments presented in section 4 were designed to produce error rates high enough to examine the ERN. It is conceivable that those flanker tasks provide an imperfect measure for small emotional effects. However, an experimental task more similar to Dreisbach's and Goschke's setting (2004) would produce a relatively low error rate (4.15 % in Dreisbach and Goschke, 2004). In addition, it would complicate integration of ERN results into previous findings. Thus, future research should develop paradigms feasible to induce emotion-caused effect on both, behavioral and ERP level. Another issue which might facilitate emotional effects on behavioral data is that Dreisbach and Goschke informed their subjects that they examine how pictures influence task performance. To avoid withdrawal of attentional resources from the demanding flanker task, subjects in the experiments presented in section 4 were not informed about the intended emotional modulation. In addition, presentation of pictures prior to flanker stimuli was shorter compared to Dreisbach and Goschke (2004) (80 ms vs. 250 ms), which might result in weakened affective responses. Those points taken together might explain why emotional modulations did not affect behavioral data.

4.6.2. ERP data

The following section discusses ERP effects related to emotional manipulation only; ERP effects specific to emotional stimuli were discussed separately for each experiment in the “summary and perspective” parts of section 4.

4.6.2.1. The flanker-locked N2

A more negative component for congruent compared to incongruent flanker stimuli was seen around 300 ms in all four experiments. This N2 effect replicates earlier findings (Falkenstein, Hoormann, & Hohnsbein, 1999; Kopp, Rist, & Mattler, 1996; Van 't Ent, 2002). Since the present thesis was not primarily concerned about whether the ERN and the N2 reflect the same mechanisms, a comparison between both components was conducted by visual inspection only. The N2 appears to be somewhat more posterior than the ERN, which is in line with some previous research (Falkenstein, Hoormann, & Hohnsbein, 1999). However, a stronger point towards the same or different underlying mechanisms can be made if both components can be independently manipulated. Falkenstein and colleagues (1999) argued that the N2 amplitude is sensitive to overall error rate (decreased in subjects with high error rate), whereas the ERN is not. This is not supported by the present data. Furthermore, here I present the reversed pattern: Experiment 4.3 distinguishes between subjects with a low and a high error rate and finds no group effect on the N2, but a less negative ERN for subjects with a high error rate. However, Falkenstein and colleagues (1999) conducted a Go/NoGo-task, which required their subjects to withhold a response. Those differences in task performance might contribute to the conflicting results. In addition, different reference methods were used (linked mastoid by Falkenstein, nose reference in all experiments of section 4). Similar to the present results, there are studies reporting decreased ERN when subjects committed more errors (Gehring, Goss, Coles, Meyer, & Donchin, 1993; Hajcak, McDonald, & Simons, 2003b).

A strong point towards different processes underlying the N2 and the ERN can be made if both components are affected differentially by emotional modulation. This was clearly the case in experiment 4.3, 4.4, and 4.5. While there was no N2 effect but an ERN/CRN when emotions were induced by IAPS pictures or by facial feedback, the N2 and the ERN/CRN-amplitudes were sensitive to the kind of feedback subjects received..

In experiment 4.5, error rates were slightly (but not significantly) lower when subjects received positive feedback. A prediction based solely on error rates would assume a larger N2 for this group. However, the pattern observed in study 4.5 is exactly the other way round; N2 amplitude was increased for the negative feedback group. This supports my argumentation that not absolute error rate, but emotional modulation is responsible for changes seen in the N2. Apparently, those affective changes have to be relatively large, so that they are only seen when emotional experience includes personal involvement. As indicated by the questionnaire, this was the case in experiment 4.5.

The N2 has been shown to be reduced in subjects recruited from a group of impulsive-violent offenders (Chen, Tien, Juan, Tzeng, & Hung, 2005) relative to matched non-violent offenders. Results were interpreted to reflect impairments in impulse inhibition. Following this line of argumentation, an increased N2 as seen in the negative feedback group in experiment 4.5 indicate increased impulse inhibition. It is conceivable that subjects under negative affect do inhibit response alternatives in favor to more established response alternatives, as suggested by previous research (Dreisbach & Goschke, 2004; Wager, Phan, Liberzon, & Taylor, 2003) and in section 4.1.3.1. Thus, the present thesis shows that the N2 might serve as an indicator of emotional engagement. Apparently, the negative emotion has to be relatively strong. Very mild negative emotions as induced by negative IAPS pictures (experiment 4.4) or possibly induced by low dosage of Yohimbine (Riba, Rodriguez-Fornells, Morte, Münte, & Barbanoj, 2005) are not powerful enough to manipulate the N2.

4.6.2.2. The response-locked ERN/CRN

A clear ERN/CRN component was seen in all four studies. The ERN was most pronounced over frontocentral areas, whereas the CRN reaches its peak somewhat more posteriorly. It remains unclear why the ERN and the CRN do not show the same distribution, as suggested by other research (Hajcak, McDonald, & Simons, 2004; Simon-Thomas & Knight, 2005). Earlier research (Falkenstein, 2004) argued that distribution differences might be caused by different reference methods (see section 4.1.2.1). However, the fact that the CRN was found to be more posteriorly across all four studies suggests that the finding is robust across the chosen flanker task and recording setting. There is also some evidence that the ERN and the CRN do not describe exactly the same mechanisms: While the ERN was susceptible to motivational factors, the CRN was not (Hajcak, Moser, Yeung, & Simons, 2005). However; the present experiments were not designed to finally decide on this topic, further research should address this issue.

There is much literature showing that the ERN is generated in the anterior cingulate cortex (see Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004, for meta analysis). As mentioned above (section 4.1), this region of the brain can be functionally separated into dorsal cognitive and a rostral affective subdivision (Bush, Luu, & Posner, 2000). In addition, the ACC shows a specialization on the cellular level: Only in humans and great apes, the ACC contains a special class of spindle-like neurons. Relative to ordinary pyramid cells, they are up to four times larger in volume and differ in dendrites properties. Those spindle neurons show a high grade of long-distance projections (Allman, Hakeem, Erwin, Nimchinsky, & Hof, 2001). Equipped with this specialization, the ACC might serve as a relay station between evolutionary old and new developed brain structures or, in other words, as “an interface between emotion and cognition” (Allman, Hakeem, Erwin, Nimchinsky, & Hof, 2001, p. 107). In line with this, the ACC has been shown to be involved in emotional self-control, focused problem solving, error recognition and adaptive responses to changing conditions; shortly in all basic aspects of intelligent behavior.

The ERN was stronger under negative affect conditions, which replicates earlier results based on between-group-designs (Hajcak, McDonald, & Simons, 2003a, 2004; Hajcak & Simons, 2002; Riba, Rodriguez-Fornells, Morte, Münte, & Barbanoj, 2005). Here, I show that an increased ERN can also be observed in the same subjects within the same sessions; even on a trial-by-trial-basis (experiment 4.3).Thus, increased ERN is not inevitably an indication for maladaptive functions. Instead, the ERN reflects flexible adjustment to environmental requirements.

To my knowledge, the present research (experiment 4.4) is the first reporting ERN decrease due to positive affect. Lack of ERN research on positive emotions might be due to several reasons: First, there are many affective disorders related to negative affect, but there are only few disorders which primary symptom are increased positive affect. Thus, from the clinical standpoint, there is less need to examine interactions of positive affect and performance monitoring. In addition, there is emerging evidence that negative affects are faster and more reliably elicited (see section 4.3.3). On the other hand, it has been shown that reduction of negative emotions (providing Oxazepam, a drug with anxiolytic properties; see section 4.1.3), diminishes the ERN amplitude (Johannes, Wieringa, Nager, Dengler, & Münte, 2001) and low dosage of alcohol, which is known to induce some kind of pleasant feeling, also diminishes the ERN amplitude (Ridderinkhof et al., 2002). Thus, there is the need to integrate both, positive and negative affect into current models of performance monitoring.

4.6.2.3. The response-locked P_e

As pointed out by Hajcak, McDonald, and Simons (2004), there is still a lack of formal examination on affective influences on the P_e. Some evidence suggest that the P_e is not susceptible to affective variables (Hajcak, McDonald, & Simons, 2003a; Luu, Collins, & Tucker, 2000) or that the P_e is somewhat smaller in highly anxious subjects (Gehring, Himle, & Nisenson, 2000; Hajcak & Simons, 2002).

An explicit examination of the P_e was provided by Hajcak, McDonald, and Simons (2004): They described the P_e to be smaller (less positive) in subjects scoring high on a negative affect scale. More negative P_e amplitudes following negative affect induction were not reported in any of the present experiments. However, visual inspection of the left panel in Figure 21 indicates a comparable pattern: The ERN as well as the P_e were more negative following negative affect induction. In the present study, this effect was not significant, because a very conservative approach was employed. In contrast to Hajcak et al. (2004), P_e analysis was conducted with baseline set to the ERN time window, which enables a distinction between emotional effects on the ERN and P_e. Thus, whereas the P_e effect reported by Hajcak et al. (2004) might still include some activity related to the ERN, I cannot be entirely sure that the baseline correction was too conservative and made an existing effect disappear. Future research is necessary to finally decide on this issue.

Analysis of the P_e for experiment 4.5 was based on the same conservative baseline-adjustment procedure. However, the P_e amplitude was more positive, which contradicts Hajcak et al.’s (2004) finding of a decreased (less positive) P_e. Hajcak and colleagues concluded “that subjects high in NA may find their errors less salient or be less aware of their errors”(p. 196). I regard this explanation as counterintuitive and not feasible, since it is well known that subjects high in negative affect (for example subjects with anxiety disorder and/or depression) tend to overestimate the significance of their errors (Wenzlaff & Grozier, 1988) and are poor in suppressing failure-related thoughts (Conway, Howell, & Giannopoulos, 1991). If the P_e is related to conscious error processing (Falkenstein, 2004) (see section 4.1.2.3), this component should be enlarged in subjects high on negative affect, and, accordingly, in subjects with induced negative affect. This is exactly the case in experiment 4.5. It remains unclear how those differences in P_e amplitude between studies might be reconciled, but the results presented here fit better into theoretical frameworks of affective disorders. A possible explanation could be that the brain adapts in subjects which are always high on negative affect. Thus, a clear P_e amplitude increase is only seen in subjects who are not permanently in a negative affective state. Interestingly, as the results presented here, earlier research by Hajcak and colleagues (Hajcak, McDonald, & Simons, 2003a) showed more positive P_e

amplitudes for subjects classified as phobic or worried relative to matched controls. However, they restricted their statistical analysis to the ERN.

4.6.2.4. Integrating affect and reinforcement learning

Previous research pointed out that there is the need to integrate affective and motivational issues into existing theories of performance monitoring (Hajcak, Moser, Yeung, & Simons, 2005). This is done in the next section. I propose that positive affect modulates performance monitoring by changing dopamine level in mesencephalic structures, whereas negative affect acts in the opposite direction.

Previous research indicated that positive affect increases activity in mesencephalic dopaminergic structures (Ashby, Isen, & Turken, 1999). According to the reinforcement learning hypothesis, a dopamine increase causes increased inhibition of the anterior cingulate cortex (Holroyd & Coles, 2002), which is measurable by a decrease of ERN amplitude. Although the present data cannot provide information regarding the exact structures involved, the less negative ERN following positive affect in experiment 4.4 corresponds with Ashby et al’s (Ashby, Isen, & Turken, 1999) as well as with Holroyd and Coles’ (2002) proposals. Here, I suggest that positive affect increases activity of dopaminergic mesencephalic structures. This increase accumulates with signals receiving from the basal ganglia; generated by evaluation of the ongoing behavior. Thus, there are more inhibiting signals forwarded to the ACC, which reduces monitoring on the given task. Importantly, the reinforcement learning theory makes only prediction about the ERN (Holroyd & Yeung, 2003), specific predictions regarding the N2 and the Pe cannot be derived.

There is some reason to assume that negative affect can be described as the other end of a positive-negative continuum(Russell & Carroll, 1999). Congruent with this, it has been argued that happiness and sadness do activate the same brain circuits (Murphy, Nimmo-Smith, & Lawrence, 2003) (see section 1.4.3). Thus, when positive affect is associated with increased dopamine level in midbrain and frontal brain areas, negative affect could be associated with decreases in dopamine level. This view receives some support from patients suffering from depression, which has increased negative affect as a central defining characteristic. Depression has been associated with a broad variety of changes in brain metabolism, among them decreased activation in left, right and bilateral prefrontal areas, in cortical- limbic and thalamocortical connections and an increased amygdala activation (see Davidson, Abercrombie, Nitschke, & Putnam, 1999, for overview). There is also burgeoning evidence of ACC involvement in depression: It was shown that patients who responded to treatment showed increased activity in the emotional rostral ACC region compared to control subjects, whereas nonresponders showed less ACC activation (Mayberg et al., 1997; Wu et al., 1999). Other researchers found that there is an increase in dopamine D2 receptor binding in the ACC and the striatum during treatment of major depression in treatment responders, but not in nonresponders (Larisch et al., 1997). Thus, here I conclude that negative affect changes ERN amplitude towards greater negativity, probably by changes in dopaminergic level. However, I do not propose that exactly the same circuits as claimed for positive effects are involved, because Ashby et al. (Ashby, Isen, & Turken, 1999) clearly stated that the theory of positive affect is not feasible to explain mechanisms in negative affect. In line with this, recent meta-analysis (Phan, Wager, Taylor, & Liberzon, 2002; Wager, Phan, Liberzon, & Taylor, 2003) and Wager et al. (Wager, Phan, Liberzon, & Taylor, 2003) linked only positive affect to the basal ganglia, which, as mentioned above, play a critical role in evaluation of behavior outcomes (Holroyd & Coles, 2002) and reward processing (Hamann & Mao, 2002).

As mentioned above, the present flanker tasks produced reliable effects on performance monitoring processes, but were not sensitive to changes in cognitive flexibility, indicated by facilitated orientation towards new requirements (Dreisbach & Goschke, 2004). Future research should focus on developing paradigms that demonstrate behavioral and neuropsychological effects within one task. In addition, only one experiment demonstrated that positive affect modulates performance monitoring. This could be due to the reason that it is easier to induce negative relative to positive emotions. Nevertheless, more research is needed to examine the effects on positive affect on performance monitoring. Unlike most previous research, the present thesis distinguished between perceiving emotional stimuli and experiencing emotions due to personal involvement (Davidson & Irwin, 1999; Reisberg & Hertel, 2004). This has been shown to be an important issue, which should be considered in future research. Since it has been shown that man and women act differently upon emotional stimuli (see section 3.2.3), subsequent research should also include male subjects and provide a direct comparison between genders.

5. Conclusion

Using memory encoding and performance monitoring as examples for cognitive functions, the present dissertation demonstrates that cognition and emotions are highly interactive. Positive background emotions facilitated recall performance (3.2) and decreases performance monitoring (experiment 4.4). This provides further evidence that positive emotions tune the cognitive system to act less focused on task requirements. This, in general, might indicate a switch towards increased flexibility and less restrictive and controlled behavior. In contrast, negative affect decreases cognitive flexibility, which is indicated by increased focus to central, task-relevant information (no increased memory performance by negative background information in experiment 3.2 and 3.3 and increased ERN when there is an error in task performance, experiments 4.3 and 4.5).

The present thesis supports the idea that examination of cognition without considering emotional aspects is incomplete. Thus, the distinction between cognition and emotions should be considered as historically developed; new neuropsychological models should no longer regard them as brain functions that can be examined independently.

There are some limitations which should be kept in mind when integrating the present results into the large body of neuropsychological findings. First of all, there is the need of replication, especially in the case of positive emotions. This is because positive emotions are harder to induce experimentally and, probably not independent from the first point, there is relatively few research on positive emotions. Second, the present thesis derived their findings mainly from ERPs; future research should feel challenged to re-examine the current results using a) methods with better spatial resolution, b) paradigms which are able to show effects also on the behavior level, c) employing subjects of both genders.

6. Acknowledgement

At first, I would like to thank PD Dr. Jascha Rüsseler and Prof. Dr. Thomas F. Münte for enabling me to conduct those experiments and supporting me on all aspects of the dissertation process. In addition, I would like to thank Dr. Marcus Heldmann, Jürn Möller and Dr. Arie van der Lugt for supporting me on methodological, technical and programming issues. I also appreciate the support I gained from our student assistants Nadine Strien and Peggy Tausche for assisting me during data acquisition and from Jan-Ole Schumann who supported me in data preprocessing. Special thanks also to Dr. Josep Pallares, who programmed the SOBI-algorithm used for artifact correction, and to Gregor Szycik for all those long discussions (and all the fun we had…) while working on this thesis. I would like to thank Dr. Julia Festman for proof reading, Esther Kluba for providing the photos in Figure 22 and to Uwe Schröder for designing the book cover. Last but not least, I would like to thank my family and my friends for all the support I gained.

7. References

Adolphs, R., Tranel, D., & Buchanan, T. W. (2005). Amygdala damage impairs emotional memory for gist but not details of complex stimuli. *Nature Neuroscience, 8*(4), 512-518.

Adolphs, R., Tranel, D., Damasio, H., & Damasio, A. (1994). Impaired recognition of emotion in facial expressions following bilateral damage to the human amygdala. *Nature, 372*(6507), 669-672.

Adolphs, R., Tranel, D., Hamann, S., Young, A. W., Calder, A. J., Phelps, E. A., et al. (1999). Recognition of facial emotion in nine individuals with bilateral amygdala damage. *Neuropsychologia, 37*(10), 1111-1117.

Aho, A. V., Kernighan, B. W., & Weinberger, P. J. (1988). *The AWK programming language*. Reading, Mass.: Addison-Wesley Pub. Co.

Allman, J. M., Hakeem, A., Erwin, J. M., Nimchinsky, E., & Hof, P. (2001). The anterior cingulate cortex: The evolution of an interface between emotion and cognition. *Annals of the New York Academy of Sciences, 935*, 107-117.

Amrhein, C., Muhlberger, A., Pauli, P., & Wiedemann, G. (2004). Modulation of event-related brain potentials during affective picture processing: a complement to startle reflex and skin conductance response? *International Journal of Psychophysiology, 54*(3), 231-240.

Anders, S., Lotze, M., Erb, M., Grodd, W., & Birbaumer, N. (2004). Brain activity underlying emotional valence and arousal: a response-related fMRI study. *Human Brain Mapping, 23*(4), 200-209.

Ashby, F. G., Isen, A. M., & Turken, A. U. (1999). A neuropsychological theory of positive affect and its influence on cognition. *Psychological Review, 106*(3), 529-550.

Averill, J. R. (1994). In teh eyes of the beholder. In P. Ekman & R. J. Davidson (Eds.), *The nature of emotion: Fundamental questions* (pp. 15–19). Oxford: Oxford University Press.

Baayen, R. H., Piepenbrock, R., & Gulikers, L. (1995). The CELEX Lexical Database (Release 2) [CD-ROM]. Philadelphia: PA: Linguistic Data Consortium, University of Pennsylvania [Distributor].

Barrett, L. F., & Wager, T. D. (2006). The Structure of Emotion: Evidence From Neuroimaging Studies. *Current Directions in Psychological Science, 15*(2), 79-85.

Beedie, C. J., Terry, P. C., & Lane, A. M. (2005). Distinguishing mood from emotion. *Cognition and Emotion, 19*, 847–878.

Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience, 8*(6), 551-565.

Bentin, S., & Deouell, L. Y. (2000). Structural encoding and identification in face processing: ERP evidence for separate mechanisms. *Cognitive Neuropsychology, 17*(1-3), 35-54.

Berntsen, D. (2002). Tunnel memories for autobiographical events: Central details are remembered more frequently from shocking than from happy experiences. *Memory and Cognition, 30*(7), 1010-1020.

Blair, R. J., & Cipolotti, L. (2000). Impaired social response reversal. A case of 'acquired sociopathy'. *Brain, 123 (Pt 6)*, 1122-1141.

Bradley, M. M., Greenwald, M. K., Petry, M. C., & Lang, P. J. (1992). Remembering pictures: pleasure and arousal in memory. *Journal of Experimental Psychology : Learning, Memory and Cognition, 18*(2), 379-390.

Bradley, M. M., & Lang, P. J. (1999). *Affective norms for English words (ANEW): Instruction manual and affective ratings*: Technical Report C-1, The Center for Research in Psychophysiology, University of Florida.

Bradley, M. M., & Lang, P. J. (2000). Measuring emotion: Behavior, feeling, and physiology. In R. D. Lane & L. Nadel (Eds.), *Cognitive Neuroscience of Emotion* (pp. 242-276). New York: US: Oxford University Press.

Breiter, H. C. (1996). Response and habituation of the human amygdala during visual processing of facial expression. *Neuron, 17*(5), 875-887.

Brown, T. A., Chorpita, B. F., & Barlow, D. H. (1998). Structural relationships among dimensions of the DSM-IV anxiety and mood disorders and dimensions of negative affect, positive affect, and autonomic arousal. *Journal of Abnormal Psychology, 107*(2), 179-192.

Buck, R. (2000). Conceptualizing motivation and emotion. *Behavioral and Brain Sciences, 23*(02), 195-196.

Bush, G., Luu, P., & Posner, M. I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in Cognitive Sciences, 4*(6), 215-222.

Cacioppo, J. T., & Berntson, G. G. (1999). The affect system: Architecture and operating characteristics. *Current Directions in Psychological Science, 8*(5), 133 137.

Calder, A. J., Keane, J., Manes, F., Antoun, N., & Young, A. W. (2000). Impaired recognition and experience of disgust following brain injury. *Nature Neuroscience, 3*(11), 1077-1078.

Canli, T., Zhao, Z., Brewer, J., Gabrieli, J. D., & Cahill, L. (2000). Event-related activation in the human amygdala associates with later memory for individual emotional experience. *Journal of Neuroscience, 20*(19), RC99.

Carter, C. S., Braver, T. S., Barch, D. M., Botvinick, M. M., Noll, D., & Cohen, J. D. (1998). Anterior cingulate cortex, error detection, and the online monitoring of performance. *Science, 280*(5364), 747-749.

Chen, C. Y., Tien, Y. M., Juan, C. H., Tzeng, O. J., & Hung, D. L. (2005). Neural correlates of impulsive-violent behavior: an event-related potential study. *Neuroreport, 16*(11), 1213-1216.

Christianson, S. A., & Loftus, E. F. (1991). Remembering emotional events: The fate of detailed information. *Cognition and Emotion, 5*(2), 81-108.

Cimbalo, R. S. (1978). Making something stand out: The isolation effect in memory performance. In M. M. Grunneberg, P. E. Morris & S. R.N. (Eds.), *Practical aspects of memory* (pp. 101-110). New York: Academic Press.

Conway, M., Howell, A., & Giannopoulos, C. (1991). Dysphoria and thought suppression. *Cognitive Therapy and Research, 15*(2), 153 166.

Cooper, E. H., & Pantle, A. J. (1967). The Total-Time Hypothesis in Verbal Learning. *Psychological Bulletin, 68*(4), 221-234.

Costa, M., Braun, C., & Birbaumer, N. (2003). Gender differences in response to pictures of nudes: a magnetoencephalographic study. *Biological Psychology, 63*(2), 129-147.

Croft, R. J. (2000). The Differential Correction of Eyelid-Movement and Globe-Rotation Artefact from the EEG (Reply to Verleger). *Journal of Psychophysiology, 14*(4), 207-209.

Cuthbert, B. N., Schupp, H. T., Bradley, M. M., Birbaumer, N., & Lang, P. J. (2000). Brain potentials in affective picture processing: covariation with autonomic arousal and affective report. *Biological Psychology, 52*(2), 95-111.

Dalbert, C. (1992). Subjektives Wohlbefinden junger Erwachsener: Theoretische und empirische Analysen der Struktur und Stabilität. *Zeitschrift für Differentielle und Diagnostische Psychologie, 13*(207-220).

Davidson, R. J. (2004). What does the prefrontal cortex "do" in affect: Perspectives on frontal EEG asymmetry research. *Biological Psychology, 67*(1,2), 219-233.

Davidson, R. J., Abercrombie, H., Nitschke, J. B., & Putnam, K. (1999). Regional brain function, emotion and disorders of emotion. *Current Opinion in Neurobiology, 9*(2), 228-234.

Davidson, R. J., & Irwin, W. (1999). The functional neuroanatomy of emotion and affective style. *Trends in Cognitive Sciences, 3*(1), 11-21.

Davidson, R. J., Maxwell, J. S., & Shackman, A. J. (2004). The privileged status of emotion in the brain. *Proceedings of the National Academy of Sciences of the United States of America (PNAS), 101*(33), 11915-11916.

de Gelder, B., Vroomen, J., Pourtois, G., & Weiskrantz, L. (1999). Non-conscious recognition of affect in the absence of striate cortex. *Neuroreport, 10*(18), 3759 3763.

Dien, J. (1998). Issues in the application of the average reference: Review, critiques, and recommendations. *Behavior Research Methods Instruments & Computers, 30*(1), 34-43.

Dimberg, U., & Thunberg, M. (1998). Rapid facial reactions to emotional facial expressions. *Scandinavian Journal of Psychology, 39*(1), 39-45.

Dolan, R. J. (2002). Emotion, cognition, and behavior. *Science, 298*(5596), 1191-1194.

Dolan, R. J., & Vuilleumier, P. (2003). Amygdala automaticity in emotional processing. *Annals of the New York Academy of Sciences, 985*, 348-355.

Dolcos, F., & Cabeza, R. (2002). Event-related potentials of emotional memory: encoding pleasant, unpleasant, and neutral pictures. *Cognitive, Affective and Behavioral Neuroscience, 2*(3), 252-263.

Dolcos, F., LaBar, K. S., & Cabeza, R. (2004). Dissociable effects of arousal and valence on prefrontal activity indexing emotional evaluation and subsequent memory: an event-related fMRI study. *Neuroimage, 23*(1), 64-74.

Donchin, E., & Coles, M.-G. (1988). Is the P300 component a manifestation of context updating? *Behavior and Brain Sciences, 11*, 357-427.

Dreisbach, G., & Goschke, T. (2004). How positive affect modulates cognitive control: reduced perseveration at the cost of increased distractibility. *Journal of Experimental Psychology : Learning, Memory and Cognition, 30*(2), 343-353.

Dubois, S., Rossion, B., Schiltz, C., Bodart, J. M., Michel, C., Bruyer, R., et al. (1999). Effect of familiarity on the processing of human faces. *Neuroimage, 9*(3), 278-289.

Easterbrook, J. A. (1959). The effect of emotion on cue utilization and the organization of behavior. *Psychological Review, 66*, 183-201.

Eimer, M. (1993). Effects of attention and stimulus probability on ERPs in a Go/Nogo task. *Biological Psychology, 35*(2), 123-138.

Eimer, M. (2000). Event-related brain potentials distinguish processing stages involved in face perception and recognition. *Clinical Neurophysiology, 111*(4), 694-705.

Eimer, M., & Holmes, A. (2002). An ERP study on the time course of emotional face processing. *Neuroreport, 13*(4), 427-431.

Ekman, P. (1993). Facial expression and emotion. *American Psychologist, 48*(4), 384-392.

Ekman, P. (1994). All emotions are basic. In P. Ekman & R. J. Davidson (Eds.), *The nature of emotion: Fundamental questions* (pp. 15–19). Oxford: Oxford University Press.

Ekman, P. (1999). Basic emotions. In T. Dalgleish & M. Power (Eds.), *Handbook of Cognition and Emotion. :* (pp. 45-60): John Wiley and Sons Ltd.

Ekman, P., & Friesen, W. V. (1976). *Pictures of facial affect*. Palo Alto: CA: Consulting Psychologists.

Eriksen, B. A., & Eriksen, C. W. (1974). Effects of noise letters upon the identification of a target letter in a nonsearch task. *Perception and Psychophysics, Vol 16*(1), 143-149.

Erk, S., Kiefer, M., Grothe, J., Wunderlich, A. P., Spitzer, M., & Walter, H. (2003). Emotional context modulates subsequent memory effect. *Neuroimage, 18*(2), 439-447.

Erk, S., Martin, S., & Walter, H. (2005). Emotional context during encoding of neutral items modulates brain activation not only during encoding but also during recognition. *Neuroimage, 26*(3), 829-838.

Fabiani, M., & Donchin, E. (1995). Encoding processes and memory organization: a model of the von Restorff effect. *Journal of Experimental Psychology : Learning, Memory and Cognition, 21*(1), 224-240.

Fabiani, M., Karis, D., & Donchin, E. (1990). Effects of mnemonic strategy manipulation in a Von Restorff paradigm. *Electroencephalography and Clinical Neurophysiology, 75*(2), 22-35.

Falkenstein, M. (2004). ERP correlates of erroneous performance. In M. Ullsperger & M. Falkenstein (Eds.), *Errors, Conflicts, and the Brain. Current Opinions on Performance Monitoring* (pp. 5-14). Leipzig: Max Planck Institute for Human Cognitive and Brain Sciences.

Falkenstein, M., Hielscher, H., Dziobek, I., Schwarzenau, P., Hoormann, J., Sunderman, B., et al. (2001). Action monitoring, error detection, and the basal ganglia: an ERP study. *Neuroreport, 12*(1), 157-161.

Falkenstein, M., Hohnsbein, J., Hoormann, J., & Blanke, L. (1991). Effects of crossmodal divided attention on late ERP components. II. Error processing in choice reaction tasks. *Electroencephalography and Clinical Neurophysiology, 78*(6), 447-455.

Falkenstein, M., Hoormann, J., Christ, S., & Hohnsbein, J. (2000). ERP components on reaction errors and their functional significance: a tutorial. *Biological Psychology, 51*(2-3), 87-107.

Falkenstein, M., Hoormann, J., & Hohnsbein, J. (1999). ERP components in Go/Nogo tasks and their relation to inhibition. *Acta Psychologica, 101*(2-3), 267-291.

Fernandez, G., Weyerts, H., Tendolkar, I., Smid, H. G., Scholz, M., & Heinze, H. J. (1998). Event-related potentials of verbal encoding into episodic memory: dissociation between the effects of subsequent memory performance and distinctiveness. *Psychophysiology, 35*(6), 709-720.

Fiedler, K. (2001). Affective states trigger processes of assimilation and accommodation. In G. L. Clore & L. L. Martin (Eds.), (pp. 85-99). Mahwah, NJ,: US: Lawrence Erlbaum Associates Publishers.

Fitzgerald, K. D., Welsh, R. C., Gehring, W. J., Abelson, J. L., Himle, J. A., Liberzon, I., et al. (2005). Error-related hyperactivity of the anterior cingulate cortex in obsessive-compulsive disorder. *Biological Psychiatry, 57*(3), 287-294.

Friedman, D., Ritter, W., & Snodgrass, J. G. (1996). ERPs during study as a function of subsequent direct and indirect memory testing in young and old adults. *Cognitive Brain Research, 4*(1), 1-13.

Friedman, D., & Sutton, S. (1987). Event-related potentials during continuous recognition memory. *Electroencephalography and Clinical Neurophysiology Supplement, 40*, 316-321.

Frijda, N. H. (2000). Emotion theory? *Behavioral and Brain Sciences, 23*(2), 199-+.

Gehring, W. J., Goss, B., Coles, M. G. H., Meyer, D. E., & Donchin, E. (1993). A neural system for error detection and compensation. *Psychological Science, 4*(6), 385–390.

Gehring, W. J., Himle, J., & Nisenson, L. G. (2000). Action-monitoring dysfunction in obsessive-compulsive disorder. *Psychological Science, 11*(1), 1-6.

Gray, J. A. (1999). Cognition, emotion, consious experience and the Brain. In T. Dalgleish & M. Power (Eds.), *Handbook of cognition and emotion* (pp. 83-102). Sussex, U.K.: John Wiley and Sons Ltd.

Hajcak, G., McDonald, N., & Simons, R. F. (2003a). Anxiety and error-related brain activity. *Biological Psychology, 64*(1-2), 77-90.

Hajcak, G., McDonald, N., & Simons, R. F. (2003b). To err is autonomic: error-related brain potentials, ANS activity, and post-error compensatory behavior. *Psychophysiology, 40*(6), 895-903.

Hajcak, G., McDonald, N., & Simons, R. F. (2004). Error-related psychophysiology and negative affect. *Brain and Cognition, 56*(2), 189-197.

Hajcak, G., Moser, J. S., Yeung, N., & Simons, R. F. (2005). On the ERN and the significance of errors. *Psychophysiology, 42*(2), 151-160.

Hajcak, G., & Simons, R. F. (2002). Error-related brain activity in obsessive-compulsive undergraduates. *Psychiatry Research, 110*(1), 63-72.

Hamann, S. (2001). Cognitive and neural mechanisms of emotional memory. *Trends in Cognitive Sciences, 5*(9), 394 - 400.

Hamann, S., & Mao, H. (2002). Positive and negative emotional verbal stimuli elicit activity in the left amygdala. *Neuroreport, 13*(1), 15-19.

Holroyd, C. B., & Coles, M. G. (2002). The neural basis of human error processing: reinforcement learning, dopamine, and the error-related negativity. *Psychological Review, 109*(4), 679-709.

Holroyd, C. B., & Yeung, N. (2003). Alcohol and error processing. *Trends in Neurosciences, 26*(8), 402-404.

Hunt, R. R., & Lamb, C. A. (2001). What causes the isolation effect? *Journal of Experimental Psychology : Learning, Memory and Cognition, 27*(6), 1359-1366.

Isen, A. M. (2001). An influence of positive affect on decision making in complex situations: Theoretical issues with practical implications. *Journal of Consumer Psychology, 11*(2), 75-85.

Isen, A. M., Daubman, K. A., & Nowicki, G. P. (1987). Positive affect facilitates creative problem solving. *Journal of Personality and Social Psychology, 52*(6), 1122-1131.

Ito, T. A., Larsen, J. T., Smith, N. K., & Cacioppo, J. T. (1998). Negative information weighs more heavily on the brain: the negativity bias in evaluative categorizations. *Journal of Personality and Social Psychology, 75*(4), 887-900.

James, W. (1884). What is an Emotion? *Mind, 9*(34), 188-205.

James, W. (1890). *The principles of psychology*. New York,: H. Holt and company, online available at http://psychclassics.yorku.ca/James/Principles/index.htm.

Jasper, H. H. (1958). The ten-twenty- electrode system of the international federation. *Electroencephalography and Clinical Neurophysiology, 10*, 371-375.

Jeffreys, D. A., & Tukmachi, E. S. A. (1992). The Vertex-Positive Scalp Potential Evoked by Faces and by Objects. *Experimental Brain Research, 91*(2), 340-350.

Johannes, S., Wieringa, B. M., Nager, W., Dengler, R., & Münte, T. F. (2001). Oxazepam alters action monitoring. *Psychopharmacology, 155*(1), 100-106.

Johnstone, T., Somerville, L. H., Alexander, A. L., Oakes, T. R., Davidson, R. J., Kalin, N. H., et al. (2005). Stability of amygdala BOLD response to fearful faces over multiple scan sessions. *Neuroimage, 25*(4), 1112-1123.

Joyce, C. A., Gorodnitsky, I. F., & Kutas, M. (2004). Automatic removal of eye movement and blink artifacts from EEG data using blind component separation. *Psychophysiology, 41*(2), 313-325.

Karama, S., Lecours, A. R., Leroux, J. M., Bourgouin, P., Beaudoin, G., Joubert, S., et al. (2002). Areas of brain activation in males and females during viewing of erotic film excerpts. *Human Brain Mapping, 16*(1), 1-13.

Karis, D., Fabiani, M., & Donchin, E. (1984). "P300" and memory: Individual differences in the von Restorff effect. *Cognitive Psychology, 16*(2), 177-216.

Keil, A., Bradley, M. M., Hauk, O., Rockstroh, B., Elbert, T., & Lang, P. J. (2002). Large-scale neural correlates of affective picture processing. *Psychophysiology, 39*(5), 641-649.

Kemp, A. H., Silberstein, R. B., Armstrong, S. M., & Nathan, P. J. (2004). Gender differences in the cortical electrophysiological processing of visual emotional stimuli. *Neuroimage, 21*(2), 632-646.

Kiehl, K. A., Liddle, P. F., & Hopfinger, J. B. (2000). Error processing and the rostral anterior cingulate: an event-related fMRI study. *Psychophysiology, 37*(2), 216-223.

Kierkels, J. J., van Boxtel, G. J., & Vogten, L. L. (2006). A model-based objective evaluation of eye movement correction in EEG recordings. *IEEE Transactions on Biomedical Engineering, 53*(2), 246-253.

Kirchhoff, B. A., Wagner, A. D., Maril, A., & Stern, C. E. (2000). Prefrontal-temporal circuitry for episodic encoding and subsequent memory. *Journal of Neuroscience, 20*(16), 6173-6180.

Kok, A. (1997). Event-related-potential (ERP) reflections of mental resources: a review and synthesis. *Biological Psychology, 45*(1-3), 19-56.

Kopp, B., Rist, F., & Mattler, U. (1996). N200 in the flanker task as a neurobehavioral tool for investigating executive control. *Psychophysiology, 33*(3), 282-294.

Krohne, H. W., Pieper, M., Knoll, N., & Breimer, N. (2002). The cognitive regulation of emotions: The role of success versus failure experience and coping dispositions. *Cognition and Emotion, 16*(2), 217 243.

LaBar, K. S., Gatenby, J. C., Gore, J. C., LeDoux, J. E., & Phelps, E. A. (1998). Human amygdala activation during conditioned fear acquisition and extinction: a mixed-trial fMRI study. *Neuron, 20*(5), 937-945.

LaBar, K. S., Gatenby, J. C., Gore, J. C., & Phelps, E. A. (1998). Role Of The Amygdala in Emotional Picture Evaluation as Revealed By fMRI. *Journal of Cognitive Neuroscience, Supplement S*, 108.

Lang, P. J., Bradley, M. M., & Cuthbert, B. (1997). *International affective picture system (IAPS): Technical Manual and affective Ratings*.

Lang, P. J., Bradley, M. M., & Cuthbert, B. (1999). *International affective picture system (IAPS): instruction manual and affective ratings. Technical Report A-4, The Center for Research in Psychophysiology*. Gainesville, Florida: University of Florida.

Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1998). Emotion and motivation: measuring affective perception. *Journal of Clinical Neurophysiology, 15*(5), 397-408.

Lang, P. J., Bradley, M. M., Fitzsimmons, J. R., Cuthbert, B. N., Scott, J. D., Moulder, B., et al. (1998). Emotional arousal and activation of the visual cortex: an fMRI analysis. *Psychophysiology, 35*(2), 199-210.

Lang, P. J., & Greenwald, M. K. (1988). *The international affective picture system standardization procedure and initial group results for affective judgement*. Gainesville, Florida: University of Florida.

Lang, P. J., Greenwald, M. K., Bradley, M. M., & Hamm, A. O. (1993). Looking at pictures: affective, facial, visceral, and behavioral reactions. *Psychophysiology, 30*(3), 261-273.

Lange, C. (1887). *Über Gemühtsbewegungen*. Leipzig: Thomas, online at http://psychclassics.yorku.ca/Lange/.

Larisch, R., Klimke, A., Vosberg, H., Loffler, S., Gaebel, W., & Muller-Gartner, H. W. (1997). In vivo evidence for the involvement of dopamine-D2 receptors in striatum and anterior cingulate gyrus in major depression. *Neuroimage, 5*(4 Pt 1), 251-260.

Lazarus, R. S. (1999). The cognition-emotion debate: a bit of history. In T. Dalgleish & M. Power (Eds.), *Handbook of cognition and emotion* (pp. 3–19). Sussex, U.K.: John Wiley and Sons Ltd.

LeDoux, J. (1997). Parallel Memories: Putting Emotions Back Into The Brain: A Talk With Joseph LeDoux: http://www.edge.org/3rd_culture/ledoux/ledoux_p1.html.

Lisman, J. E., & Grace, A. A. (2005). The hippocampal-VTA loop: controlling the entry of information into long-term memory. *Neuron, 46*(5), 703-713.

Lundqvist, D., Flykt, A., & Öhman, A. (1998). *The Karolinska Directed Emotional Faces*. Stockholm, Sweden: Department of Neurosciences Karolinska Hospital.

Luu, P., Collins, P., & Tucker, D. M. (2000). Mood, personality, and self-monitoring: negative affect and emotionality in relation to frontal lobe mechanisms of error monitoring. *Journal of Experimental Psychology: General, 129*(1), 43-60.

Luu, P., & Pederson, S. M. (2004). The Anterior Cingulate Cortex: Regulating Actions in Context. In M. I. Posner (Ed.), *Cognitive Neuroscience of Attention*: New York, NY, US: Guilford Press.

Maratos, E. J., Allan, K., & Rugg, M. D. (2000). Recognition memory for emotionally negative and neutral words: an ERP study. *Neuropsychologia, 38*(11), 1452-1465.

Mayberg, H. S., Brannan, S. K., Mahurin, R. K., Jerabek, P. A., Brickman, J. S., Tekell, J. L., et al. (1997). Cingulate function in depression: a potential predictor of treatment response. *Neuroreport, 8*(4), 1057-1061.

McIntosh, D. N. (1996). Facial feedback hypotheses: Evidence, implications, and directions. *Motivation and Emotion, 20*(2), 121-147.

McNair, D. M., Lorr, M., & Doppleman, L. F. (1971). *EITS – manual for Profile of Mood States*. San Diego, California: Educational and Industrial Testing Service.

Menon, V., Adleman, N. E., White, C. D., Glover, G. H., & Reiss, A. L. (2001). Error-related brain activation during a Go/NoGo response inhibition task. *Human Brain Mapping, 12*(3), 131-143.

Morris, J. S., Ohman, A., & Dolan, R. J. (1998). Conscious and unconscious emotional learning in the human amygdala. *Nature, 393*(6684), 467-470.

Murphy, F. C., Nimmo-Smith, I., & Lawrence, A. D. (2003). Functional neuroanatomy of emotions: a meta-analysis. *Cognitive, Affective and Behavioral Neuroscience, 3*(3), 207-233.

Neville, H. J., Kutas, M., Chesney, G., & Schmidt, A. L. (1986). Event-related brain potentials during initial encoding and recognition memory of congruous and incongruous words. *Journal of Memory and Language, 25*(1), 75-92.

Nieuwenhuis, S., Ridderinkhof, K. R., Blom, J., Band, G. P., & Kok, A. (2001). Error-related brain potentials are differentially related to awareness of response errors: evidence from an antisaccade task. *Psychophysiology, 38*(5), 752-760.

Ochsner, K. N. (2000). Are affective events richly recollected or simply familiar? The experience and process of recognizing feelings past. *Journal of Experimental Psycholology: General, 129*(2), 242-261.

Ochsner, K. N., & Gross, J. J. (2005). The cognitive control of emotion. *Trends in Cognitive Sciences, 9*(5), 242-249.

Ohman, A., Flykt, A., & Esteves, F. (2001). Emotion drives attention: detecting the snake in the grass. *Journal of Experimental Psychology: General, 130*(3), 466-478.

Otten, L. J., & Donchin, E. (2000). Relationship between P300 amplitude and subsequent recall for distinctive events: dependence on type of distinctiveness attribute. *Psychophysiology, 37*(5), 644-661.

Paller, K. A., Kutas, M., & Mayes, A. R. (1987). Neural correlates of encoding in an incidental learning paradigm. *Electroencephalography and Clinical Neurophysiology, 67*(4), 360-371.

Palomba, D., Angrilli, A., & Mini, A. (1997). Visual evoked potentials, heart rate responses and memory to emotional pictorial stimuli. *International Journal of Psychophysiology, 27*(1), 55-67.

Patrick, C. J., & Lavoro, S. A. (1997). Ratings of emotional response to pictorial stimuli: Positive and negative affect. *Motivation and Emotion, 21*(4), 297-321.

Phan, K. L., Wager, T., Taylor, S. F., & Liberzon, I. (2002). Functional neuroanatomy of emotion: a meta-analysis of emotion activation studies in PET and fMRI. *Neuroimage, 16*(2), 331-348.

Phan, K. L., Wager, T. D., Taylor, S. F., & Liberzon, I. (2004). Functional neuroimaging studies of human emotions. *CNS Spectrums, 9*(4), 258-266.

Phelps, E. A., O'Connor, K. J., Gatenby, J. C., Gore, J. C., Grillon, C., & Davis, M. (2001). Activation of the left amygdala to a cognitive representation of fear. *Nature Neuroscience, 4*(4), 437-441.

Polich, J., & Kok, A. (1995). Cognitive and Biological Determinants of P300 - an Integrative Review. *Biological Psychology, 41*(2), 103-146.

Posner, M. I., & Petersen, S. E. (1990). The attention system of the human brain. *Annual Review of Neuroscience, 13*, 25-42.

Rabbitt, P. M. A. (1981). Sequential reactions. In D. Holding (Ed.), *Human skills* (pp. 153-175). New York: Wiley.

Rabbitt, P. M. A. (2002). Consciousness is slower than you think. *The Quarterly Journal of Experimental Psychology: Section A: Human Experimental Psychology, 55*(4), 1081-1092.

Ranganath, C., & Rainer, G. (2003). Neural mechanisms for detecting and remembering novel events. *Nature Reviews Neuroscience, 4*(3), 193-202.

Reisberg, D., & Hertel, P. (2004). Memory for Emotional Events. In D. Reisberg & F. Heuer (Eds.), *Memory and Emotions* (pp. 3-41). New York: US: Oxford University Press.

Riba, J., Rodriguez-Fornells, A., Morte, A., Münte, T. F., & Barbanoj, M. J. (2005). Noradrenergic stimulation enhances human action monitoring. *Journal of Neuroscience, 25*(17), 4370-4374.

Ridderinkhof, K. R., de Vlugt, Y., Bramlage, A., Spaan, M., Elton, M., Snel, J., et al. (2002). Alcohol consumption impairs detection of performance errors in mediofrontal cortex. *Science, 298*(5601), 2209-2211.

Ridderinkhof, K. R., Ullsperger, M., Crone, E. A., & Nieuwenhuis, S. (2004). The role of the medial frontal cortex in cognitive control. *Science, 306*(5695), 443-447.

Robinson, M. D. (1998). Running from William James' bear: A review of preattentive mechanisms and their contributions to emotional experience. *Cognition and Emotion, 12*(5), 667-696.

Rolls, E. T. (1999). *The brain and emotion* (Reprinted ed.). Oxford [u.a.]: Oxford Univ. Press.

Rolls, E. T. (2000). Precis of The brain and emotion. *Behavioral and Brain Sciences, 23*(2), 177-191; discussion 192-233.

Rolls, E. T. (2004). *The brain and emotion* (Reprinted ed.). Oxford [u.a.]: Oxford Univ. Press.

Rüsseler, J., Hennighausen, E., Münte, T. F., & Rösler, F. (2003). Differences in incidental and intentional learning of sensorimotor sequences as revealed by event-related brain potentials. *Cognitive Brain Reseach, 15*(2), 116-126.

Rüsseler, J., & Rösler, F. (2000). Implicit and explicit learning of event sequences: evidence for distinct coding of perceptual and motor representations. *Acta Psychologica, 104*(1), 45-67.

Russell, J. A., & Carroll, J. M. (1999). On the bipolarity of positive and negative affect. *Psychological Bulletin, 125*(1), 3-30.

Sawamoto, N., Honda, M., Okada, T., Hanakawa, T., Kanda, M., Fukuyama, H., et al. (2000). Expectation of pain enhances responses to nonpainful somatosensory stimulation in the anterior cingulate cortex and parietal operculum/posterior insula: an event-related functional magnetic resonance imaging study. *Journal of Neuroscience, 20*(19), 7438-7445.

Scherer, K. R. (1994). Towards a concept of "Modal emotions". In P. Ekman & R. J. Davidson (Eds.), *The nature of emotion: Fundamental questions* (pp. 25-31). Oxford: Oxford University Press.

Scherer, K. R. (2000). Psychological models of emotion. In J. C. Borod (Ed.), *The neuropsychology of emotion.*: New York, NY, US: Oxford University Press.

Scherer, K. R. (2005). What are emotions? And how can they be measured? *Social Science Information, 44*(4), 693-727.

Schupp, H. T., Cuthbert, B. N., Bradley, M. M., Cacioppo, J. T., Ito, T., & Lang, P. J. (2000). Affective picture processing: the late positive potential is modulated by motivational relevance. *Psychophysiology, 37*(2), 257-261.

Schupp, H. T., Junghöfer, M., Weike, A. I., & Hamm, A. O. (2003). Emotional facilitation of sensory processing in the visual cortex. *Psychological Science, 14*(1), 7-13.

Schupp, H. T., Junghöfer, M., Weike, A. I., & Hamm, A. O. (2004). The selective processing of briefly presented affective pictures: an ERP analysis. *Psychophysiology, 41*(3), 441-449.

Schupp, H. T., Ohman, A., Junghöfer, M., Weike, A. I., Stockburger, J., & Hamm, A. O. (2004). The facilitated processing of threatening faces: an ERP analysis. *Emotion, 4*(2), 189-200.

Simon-Thomas, E. R., & Knight, R. T. (2005). Affective and cognitive modulation of performance monitoring: behavioral and ERP evidence. *Cognitive, Affective and Behavioral Neuroscience, 5*(3), 362-372.

Simons, R. F., Graham, F. K., Miles, M. A., & Chen, X. (2001). On the relationship of P3a and the Novelty-P3. *Biological Psychology, 56*(3), 207-218.

Soussignan, R. (2002). Duchenne smile, emotional experience, and autonomic reactivity: a test of the facial feedback hypothesis. *Emotion, 2*(1), 52-74.

Strack, F., Martin, L. L., & Stepper, S. (1988). Inhibiting and facilitating conditions of the human smile: a nonobtrusive test of the facial feedback hypothesis. *Journal of Personality and Social Psychology, 54*(5), 768-777.

Strange, B. A., & Dolan, R. J. (2001). Adaptive anterior hippocampal responses to oddball stimuli. *Hippocampus, 11*(6), 690-698.

Strange, B. A., Henson, R. N. A., Friston, K. J., & Dolan, R. J. (2000). Brain mechanisms for detecting perceptual, semantic, and emotional deviance. *Neuroimage, 12*(4), 425-433.

Strange, B. A., Hurlemann, R., & Dolan, R. J. (2003). An emotion-induced retrograde amnesia in humans is amygdala- and beta-adrenergic-dependent. *Proceedings of the National Academy of Sciences of the United States of America (PNAS), 100*(23), 13626-13631.

Talairach, J., & Tournoux, P. (1988). *Co-Planar Stereotaxic Atlas of the Human Brain: Three-Dimensional Proportional System*. Stuttgart: Georg Thieme.

Tracey, I., Ploghaus, A., Gati, J. S., Clare, S., Smith, S., Menon, R. S., et al. (2002). Imaging attentional modulation of pain in the periaqueductal gray in humans. *Journal of Neuroscience, 22*(7), 2748-2752.

Tucker, D. M., Liotti, M., Potts, G. F., Russell, G. S., & Posner, M. I. (1994). Spatiotemporal analysis of brain electrical fields. *Human Brain Mapping, 1*(2), 134-152.

Van 't Ent, D. (2002). Perceptual and motor contributions to performance and ERP components after incorrect motor activation in a flanker reaction task. *Clinical Neurophysiology, 113*(2), 270-283.

van Veen, V., & Carter, C. S. (2002a). The anterior cingulate as a conflict monitor: fMRI and ERP studies. *Physiology and Behavior, 77*(4-5), 477-482.

Van Veen, V., & Carter, C. S. (2002b). The timing of action-monitoring processes in the anterior cingulate cortex. *Journal of Cognitive Neuroscience, 14*(4), 593-602.

Verleger, R. (2000). Should We Really Use Different Estimates for Correcting EEG Artefacts Produced by Blinks and by Saccades? *Journal of Psychophysiology, 14*(4), 204-206.

von Restorff, H. (1933). Ueber die Wirkung von Bereichsbildungen im Spurenfeld. *Psychologische Forschung, 18*, 299-342.

Wager, T. D., Phan, K. L., Liberzon, I., & Taylor, S. F. (2003). Valence, gender, and lateralization of functional brain anatomy in emotion: a meta-analysis of findings from neuroimaging. *Neuroimage, 19*(3), 513-531.

Wager, T. D., Rilling, J. K., Smith, E. E., Sokolik, A., Casey, K. L., Davidson, R. J., et al. (2004). Placebo-induced changes in FMRI in the anticipation and experience of pain. *Science, 303*(5661), 1162-1167.

Wagner, A. D., Koutstaal, W., & Schacter, D. L. (1999). When encoding yields remembering: insights from event-related neuroimaging. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences, 354*(1387), 1307-1324.

Wallace, W. P. (1965). Review of the historical, empirical, and theoretical status of the von Restorff phenomenon. *Psychological Bulletin, 63*(6), 410-424.

Wallstrom, G. L., Kass, R. E., Miller, A., Cohn, J. F., & Fox, N. A. (2004). Automatic correction of ocular artifacts in the EEG: a comparison of regression-based and component-based methods. *International Journal of Psychophysiology, 53*(2), 105-119.

Watson, D., Clark, L. A., & Tellegen, A. (1988). Development and validation of brief measures of positive and negative affect: the PANAS scales. *Journal of Personality and Social Psychology, 54*(6), 1063-1070.

Wenzlaff, R. M., & Grozier, S. A. (1988). Depression and the magnification of failure. *Journal of Abnormal Psychology, 97*(1), 90-93.

Whalen, P. J., Rauch, S. L., Etcoff, N. L., McInerney, S. C., Lee, M. B., & Jenike, M. A. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *Journal of Neuroscience, 18*(1), 411-418.

Wierzbicka, A. (1999). *Emotions across languages and cultures : diversity and universals*. Cambridge: University Press.

Wiswede, D., Rüsseler, J., Hasselbach, S., & Münte, T. F. (2006). Memory recall in arousing situations - an emotional von Restorff effect? *BMC Neuroscience, 7*, 57.

Wiswede, D., Rüsseler, J., & Münte, T. F. (2007). Serial position effects in free memory recall – an ERP-study *Biological Psychology, 75*, 185-193.

Wrase, J., Klein, S., Gruesser, S. M., Hermann, D., Flor, H., Mann, K., et al. (2003). Gender differences in the processing of standardized emotional visual stimuli in humans: a functional magnetic resonance imaging study. *Neuroscience Letters, 348*(1), 41-45.

Wright, C. I., Martis, B., Schwartz, C. E., Shin, L. M., Fischer, H. H., McMullin, K., et al. (2003). Novelty responses and differential effects of order in the amygdala, substantia innominata, and inferior temporal cortex. *Neuroimage, 18*(3), 660-669.

Wu, J., Buchsbaum, M. S., Gillin, J. C., Tang, C., Cadwell, S., Wiegand, M., et al. (1999). Prediction of antidepressant effects of sleep deprivation by metabolic rates in the ventral anterior cingulate and medial prefrontal cortex. *American Journal of Psychiatry, 156*(8), 1149-1158.

Wundt, W. (1905). *Grundzüge der physiologischen Psychologie*. Leipzig: Engelmann.

Yeung, N., Cohen, J. D., & Botvinick, M. M. (2004). The neural basis of error detection: conflict monitoring and the error-related negativity. *Psychological Review, 111*(4), 931-959.

Yip, J. T., & Lee, T. M. (2006). Selective impairment of sadness and disgust recognition in abstinent ecstasy users. *Neuropsychologia, 44*(6), 959-965.

Young, A. W., Perrett, D. I., Calder, A. J., Sprengelmeyer, R., & Ekman, P. (2002). Facial expressions of emotion: stimuli and tests (FEEST). Bury St. Edmunds (UK): Thames Valley Test Company.

Zald, D. H. (2003). The human amygdala and the emotional evaluation of sensory stimuli. *Brain Research Reviews, 41*(1), 88-123.

Zalla, T., Koechlin, E., Pietrini, P., Basso, G., Aquino, P., Sirigu, A., et al. (2000). Differential amygdala responses to winning and losing: a functional magnetic resonance imaging study in humans. *European Journal of Neuroscience, 12*(5), 1764-1770.

8. Appendix

IAPS #	motive	arousal	valence
3000	Mutilation	7.3	1.5
3010	Mutilation	7.2	1.7
3030	Mutilation	6.8	1.9
3053	Burn_victim	6.9	1.3
3060	Mutilation	7.1	1.8
3080	Mutilation	7.2	1.5
3170	Baby tumor	7.2	1.5
3266	Injury	6.8	1.6
3530	Attack	6.8	1.8
4490	Erotic male	6.1	6.3
4607	Erotic couple	6.3	7.0
4608	Erotic couple	6.5	7.1
4656	Erotic couple	6.4	6.7
6230	Aimed Gun	7.4	2.4
6260	Aimed Gun	6.9	2.4
6313	Attack	6.9	2.0
6350	Attack	7.3	1.9
6540	Attack	6.8	2.2
9405	Sliced hand	6.1	1.8
9410	Soldier	7.1	1.5
total mean		**6.9**	**2.8**
total SD		**.4**	**2.1**

Appendix 1: Arousal and valence ratings for arousing background stimuli, study 3.2

IAPS #	motive	arousal	valence
1120	Snake	7.2	3.0
3030	Mutilation	7.1	1.5
3064	Mutilation	7.3	1.2
3071	Mutilation	7.1	1.7
3120	Dead body	7.5	1.3
3140	Dead body	6.9	1.5
3170	Baby tumor	7.6	1.2
6350	Attack	7.5	1.4
6510	Attack	7.2	2.1
6540	Attack	7.1	1.9
total mean		**7.3**	**1.7**
total SD		**0.2**	**0.6**

Appendix 2: Arousal and valence ratings for arousing background stimuli, study 3.3

neutral	Happy	Fearful
MC01_Hap_000%	MC01_Hap_100%	MC01_Fea_100%
MC02_Hap_000%	MC02_Hap_100%	MC02_Fea_100%
MC03_Hap_000%	MC03_Hap_100%	MC03_Fea_100%
MC04_Hap_000%	MC04_Hap_100%	MC04_Fea_100%
MC05_Hap_000%	MC05_Hap_100%	MC05_Fea_100%
MC06_Hap_000%	MC06_Hap_100%	MC06_Fea_100%
MC07_Hap_000%	MC07_Hap_100%	MC07_Fea_100%
MC08_Hap_000%	MC08_Hap_100%	MC08_Fea_100%
MC09_Hap_000%	MC09_Hap_100%	MC09_Fea_100%
MC10_Hap_000%	MC10_Hap_100%	MC10_Fea_100%.

Appendix 3: list of all face pictures used in study 4.2.

Emotion	IAPS #	Motive	Valence	Arousal
neutral	7020	Fan	2.2	4.9
	7175	Lamp	1.9	5.0
	7050	Hairdryer	2.9	5.0
	7080	Fork	2.7	5.1
	7217	Clothes rack	2.6	5.0
	7006	Bowl	2.6	5.1
	7035	Mug	2.8	5.2
	7034	Hammer	3.0	4.9
	7010	Basket	2.0	4.9
	7185	Abstract art	2.7	5.1
Mean neutral			**2.5**	**5.0**
SD neutral			**0.4**	**0.1**
pleasant	5760	Nature	3.7	8.4
	2057	Father	4.7	8.4
	2260	Baby	4.8	8.5
	1610	Rabbit	3.3	8.4
	1710	Puppies	5.3	8.6
	5830	Sunset	4.9	8.5
	2050	Baby	5.1	8.6
	1460	Kitten	4.4	8.6
	1750	Bunnies	4.0	8.6
	2040	Baby	5.0	8.7
Mean pleasant			**4.5**	**8.5**
SD pleasant			**0.6**	**0.1**
unpleasant	3060	Mutilation	7.3	1.7
	3051	Mutilation	6.0	2.1
	6550	Attack	7.2	2.1
	3261	Tumor	5.9	1.7
	9571	Cat	6.5	1.4
	3400	Severed hand	7.1	2.1
	3102	Burn victim	7.2	1.2
	6313	Attack	7.3	1.6
	3100	Burn victim	7.0	1.4
	3000	Mutilation	7.8	1.2
Mean unpleasant			**6.9**	**1.6**
SD unpleasant			**0.6**	**0.3**

Appendix 4: Arousal and valence ratings for arousing background stimuli, study 4.3.

ASTS © Dalbert, Martin-Luther-Universität Halle-Wittenberg

MOMENTANES BEFINDEN

Nachfolgend finden Sie eine Liste mit Wörtern, die verschiedene Gefühle und Gefühlszustände beschreiben. Bitte lesen Sie sorgfältig jedes einzelne Wort und kreuzen Sie dann die Zahl an, die am besten Ihren Gefühlszustand **im Moment** beschreibt. Bitte machen Sie bei jeder Aussage ein Kreuz.

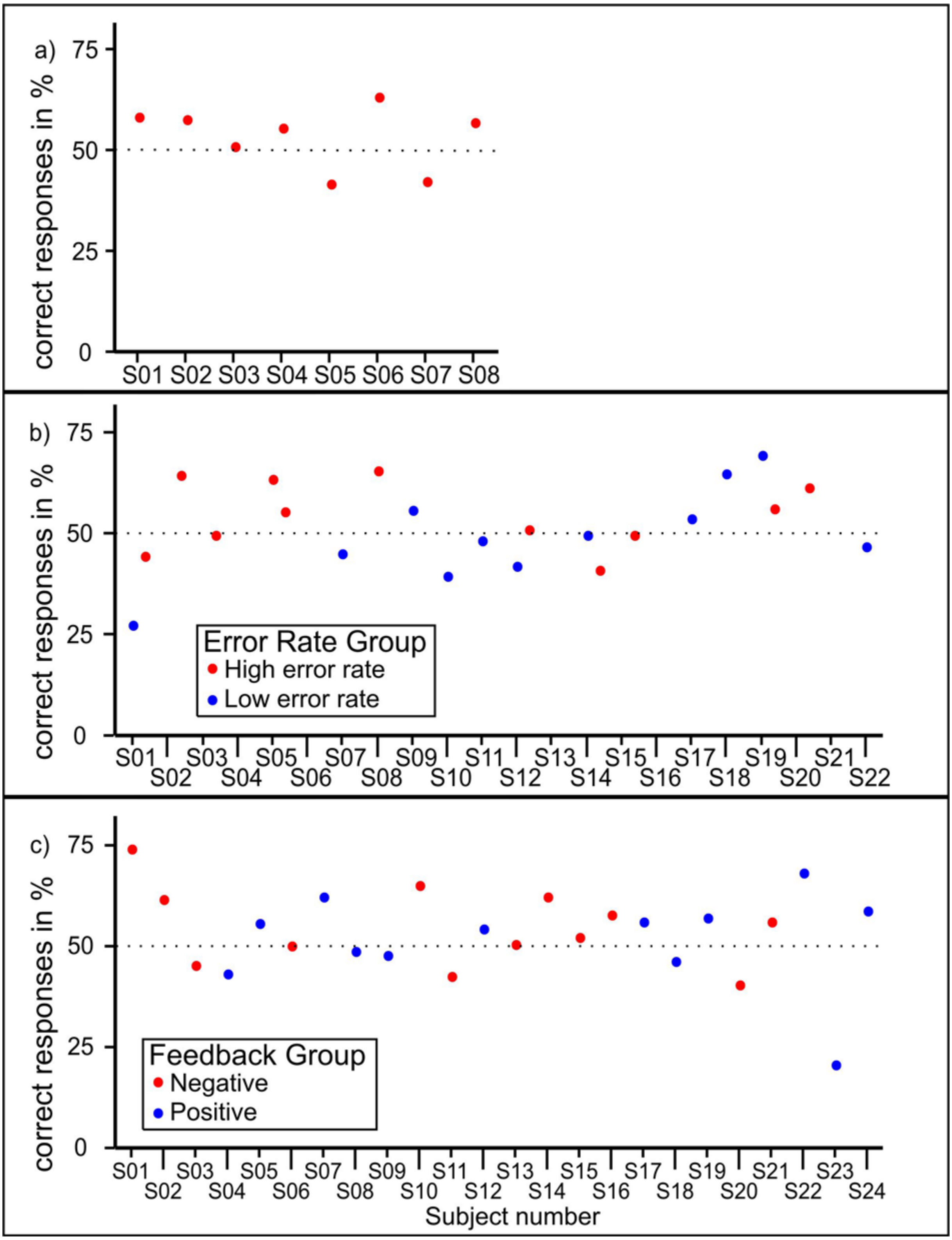
		sehr stark	stark	ziemlich	etwas	schwach	sehr schwach	überhaupt nicht
1	zornig	7	6	5	4	3	2	1
2	abgeschlafft	7	6	5	4	3	2	1
3	unglücklich	7	6	5	4	3	2	1
4	traurig	7	6	5	4	3	2	1
5	angenehm	7	6	5	4	3	2	1
6	betrübt	7	6	5	4	3	2	1
7	freudig	7	6	5	4	3	2	1
8	hoffnungslos	7	6	5	4	3	2	1
9	müde	7	6	5	4	3	2	1
10	verärgert	7	6	5	4	3	2	1
11	frohgemut	7	6	5	4	3	2	1
12	entmutigt	7	6	5	4	3	2	1
13	fröhlich	7	6	5	4	3	2	1
14	erschöpft	7	6	5	4	3	2	1
15	heiter	7	6	5	4	3	2	1
16	verzweifelt	7	6	5	4	3	2	1
17	wütend	7	6	5	4	3	2	1
18	entkräftet	7	6	5	4	3	2	1
19	lustig	7	6	5	4	3	2	1

Bitte überprüfen Sie nochmals, ob Sie kein Wort ausgelassen haben.

Appendix 5: The ASTS Questionaire "Aktuelle Stimmungsskala"; "current feeling".

German word	English translation
zornig	angrily, angry, irate, wrathful
abgeschlafft	?
unglücklich	to feel blue, unhappy
traurig	sad, cheerless, doleful
angenehm	convenient
betrübt	unhappy, sad, afflicted
freudig	glad, joyful
hoffnungslos	hopeless
müde	tired
verärgert	angry, annoyed, displeased
frohgemut	cheerful, in good spirit
entmutigt	discouraged
fröhlich	cheerful, happy, blitheful
erschöpft	exhausted, jaded
heiter	blithe
verzweifelt	desperate
wütend	enraged, furious
entkräftet	enervated, devitalized
lustig	blithe, merry

Appendix 6: Translation of German ASTS questionnaire, source for translation: http://dict.leo.org/.



Appendix 7: Figures a) to c) show the percentage of correct responses given when 50% of the errors were committed; separately for each subject. A value close to 50 (dashed line) indicates that errors were equally distributed across the experiment. Values lower than 50 indicate that the subject made more errors at the beginning of the experiment. a) experiment 4.2 b) experiment 4.3 c) experiment 4.5.

List of Tables

List of Figures

Curriculum Vitae

Persönliche Daten

Geburtsdatum:	07.03.1978
Geburtsort:	Salzwedel, Deutschland
Nationalität:	deutsch
Kontaktadresse:	Ristedter Strasse 1 38486 Immekath

Ausbildungsweg

09/1984 – 06/1996	Schulausbildung, Beendet mit Abitur
07/1996 – 04/1997	Grundwehrdienst
10/1997 – 02/2001	Psychologiestudium an der Otto–von–Guericke-Universität Magdeburg
02/2001 – 12/2002	Master of Science Studiengang an der Universität Auckland/Neuseeland
04/2002	Universitätsabschluss zum Bachelor of Science Honours im Fach Psychologie, University of Auckland Supervisor: Prof. Dr. M. C. Corballis
02/2002 – 12/2002	Forschungsassistent im „Research Centre for Cognitive Neuroscience“ an der Universität Auckland/Neuseeland
2002	Diplomarbeit, Thema: „ERPs following familiar, unfamiliar and the subject’s own face.”

	Supervisor: Prof. Dr. M. C. Corballis, Prof. Dr. Lutz Jäncke (Universität Zürich)
03/2003	Abschluss als Master of Science (Fachrichtung Psychologie) Thema der Masterthesis: „Do you know this person? Event-related brain potentials used for detecting person familiarity”.
09/2003	Diplom in Psychologie an der Otto-von-Guericke-Universität Magdeburg
01/2004 – 12/2006	Promotion an der Otto-von-Guericke-Universität Magdeburg.
2005	Dozententätigkeit für folgende Seminare: „Aspekte der klinischen Neuropsychologie“ Empiriepraktikum Experimentalpraktikum
Seit 01.01.2007	Fellow am Hanse Wissenschaftskolleg Delmenhorst. Thema „Neurobiologische und psychometrische Veränderungsprozesse bei psychoanalytischen Behandlungen von depressiven Patienten“

Auszeichnungen

02/2001 – 12/2001	DAAD Stipendium für das Auslandsstudium
02/2002 – 12/2002	Human Frontiers Science Project Masters Scholarship (Stipendium)

Wissenschaftliche Beiträge

Publikationen

Wiswede, D., Rüsseler, J., Hasselbach, S., & Münte, T. F. (2006). Memory recall in arousing situations - an emotional von Restorff effect? *BMC Neuroscience, 7*, 57.

Wiswede, D., Rüsseler, J., & Münte, T. F. (2007). Serial position effects in free memory recall – an ERP-study *Biological Psychology, 75*, 185-193.

Publizierte Abstracts

Wiswede, D., Hasselbach, S., Rüsseler, J. & Münte, T.F. (in press). Enkodierung in emotionalen Situationen – gibt es einen emotionalen „von Restorff“ Effekt? Tagungsband der 47. Tagung experimentell arbeitender Psychologen, Regensburg, April 2005

Wiswede, D., Rüsseler, J., Heldmann, M. & Münte, T.F. (2005). Error monitoring in a sequence learning task. *Journal of Cognitive Neuroscience, Supplement*, 89.

Wiswede, D., Rüsseler, J., Goschke, T., Münte, T.F. (2006). Error monitoring is modulated by induced short-term mood changes: an event-related brain potential study. *Journal of Cognitive Neuroscience, Supplement,* 162.

Persönliche Erklärung

Hiermit erkläre ich, die Dissertation selbständig und ohne unerlaubte Hilfe angefertigt zu haben. Ich erkläre die Kenntnisnahme der dem Verfahren zugrunde liegenden Promotionsordnung der Fakultät für Naturwissenschaften der Otto-von-Guericke Universität Magdeburg.

Daniel Wiswede

April 2007