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Emotions in Motion:

Processing of Dynamic and Static Facial Expressions of Happiness and Disgust Investigated by FMRI and EEG

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“Wenn wir an unsere Stärken glauben,

werden wir täglich stärker.”

(Mahatma Gandhi)

Contents

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Zusammenfassung

Die emotionale Gesichterwahrnehmung nimmt einen sehr großen und wichtigen Part in unserem Alltag, vor allem in sozialen Situationen und Gesprächen, ein. Die Gesichterwahrnehmung mit dynamischen, anstelle von statischen Gesichtern zu untersuchen erwies sich in vorigen Studien als vielversprechender und ökologisch valider Ansatz. Ein möglicher Grund dafür könnte sein, dass sich Gesichter in sozialem Kontext sehr schnell verändern und sich eher selten in statischer Natur zeigen. Deshalb wurde die emotionale Gesichterwahrnehmung von Ekel und Freude bei statischen und dynamischen Gesichtern mit der funktionellen Magnetresonanztomographie (fMRT) und der Elektroenzephalographie (EEG) untersucht.

Nach gegenwärtiger Kenntnis der Autorin wurden bisher wenige fMRT-Studien und noch keine EEG-Studie veröffentlicht, die sich mit der dynamischen emotionalen Gesichterwahrnehmung auseinandersetzten. Dies weist auf den dringenden Bedarf an weiteren Erkenntnissen über die Verarbeitung dynamischer im Vergleich zu statischen emotionalen Gesichtern hin.

Die erste Studie verfolgte zwei Ziele: Mit Hilfe der fMRT sollten, erstens, die neuronalen Korrelate der Emotionswahrnehmung getrennt für statische und dynamische Gesichter untersucht werden und, zweitens, sollte der Einfluss der Bewegung auf die Emotionswahrnehmung überprüft werden.

Sechzehn deutsche, weibliche Probandinnen nahmen an der fMRT-Studie teil. Ihre Aufgabe bestand darin, statische und dynamische Gesichter mit neutralen, glücklichen und angeekelten Gesichtsausdrücken passiv zu betrachten. Die Stimuli wurden einer neu entwickelten Gesichterdatenbank entnommen. Probandinnen bewerteten alle Gesichter nach der Kernspinuntersuchung auf den Skalen „Arousal“ (Erregbarkeit) und „Valenz“ (Wertigkeit der Emotion). Dynamische Gesichter zeigten konsistente Netzwerkaktivierungen im parahippokampalen Gyrus und der Amygdala, im fusiformen Gyrus (FuG), im superior temporalen Gyrus (STG), inferior frontalen Gyrus, okzipitalen und orbitofrontalen Gyrus. Diese Regionen wurden in Zusammenhang mit Gedächtnisenkodierung, der Wahrnehmung von Bedrohung, der Gesichteridentitätswahrnehmung, der Wahrnehmung biologischer Bewegung, dem Spiegelneuronensystem, dem Anstieg von Arousal und dem Belohnungssystem diskutiert. Dynamische im Vergleich zu statischen Stimuli wurden in der posthoc Bewertung akkurater erkannt. Schlussfolgernd lässt sich zusammenfassen, dass dynamische, im Gegensatz zu statischen emotionalen Gesichtsausdrücken, anscheinend einen

ökologisch valideren Ansatz darstellen, um die Verarbeitung von Emotionen zu untersuchen.
Das Ziel der zweiten Studie war, mit Hilfe der EEG, erstens, den zeitlichen Verlauf anhand von ereignis-korrelierten Potenzialen (EKP) zu untersuchen und, zweitens, den zeitlichen Verlauf diskreter regionaler Quellenmodelle von statischen und dynamischen emotionalen Gesichtern zu beschreiben. Der Ansatz für die Quellenanalysemodelle basierte auf den Aktivierungsmustern der Kernspinstudie, die mit zusätzlich angepassten Quellen erweitert wurden.
Neunzehn gesunde spanische Probandinnen bekamen dieselbe Aufgabe wie die deutschen Probandinnen in der fMRT-Studie, damit die Studien für die geplanten Quellenmodelle vergleichbar blieben.
Ereigniskorrelierte Potentiale (EKP) der statischen Gesichter zeigten eine emotionale Modulierung der N170-Amplitude in rechts lateralisierten posterioren Elektroden bei glücklichen und angeekelten verglichen mit neutralen Gesichtern. Die „early posterior negativity“ (EPN) Komponente zeigte eine erhöhte Amplitude in ähnlichen Regionen. Darüber hinaus zeigten statische und dynamische emotionale Gesichtsausdrücke eine anhaltende Positivierung über zentro-parietalen Regionen verglichen mit neutralen Gesichtern, die für dynamische Gesichter deskriptiv stärker ausgeprägt war.
Regionale Quellen für statische Gesichtsausdrücke zeigten eine höhere Quellenstärke in der Insula für angeekelte verglichen mit neutralen Gesichtern zwischen 300 und 350 ms. Darüber hinaus modulierten emotionale Gesichter vor allem okzipito-temporale Regionen.
Im Gegensatz dazu, aktivierten dynamische emotionale Gesichtsausdrücke ein weiter verbreitetes Netzwerk an regionalen Quellen. Ekel zeigte höhere Quellenstärken im linken superior temporalen Gyrus (200 ms), linken präzentralen Gyrus (250 ms, 400ms), und rechten inferior frontalen Gyrus (300, 450 ms) verglichen mit neutralen Stimuli. Die Verarbeitung positiver Gesichtsausdrücke resultierte in einer höheren Quellenstärke im linken Cuneus (200 ms, 500 ms), linken fusiformen Gyrus (250ms), inferior frontal Gyrus (250 ms), und rechten medial frontal Gyrus (400 ms) im Vergleich zu neutralen Gesichtern.
Im Gegensatz zu den Quellenaktivierungen der statischen Stimuli, die Modulierungen vor allem in posterioren Regionen aufwiesen, zeigten dynamisch Stimuli ein Netzwerk von sowohl frontalen, als auch okzipito-temporalen Regionen. Dies könnte darauf hinweisen, dass statische emotionale Gesichter vor allem in Regionen verarbeitet wurden, die für die kontinuierliche strukturelle Analyse der Gesichter zuständig ist. Dynamische Stimuli wurden neben der strukturellen Analyse womöglich komplexer verarbeitet, da auch präfrontale Areale aktiviert wurden. Dies könnte durch den unterschiedlichen sozialen Kontext

(Momentaufnahme versus soziale Interaktionen), in denen man statischen Gesichtern begegnet, erklärt werden.

Die dynamischen Gesichtsausdrücke wiesen keine bessere Erkennungsgenauigkeit in der EEG-Studie im Vergleich zu statischen Gesichtern auf. Dieses Ergebnis wurde im Zusammenhang der unterschiedlichen kulturellen Herkunft der Probandinnen beider Studien diskutiert.

Funktionelle Aspekte der gefundenen Quellen wurden unter anderem im Kontext der Wahrnehmung von Ekel (v.a. in der Insula) und biologischer Bewegung (STG), Identitätswahrnehmung (FuG), und dem Spiegelneuronensystem beleuchtet. Die Ergebnisse der EEG-Studie unterstützen den Standpunkt, dass die Kombination von fMRT und EEG Erkenntnisse über die zeitlich-räumliche Verarbeitung der emotionalen Gesichterwahrnehmung erweitern.

Die Autorin der vorliegenden Dissertation integriert die Ergebnisse der beiden Studien, indem sie methodologische Herausforderungen und Limitationen der Kombination von fMRT und EEG aufzeigt, die Ergebnisse mit dem verbreiteten Emotions-Gesichterwahrnehmungsmodell von Adolphs (2002) in Verbindung bringt, und die Verarbeitung von dynamischen und statischen Gesichtern im Zusammenhang mit jüngsten Netzwerktheorien assoziiert.

Abstract

Emotional face processing is a very essential part of everyday life, especially during social communication. Studying emotion perception on dynamic facial expressions has been discussed as a promising and ecologically valid approach. In social contexts, facial expressions are of dynamic nature varying rapidly in relation to situational requirements and rarely appear static by nature. Therefore, emotion processing of happiness and disgust was investigated by dynamic and static facial expressions in two separate studies applying functional magnetic resonance imaging (fMRI) and electroencephalography (EEG).

To the author's knowledge, there are only few fMRI studies (no study examining dynamic disgust) and no EEG study using dynamic emotional stimuli. Consequently, further research of the processing of dynamic compared to static facial expressions is urgently required.

The aim of the first study applying fMRI was (1) to examine the neural networks involved in emotion perception of static and dynamic facial stimuli separately, and (2) to examine the impact of motion on emotional processing of dynamic compared to static facial stimuli.

Sixteen German females participated in an fMRI study performing a passive emotion perception task including static and dynamic faces with neutral, happy, and disgusted expressions. Stimuli were derived from a new face database. Therefore, participants rated static and dynamic facial expressions according to their arousal and valence.

Dynamic stimuli compared to static faces produced enhanced emotion-specific brain activation patterns in the parahippocampal gyrus including the amygdala, fusiform gyrus, superior temporal gyrus, inferior frontal gyrus, and occipital and orbitofrontal cortex. These regions have been discussed to be associated with emotional memory encoding, the perception of threat, facial identity, biological motion, the mirror neuron system, an increase of emotional arousal and reward processing, respectively. Posthoc ratings of the dynamic stimuli confirmed a better recognizability in comparison to the static stimuli. In conclusion, the display of dynamic facial expressions is assumed to provide a more appropriate approach to examine the processing of emotional face perception than the display of static stimuli.

The aim of the second study was (1) to study the time course of emotion processing via event-related potentials (ERP) recorded with 62-channel EEG and (2) to examine discrete regional source models of static and dynamic facial emotional stimuli based on previous fMRI activations complemented with additional sources. Nineteen healthy Spanish females performed the exact same design as applied for the fMRI study to keep both studies comparable for planned source model analysis.

ERP data of static facial expressions indicate a stronger deflection of the N170 amplitude in right-lateralized posterior electrode sites for emotional compared to neutral stimuli. Early posterior negativity (EPN) was modulated during disgust processing in similar regions. Both, static and dynamic facial expressions showed a sustained positivity (late positive potential, LPP) over centro-parietal areas for happy and disgusted compared to neutral facial expressions. LPP was descriptively enhanced for dynamic compared to static stimuli.

The constrained regional source model of static stimuli revealed an emotional modulation of the insula with an enhancement of activity of disgust compared to neutral stimuli between 300 and 350 ms. Furthermore, processing of static facial expressions was demonstrated predominantly in occipito-temporal regions.

In contrast, dynamic stimuli activated a wider network of anterior and posterior sources. Source power in dynamic stimuli yielded an enhancement of left superior temporal gyrus (STG) (200 ms), left precentral gyrus (250 ms, 400ms), and right inferior frontal gyrus (300, 450 ms) for disgust. In addition, an enhancement was shown in left cuneus (200 ms, 500 ms), left fusiform gyrus (FuG) (250ms), inferior frontal gyrus (250 ms), and right medial frontal gyrus (400 ms) for the positive compared to the neutral facial expressions.

While static stimuli resulted in predominantly posterior activations, which were presumably associated with the continuous structural analysis of stimuli, dynamic faces showed a more complex network of frontal, temporal and occipital sources. Thus, dynamic stimuli recruited networks involved in structural analysis, biological motion analysis and mirroring aspects. These results led to the assumption that static and dynamic facial expressions are processed due to diffent experience with them in different contexts (snapshot versus social interactions).

Better recognizability was not confirmed for dynamic compared to static faces. This result was discussed within the scope of possible cultural differences between samples.

Functional aspects of sources in the context of, for example, disgust perception (insula), biological motion (STG), facial identity perception (FuG), and the mirror neuron system are discussed. Results of the second study support the view that a combined fMRI and EEG approach of studying emotional perception enhances the present knowledge about the temporo-spatial relationships of different brain regions during emotion processing.

Integrating both studies, the author of the present thesis addresses methodological challenges and limitations by combining fMRI and EEG. Results are integrated with the emotional face perception model proposed by Adolphs (2002). Furthermore, the modality aspects of static compared to dynamic stimuli are addressed with regard to recent network theories.

Keywords

Emotion perception, static and dynamic stimuli, disgust, happiness, facial expressions, faces, EEG, ERP, topography, fMRI, fMRI constrained source analysis, combination of EEG and fMRI.

Abbreviations

(in alphabetic order)

AMG	amygdala
ANOVA	Analysis of Variance
AP	ANTERIOR-POSTERIOR (factor for repeated measurement ANOVAs)
BG	basal ganglia
rCBF	regional cerebral blood flow
DIS	disgust
ECD	Equivalent current dipole
EEG	electroencephalogram, electroencephalography
EMO	EMOTION (factor for repeated measurement ANOVAs)
ERP(s)	Event-related potentials
FFA	fusiform face area
fMRI	functional magnetic resonance imaging
FuG	fusiform gyrus
GLM	general linear models
H	height
HAP	happiness/happy
HPF	high pass filter
IAPS	International Affective Picture System
INS	insula
LAT	LATERALITY (factor for repeated measurement ANOVAs)
LAURA	Local Auto-Regressive Average Model
LORETA	low resolution brain electromagnetic tomography
LPF	low pass filter
LPP	late positive potential
MEG	magnetencephalography
MNS	mirror neuron system
MOD	MODALITY (factor for repeated measurement ANOVAs)
MOG	middle occipital gyrus
mm	millimeter
ms	millisecond(s)
µV	microvolt

nAm	nanoamperemeter
NEU	neutral
OFC	orbitofrontal cortex
PCA	principal component analysis
PHG	parahippocampal gyrus
PMA	premotor area
RMS	root mean square
ROI	region of interest
RS(s)	regional source(s)
SCR	skin conductance response
SD	standard deviation
sec	second(s)
SEM	standard error of mean
SEQ	SEQUENCE (factor for repeated measurement ANOVAs)
SMA	supplementary motor area
SMI	smile
SPM	statistical parametric mapping
STG	superior temporal gyrus
STS	superior temporal sulcus
SW	slow wave
VPP	vertex positive potential
W	width

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1 General introduction[1]

1.1 Structure of the present thesis

The present dissertation examines the neural correlates of the perception of static and dynamic emotional facial expressions of happiness and disgust compared to neutral faces. By applying functional magnetic resonance tomography (fMRI) and electroencephalography (EEG), the present thesis gives an overview of the spatio-temporal dynamics of face perception in static and dynamic modality.

The first chapter gives an overview of concepts of defining emotion and folk concepts of emotion. Furthermore, the importance of emotional face perception and its neural correlates are emphasized followed by a brief introduction of the used methods (fMRI and EEG). The chapter closes with the general aims and scope of the present thesis.

The following two chapters (Chapter 2 and 3) present the fMRI and the EEG studies of emotional face perception. Chapter four intends to integrate the results of those two mutually complementing methods. Chapter five finishes by suggesting an outlook for possible future lines of research of emotion perception.

1.2 Definition of emotion

"Everyone knows what an emotion is until asked to give a definition." (Fehr and Russell, 1984, p. 464).

Giving a definition of emotion is difficult. Defining the importance of emotions for human beings is slightly easier. From an evolutionary perspective, the detection of emotional events, which convey a strong value for the human being, has been shown to be important for survival. For example, rapidly detecting a dangerous animal used to be of high importance for survival in order to prepare oneself to either fight or flight (LeDoux, 1996). From a social perspective, the impact of emotions on one's thoughts, memory, concentration, decisions and behavior is (well known and) part of everyday life experience (Dolan, 2002). Emotions have been shown to be processed preferentially resulting in an increase of attention and a fast detection of those emotional events (for review see Dolan, 2002). Human beings are daily

[1] Chapters one, two, and four are in part modified from a manuscript which has previously been submitted to "Neuropsychologia" for publication.

confronted with the perception of, the interpretation of and the adequate reactions to different emotional facial expressions and complex emotional situations. Emotional events or scenes convey a high salience and are memorized better (LaBar and Cabeza, 2006). Besides emotions influence reason and motivational behavior and exhibit a strong importance in human relationships (Dolan, 2002). In a broader sense, emotions play an important role in regulating social behavior (Adolphs, 2002, 2003).
Emotions can be regarded from various perspectives and therefore, many different concepts of emotion have been suggested in the past (see Scherer, 2005, for review). Adolphs (2002) suggested a one-sentence-definition of emotions:

"Neurobiologists and psychologists alike have conceptualized an emotion as a concerted, generally adaptive, phasic change in multiple physiological systems (including both somatic and neural components) in response to the value of a stimulus" (Adolphs, 2002; p. 24).

According to Adolphs, emotions are complex psychological and physiological states which have an onset, a finite duration and an offset. Moreover, they are an important factor for social communication (Adolphs, 2002).
Emotions should not be confused with mood or affect. Mood can be distinguished by rather diffuse affective states, which can last from hours to days and which do not have an apparent cause (Levine, 2007). Affect has been defined as the outward, physical signs of emotions evoked by the autonomic nervous system resulting in a change of heart rate, blood pressure, perspiration, breathing etc. (e.g., Levine, 2007; Williams et al., 2005). Somatic changes in correlation with emotion perception are a wide and a very interesting field of research, but it would be beyond the scope of the present thesis to further discuss it. The present thesis addresses the neural processing of emotions. A more detailed definition follows below.
The next chapter (Chapter 1.2.1) gives an overview of a portion of the vast amount of different psychological concepts which have been proposed to classify emotions (see Scherer, 2005, for review).

1.2.1 Psychological concepts of emotion

The *discrete emotion theory*, which was inspired by Darwin (Darwin, 1965) and elaborately pursued by Paul Ekman and colleagues (Ekman, 1994), suggests that emotions can be defined as discrete emotional states (Adolphs, 2002). This approach is based on semantic concepts of language which enable to classify and to describe basic emotions. The number of basic

emotions varies from six to 14 depending on the approach (for review, see Scherer, 2005). Some emotions, like joy (or happiness), anger, disgust, fear, surprise, and sadness, have been shown to be recognized and generated universally across cultures. Therefore, they were defined *basic emotions* (Ekman et al., 1987; for review, see Scherer, 2005). Basic emotions facilitate adaptation to external events and have been shown to be important for survival because of the necessity to react rapidly (Scherer, 2005). The present thesis applied two basic emotions: happiness and disgust.

The *dimensional approach*, which was pioneered by Wilhelm Wundt (1905; in Scherer, 2005), suggests categorizing emotions in two dimensions. These include valence (pleasant to unpleasant or positive to negative) and arousal (low to high arousal or also excitement). Hence, the emotional state is described by a point in a two dimensional grid (Russel, 1983; in Scherer, 2005).

Adolphs (2002; e.g., see Table 1 on page 28) summarized possible categorization approaches which propose to classify emotions according to their motivational state (reward versus punishment), moods (depression, anxiety, contentment), approach and withdrawal (see also Davidson and Irwin, 1999, for neural correlates of the approach-withdrawal approach), or social emotions (pride, embarrassment, guilt etc.).

Further psychological concepts to categorize emotions have been reviewed extensively, for example, by Scherer (2005).

1.2.2 Excursion: folk concepts versus scientific concepts of emotion

Based on the above mentioned concepts of emotion the author of the present dissertation was wondering how people define emotions and in how far their concepts are in line with the above mentioned theoretical frameworks.

Asking folks (only women) how they would define “emotions” the following answers were given:

- “Emotions are feelings which can either be positive or negative. “
- “Emotions are short in comparison to feelings which are rather prolonged, like, for example, romantic love.”
- “Emotions evoke reactions in the body.”
- “Emotions are evoked by, for example, situations, thoughts, objects or pictures which can either make me sad or happy.”
- “Emotions can be defined as excitement, fear, joy, happiness, sadness, being in love

among many other emotions. Emotions touch my soul and my heart, but less my brain."

- "Emotions act on instinct."
- "Life would be boring and unspectacular without emotions."
- "Emotions cannot always be controlled and have a big impact on our behavior and thoughts. Sometimes it is hard to inhibit emotions."[2]

The above introduced folk concepts of emotion are reflected in the vast amount of scientific theories, which tried to define and classify emotions (Adolphs, 2002; Scherer, 2005). Folks have mentioned the classification of emotions as being either positive or negative which has been reflected by the *dimensional approach* (see above*)*. The notion of "Life would be … unspectacular without emotions" might be associated to arousal, which has been shown to be induced by emotions, and to be part of the *dimensional emotion approach* (for review, see Scherer, 2005). On the other hand, individuals defined emotions by finding semantic labels like happiness, joy, sadness, love etc., which can be related to the *discrete emotion approach* (see Chapter 1.2.1). Furthermore, they mentioned "reactions in the body" which could be related to the complex somatic changes, like endocrine, visceral, and autonomic changes during an emotional reaction (Adolphs, 2002). "Emotions act on instinct" or "Emotions cannot always be controlled …" support previous findings that emotions have a high impact on behavior, thoughts, memory, decisions (Dolan, 2002). In summary, theoretical concepts of emotions seem to be concordant with folk concepts and vice versa.

Chapter 1.2 overviewed the importance of emotion in everyday life. The following chapters (Chapter 1.3 and 1.4) highlight current neuroscientific research of emotional face processing. One of the best understood ways in neuroscience to study emotion processing is by the application of static facial expressions.

1.3 The fascination of facial expressions

Faces are fascinating, surprising, amazing, interesting, complex, different, unique, expressive, sad, happy, angry, informative, exciting, arousing, capturing, and probably hundreds additional character traits. There are several reasons why faces are fascinating and an important and appropriate approach to study emotion:

1. Darwin (1965) has already highlighted the evolutionary role of faces and emotional

2 These definitions were gratefully received by the author's female friends who gave informed consent about the anonymous inclusion of those definitions in the current thesis.

facial expressions. Being able to perceive, recognize and interpret facial expressions poses an advantage for survival. Fearful expressions indicate possible danger and the importance for fight or flight reactions (Darwin, 1965). Understanding facial expressions of, for example, disgust could pose an advantage for survival. Assumed, the food in front of one's counterpart might be contaminated and poisoned. Consequently, it should better be avoided (Rozin and Fallon, 1987). It would be of high importance for survival to be able to understand this facial expression, and to be able to avoid the contaminated food. Thus, emotional facial expressions give rise to the emotional state of the people with whom one interacts.

2. Therefore, it is essential that facial expression and emotional context are analyzed and interpreted appropriately because they constitute the basis for social interactions (Adolphs, 2002; Posamentier and Abdi, 2003; Vuilleumier and Pourtois, 2007). Facial expressions convey information that are inevitably important for everyday social interactions in humans because they comprise a large array of social signs (Adolphs, 2002). Being able to analyze, comprehend, interpret and react to these signs is extremely important for human beings.
3. Faces consist of multi-dimensional information. They communicate structural information about features and configurations, which are integrated into a holistic percept during the processing of faces. Hence, important and complex social signals (like emotional expressions and nonverbal gestures) with high motivational significance can be extracted from a face (Vuilleumier and Pourtois, 2007). These signals include information about the identity, emotional condition, gender, age, trustworthiness, attractiveness, gaze, and intention which can be derived from a face (Adolphs, 2002; Phan et al., 2002; Posamentier and Abdi, 2003).
4. Human beings encounter innumerable faces during their lives. According to Haxby and colleagues, they are experts for face perception and recognition (Haxby et al., 2000).
5. Faces displaying basic emotional expressions are recognized independently from cultural background. Thus, basic emotional expressions are recognized across various cultures and are, therefore, called "universal" (Ekman et al., 1987).
6. The human brain is able to distinguish a large amount of different faces even under different physical circumstances, like complex changes in viewing angle, appearance, and age (Posamentier and Abdi, 2003).
7. Emotional expressions are contagious (Wild et al., 2001) and thus, convey a high

relevance which presumably facilitates the processing of emotions and accompanying perceptual and cognitive processing demands.

Some of the mentioned aspects are discussed in more detail in the following chapters. They comprise an incomplete, small number of reasons why the face and facial expressions are fascinating and a very interesting and appropriate approach to study emotions. The present thesis focuses on two discrete and opposing emotional valences, namely happiness and disgust.

Smiling - or synonymous happy or positive - faces are related to positive emotions, the sole positive emotion out of the six basic emotions: happiness, fear, anger, disgust, surprise, and sadness. Happiness has various representations: enjoyment, dampened, miserable, compliance, coordination, flirtations (McNeill, 1998, p. 206-208), but this work will focus on the basic emotion of happiness displayed as smiling faces. Smiling faces are rewarding and apparently processed faster than other emotional valences (Leppanen and Hietanen, 2004).

Disgust is an emotion which is probably less often encountered by people in everyday life compared to happy facial expressions. However, the evolutionary role of disgust refers to the importance of avoiding contamination and poisoning, for example, in regards to rejection of harmful food (Rozin and Fallon, 1987).

So far, the importance of emotions and emotional face processing was illustrated. The following Chapter 1.4 elucidates recent neuropsychological models of emotional face processing.

1.4 General models of face and emotional face perception

Before the implementation of fMRI to neuroscientific research was introduced in the nineties, research on the neural correlates of emotion processing were predominantly based on pharmacological and electrophysiological approaches, as well as on lesion studies (Murphy et al., 2003). These studies resulted in many different models of emotion processing.

For example, single- and dual-system models of emotion processing intended to describe the relationship between the function and structure of the brain in emotional processing (for review, see Murphy et al., 2003).

One of the earliest single-system approaches was introduced by MacLean (1949, 1952; cited in Murphy et al., 2003) who suggested that the neural basis for emotion processing was located within the limbic system. Alternatively, the “right-hemisphere hypothesis” suggested that all aspects of positive and negative emotions were processed solely within the right hemisphere (e.g., Sackeim & Gur, 1978; in Murphy et al., 2003). The “valence hypothesis” - a

dual-system approach - proposed that the left hemisphere processed positive and the right hemisphere processed negative emotions (e.g., Davidson, 1984; in Murphy et al., 2003). For a more detailed discussion of those models, the author refers the reader to Adolphs and Murphy and colleagues, respectively (Adolphs, 2002; Murphy et al., 2003).

By applying fMRI, these models could be reassessed with a higher spatial resolution. To date, there have been a vast amount of papers reviewing the neural basis of emotion perception, emotion recognition, and emotional experience (Adolphs, 2002; Davidson and Irwin, 1999; Murphy et al., 2003; Phan et al., 2002). Two contemporary models of face (Haxby et al., 2000) and emotion perception (Adolphs, 2002) are introduced in the following chapters (Chapter 1.4.1 and 1.4.2), which have extended previous models and which display a network of interacting brain regions during emotion processing.

1.4.1 The modified face perception model by Haxby and colleagues (2000)

When studying face and emotional face perception, one obligatorily encounters the face perception model proposed by Bruce and Young (Bruce and Young, 1986). Based on this face perception model by Bruce and Young (1986), Haxby, Hoffman, and Gobbini (2000) modified the latter model. This modified model is based on a core and an extended system of face perception (see Fig. 1 for illustration). The core system represents the visual analysis of faces and comprises the inferior occipital gyri for early visual analysis, the fusiform face area (FFA) for the processing of facial features and identity, and the superior temporal sulcus (STS) area for the processing of changeable facial features (i.e., eyes, mouth, expressions; see also Allison et al., 2000, for review). The extended system is reciprocally linked to the core system and comprises the auditory cortex (i.e., for lip reading), parietal areas (i.e., for spatial attention to changeable features), the temporal pole (TP, associated with autobiographical information, names, and personal identity), and the amygdala (AMG, emotion, facial expressions).

Haxby and colleagues claimed that the temporal sequence of processing of the different stages of the model should be addressed in detail in future studies (Haxby et al., 2000). The emotional face perception model by Adolphs (2002) addressed this aspect.

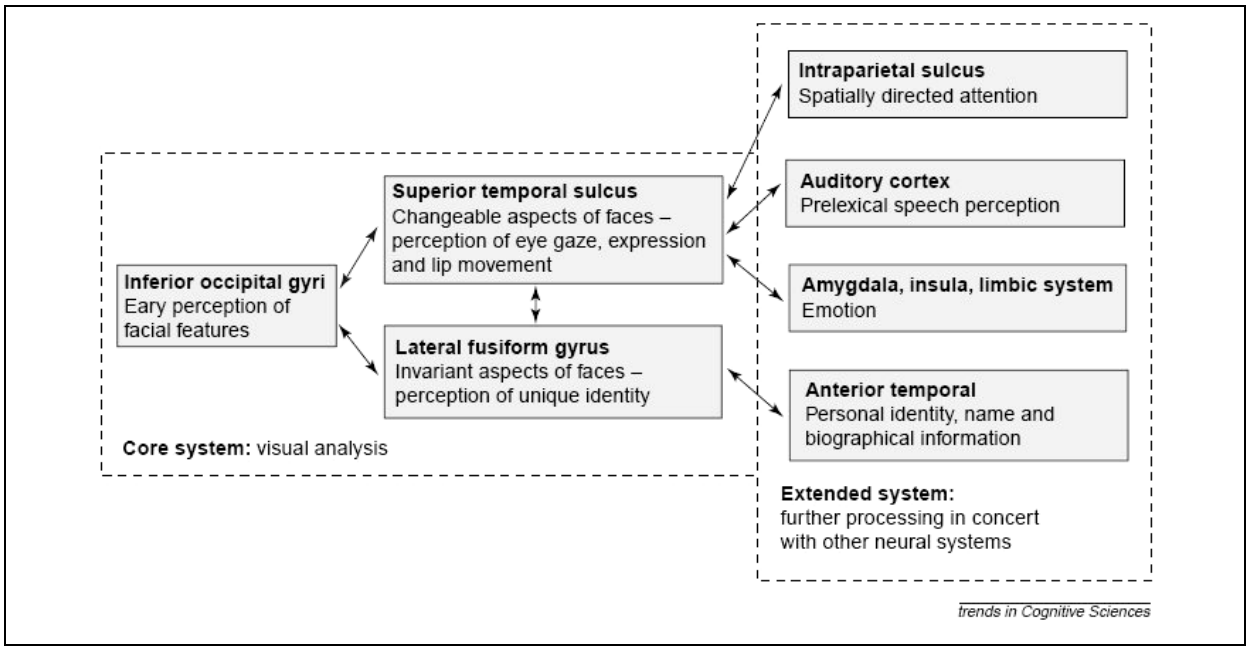

Figure 1: Reprint of Haxby's and colleagues (2000, see p. 230) modified face perception model which was originally based on the face perception model by Bruce and Young (1986).

1.4.2 The emotional face perception model by Adolphs (2002)

Adolphs (2002) extended the face perception model (Haxby et al., 2000) by adding the temporal dimension of face and emotion perception and recognition (Fig. 2). Within the first 120 ms after emotion onset, the amygdala (AMG), early (at this point, the AMG is activated in the early processing stage), the striate cortex and the thalamus are proposed to process and encode automatically very early perceptual structures of salient emotional stimuli. This is considered to be equivalent to the "core system" suggested by Haxby and colleagues (Adolphs, 2002; Haxby et al., 2000).

The "extended system" of emotion recognition modules comprises the striate cortex, the fusiform face area (FFA; early), superior temporal gyrus (STG; early), the AMG, late (reactivation of the AMG), the orbitofrontal cortex (OFC) and the basal ganglia (BG). The latter regions are proposed to play a role in processing the motion of emotional expressions, even if simply implied in static stimuli (superior temporal sulcus area [STS], especially for changes in mouth and eye area; for review, see Allison et al., 2000; Haxby et al., 2000; Hoffman and Haxby, 2000). Moreover, they are involved in allocation of attention, in planning of motor components of facial expressions, in triggering autonomic body changes and in the more detailed face perception and identification about 170 ms after stimulus onset (FFA; for review, see Haxby et al., 2000; see also Kanwisher et al., 1997).

Magnetencephalography (MEG) and/or EEG studies of face recognition of pleasant, unpleasant and neutral faces confirmed a face- and emotion-specific N170 component in occipito-temporal areas (Batty and Taylor, 2003; Pizzagalli et al., 2002; Righart and de Gelder, 2006). Deeper cognitive evaluation and the combination of the conceptual knowledge of the perceived emotion of the stimuli is processed by FFA (late), STG, OFC, somatosensory and insular cortex at about 300 ms after stimulus onset represented by the "cognitive system" (Adolphs, 2002; see also Fig. 2).

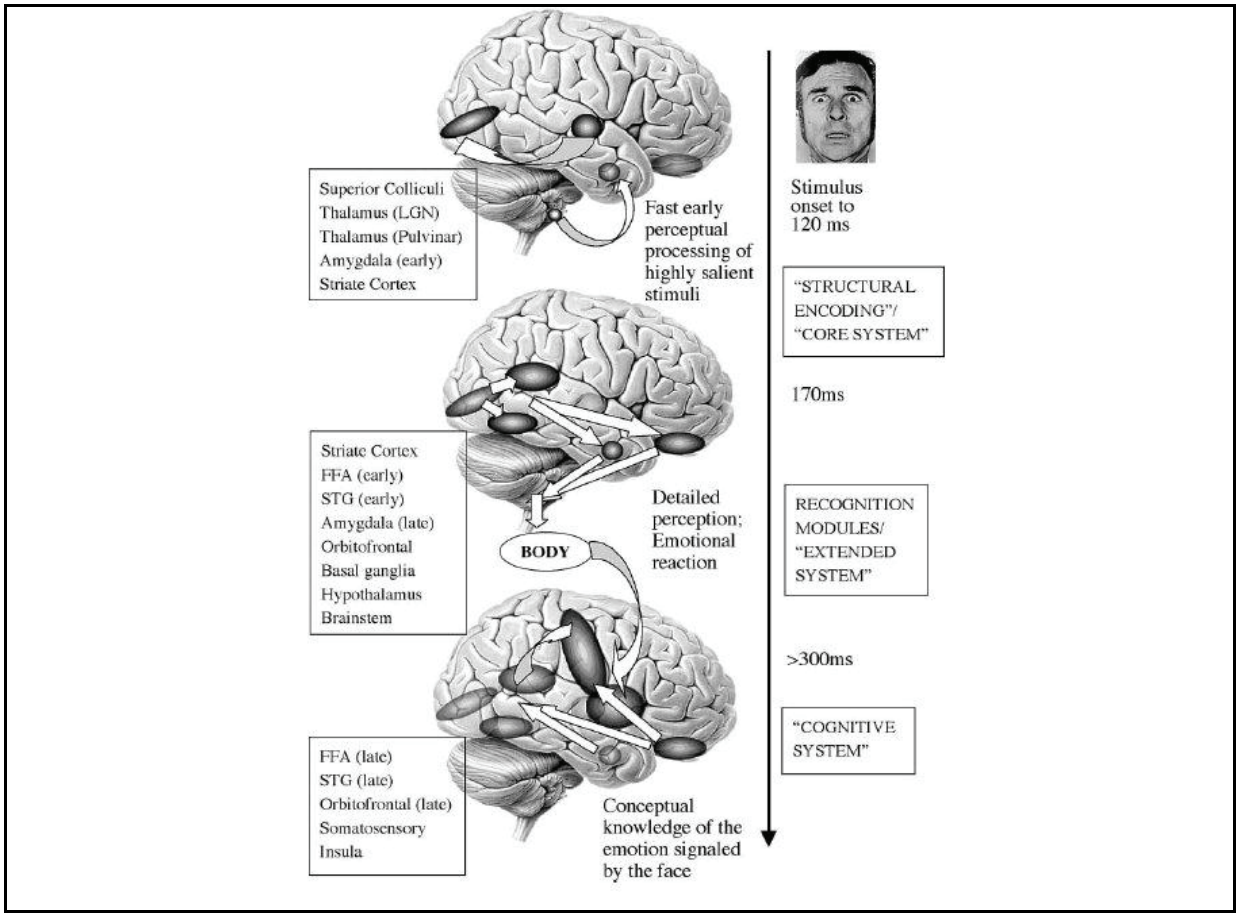

Figure 2: Emotion perception model by Adolphs (2002, p. 52) incorporating both temporal and spatial information of emotion perception.

Based on these two models, recent findings in emotion perception applying fMRI and EEG will be discussed in more detail in Chapter 2 for fMRI and in Chapter 3 for recent EEG studies. In Chapter 4, results of both studies are integrated into the emotional face perception model by Adolphs (2002).

1.5 Emotional face processing in static versus dynamic stimuli

The majority of studies on emotion perception (for review, see Adolphs, 2002; Davidson and Irwin, 1999; Murphy et al., 2003; Phan et al., 2002) have used stimuli displaying static emotional facial expressions (see also Ekman and Friesen, 1976) neglecting the dynamic features of facial expressions which seem to be necessarily involved in an ecologically more valid approach. Even though their natural and ecological validity has been questioned by many researchers as discussed in a review article by Posamentier and Abdi (2003), most of the emotion perception studies have used static facial expressions. To date, there have been only a small amount of publications studying dynamic face perception in fMRI, none examining the dynamic face perception of disgust neither in EEG nor in fMRI, and no EEG study applying dynamic facial expressions per se.

Natural features (Harwood et al., 1999; Sato et al., 2004), however, should be considered for stimulus construction because they convey an increased richness of temporal and structural facial object properties, which improve the three-dimensional perception (Knight and Johnston, 1997). These features, in turn, potentially facilitate emotion recognition and might even support the processing of social interactions in a more natural way (Bassili, 1979; Berry, 1990; LaBar et al., 2003; Sato et al., 2004). Behavioral studies on moving facial expressions corroborated this line of argumentation and showed higher arousal reactions such as an increase of skin conductance and electromyographic responses (Simons et al., 1999; Weyers et al., 2006), as well as better recognition performance (Ambadar et al., 2005; Bassili, 1979; Harwood et al., 1999) during a rating task on dynamic compared to static emotional facial expressions.

Relating those aspects to daily communication among human beings, it is important to include dynamic emotional face perception into current scientific investigations to broaden the knowledge about dynamic emotion perception because when humans communicate, they do so by incessantly moving their faces, changing quickly from one expression to another. Thus, one must be able to interpret the nonverbal, temporal changes of the face quickly in order to be able to characterize the type of conversation aside from the verbally conveyed content. In contrast, people do not simply stare and do not move their faces during communication. This is, however, what photos of facial expressions actually convey and what is, hence, not natural and realistic. That is the reason why the use of dynamic stimuli is recommendable and will be investigated in the present thesis with fMRI and EEG.

1.6 A brief overview of applied methods

Scientists aspire to understand the neuronal processing mechanisms by revealing spatio-temporal dynamics with fMRI and EEG. A short outline of both methods is presented in the following paragraphs.

1.6.1 FMRI and BOLD signal

The first study applied fMRI and examined the BOLD signal during emotion processing. Neuronal activity results in changes of regional cerebral blood flow (rCBF), blood volume and blood oxygenation which has been called neurovascular coupling (Arthurs, 2002). FMRI is sensitive to detect changes of oxygenated and deoxygenated blood/hemoglobin because of its magnetic and paramagnetic characteristics, respectively. These properties have an impact on the strength of the MR signal (T2*). Activation of local brain regions, which is evoked by, for example, a cognitive task, results in the consumption of oxygenated hemoglobin which in turn increases the concentration of deoxygenated hemoglobin in a first step. Deoxygenated hemoglobin produces inhomogeneities in the magnetic field of the MRI because of its paramagnetic properties and leads to a decrease in (T2*-weighted) MR signal. An increase in the flow of oxygenated blood follows in a second step which leads to an increase of MR signal due to its magnetic properties before the signal returns to baseline in a last step (Heeger and Ress, 2002; Hopfinger et al., 2005). The hemodynamic response increases slowly with neuronal activity, and is, hence, an indirect and temporally delayed measure of brain activation (Hopfinger et al., 2005; Huettel et al., 2004). FMRI typically measures the ratio of oxygenated and deoxygenated hemoglobin, the so-called “blood-oxygenation level dependent” or “BOLD” effect, in the brain (Kwong et al., 1992; Ogawa et al., 1990). FMRI allows precise localization of brain regions within the range of one to three millimeter with the drawback of a low temporal resolution between five and eight seconds (Arthurs, 2002). But on the other hand, one should keep in mind that the correlation of neural activity, increases of rCBF, oxygen metabolism (increase of ratio oxygenated to deoxygenated hemoglobin), and increased BOLD signal have still not been 100 per cent elucidated (Arthurs, 2002; Hopfinger et al., 2005).

1.6.2 EEG, ERPs, source analysis

The second study of the present thesis applied EEG to examine event-related potentials (ERPs) and fMRI constrained source analysis to describe the spatiotemporal dynamics of emotional face perception (Chapter 3).

The electroencephalogram (EEG) is based on spontaneous electrical brain activity and is, more specifically, based on postsynaptic potentials of the cell body of neurons. Measurable voltage develops as followed: an excitatory neurotransmitter is released at the apical dendrites of a cortical pyramidal cell, a net negativity around the apical dendrites outside the cell results, whereas a net positivity around cell body results due to the current flow which leaves the cell body (Luck, 2005b). These processes generate a small dipole. However, voltage can only be measured on the scalp if large assemblies of neurons receive the same sort of input (inhibitory or excitatory), are of similar orientation (best in pyramidal cells which are aligned in perpendicular orientation to the scalp surface), and occur at approximately the same time so that their dipoles summate. If those conditions are not fulfilled, dipoles are too weak to be recorded or cancel themselves out (e.g., during simultaneous inhibitory and excitatory activation; Luck, 2005b). These voltage differences are called electroencephalogram (EEG) and represent a rather direct neural activity compared to the BOLD effect measured by fMRI.

Event-related potentials (ERPs) represent averaged time windows of EEG fluctuations which are time-locked to repeated occurrences of internal or external events. Random EEG fluctuations are averaged out and, therefore, the event-related brain potentials remain. ERP components represent a sequence of positive and negative deflections which represent different sensory, motor, and or cognitive processes with a high temporal resolution in milliseconds, but with the drawback of a low spatial resolution (Luck, 2005b).

In addition to the temporal information derived by ERP analysis, ERPs can provide spatial information to a limited extent by applying free source analysis approaches (Hopfinger et al., 2005; Luck, 2005a; Slotnick, 2005). While a specific source configuration results in a unique scalp topography (forward solution), the opposite is the case in ERP studies because only the voltage topography of ERPs are known. Thus, an infinite number of different source configurations can result in the same topography which is called the “inverse problem” (the so called “illposedness of EEG”). The “inverse problem” can be approached by the “inverse solution” which depends on the “forward solution” (Slotnick, 2005). A model of dipole configurations is compared to the actual topography of the recorded data by:

- the determination of head models which represent the head as, for example, a sphere which takes into account different conductance characteristics (brain, bone, cerebrospinal fluid, and scalp),
- the determination of the number of the to be fitted dipoles, and
- the use of iterative error minimization algorithms at each time point, as - among other programs - implemented in, e.g., BESA®.

To what extent the two models match is expressed by the unexplained variance, also called the residual variance of the model (Hopfinger et al., 2005; Luck, 2005a; Slotnick, 2005). Additional sources, sequentially fitted, help to reduce the unexplained variance. The problem of this approach is the high influence of input by the investigator who is supposed to determine the head model and the number of sources a priori.

Combining the advantages of both fMRI and EEG yields an even better approach to modeling the spatio-temporal dynamics of cognitive and emotional processes. Using prior knowledge of anatomy and physiology like, e.g., activation clusters as specified by BOLD contrasts in an fMRI measurement, in an identical design is called an fMRI constrained or seeded source model approach (Luck, 2005a). Constraints have been shown to improve the explanation of the model of the recorded data (Hopfinger et al., 2005; Michel et al., 2004; Scherg and Berg, 1991) because spurious sources can largely be ruled out (see Im, 2007, for more detailed methodological discussion of mismatched sources in EEG and fMRI). Since mismatches between BOLD activations and EEG sources have previously been reported, additional sources even enhance the quality of the seeded source model (Im, 2007). That is why additionally fitted sources were added to the seeded source model in the present EEG study (Chapter 3). This is an appropriate approach because identical stimulus designs were applied in the current two studies (see Chapter 2.2.3 and 3.2.3).

1.7 Aims and scope of the present studies

Emotion and face perception are two fundamental processes the human brain encounters everyday. Since most of the studies have previously investigated static face perception, which is not as natural as moving facial expressions (Chapter 1.5), it appears that there is a large need to broaden the knowledge about the temporo-spatial relationship of static and dynamic face processing.

The present thesis mainly focuses on the processing of two basic emotions (happiness and disgust), and its basic neuronal processing which is examined by its spatial (fMRI) and temporal (EEG) correlates because basic emotions have been shown to be universal across cultures. Consequently, human beings from different cultural background (European, Asian etc.) have been able to categorize those expressions appropriately according to their valence (Ekman et al., 1987).

As mentioned above, there have only been few emotion perception studies applying dynamic stimuli in fMRI (Kilts et al., 2003; LaBar et al., 2003; Sato et al., 2004). To date, there has been no fMRI study investigating the perception of dynamic facial expressions of disgust and

no study examining dynamic emotional face perception with EEG or fMRI constrained source analysis. The latter aspects emphasize the importance of the following studies and analyses. They address the combination of two methods because they complement each other due to the excellent temporal (EEG, in ms) and spatial resolution (fMRI, in mm; see also Chapter 1.6).

Two studies applying the same experimental design were conducted (1) with fMRI and (2) with EEG measuring two different samples of participants. In both studies, female participants were asked to watch dynamic and static stimuli of disgusted, happy, and neutral expressions passively and empathize with the presented expression.

The aim of the first study (Chapter 2) was (1) to investigate the BOLD response in a network of brain regions processing the presentation of static and dynamic facial expressions, (2) to discover differences in the processing of both valences compared to neutral condition, and (3) to specify differences during the processing of static and dynamic faces.

In a second EEG study (Chapter 3), the goal was (1) to characterize emotion-specific differences in topographies and typical ERP components for each static and dynamic stimulus material. Furthermore, the aim was (2) to examine the time course of emotional processing in several brain regions represented by an fMRI constrained source model complemented with additional regional sources. Due to the high temporal resolution in EEG and the different physical characteristics of the videos and the photos, ERPs and source waveforms of static and dynamic faces were compared descriptively.

In summary, the thesis investigates the basic neural correlates and temporal dynamics of static and dynamic emotional face processing of disgust and happiness.

2 Study 1: fMRI study of dynamic and static facial expression processing of happiness and disgust

2.1 Introduction: evidence from fMRI studies investigating emotion processing

2.1.1 Distinct networks of emotion processing revealed by fMRI

Numerous studies provided evidence for an involvement of emotion-related neural networks in the perception of emotional face expressions (for reviews, see Adolphs, 2002; Davidson and Irwin, 1999; LeDoux, 1996; Murphy et al., 2003; Phan et al., 2002). Brain areas involved in emotional face processing are the amygdala (predominantly related to the perception of negative stimuli; Anderson et al., 2003; Breiter et al., 1996; Morris et al., 1998; Murphy et al., 2003), the insula (disgust perception; Phillips et al., 2004; Phillips et al., 1998; Phillips et al., 1997; Sprengelmeyer et al., 1998; Sprengelmeyer et al., 1996), the superior temporal sulcus and anatomically adjacent areas, e.g., middle, superior temporal gyrus and angular gyrus (referred to as the STS area, biological motion of facial expressions; STS area reviewed in Allison et al., 2000; see also Haxby et al., 2000; Narumoto et al., 2001; Pessoa et al., 2002; Phillips et al., 1998), lateral inferior temporal and fusiform gyrus (referred to as the fusiform face area, FFA, for structure and identity of faces; Haxby et al., 2000; Hoffman and Haxby, 2000; Kanwisher et al., 1997), the orbitofrontal cortex (OFC, pleasant stimuli associated with social reward; Gorno-Tempini et al., 2001; O'Doherty et al., 2003), and primary and secondary visual areas (visual analysis modulated by emotion and attention; Lane et al., 1999; Lang et al., 1998). Confirmatively, studies concerning Huntington disease gene carriers (Gray et al., 1997) and lesion studies of the basal ganglia and insula (Calder et al., 2000) have indicated a selective impairment of disgust recognition confirming the latter results.

The processing of positively valenced faces has been reported more ambiguously. While Murphy and colleagues (2003) associated the perception of happy faces to rostral supracallosal ACC structures, Davidson and Irwin (1999) and Phan and co-workers (2002) reported activation of the basal ganglia (ventral striatum and putamen) linked to happy face processing.

2.1.2 The use of dynamic stimulus material in emotion perception

To date, there are only few neuroimaging studies addressing the perception of dynamic

emotional stimuli, and, to the author's knowledge, there is no fMRI study examining the neural processing of dynamic facial expressions of disgust. In a PET study, Kilts et al. (2003) contrasted dynamic and static emotional face stimuli showing smiling and angry facial expression. They reported increased activity in V5, STS area and periamygdaloid area for dynamic versus static angry faces and cuneus, V5, lingual, middle temporal and medial frontal gyrus for dynamic versus static happy faces. LaBar and co-workers (2003) using fMRI presented photographs and morphed videos of emotional expressions of anger and fear and reported an enhancement of activation for emotional compared to neutral expressions in - among other - the fusiform gyrus (FuG), the ventromedial prefrontal (also orbitofrontal) cortex and the STS area for dynamic stronger than for static faces. This data support the idea that the processing of dynamic aspects of emotional stimuli facilitate the recognition of emotional faces because they convey, in addition to structural aspects, temporal cues of the changing face (Kilts et al., 2003; LaBar et al., 2003). Sato and colleagues (2004) applied a passive viewing task including happy and fearful dynamic faces. They described more widespread activations for dynamic compared to static facial expressions in happy and fearful expressions when compared to neutral faces or mosaics of scrambled faces. In line with the work of Kilts and colleagues (2003) and Labar and colleagues (2003), Sato and co-workers (2004) concluded that dynamic stimuli convey more lively and realistic aspects of faces occurring in social interactions leading to more widespread activation patterns.

The above mentioned studies demonstrated that the processing of dynamic in contrast to static facial expressions appear to more consistently recruit neural networks of emotion processing such as the amygdala (Kilts et al., 2003; LaBar et al., 2003), fusiform gyrus, inferior occipital, middle and superior temporal regions STS area (for reviews, see Allison et al., 2000; Haxby et al., 2000), motion sensitive areas (MT+/V5), and the lateral inferior frontal cortex (mirror neuron system; Buccino et al., 2001; Kilts et al., 2003; LaBar et al., 2003; Leslie et al., 2004; Sato et al., 2004). Although studies addressing the processing of dynamic and static facial expressions appear to present rather convincing results, one might argue that the validity of the inferred conclusions might be biased by the use of artificial and non-natural stimuli. In several studies, dynamic stimuli including computer generated faces (Krumhuber and Kappas, 2005) or morphed stimuli which were constructed on the basis of static stimuli, e.g., the face inventory introduced by Ekman and Friesen (1976; see also Sato et al., 2004), or other emotional face databases (Biele and Grabowska, 2006), have been used as stimulus material. For instance, video streams were constructed by arranging pictures of faces, representing different stages of facial expressions, in consecutive order (Biele and Grabowska, 2006;

Krumhuber and Kappas, 2005; Sato et al., 2004). Thus, faces displayed an "artificial" motion from a neutral to an emotional target expression. Natural moving faces are assumed to provide a more valid stimulus basis for the examination of neuronal correlates of facial expression perception. Gepner and colleagues (2001) produced videos showing an actress displaying different emotional expressions. However, since the stimuli repeatedly displayed exclusively one individual, study participants might have run the risk of habituation. For this reason, a new stimulus data set was developed based on 80 different actors and actresses (for detailed description, see Chapter 2.2.3).

2.1.3 Goals and hypotheses of the present fMRI study

The present study aimed at two central points:
Firstly, by using a new stimulus database, the emotion-specific neural activation patterns of emotional (happiness/disgust) compared to neutral faces should be examined. The above discussed network of emotion-specific areas was expected to be more consistent in dynamic compared to static emotional face stimuli, especially in striate and extrastriate regions (happy), inferior temporal gyrus (FFA), middle and superior temporal gyrus (STS area), medial superior frontal (supplementary motor area, SMA) and inferior frontal areas, insula and amygdala (disgust), and ventromedial frontal/orbitofrontal regions.
Secondly, neural activation patterns of both emotional valences during perception in dynamic compared to static stimuli were examined. A more widespread activation pattern in dynamic face processing was expected resulting in a signal increase in areas associated with emotion perception (insula and amygdala for disgust), the processing of biological motion (such as the medial and superior temporal gyrus; see also Allison et al., 2000), facial identity (FFA; Kanwisher et al., 1997), mirroring neuron system (inferior frontal gyrus; Buccino et al., 2001), and reward processing (ventromedial and OFC; Gorno-Tempini et al., 2001). This enhanced "emotion by motion" effect should also result in a better recognition rate of the different facial expressions in dynamic compared to static stimuli.

2.2 Material and methods: fMRI study

2.2.1 Participants

The study group consisted of 16 female adults between 19 and 27 years (mean: 21.6 years ± standard deviation [SD] 2.3) from Bremen University campus in order to avoid gender-specific confounds (for review, see Wager et al., 2003). All participants were right-handed

according to a modified version of the Edinburgh Handedness Inventory Questionnaire (Laterality Quotient: 92.3 % SD 9.7, range 69.2 - 100 %; Oldfield, 1971), did not report any history of neurological or psychiatric illness, and were under no current medication affecting the central nervous system. All participants were native German speakers with 14 to 18 years of education (15.1 ± 1.5 years) and had normal or corrected to normal visual acuity.

Only female participants were included in the study group because previous fMRI-studies about gender differences in emotion perception have been controversial (for review, see Wager et al., 2003). Wager and colleagues (2003) concluded in their meta-analysis of 65 neuroimaging studies of emotion that gender differences have been reported in regard to stronger lateralization of emotion perception in men compared to women (Wager et al., 2003). Furthermore, since they also mentioned that women usually showed stronger activation during subjective emotional processing tasks, an exclusively female sample was chosen in order to achieve a better signal to noise ration (SNR) and to avoid confounding gender differences. A similar line of argumentation has been confirmed in EEG studies reporting increased amplitudes for emotional stimuli in women compared to men (Orozco and Ehlers, 1998).

2.2.2 Data protection, data security and legal framework

The participants gave informed and written consent to participate in the fMRI experiment (see Appendix A.1 - A.3). The study protocol was designed and performed according to the Helsinki Declaration (1964/2004) and was approved by the local ethics committee of the University of Bremen.

Participants were informed about data collection, data protection, and data security of all experimental and personal data belonging to the participant. Furthermore, participants were informed about general and specific risks of the experimental equipment used during functional magnetic resonance imaging (fMRI; see Appendix A.1-A.3). According to this information and their right to quit the experiment during the entire course of the examination, participants gave written and informed consent for their participation prior to the beginning of the experiments (see Appendix A.1-A.3). Participants were naïve to both the working hypotheses and the stimulus material.

2.2.3 Experimental procedure: study design and strategies of data analyses

2.2.3.1 Stimulus material

A set of emotional videos and video screen captures was introduced showing different facial expressions. The stimuli were taken from a newly developed stimulus database of 40 female and 40 male non-professional actors displaying each of eight different emotional facial expressions (happiness (smiling and laughing), surprise, enjoying, fear, anger, sadness, and disgust) and neutral expressions. Forty female and 40 male non-professional actors, mainly students (between 19 and 38 years), were recruited on campus or by advertisement on different notice boards. Participants were supposed to appear as authentic and close to the normal population as possible (see also Fig. 3).

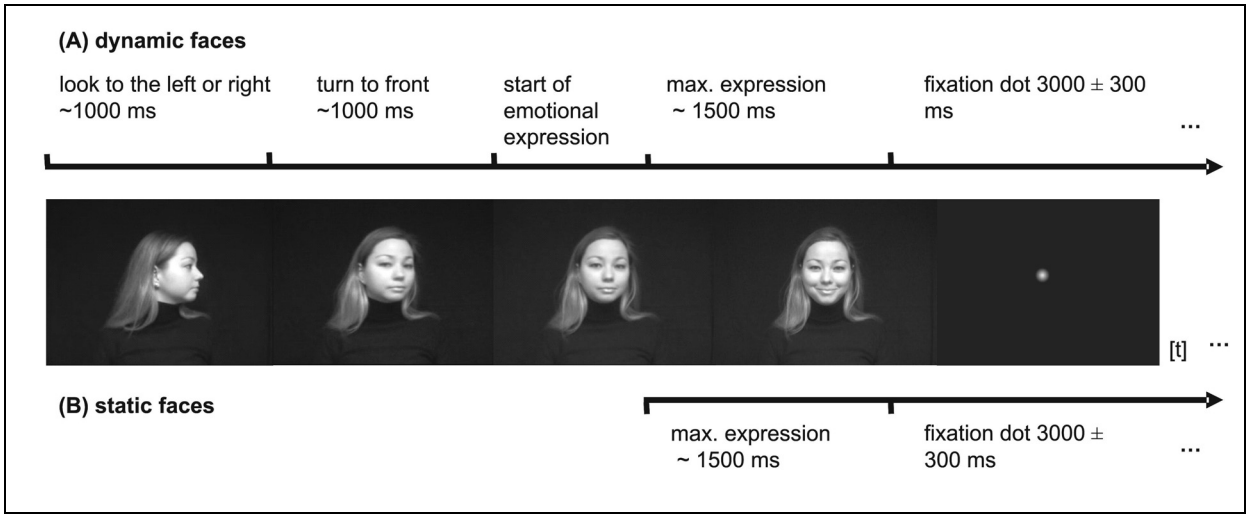

Figure 3: Example for trial sequences for dynamic (A, upper row) and static faces (B, lower row). Please note that even though the above stimuli are displayed in grayscale, participants viewed facial stimuli in color. The structure of the videos is exemplarily presented in the upper row (A). The actress looked to the right (left) with an angle of 90° to the camera (black background) with a neutral expression, turned towards the camera after approximately one second. Her face either remained neutral or started expressing a happy or disgusted face as soon as she faced the camera frontally. The turn aspect contributed to the authenticity of the stimuli because if a person turns towards someone the social relevance is suggested to increase. The design included videos with 50 percent of the actresses turning from the right and 50 percent turning from the left side to the front. Videos were recorded in mpg2-format and then converted to mpg1-format (PAL: 25 frames/s, 352x576, ratio 4:3; TMPGEnc Plus, version 2.510.49.157). (B) Static stimuli were captured from the videos at the maximum of each frontally presented neutral or emotional expression saved in jpg-format, 96x96 dpi resolution, 24 bit depth; Paint Shop Pro, version 5.01, Jasc software, Inc.). Each of the four emotional face perception blocks included 10 stimuli of happiness, disgust, and neutral, respectively. Each stimulus was followed by a fixation dot (for 3000±300 ms), thus, resulting in an average trial duration of about 4.5 sec for the static and about 6.7 sec for dynamic stimuli.

Actors were placed in front of a video camera (70 cm distance between face and camera, black background, darkened room with virtually equally held illumination). Emotional expressions of actresses were triggered by a mood induction strategy (e.g., for disgust: “imagine, you come home after two weeks of vacation but you forgot to take out the biowaste

container" or happiness: "imagine you meet someone unexpectedly on the street who you really like and give him a smile because you are happy to see him"). For details of stimuli construction see Fig. 3 A and B.

For the purposes of the present study, exclusively female dynamic and static emotional face stimuli (N=40) displaying positive (happiness), disgust, and neutral expressions were used in order to avoid gender-related differences in activation patterns in fMRI (Garrett and Maddock, 2001; Wager et al., 2003) and in amplitudes in EEG as reported in previous studies (Orozco and Ehlers, 1998) because men and women perceive and process their own and their opposite gender in different ways.

Besides, three different valences displaying smiling, disgusted and neutral facial expressions were applied to increase the signal-to-noise (SNR) ratio and to keep the design as clean and with as little sources of artifacts as possible.

2.2.3.2 Trials and sequence

Each video followed the same type of scenario (see below and Fig. 3 A, for illustration). Static stimuli were captured from the videos at the maximum of each emotional expression (see Fig. 3 B). Videos and static video frame captures were presented in color using Presentation®-software (Neurobehavioral Systems, https://nbs.neuro-bs.com) via a digital projector on a mirror in the scanner tube.

Average video duration was 3700 ms and emotional expressions were displayed for an average of 1500 ms. The timing was determined by applying a hitpoint analysis in which the time points of each video of the beginning of the turn, the frontal position, the first hint of emotion, the first subjective recognition of the emotion, the apex of emotional expression and the entire duration of the video were assigned.

Hitpoint analyses were conducted by the author of the present thesis and by two independent female students. Hitpoint raters determined the first subjective recognition of happiness and disgust and their maximum. Correlating the data of all raters (Pearson Correlation) showed a significant correlation (all $p<.001$) among independent raters, which supported the reliability of the applied hitpoints for the present two studies.

The results of this hitpoint analysis confirmed an average video-length of 3.7 sec (for neutral, smile and disgust) and showed an average duration of the maximum of emotional expression (for neutral, average time of the frontal position of the face till the end of the video was chosen) of 1499 ms. Thus, an average presentation time of 1500 ms was chosen for the static modality in order to allow for a comparable fMRI data modeling for both static and dynamic

stimulus modalities.

Each stimulus was followed by a fixation dot displayed 3000 ± 300 ms. Static and dynamic stimuli (120 stimuli for each modality: 40 disgust, 40 smile and 40 neutral, respectively) were presented in two separate and counterbalanced runs during one fMRI-session. Each run consisted of four blocks (average duration: 18 min for static and 23 min for dynamic faces) which were separated by two minutes sequences of stimulus-response-compatibility tasks and a 15 sec resting period in order to ensure an appropriate vigilance level. Stimuli were presented in a pseudo-randomized non-stationary probabilistic sequential order (Friston et al., 1999c; for details of stimulus sequence, see Fig. 4), based on the assumption that the effect of emotional stimuli persist up to half a minute or longer after stimulation (Garrett and Maddock, 2001). This procedure provides an appropriate compromise between event-related and block design, thus avoiding habituation effects usually appearing in emotion perception studies with block designs (Breiter et al., 1996) especially in subcortical, emotion-sensitive areas like the amygdala. Between runs, participants had between three to five minutes to rest.

Participants were asked to fixate a dot in the center of the screen, to watch the videos and the static video frame captures carefully, and to 'empathize' the perceived expressions. They were naïve to the displayed emotional valences. Stimuli were presented with a vertical and horizontal visual angle of 14.7° and 17.8°, respectively (distance to projection screen: 42 cm, height (H) 11 cm, width (W) 13,44cm).

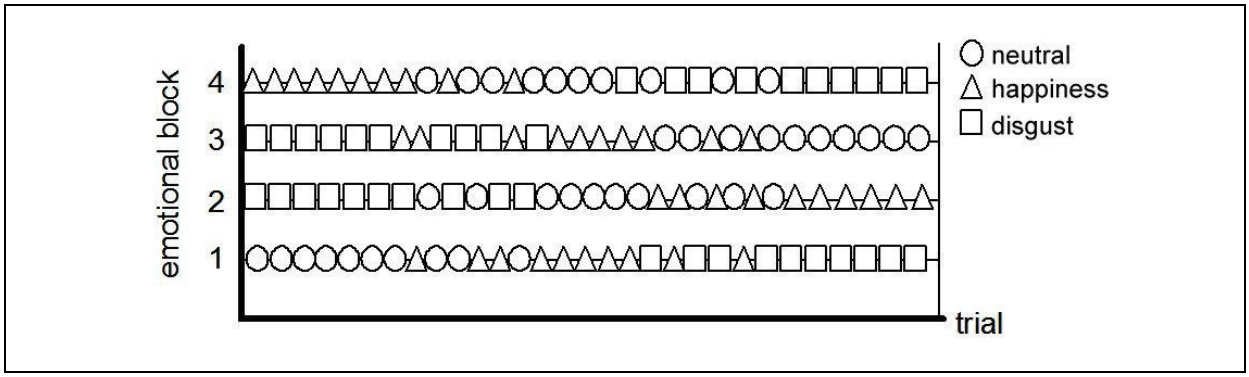

Figure 4: The graph displays the pseudo randomized non-stationary probabilistic balanced stimulus sequence for 30 trials (x-axis) and four blocks (y-axis). Static and dynamic faces were presented in two separate, but counterbalanced runs, and were both presented with identical sequence. Each symbol represents one emotional valence: circle = neutral, triangle = smile/happiness, square = disgust.

2.2.4 Behavioral measures: rating of stimulus material

After the fMRI scanning session, participants rated the presented stimuli according to arousal (on a scale from 0 [no arousal] to 10 [very high arousal]) and valence (happiness, neutral, disgust).

2.2.5 Evaluation study of stimulus material

In addition, a sample of 30 psychiatrically and neurologically healthy female adults (mean age 22.7 ± 2.9 years, education 15.4 ± 1.9 years, LQ 95.3 ± 15.5; Oldfield, 1971) was tested because a newly developed stimulus set of dynamic emotional expressions was applied. Therefore, it needed to be ensured that emotional valences like, e.g., disgust were actually perceived as disgust even among a choice of additional negative stimuli aside from disgust (here: fear and anger). Participants rated the emotional videos (200), which were also presented in a pseudo-randomized non-stationary probabilistic sequence, according to arousal (on a scale from 0 [no arousal] to 10 [very high arousal]) and valence (happiness, neutral, disgust, fear, anger, 40 of each valence).

2.2.6 Functional magnetic resonance imaging (fMRI)

2.2.6.1 Data acquisition

Functional (T2*-weighted gradient echo-planar imaging, EPI, sequence, 44 contiguous slices aligned to the AC-PC line, slice thickness 3 mm, no gap, interleaved acquisition, TR= 2500 ms, TE=30 ms, flip angle 90°, 64 x 64 matrix, FOV 192 x 192) and structural (MPRAGE, T1-weighted sequence, 160 slices, TR 2300 ms, TE 4.38 ms, flip angle = 8°, TI 900 ms, FOV 256 x 256, 1 mm^3 voxel, saggital orientation) MRI data were recorded on a 3-T SIEMENS Allegra System (Siemens, Erlangen, Germany). FMRI data analyses were performed using the statistical parametric mapping software SPM2 (Wellcome Department of Cognitive Neurology, London, UK, http://www.fil.ion.ucl.ac.uk/spm/). Parameter estimates for percent signal change were calculated using the Marsbar toolbox (http://marsbar.sourceforge.net).

2.2.6.2 Data analysis

After discarding the first two volumes of each run to allow for magnetic saturation, all functional data were slice-time corrected, realigned and unwarped to the 10^{th} volume, spatially normalized (bounding box, template: 90:90, -126:90, -72:108, trilinear interpolation) to the Montreal Neurological Institute (MNI) stereotactic EPI template and resampled to 2x2x2 mm voxel size. Thereafter, data were smoothed with a Gaussian Kernel of 8 mm (full width half maximum, FWHM) in order to increase the signal-to-noise (SNR) ratio of the data and to compensate for anatomical variability between participants (Glascher et al., 2004; Sato et al., 2004). To model the data at first level, trial related stimulus durations were convolved with the canonical hemodynamic response function (Della-Maggiore et al., 2002; Friston et

al., 1999a; Friston et al., 1999b) and locked to the respective stimulus onsets. Data were corrected for intrinsic autocorrelation (AR (1)) and high-pass filtered (128 Hz) to remove low frequency signal drifts. The design matrix comprised 8 regressors for the embedded inter-block stimulus-response-compatibility task, which was no further subject of the present study, three regressors for the facial expression categories (plus three regressors, exclusively for the videos, modeling the onset of the actress´ head until the first emotional expression could be recognized), one regressor covering dummy variables (instruction text and resting epochs), one regressor for errors and misses during the embedded stimulus-response-compatibility task, and 6 realignment parameters (x,y,z, and the three rotation angles, as regressors of no interest in order to minimize false-positive activations due to task-related motion of the participants, see also Johnstone et al., 2006). Second-level whole-brain random effects analyses (Holmes and Friston, 1998) were performed by calculating a t-statistic for predetermined condition effects at each voxel for each participant and run and producing a statistical image for the contrasts disgust > neutral, happiness > neutral, and vice versa, separately for both static and dynamic stimulus modalities. These individual contrast images were used to identify the main task effects by means of a one sample t-test. To detect modality-specific differences between the dynamic and static face perception processing, interaction analyses (one-way ANOVA) for stimulus modality (static vs. dynamic) were calculated including the respective contrast images as defined above ([dynamic disgust > dynamic neutral] / [dynamic happiness > dynamic neutral] versus [static disgust > static neutral] / [static happiness > static neutral]).

Functional regions of interest (ROIs) were determined on the basis of significant cluster peak activations revealed by the interaction analysis. For each ROI, stimulus modality, and emotional category, percent signal change values were calculated. For percent signal change values for the amygdala, a spatial ROI mask for this region was determined using the wfu-pickatlas toolbox (Brodmann areas, 3-D, dilatation 0, http://www.fmri.wfubmc.edu/download.htm). MNI-coordinates of significant voxel clusters from MNI (Montreal Neurological Institute) were converted to Talairach space (http://imaging.mrc-cbu.cam.ac.uk/imaging/MniTalairach, see also Talairach, 1988) using a Matlab® tool (mni2tal.m, http://imaging.mrc-cbu.cam.ac.uk/imaging/MniTalairach), and the corresponding anatomical regions were determined using the Talairach Daemon Client software (http://ric.uthscsa.edu/projects/talairachdaemon.html).

2.3 Results

2.3.1 Behavioral data

2.3.1.1 Behavioral data (evaluation study)

Data show a correct categorization rate of 94.1 % (± 9.8) for neutral, 98.1 % (± 5.2) for positive, 94.2 % (± 4.5) for disgust, 95.3 % (± 6.4) for fearful, and 88.8 % (± 5.1) for angry expressions (see Fig. 5 A). Repeated measurement ANOVAs with the factor EMOTION (5 levels: neutral, happiness, disgust, fear, anger), calculated for arousal and categorization separately, revealed significant main effects of emotion for both category ($F_{[2.5, 72.1]} = 10.2$, Greenhouse Geisser (GG) corrected, $p<.001$) and arousal ($F_{[1.8, 52.2]} = 23.6$, GG corrected, $p<.001$) explained by a higher categorization rate of happy compared to neutral ($p=.049$), disgust ($p=.005$), fearful ($p=.002$), and angry ($p<.001$) faces and a better categorization rate of neutral, disgust and fearful faces compared to angry faces ($p=.002$, $p<.001$, $p<.001$, respectively). Happy faces showed a higher arousal compared to faces of disgust ($p=.02$), fear ($p<.001$), and anger ($p<.001$), faces of disgust showed higher arousal compared to fear ($p=.046$) and anger ($p<.001$), and fearful facial expressions showed a higher arousal compared to angry ones ($p<.001$, Fig. 5 B).

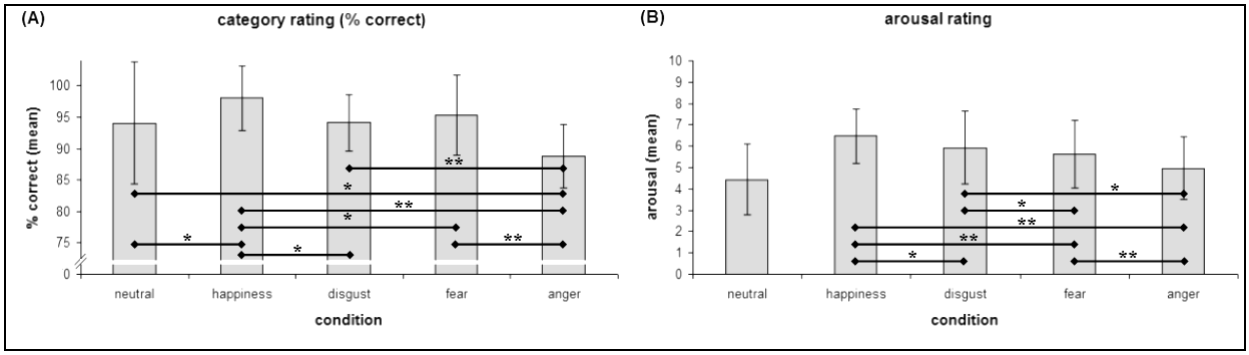

Figure 5: (A) Results of evaluation study displaying the mean (± 1 SD) of categorization accuracy in percent (y-axis) for each emotional valence (x-axis). (B) Results of arousal ratings (mean, ± 1 SD, y-axis) for different emotional valences (x-axis). Black lines indicate p-value of posthoc comparisons: * p<.05, ** p<.001.

2.3.1.2 Behavioral data (fMRI study)

Post hoc evaluation of the facial expression stimuli revealed a categorization rate for the static faces of 98.0 % (± 3.9) for neutral, 97.8% (± 3.4) for happy, and 97.5 % (± 2.0) for disgust, and for the dynamic faces of 95.9% (± 8.7) for neutral, 99.5 % (± 1.4) for positive, and 98.9 % (± 2.0) for disgust expressions (see Fig. 6 A). A MODALITY (2 levels: static and dynamic) x EMOTION (three levels: happiness, disgust, and neutral) x SEQUENCE (2 levels: start

with static or start with dynamic stimuli) repeated measurement ANOVA, separately conducted for the category and arousal ratings, revealed a significant EMOTION x MODALITY interaction ($F_{[1.7,\ 24.1]} = 3.7$, $p<.05$, Huynh Feldt corrected) for category. This effect was explained by a significantly higher categorization rate for dynamic compared to static disgust facial expressions (post hoc t-test, $p = .01$), and by a trend for better categorization rate for dynamic compared to static positive facial expressions (post hoc t-test, $p = .07$, see Fig. 6 A).

Arousal showed a main effect for EMOTION ($F_{[2,\ 28]} = 11.08$, $p<.001$) resulting in higher arousal rates for emotional expressions independent from motion and a trend for MODALITY ($F_{[1,\ 14]} = 4.26$, $p=.058$) yielding higher arousal rates for dynamic compared to static stimuli independent of emotion (see Fig. 6 B). However, the EMOTION x MODALITY interaction did not reach significance.

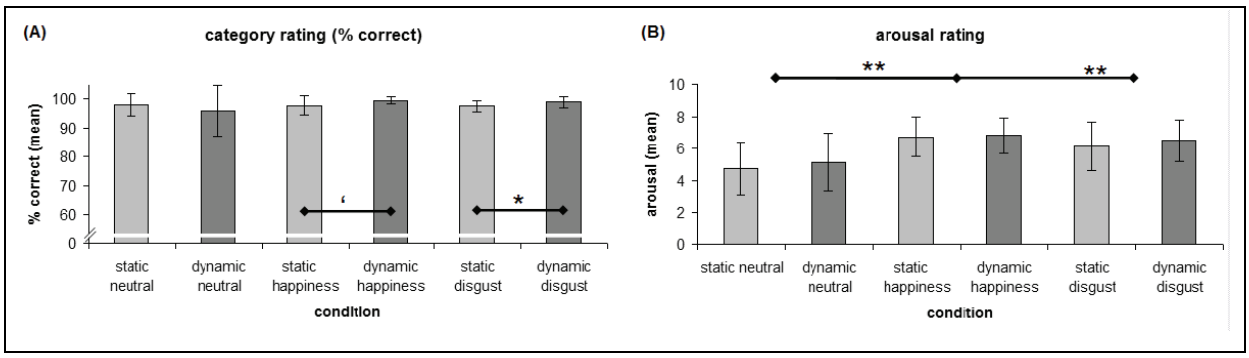

Figure 6: (A) Results of postscan rating displaying the mean (± 1 SD) of categorization accuracy in percent (y-axis) for each modality and emotional valence (x-axis). (B) Results of arousal ratings (mean, ± 1 SD, y-axis) for different emotional valences (x-axis). Static modality: light gray, dynamic modality: dark gray, black lines indicate results of posthoc comparisons: ' $p< .1$ (trend), * $p < .05$, ** $p < .001$.

2.3.2 FMRI data

2.3.2.1 Emotion effects for dynamic and static stimulus material

For comparison between static facial stimulus conditions, all contrasts were fixed ad hoc at a significance level of $p<.005$ (uncorrected, $k=20$). Disgust in contrast to neutral static facial expressions showed an activation pattern comprising left inferior and middle frontal gyrus, left medial superior frontal gyrus, and left putamen (see Table 1 and Fig. 7 A, lower row, see also Appendix B.1, for glassbrains). Positive in contrast to neutral static facial expressions showed an activation pattern in the left medial superior frontal gyrus (supplementary motor area, SMA), the left precentral gyrus and the right cerebellar tonsil (see Table 1 and Fig. 7 B, lower row, see also Appendix B.3, for glassbrains).

		dynamic: disgust>neutral		static: disgust>neutral		dynamic: happiness>neutral		static: happiness>neutral	
brain area	*H*	*x y z*	*T*	*x y z*	*T*	*x y z*	*T*	*x y z*	*T*
Inferior Frontal Gyrus	L	-55 18 6	5.75						
	L	-57 17 -6	5.67	-46 24 17	4.28				
	L	-59 22 12	5.09	-46 27 2	4.18				
	R	63 9 16	6.47						
Medial Frontal Gyrus	L	-10 44 25	4.23			-4 52 -4	4.44		
	L					-2 48 -14	4.07		
Middle Frontal Gyrus	L			-53 30 21	4.07				
	R	59 12 36	4.47						
	R	55 4 40	4.09						
Superior Frontal Gyrus	L	0 5 61	5.25	-2 5 53	3.90			-2 5 51	3.22
	L	-2 17 60	4.95						
	R	6 15 62	6.28			4 21 63	5.86		
Precentral Gyrus	L							-40 -5 61	3.37
	L							-38 -12 63	3.24
Precuneus	L					-32 -74 37	4.36		
Supramarginal Gyrus	L	-53 -41 35	5.68						
	R	67 -43 28	4.21						
Cuneus	L					-18 -92 27	4.56		
	R					14 -95 10	5.85		
	R					12 -94 23	4.27		
	R					10 -84 30	4.34		
Lingual Gyrus	R					16 -90 -4	6.44		
Middle Occipital Gyrus	L					-26 -97 10	4.64		
	R	55 -68 -5	7.44						
Angular Gyrus	L					-44 -74 31	4.79		
Superior Temporal Gyrus	L	-50 -53 21	8.10						
	R	67 -44 13	8.46						
	R	46 -35 5	4.93						
	R	28 7 -24	6.12						
Middle Temporal Gyrus	L	-40 -64 9	6.76			-53 -67 25	4.15		
	L	-51 -69 13	6.40						
	R	55 -66 3	10.66			51 -62 12	5.12		
	R	50 -79 9	4.09						
Fusiform Gyrus	L	-42 -43 -15	6.92			-42 -57 -16	4.43		
	L					-42 -78 -15	4.33		
	L					-26 -80 -16	4.05		
	R					46 -67 -17	4.59		
Culmen	L					-36 -55 -21	4.17		
Declive	R					14 -78 -11	5.24		
Cerebellar Tonsil	R							26 -56 -38	3.35
	R							20 -64 -34	3.28
Amygdala	L	-20 -6 -13	6.24						
Uncus	L	-24 4 -34	6.90						
	R	18 1 -20	6.51						
	R	22 -5 -30	5.17						
Parahippocampal Gyrus	L					-18 -28 -10	6.22		
	R	20 -12 -13	5.26			18 -43 4	6.33		
Hippocampus	L					-28 -29 -7	6.40		
Posterior Cingulate	R	0 -54 12	4.59			16 -50 8	6.19		
	R					4 -52 12	5.51		
Mammillary Body	R	4 -12 -11	4.60						
Putamen	L			-20 4 0	3.43				
Extra-Nuclear/Claustrum	L					-28 18 8	4.92		

Table 1: Talairach coordinates of simple BOLD contrasts of dynamic (disgust > neutral, happiness > neutral, p<.001, uncorrected, k=20) and static (disgust > neutral, happiness > neutral, p < .005, uncorrected, k=20) facial expressions.

Furthermore, Figure 7 also depicts the contrast between dynamic facial stimulus conditions (p<.001, uncorrected, k=20). Disgust in contrast to neutral dynamic facial expressions resulted in a signal increase in bilateral inferior frontal, right middle frontal (premotor area, PMA), left medial frontal, bilateral superior frontal areas (SMA), right posterior cingulate cortex (PCC), bilateral supramarginal regions, in left fusiform gyrus (FuG, FFA), and in bilateral superior and middle temporal regions (STS area; see also Table 1 and Fig. 7 A, upper row). Furthermore, disgust versus neutral dynamic facial expression stimuli showed an increased activation pattern comprising right parahippocampal gyrus (PHG), left uncus, and

the amygdala (AMG) for disgust (see Fig. 7 A, upper row and Table 1 for further details, see also Appendix B.1, for glassbrains).

Positive in contrast to neutral dynamic facial expressions resulted in a signal increase in right superior frontal gyrus, left medial frontal gyrus (spreading ventrally to OFC), right posterior FuG, left FuG (FFA), bilateral middle temporal gyrus (MTG, STS area) posterior, left angular gyrus including parts of the middle temporal gyrus (STS area), right PCC, bilateral PHG, left precuneus, and occipital brain regions (see Table 1 and Fig. 7 B, upper row, see also Appendix B.3, for glassbrains).

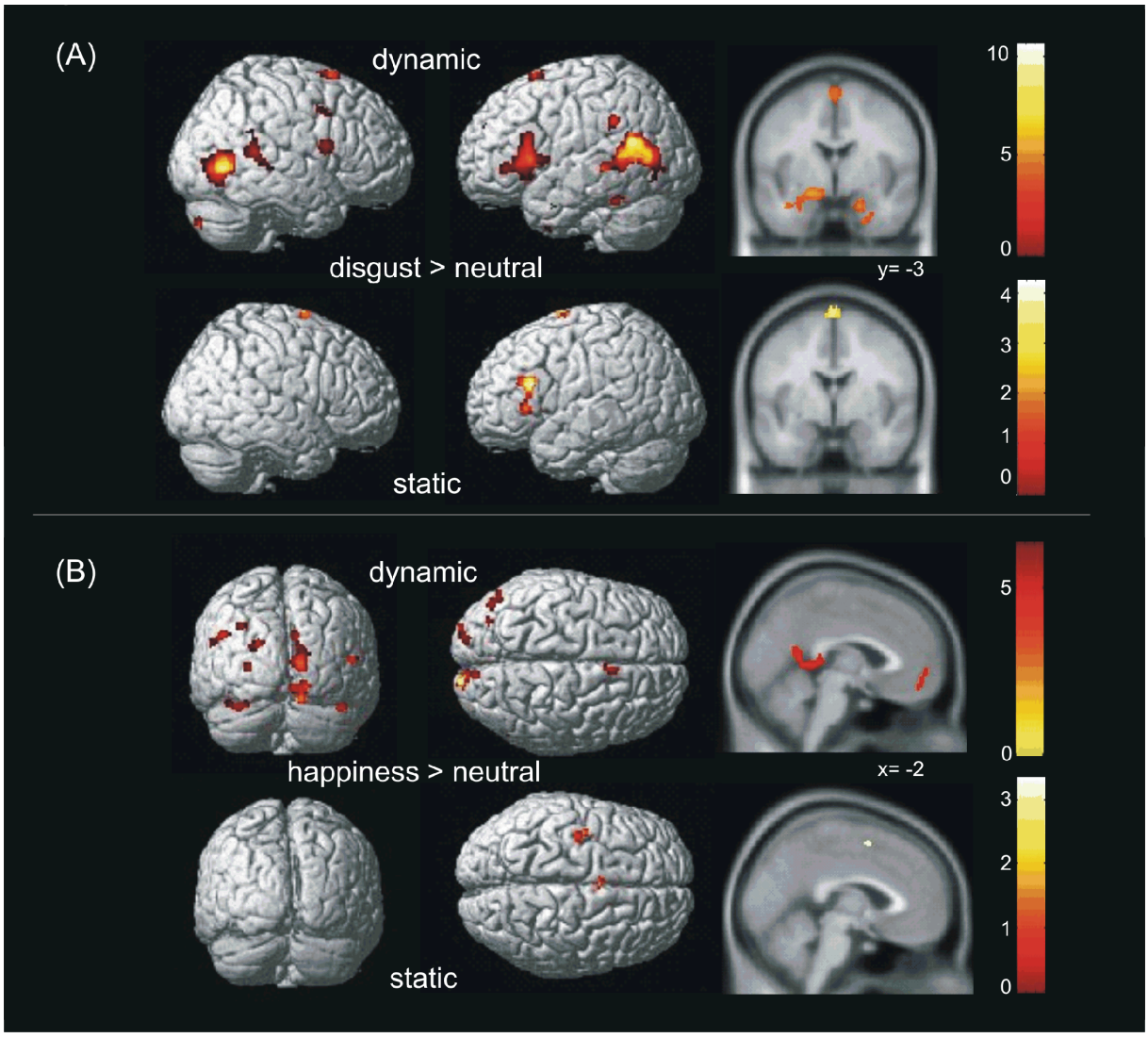

Figure 7: Contrasts of emotional compared to neutral facial expressions (p<.001, uncorrected, k=20) showed stronger and more widespread emotion-specific activations. (A) Emotion effect of disgust for the dynamic (upper row, p<.001, uncorrected, k=20) and static modality (lower row, p<.005, uncorrected, k=20). (B) Emotion effect for happiness for the dynamic (upper row, p<.001, uncorrected, k=20) and static modality (lower row, p<.005, uncorrected, k=20). Color bars on the right indicate grading of T-values.

2.3.2.2 Enhanced emotion by motion effect for dynamic and static stimuli

Interaction analysis including the contrasts disgust > neutral expressions for each static and dynamic stimuli revealed larger activation differences for dynamic compared to static stimuli in left rectal gyrus (part of the OFC), left inferior frontal gyrus, left superior temporal gyrus, bilateral middle temporal gyri (both STS area), left inferior temporal gyrus (lateral FFA), and right middle occipital gyrus (see Table 2 and Fig. 8 A for further details, see also Appendix B.2, for glassbrains).

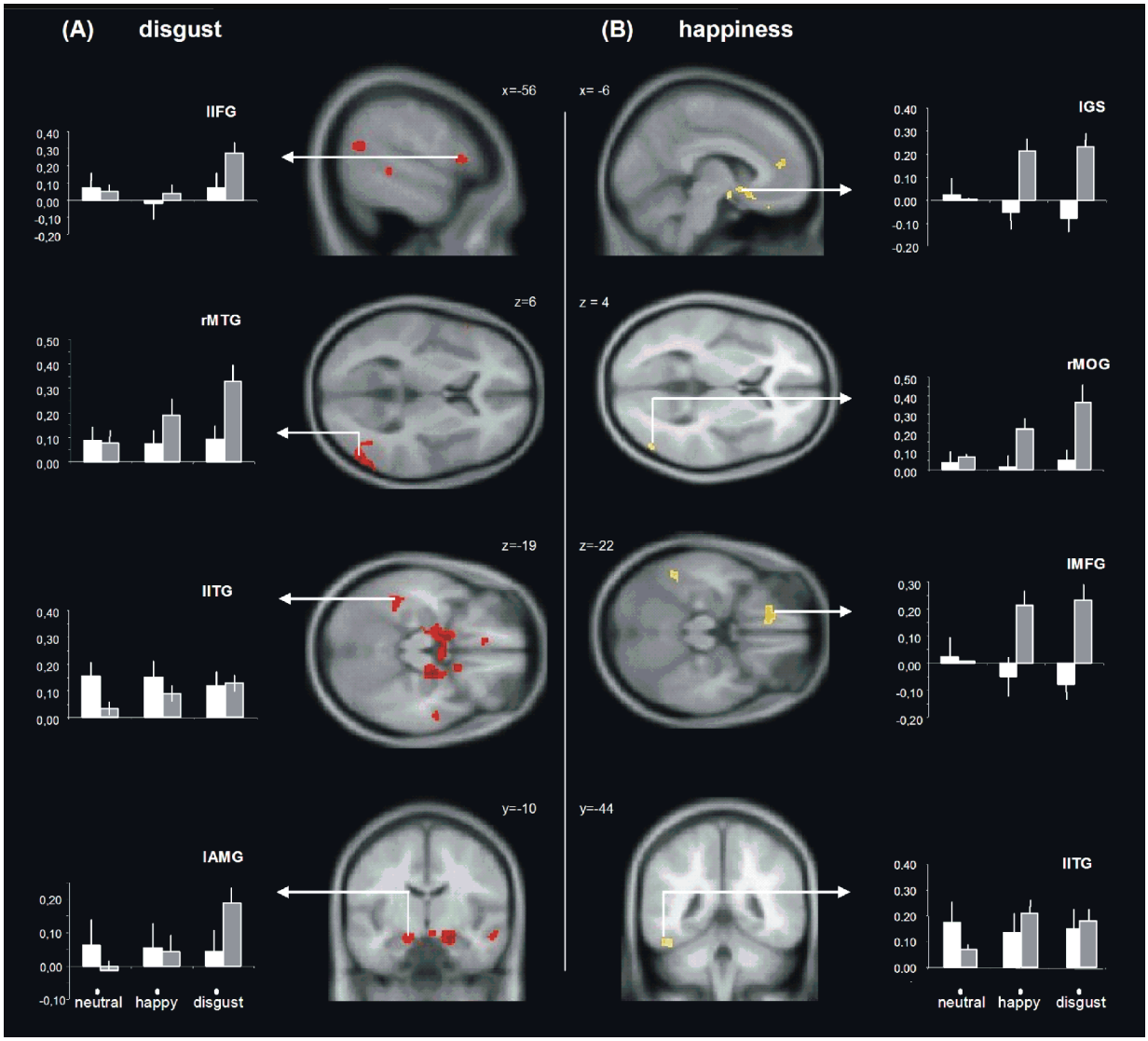

Figure 8: Interaction analysis (p<.001, k=20) showed an enhanced emotion by motion effect for (A) disgust ([dynamic disgust > dynamic neutral] > [static disgust > static neutral] in left inferior frontal gyrus (lIFG), right middle temporal gyrus (rMTG, → STS area), left inferior temporal gyrus (lITG, → FFA) and left amygdala (lAMG), and (B) happiness ([dynamic happiness > dynamic neutral] > [static happiness > static neutral] in left subcallosal gyrus (lGS), right middle occipital gyrus (rMOG, including MT+/V5 and STS), left medial frontal gyrus (lMFG), and left inferior temporal gyrus (lITG, including fusiform face area (FFA)). Sort of percent signal change graphs were derived from the Marsbar toolbox (http://marsbar.sourceforge.net). White bars indicate the static stimulus modality (±1 SEM, standard error of mean), gray bars show the dynamic stimulus modality (± 1 SEM).

Furthermore, dynamic disgusted facial expressions showed larger bilateral differences in parahippocampal gyrus (PHG) comprising the uncus and amygdala (see Table 2 and Fig. 8 A). Mean percent signal change revealed an enhanced signal for dynamic disgust facial expressions compared to static and dynamic faces of happy and neutral valence in left inferior frontal gyrus (IFG), right MTG (STS area), left lateral inferior temporal gyrus (FFA), and left AMG (see Fig. 8 A).

Interaction analysis based on the positive compared to neutral contrasts for both static and dynamic stimuli showed larger differences for dynamic compared to static stimuli in left inferior frontal (IFG, part of the OFC) and subcallosal gyrus, left medial anterior STG, left anterior middle temporal gyrus, left posterior inferior temporal gyrus (ITG, FFA), left precuneus comprising the superior and inferior parietal lobule, right cuneus, and right middle occipital gyrus (comprising MT+/V5 and STS area, see Table 2, Fig. 8 B for details, see also Appendix B.4, for glassbrains). Corresponding percent signal change data support a stronger signal increase for the dynamic positive facial expressions compared to the static modality in ventromedial and subcallosal regions, right middle occipital gyrus (including MT+ and STS area) and left inferior temporal gyrus (FFA, see Fig. 8 B).

		motion faces > static faces (disgust)		**motion faces > static faces (happiness)**	
brain area	H	x y z	T	x y z	T
Inferior Frontal Gyrus	L	-55 18 8	3.88	-12 32 -17	3.83
	L	-59 24 12	3.53	-20 32 -18	3.75
Medial Frontal Gyrus	L			-4 45 12	3.83
Rectal Gyrus	L	-10 34 -20	4.12		
sub-lobar	L			-6 7 -7	3.75
Subcallosal Gyrus	L			-6 19 -14	3.66
Middle Frontal Gyrus	L	-24 23 36	4.22		
Precuneus	L			-32 -74 37	4.13
Cuneus	R			12 -96 21	4.28
	R			26 -92 27	3.97
	R			12 -94 29	3.89
Middle Occipital Gyrus	R	28 -82 1	3.73	51 -70 7	3.89
	R	20 -89 15	3.68		
	R	22 -96 23	3.51		
Superior Temporal Gyrus	L	-51 -53 21	4.52	-38 16 -23	3.96
Middle Temporal Gyrus	L	-57 -35 2	3.90	-55 1 -27	4.39
	R	61 -60 9	4.83		
	R	42 -62 10	3.79		
	R	55 -8 -13	4.13		
Inferior Temporal Gyrus	L	-44 -43 -15	4.19	-46 -44 -16	4.20
Middle Occipital Gyrus	R	53 -68 7	4.70		
Parahippocampal Gyrus	L	-12 -1 -13	5.43		
	R	20 -12 -15	5.37		
Uncus	L	-22 9 -21	5.08		
Hypothalamus	L			-4 -3 -12	4.67

Table 2: Talairach coordinates of dynamic versus static stimuli (interaction analysis, p<.001, uncorrected, k=20) for disgust ([dynamic disgust > dynamic neutral] > [static disgust > static neutral] and happiness ([dynamic happiness > dynamic neutral] > [static happiness > static neutral].

2.4 General discussion of imaging data

In the present study, two central questions were pursued. First, the newly introduced stimulus

database was expected to evoke emotion-specific networks, especially in striate and extrastriate regions (happiness), inferior temporal gyrus (e.g., FFA), middle and superior temporal gyrus (e.g., STS area), supplementary motor (SMA), inferior frontal areas, insula (disgust), parahippocampal area including the amygdala (disgust), and orbitofrontal regions (OFC). Second, more widespread neural activation patterns for dynamic compared to static facial expressions in those emotion-specific regions were expected resulting in a higher recognition accuracy of emotional stimuli for the dynamic modality.

Dynamic - but not static - emotional versus neutral stimuli showed a consistent emotion-specific network comprising the amygdala (only for disgust), parahippocampal regions, the STS area, FFA, supplementary motor areas (SMA), inferior frontal regions (only for disgust), visual and orbitofrontal regions, but no insula. This emotion-specific network was shown to be enhanced by motion for the dynamic compared to static stimulus modality. Furthermore, ratings of the stimulus material confirmed a higher recognition accuracy of dynamic compared to static stimuli.

The following paragraphs discuss the current findings in more detail.

2.4.1 Emotional stimulus processing

Emotion perception has been extensively described in previous studies and a network of anatomical regions such as visual areas, FFA, STS region, amygdala, orbitofrontal cortex, premotor as well as inferior frontal areas have been shown to take part in processing, analyzing and evaluating emotional face stimuli (for review, see Adolphs, 2002; Phan et al., 2002). These brain regions are known to subserve multiple emotional and cognitive functions and will be discussed in more detail.

According to Haxby's adapted face perception model (Haxby et al., 2000), face perception can be divided into a core and an extended system which act in concert. The core system is responsible for the early visual analysis of faces (visual areas), for the perception of changeable (STS area) and invariant aspects, e.g., identity (lateral fusiform gyrus, FFA). In the present study, all of those areas activated by emotional face stimuli could be confirmed. Striate and extrastriate areas have been attributed to early stages of visual processing (Kilts et al., 2003), and to an enhancement of selective attention due to an increase of arousal in emotional compared to neutral stimuli (Kosslyn et al., 1996; Lane et al., 1997; Phillips et al., 1997; Schienle et al., 2002) emphasizing the interaction of emotion and attention in posterior regions. In the present study, participants watched the emotional faces and presumably automatically analyzed their structure and valence. This might have triggered arousal as

indicated by corresponding behavioral data showing higher arousal values for emotional compared to neutral faces. An increase of arousal for dynamic emotional faces has previously been described in behavioral studies (Simons et al., 1999; Weyers et al., 2006).

Another aspect of dynamic face perception includes the perception of (1) structural details such as identity and (2) moving characteristics of the perceived faces such as gaze or facial expressions. The inferior temporal and fusiform gyrus (e.g., FFA) has been discussed to be involved in the processing of identity of faces (Grill-Spector et al., 2004; Haxby et al., 2000; Hoffman and Haxby, 2000; Kanwisher et al., 1997) and - in more detail - the detection, encoding and/or analysis of invariant facial features such as eyes, mouth, and nose (Halgren et al., 1999). Furthermore, activation of FFA was reported in many studies addressing attentional demands in the context of emotion perception (Narumoto et al., 2001; Pessoa et al., 2002; Vuilleumier et al., 2001; Vuilleumier et al., 2004), and motion processing of dynamic facial expressions (Kilts et al., 2003; LaBar et al., 2003; Sato et al., 2004). According to the hypotheses of the present study, FFA activity was enhanced by emotional salience of both disgust and positive stimuli, hence emotion per se, and further by dynamic characteristics in both valences. Therefore, the author of the present thesis suggests that the FFA might be modulated by emotional characteristics of faces and that it probably recruited more attentional resources in dynamic compared to static stimuli resulting in more widespread activation patterns.

The perception of movement in a face plays an important role for emotional face perception. STS area activation for smile and disgust spreading to V5/MT+ in the dynamic modality were found. Thus, dynamic face characteristics might result in an enhanced visual motion analysis (Dumoulin et al., 2000) possibly induced by more natural and complex stimulus properties, hence, recruiting more attentional resources and resulting in stronger and more widespread activation patterns. Moreover, V5/MT+ activation is assumed to be temporally followed by a more detailed analysis of dynamic features - the biological motion - of the facial expressions in the STS region. The STS area has been associated with the processing of biological motion of changeable aspects in studies of, e.g., body and face perception (Allison et al., 2000; Grossman and Blake, 2002; Haxby et al., 2000; Pelphrey et al., 2003; Puce et al., 1998) and with the perception of dynamic facial emotions of anger and fear indicating an interaction of emotion and motion (Kilts et al., 2003; LaBar et al., 2003; Sato et al., 2004; Wicker et al., 2003). Besides, the STS region was suggested to rapidly assess actions, interests and intentions of other people by analyzing social cues (e.g., by extracting the perceived changeable facial features) which might facilitate the interpretation of social perception,

gestures and, in a broader context, social communication (Allison et al., 2000; Hoffman and Haxby, 2000; Kilts et al., 2003; Narumoto et al., 2001). Confirming the hypothesis of the present study, STS area activation patterns were confirmed for the perception of dynamic disgust (STS area) and happiness (V5/MT+ and STS area) facial expressions. Biological motion aspects of stimuli (e.g., gaze, muscular changes of the face) apparently convey a higher complexity of social cues which are important for adequate social communication, and probably evoke stronger neural activation patterns.

The STS area, the FuG, and striate and extrastriate areas have been linked to the face perception model by Haxby, Hoffman, and Gobbini (2000; see also Fig. 1). It is however important to mention that they have postulated the need to discover the underlying temporal course of those brain regions acting in "in concert". This suggestion has been partly seized by Adolphs (Adolphs, 2002; see also Fig. 2) who has proposed a time course regarding emotion perception. The time course of emotion processing will be addressed in Chapter 3.

Since study participants watched the stimulus material for the first time, dynamic faces conveyed strong salience. Emotional face perception of potentially salient and negative facial stimuli was reported to be linked to amygdala activation (Anderson et al., 2003; Fitzgerald et al., 2004; LaBar et al., 2003; Phillips et al., 1998; Williams et al., 2005) which was even enhanced when dynamic negative facial expressions have been presented (e.g., fear and anger; Kilts et al., 2003; LaBar et al., 2003; Sato et al., 2004). In the present study, amygdala activation was exclusively revealed for dynamic disgust perception but not for the perception of positive dynamic stimuli. This finding strongly supports the view that the amygdala plays a role in processing exclusively negative salient stimuli which might be even intensified by motion possibly due to stronger complexity, authenticity, and salience of dynamic disgust faces (Harwood et al., 1999; Sato et al., 2004).

The salience of the applied stimulus material might have furthermore enhanced incidental memory encoding for both emotional valences thus leading to parahippocampal, hippocampus and amygdala activation as hypothesized above and as previously discussed in the context of (1) in the context of memory encoding, consolidation and retrieval (for review, see LaBar and Cabeza, 2006; Phelps, 2004) and (2) in the context of acquisition and consolidation of emotion-related long-term memory contents (amygdala, especially for aversive stimuli; Garrett and Maddock, 2006; McGaugh, 2004).

Inferior frontal regions including Broca's area have traditionally been associated with motor speech production and semantic interpretation, but also - among other regions - with the human "mirror neuron system" (MNS; for review, see Rizzolatti et al., 2001). In humans, the

MNS has been shown to be activated during passive observation of mouth, hand or foot movements (Buccino et al., 2001; Iacoboni et al., 1999) and during passive observation of emotional facial expressions (Hennenlotter et al., 2005; Lee et al., 2006; Leslie et al., 2004; Sato et al., 2004). Furthermore, the visual representation of facial affect has been shown to be related to its internal motor representations (Hennenlotter et al., 2005). Thus, the present finding of inferior frontal cortex and premotor area activation might reflect "mirroring" and/or activating internal representations of the observed action without actual execution (Iacoboni et al., 1999; Rizzolatti et al., 2002). The lack of activation in inferior frontal regions for positive faces might be explained by a faster and more automatic processing (Leppanen and Hietanen, 2004) due to a more frequent exposure to positive facial expressions in general, hence, recruiting less cortical resources (Fuster, 2006). Supplementary motor area (SMA) activation was shown for happiness, which has also been associated with the MNS (Lee et al., 2006; Leslie et al., 2004).

The present data additionally corroborate the importance of ventromedial/orbitofrontal regions during the processing of positive stimuli related to reward processing and social reward (Gorno-Tempini et al., 2001; Kim et al., 2003; O'Doherty et al., 2003). Activation in the OFC for dynamic positive stimuli was also enhanced when compared to the static stimuli. The attractiveness of a face is a highly salient social signal with a strong stimulus-reward value and has been associated with the OFC (O'Doherty et al., 2003).

Even though posterior cingulate cortex (PCC) activation was not expected, the present data revealed the involvement of the PCC in the processing of dynamic emotional versus neutral facial expressions. Activations in posterior cingulate regions have been discussed in association with the evaluation of emotionally arousing stimuli by the involvement of corresponding memory content (Fitzgerald et al., 2004; Phillips et al., 1997; Winston et al., 2003). With respect to the present data, the author of the present thesis assumes that the processing of dynamic emotional stimuli caused PCC activation because the participants were asked to watch the faces attentively and empathetically. This might have led to a retrieval of previous experience of people showing emotional faces yielding a higher arousal of dynamic compared to static stimuli. The behavioral data underpin this assumption: arousal rates for happiness and disgust compared to neutral facial expressions were found to be significantly higher.

2.4.2 Possible reasons for the lack of insula activation in disgust

In contrast to the working hypothesis, insula activation could not be confirmed during disgust

perception of facial expressions. As far as the author knows, there is solely one fMRI study focusing on the rating of valence, arousal and dominance of fearful and disgusting scenes (IAPS pictures; Stark et al., 2003). Stark and colleagues (2003) did not report insula activation, but amygdala, medial prefrontal and fusiform gyrus activation during the disgust modality. These reported areas actually reflect a previous network of brain regions reported during emotion processing tasks. Therefore, the question arises why insula could not be confirmed in the present fMRI study.

A major detail where the present study differs from other studies is the presentation duration. Some studies reporting insula activation used presentation durations of 2.5 sec, 3 sec or even longer (Gorno-Tempini et al., 2001; Phillips et al., 1998; Phillips et al., 1997; Sprengelmeyer et al., 1998; Williams et al., 2005). A presentation of 1.5 sec in the present study was presumably too short to capture the necessary resources for a parasympathetic reaction which takes more time than, e.g., a fast sympathetic fear response (Rozin and Fallon, 1987; Williams et al., 2005).

A further reason for the lack of insula activation might be that participants were simply mirroring or empathizing the shown expressions perceiving them as generally negative per se, but not directly "feeling" disgust. Leslie and colleagues (2004) reported that participants passively watched smiling and frowning faces and showed stronger right lateralized inferior frontal activation. They hypothesized that this activation was related to emotion processing and played an important role for the motor theory of empathy. Since inferior frontal activation was confirmed for disgust perception, the author speculates that participants simply empathized with a negative expression instead of "feeling" disgust per se.

2.4.3 Validity of dynamic compared to static facial expressions

The author intends to discuss the finding of a larger, more widespread, and more consistent network of brain areas involved in emotion perception for dynamic compared to static stimuli with regard to two major aspects:

First, on a feature-based level, static and moving faces displaying an emotional expression convey both specific structural features (eyes, mouth, nose, hair etc.) whereas dynamic face stimuli additionally mediate very complex and rapid changing temporal cues of information via movement. Thus, a face switching from a neutral to a happy expression displays a change of facial muscles in a certain temporal sequence. Participants, therefore, were able to relate the different changing features to one another, which was assumed to specifically improve the three-dimensional perception of faces (Knight and Johnston, 1997), to enhance the perception

of emotional expressions (Ambadar et al., 2005), to facilitate appropriate emotion recognition, and to reflect social interactions in a more natural way (Bassili, 1979; Berry, 1990; Knight and Johnston, 1997; LaBar et al., 2003; Sato et al., 2004). Better recognition accuracy of dynamic compared to static stimuli have also been confirmed in autism (Gepner et al., 2001), mentally retarded children (Harwood et al., 1999) and agnostic patients (Humphreys et al., 1993) on the behavioral level, and have been linked to enhanced activation in neuroimaging studies (Kilts et al., 2003; LaBar et al., 2003; Sato et al., 2004).

Second, dynamic facial expressions were described to enrich emotional perception of facial expressions (Biele and Grabowska, 2006) and to capture the liveliness and true form of facial expressions because they typically occur in everyday life (Harwood et al., 1999) and, hence, appear more natural and ecologically valid. Indeed, human beings do not face static faces when they socially interact with other people. Humans have a long learning history of analyzing and interpreting facial emotional expressions "in motion" from childhood on which results in a large amount of experience and memory of dynamic faces.

These two aspects are largely corroborated by the present neuroimaging and behavioral findings: the more widespread activation pattern of dynamic compared to static emotional faces might be explained by (1) a higher complexity of stimuli, and (2) a higher authenticity and appropriateness of dynamic faces. The present data furthermore showed a significantly higher accuracy rate for disgust (and a trend for smile) for dynamic in contrast to static facial expressions (see also Biele and Grabowska, 2006; Simons et al., 1999). These data were also confirmed by an additional evaluation study of the dynamic stimulus material conducted by 30 women with respect to 5 different emotions (neutral, happiness, disgust, fear, anger) which showed accuracy rates of 93, 98 and 94 percent of neutral, happy and disgusted dynamic facial expressions, respectively.

2.4.4 BOLD activation in static emotional facial expressions

In the present investigation perceptual processing of static emotional stimuli hardly produced consistent significant BOLD-activation despite a lower significance threshold than dynamic facial expressions. This data additionally corroborate the above proposed assumption that dynamic stimuli provide a more ecologically valid approach for triggering brain responses related to emotional face processing. There might be different reasons for this line of argumentation: first, static stimuli might not have equivalent salience compared to dynamic stimuli because they do not convey rapidly changing cues of information. Consequently, as discussed above, static faces are not perceived as natural and powerful as dynamic facial

stimuli resulting in lower recognition accuracy rates. Second, the author of the present thesis speculates that the perception of static facial expressions might result in a higher interindividual-variance and/or a higher intertrial-variability compared to dynamic stimuli. Thus BOLD-activation might not have reached statistical significance as consistently as dynamic stimuli resulting in less widespread activation patterns.
Furthermore, since fMRI has a high spatial resolution, but a limited temporal solution (Hopfinger et al., 2005), one possibility might be that fMRI cannot capture these very fast and transient processing stages (Im, 2007). For that reason, an EEG study applying the exact same experimental design was conducted as described in Chapter 3 of the present thesis.

2.4.5 Network complexity

On the one hand, dynamic facial expressions are more complex, but on the other hand, they are recognized more accurately and probably easier than static faces. These results might sound contradictory even though other groups have reported similar results (Kilts et al., 2003; LaBar et al., 2003; Sato et al., 2004). However, the question arises why dynamic facial expressions evoke more widespread activation patterns even though they have been shown to be easier to recognize. A recent fMRI study of the author's working group (Fehr et al., 2008) reported a similar dissociation by revealing more widespread activation patterns for complex visually presented calculation tasks compared to complex auditorily presented calculation task. Even though one might assume that the visual task might have recruited a wider network of brain areas because of an assumed higher complexity of the visual compared to the auditory task, they proved the opposite by showing faster behavioral responses for the visual task. Thus, an "easier" task resulted in more widespread neural activation patterns. Fehr and colleagues (2008) suggested that the visual presentation modality recruited a wider network because visually presented calculation tasks might have been processed in a parallel way whereas the auditory presented tasks might have been processed in a sequential way and hence recruiting fewer neural resources. The same line of argumentation might hold true for the interpretation of the present data. Since human beings are frequently confronted with the interpretation of moving faces in social interactions of everyday life, they have learned to be experts in face and emotion recognition during communication with other people. This fact might result in a more efficient and adequate processing of dynamic faces resulting in a recruitment of a wider network of neural resources. Since a wide network of regions was revealed, which was activated by 'simple' perception of dynamic facial expressions, the author of the present thesis suggests to consider emotional face processing as a complex

process. This process might be embedded in a large neural network which is distributed across distant places and which is processed in a parallel fashion in the brain instead of modularly organized functions acting independently of each other. Thus, information processing of even putatively simple mental domains must be recognized as potentially triggering activation dedicated to memory and action widely distributed all over the brain (Basar, 2006; Fuster, 2006; for a more detailed discussion of network theories, see Chapter 4.4).

2.5 Preliminary conclusions of the fMRI study

The results of the present study indicate that dynamic face stimuli result in more pronounced and distributed activation patterns when compared to static faces. This finding is interpreted in terms of higher ecological validity of the dynamic face stimuli facilitating the perception of emotional facial expression, and recruiting more widespread emotion-specific neuronal networks. Except for two studies focusing on the perception of disgust-inducing film clips (Stark et al., 2005) and videos showing people smelling disgusting, pleasant or neutral odors (Wicker et al., 2003), to the author's knowledge, there has been no study reporting an enhancement of activation for dynamic compared to static facial expressions of disgust inducing network activation, e.g., in the amygdala, fusiform face area, the superior temporal sulcus area, and lateral inferior frontal areas as discussed in the present investigation.

In the author's view, the research of emotion perception is "in motion". Humans are experts for the processing of authentic moving faces in social interactions. This is one of the main reasons why the author suggests to examine face and emotion processing considering authentic dynamic stimuli in order to more appropriately quantify and qualify the respective both normal and impaired brain physiological processing (Gepner et al., 2001; Harwood et al., 1999; Humphreys et al., 1993).

3 Study 2: EEG study of static and dynamic facial expression processing of happiness and disgust

3.1 Introduction: evidence from ERP and source analysis studies examining emotion processing

Among many studies examining emotion perception with functional MRI and PET (for review, see Adolphs, 2002; Davidson and Irwin, 1999; Murphy et al., 2003; Phan et al., 2002; see also Chapter 2.1 and 2.4 of the present thesis), there is a vast amount of EEG studies pointing to the temporal dynamics of emotional perception applying photos of faces like the "Pictures of facial affect" (Ekman and Friesen, 1976; for review, see Posamentier and Abdi, 2003; and Vuilleumier and Pourtois, 2007), or pictures of scenes, people and objects like "International Affective Picture Set" (Lang et al., 2005; for review, see Olofsson et al., 2008). Emotional stimuli (e.g., happy, disgusted faces or pleasant and unpleasant pictures) are usually compared to neutral control stimuli to examine spatio-temporal differences among conditions. Others have investigated the perception of emotional words (Kissler et al., 2008; Scott et al., 2008), emotional sounds (Spreckelmeyer et al., 2006), or the neural basis of romantic love (for oscillatory changes, see Basar et al., 2008; for ERPs, see Langeslag et al., 2007). The present study, however, addresses the perception of facial emotional expressions in two modalities: static and dynamic facial expressions of disgust and happiness compared to neutral faces.

One of the major advantages of electrophysiological approaches to emotion perception over fMRI is the high temporal resolution in milliseconds compared to fMRI. In contrast, fMRI signal is based on neuronal blood flow which increases slowly with neuronal activity and is, hence, an indirect and temporally delayed measure of brain activation (Hopfinger et al., 2005; Huettel et al., 2004; see also Chapter 1.6 of the present thesis). Thus, by applying EEG, it is possible to show the temporal dynamics of emotion perception represented by several topographically specific event-related components. Despite the low spatial resolution in EEG, multiple channel/high density EEG (60 to up to 240 electrodes) provides spatial information to a limited extent which can be investigated by the application of different source analysis approaches, e.g., low resolution brain electromagnetic tomography LORETA (Pascual-Marqui et al., 2002), or the equivalent current dipole (ECD) approach implemented in BESA® software (Luck, 2005b; Scherg and Berg, 1991).

The following section outlines commonly reported event-related components and its

functional associations in emotion perception, i.e., P1 (positive potential around 100 ms), N170 (negative potential around 170 ms), early posterior negativity (EPN, around 250 ms) component, P3 or also called late positive potential (LPP) or late positivity complex (LPC, from about 300ms, up to 1-6 sec). The section continues with an overview of previous findings from different source analysis approaches and by the definition of goals and working hypotheses of the present study. Latency differences (for review, see Olofsson et al., 2008; Pizzagalli et al., 2002; Williams et al., 2006) and lateralization effects (for review, see Wager et al., 2003) will not be discussed and examined in the present study because (1) findings have been questioned and reported controversially and (2) it would be beyond the scope of the present thesis.

3.1.1 P100

The following paragraph introduces the P1 component at approximately 100 ms over posterior regions. The emotional modulation of the P100, which reflects a positive exogenous event-related deflection, has been reported controversially in literature regarding emotion processing.

Pizzagalli and colleagues (1999) were one of the first groups to report an enhanced positive amplitude over posterior electrodes starting at 80 ms in the right and around 100 ms in the left hemisphere in participants passively viewing liked compared to disliked faces. They argued that fast processing of faces is evolutionarily fundamental and has a high survival value. They related the enhanced P1 to the fast subcortical emotion perception route (LeDoux, 1996) and to reentrant pathways of the amygdala to extrastriate brain structures (Amaral et al., 2003; Vuilleumier et al., 2003). These connections have also been linked to attentional and motivational processes in a recent fMRI study (Lang et al., 1998). The P1 has also been shown to be enhanced for emotional faces compared to neutral faces over fronto-central regions (Eimer and Holmes, 2002; Williams et al., 2006) and over lateral occipital electrodes (Batty and Taylor, 2003; Pizzagalli et al., 1999; Pourtois et al., 2005) about 100 ms after stimulus onset. Neural generators have been discovered by source analysis approaches in the extrastriate cortex (Pourtois et al., 2005). Moreover, it has been suggested for both regions that the meaning of salient, affective information is extracted by a coarse emotional feature analysis of the stimuli by the AMG (see also LeDoux, 1996; subcortical emotion perception route) - especially during the perception of fearful faces - before the face is completely processed as a whole as represented by the following, by some authors called “face-specific” N170 (for review, see Vuilleumier and Pourtois, 2007). This argument is in line with the

interpretation suggested by Pizzagalli and Vuilleumier and co-workers (Pizzagalli et al., 1999; Vuilleumier et al., 2003). These findings cannot be generalized because those differences were predominantly based on fearful compared to neutral stimuli.

In contrast, other studies did not report enhanced P1 by emotion (Eimer et al., 2003; Krolak-Salmon et al., 2001; Leppanen et al., 2007) claiming that the P1 was not sensitive to emotional facial expressions. Instead, it was argued to be associated with early visual processing, selective spatial attention (Hillyard and Anllo-Vento, 1998), and sensitive to basic stimulus features like luminance instead of emotional or facial features (Allison et al., 1999). The reason for these controversial findings are unknown and need to be investigated in more detail also in regard to other emotional valences (Leppanen et al., 2007).

Since the present study investigated the processing of disgust and happiness conveyed by facial expressions, an emotional modulation of the P1 was not expected.

3.1.2 N170

One of the most discussed components aside from the late positive potential (LPP) in emotional face perception is the N170. The N170 component has been reported in several EEG and MEG studies of face and emotional face perception (for reviews, see Eimer and Holmes, 2007; Posamentier and Abdi, 2003; Vuilleumier and Pourtois, 2007). It represents a negative deflection at approximately 170 ms over lateral occipito-temporal electrode sites (e.g., T5/6, P7/8) recorded from the scalp in healthy participants which has been shown to be highly sensitive to faces (Caharel et al., 2005; Eimer, 2000; Eimer and Holmes, 2002; Halgren et al., 2000; Herrmann et al., 2002; Rossion et al., 2003). The counterpart of the N170 with equivalent latency, but reverse polarity is the vertex positive potential (VPP) over centro-parietal, centro-frontal electrode sites (Krolak-Salmon et al., 2001; Rossion et al., 2003). In patients with implanted intracranial electrodes in ventral occipito-temporal areas the face-specific N170 component has been recorded with a latency of 200 ms (Allison et al., 1999; McCarthy et al., 1999; Puce et al., 1999). Previous fMRI studies have emphasized the role of the FuG in invariant face perception and identity naming this anatomical region the fusiform face area (FFA; see Kanwisher et al., 1997). Inferior temporal, fusiform gyrus and ventral occipital regions (Halgren et al., 2000; Rossion et al., 2003) or superior temporal regions (Itier and Taylor, 2004) have been related to the N170 in different source analyses approaches examining face perception.

A question that has often arisen in the current literature is whether the face-specific N170 is modulated by emotion. There are two contrary positions:

N170 is face-specific, but not modulated by emotion

The N170 was discussed to be involved in the structural processing of facial features and the integration into a holistic face percept (structure, internal, external features) in several face discrimination studies (Bentin et al., 1996; Bentin and Deouell, 2000; Eimer, 2000; Rossion et al., 2000; Schweinberger et al., 2002). Some studies examining the time course of emotional face processing showed that the N170 is totally independent and unaffected by emotional valence (Eimer and Holmes, 2002; Holmes et al., 2003; Leppanen et al., 2007; Streit et al., 2000) and that emotional face processing does not take place until structural encoding of facial features is completed. Therefore, the face perception model by Bruce and Young (1986) supported the assumption that structural encoding of facial features is sequentially followed by recognition and identification of the face and emotional expressions. For the modified version of this model, see also Haxby and colleagues (2000; see also Fig. 1 for a reprint of the model).

Single cell recordings in non-human primates have supported this view by reporting cells responding to different identities of faces in inferior temporal areas (Hasselmo et al., 1989), but not to different emotional expressions. In contrast, cells in superior temporal areas responded specifically to emotional expressions, but were not face-specific. In humans, this view has been supported by the double dissociation found in several patient studies: patients with prosopagnosia due to brain lesions in either bilateral inferior occipito-temporal areas or right occipital and parietal areas were unable to recognize faces, but are able to distinguish different emotional valences (Posamentier and Abdi, 2003; Tranel et al., 1988), whereas patients with, e.g., bilateral amydalae lesions had difficulties to distinguish emotional valences, but were able to recognize different facial identities (Adolphs et al., 1994). Patients with prosopagnosia have shown non-selective or absent N170 during the presentation of faces (for review, see Posamentier and Abdi, 2003).

A large study of 98 epileptic patients with intracranially implanted electrodes on the cortex surface participated in studies of face and object perception reported in three different studies supported the face-specificity of the N170 component (Allison et al., 1999; McCarthy et al., 1999; Puce et al., 1999). Allison and colleagues (1999) reported of the face-specific N200 - among other ERP components - which has been found bilaterally with a non-significant dominance to the right hemisphere in ventral occipital, inferior temporal, and lateral middle temporal regions. The N200 has been shown to be enhanced during the initial structural encoding of complex facial features versus objects, letter strings, or sinusoidal gratings. Further examination of the N200 revealed that the face-specific component was found to be

insensitive to colors, to the size of the faces, to habituation, to semantic priming, and to familiarity of the face (see also Bentin and Deouell, 2000; Eimer, 2000). The N200 showed faster latencies for upright than for inverted faces (see also Ashley et al., 2004), for full faces than for face parts, it was enhanced by the full representation of a face in contrast to parts of faces like lips, eyes, nose (which however still show larger face-specific N200 than objects), and yielded higher amplitudes for faces compared to affective stimuli (McCarthy et al., 1999; Puce et al., 1999). Furthermore, they also supported the point of view that the posterior early negative component was not emotionally modulated (Allison et al., 1999).

Functional neuroimaging and recent EEG data have challenged this point of view. Especially the FuG has been shown to be modulated by emotional valence in many fMRI studies (Kilts et al., 2003; LaBar et al., 2003; Pessoa et al., 2002), and in the present fMRI as described in Chapter 2.

Emotional modulation of the N170

Missing emotional modulation of the N170 component might be explained by different study designs. Studies, in which participants were asked to watch emotional faces passively or attentively without intentionally evaluating the displayed emotional valence (e.g., by button press), have revealed this modulation quite consistently (Batty and Taylor, 2003; Blau et al., 2007; Pizzagalli et al., 2002; Williams et al., 2006). This modulation was reflected by an increase of amplitude for emotion over ventral occipito-temporal regions. The latter regions have been shown to be enhanced in source analysis approaches in similar time windows (Lewis et al., 2003; Sprengelmeyer and Jentzsch, 2006; Williams et al., 2006) and have been attributed to lateral occipito-temporal (possibly the STS area) and the fusiform gyrus area (Batty and Taylor, 2003; Blau et al., 2007; Caharel et al., 2005; Pizzagalli et al., 2002; Williams et al., 2006). These cortical regions have consistently been shown to be activated in previous fMRI studies reporting enhanced BOLD signal in emotion when compared to neutral facial expressions in the respective brain regions (Sato et al., 2004). Additionally, emotional modulation of the N170 has been related to feedback projections of the AMG to the ventral path of visual perception (Amaral et al., 2003; Blau et al., 2007).

Furthermore, Vuilleumier and Pourtois (2007), concluded in a recent review of fMRI and EEG studies, which addressed emotion perception, that processing of faces and emotional facial expressions and its valence could not entirely be separated from structural face processing as discussed in many previous studies and as suggested by Bruce and Young (1986). Consequently, Vuilleumier and Pourtois (2007) suggested that emotional face processing might be independent of, but temporally parallel to face processing.

The present study intends to address the above mentioned debate and intends to closely examine the "behavior" of the N170 in static facial expressions.

3.1.3 EPN (Early Posterior Negativity)

The EPN (Early Posterior Negativity) component temporally follows the N170 and reflects a relative negative shift peaking after approximately 250 to 300 ms over occipito-temporal regions. The topography of the EPN has been shown to be similar for facial expressions and emotional IAPS pictures (Schupp et al., 2003, 2004a; Schupp et al., 2004b), and to yield increased negativity in lateral posterior regions. The latter regions have been associated with the fusiform gyrus (FuG) and lateral occipital regions (Schupp et al., 2004b) suggesting that visual structures contribute to the modulation of the EPN. Applying topographical current source density distributions (Laplacian) - a specific source analysis approach - in this time window has recently revealed neural generators being enhanced for pleasant and unpleasant versus neutral IAPS stimuli over temporo-parieto-occipital regions. The latter regions have been associated with the posterior visual processing system and early perceptual level processing (Junghofer et al., 2001).

An increased EPN has been reported in a variety of different study designs:

- in individuals passively viewing threatening (angry) facial expressions compared to neutral facial expression without being instructed to pay attention to the emotional valence (Schupp et al., 2004b),
- in individuals viewing emotional faces of disgust, but not fear or happiness, compared to neutral condition (neutral = control) and pressing a button when a face of the same identity and expression was repeated (Ashley et al., 2004),
- in individuals who were asked to determine the gender of fearful, happy, and neutral faces (Sato et al., 2001), and of fearful, angry and disgusted faces (Sprengelmeyer and Jentzsch, 2006), again without paying attention to the emotional valence of the faces,
- in individuals attending to and categorizing faces as either emotional or neutral (Eimer et al., 2003) or as happy or fearful (Leppanen et al., 2007), and
- in individuals categorizing pleasant, unpleasant, and neutral pictures (IAPS) (Schupp et al., 2003, 2004a).

All of these studies have in common that - independent of whether attention was focused on the emotional valence of both, faces and pictures, or not - emotional salience and increased intensity of stimuli seemed to modulate the EPN.

EPN and emotional valence

Whether this modulation depends on positive, negative or both emotional valences versus neutral stimuli has been discussed controversially. On the one hand, modulation of the EPN has been shown only for unpleasant IAPS pictures (Leppanen et al., 2007), for threatening compared to pleasant and neutral faces (Schupp et al., 2004b), and for faces of disgust, fear, and anger with high compared to low intensity (Sprengelmeyer and Jentzsch, 2006). Ashley and colleagues (Ashley et al., 2004) have reported a disgust specific EPN in occipito-temporal areas (O1 and O2, less pronounced in T5/T6) for upright faces peaking around 300 ms compared to upright neutral and happy faces. On the other hand, both pleasant and unpleasant pictures evoked EPN (Herrmann et al., 2008; Schupp et al., 2003, 2004a). Therefore, the emotional specificity of this component needs further exploration, especially for the perception of positive and negative faces.

EPN and stimulus material: emotional scenes versus emotional faces

An additional aspect of the above mentioned variety of experimental designs needs to be discussed: Eimer and colleagues (2003) argued that the emotion-specific increase of negative amplitude in occipito-temporal regions depends on the focal and selective attention to emotion. In contrast, the increase of EPN for emotional compared to neutral stimuli in different task requirements as listed above support increasing evidence that the process displayed by the EPN is automatic and independent of simultaneous explicit attention to emotion (Schupp et al., 2004b). The latter argument can be emphasized by the affective modulation of EPN (1) during a rapid serial stream stimulation design limiting attentional capacities (e.g., Junghofer et al., 2001) or (2) during gender decision tasks, in which the emotional content were ignored (Sato et al., 2001; Sprengelmeyer and Jentzsch, 2006).

Schupp and co-workers (2004b) have related their finding of increased EPN to threatening facial stimuli to the - by Ohman and Mineka (2001) proposed - module of fear and fear learning. They argued that especially faces displaying threat convey high evolutionary significance (fear in this case) and that they must be detected fast, automatically, and reflexively based on pre-existing knowledge which needs to be rapidly activated. Thus, attention is captured automatically. The EPN might therefore represent the tagging of those stimuli facilitating further, more elaborate processing. This interpretation approach has been predominantly related to fearful stimuli. Since EPN enhancement has also been found in other negative emotional stimuli (disgust, anger, unpleasant and pleasant pictures) which could per se convey potential threat, the question arises whether the EPN could possibly be related in

general to the processing of negative, highly arousing, evolutionary, and socially relevant stimuli.

Considering the involvement of subcortical and limbic structures, especially of the amygdala, to emotion perception as reported in many fMRI studies (for review, see Adolphs, 2002; Phan et al., 2002), enhanced EPN has also been associated with reentrant amygdalar pathways which project back to the ventral path of higher level visual regions (Leppanen et al., 2007; Sato et al., 2001; Schupp et al., 2004b) resulting in the recruitment of attentional resources and followed by a more elaborate processing of emotions (Schupp et al., 2004a).

Based on the above mentioned findings, EPN enhancement is expected for the perception of disgust in the present study because EPN has been predominantly shown for negative facial expressions in temporo-occipital regions.

At this point, the P3 and late positivity potential (LPP) over predominantly centro-parietal and fronto-central electrode sites should be introduced.

3.1.4 LPP (Late Positive Potential)

While the P1, N170, and EPN reflect early perceptual and sensory processing stages (Herrmann et al., 2008; Schupp et al., 2004b), which differ due to physical features of stimuli, the late positive potential (LPP) refers rather to the later, postsensory and higher order processing stages.

After emotional stimuli have been "tagged" as motivationally relevant represented by the EPN (see Chapter 3.1.3), which facilitates the processing of emotional stimuli, stimuli are elaborated continuously and in more detail. This is reflected by an increase of positive amplitudes called the LPP. The LPP has several synonyms in EEG literature of emotion. It has been labeled predominantly LPP, but also positive slow wave (SW) or late positivity complex (LPC). The present thesis will adopt the first synonym throughout this work. The LPP is a slow and sustained positive wave which starts at approximately 300 ms (Leppanen et al., 2007), and which is sustained for several hundred ms (Leppanen et al., 2007; Schupp et al., 2004b) or for up to 6 sec (Cuthbert et al., 2000) after emotional compared to neutral stimulus onset. LPP is most pronounced over midline parietal, central and frontal electrodes.

It is important to note that the LPP is preceded by the P3 after about 300 ms. The P3 component has first been described by Sutton and colleagues (1965) about 43 years ago during a stimulus uncertainty task, and has been widely studied in many different task designs (for reviews, see Polich, 2007; Polich and Kok, 1995). It is considered as the classic index of attention, recognition, and stimulus probability, e.g., in oddball tasks (Donchin and Coles,

1988). The P3 can be divided into 2 subcomponents (P3a, P3b), is modulated by many different cognitive (attention allocation, memory formation) and biological determinants (i.e., natural and environmentally induced state variables, for review, see Polich and Kok, 1995), which will not be further discussed in the present thesis (for review, see also Polich, 2007). In emotion perception studies, enhanced amplitudes of P3 have been reported to be most pronounced in oddball tasks, to be associated with tasks in which the stimuli are task-relevant and involve a cognitive evaluation, and to be attenuated in passive viewing designs (for review, see Olofsson et al., 2008).

The P3 and the LPP are usually considered to be one processing complex. While the P3 has been suggested to be involved in attention and initial memory storage events, the subsequent LPP has been related to the transfer of information to working memory (Schupp et al., 2004b), and furthermore, to enhanced encoding processes in incidental memory for emotional and arousing IAPS pictures (Dolcos and Cabeza, 2002).

Regarding emotional face perception studies, LPP has been associated with selective attention to the emotional content of the facial expressions facilitating the continued and deeper evaluation of the stimuli (Eimer et al., 2003; for review, see Vuilleumier and Pourtois, 2007). Eimer, Holmes and McGlone (2003) reported enhanced LPP in midline frontal, central and parietal electrodes during an emotional decision task, which required the allocation of focal attention to both positive and negative emotions. However, this enhancement was not found during a complex line decision task during which the emotional stimuli were ignored. This led Eimer and co-workers (2003) to the conclusion that the LPP was modulated by explicit emotional processing requiring focal attention allocated to the emotional stimuli.

In general, several research groups have supported the latter findings by applying emotional discrimination or evaluation tasks during the perception of facial expressions with the exception that they either found LPP increased for fearful compared to happy (Leppanen et al., 2007) or neutral (Eimer and Holmes, 2002) expressions, or for sad compared to happy expressions (Orozco and Ehlers, 1998); hence, predominantly for negative compared to positive or neutral facial stimuli. Thus, results are in line with the hypothesis that threatening faces facilitate processing reflected by increased LPP (Schupp et al., 2004b). Schupp and colleagues (2004b) have discussed those results in line with accompanying increased EPN amplitudes. EPN and LPP correlated positively with increased arousal ratings and were linked to the above mentioned evolved module of fear by Ohman and Mineka (2001). In summary, they suggested that the processing of threatening faces is facilitated because of their evolutionary significance.

Unlike Schupp and coworkers (Schupp et al., 2004b) who reported emotional modulation of LPP for negative or threatening facial expressions, Eimer and colleagues (2003) showed enhanced LPP for *all* emotional categories compared to neutral facial expressions. Finding both positive and negative valences to contribute to LPP has been predominantly reported in studies applying IAPS stimuli of pleasant and unpleasant valence (Cuthbert et al., 2000; Schupp et al., 2003, 2004a). This aspect would rather suggest that LPP depended on arousal or emotional salience per se, and not on the emotional valence of the stimuli.

Aside from varying results regarding LPP and valence, it is important to mention that increased LPP has also been reported in emotional perception studies applying different task designs like e.g. a one-back task (Eimer and Holmes, 2002), a passive viewing task (Schupp et al., 2004b), in which attention was not directed to emotions, and a task, in which participants attended to faces without executing a button press (Williams et al., 2006). All of the latter three studies have also shown enhanced LPP exclusively for the fearful/threatening faces, but not for happy expressions. Consequently, latter results contradicted those reported by Eimer, Holmes, and McGlone (2003) suggesting that LPP depends on selective attention. Thus, LPP might not require full selective attention to the emotional stimulus because it has also been found in passive viewing designs, but might be enhanced by arousal compared to other stimuli (Schupp et al., 2004b). Besides, increased arousal of emotional stimuli has been found to enhance both EPN and LPP (Schupp et al., 2007).

Due to these controversial results, the question arising for the present study is whether LPP is modulated solely by negative, hence, disgusted faces or also by happy faces. Furthermore, it will be investigated in how far the dynamic modality of the presently used stimulus material influences the emotional processing per se.

3.1.5 Source analysis approaches in emotion processing studies

After discussing the different ERP components in emotion perception yielding a high temporal resolution, the following section gives a brief overview of different source analysis approaches which combine temporal and spatial information in emotion perception by revealing possible underlying generators.

To date, taking advantage of the high temporal resolution, there have been many studies applying different source analysis strategies to enhance knowledge about the spatio-temporal progress of neuronal processes in, for example, primary visual (Singh et al., 2003), primary somatosensory (Arthurs et al., 2000), and higher order cognitive tasks (e.g., see different working memory tasks; Bledowski et al., 2006; Wibral et al., 2008).

However, there is only a limited number of studies applying source analysis approaches to study the temporal dynamics of different brain regions during emotion perception of either facial expressions (Batty and Taylor, 2003; Lewis et al., 2003; Sprengelmeyer and Jentzsch, 2006; Streit et al., 1999; Williams et al., 2006) or emotional pleasant or unpleasant scenes (Junghofer et al., 2001; Schupp et al., 2003), and an even more limited number of studies combining fMRI BOLD activations with EEG source models, the so-called fMRI constrained approach (Sabatinelli et al., 2007).

The comparability of those studies is possible, but limited because of the high variety of different source localization methods. While some groups applied Current Source Density (CSD) distribution analysis to determine underlying brain regions of emotional scene perception (Junghofer et al., 2001; Schupp et al., 2003), others applied Low Resolution Brain Electromagnetic Tomography (LORETA; Esslen et al., 2004; Williams et al., 2006), or Local Auto-Regressive Average Model (LAURA; Batty and Taylor, 2003) for modeling underlying sources of emotional face perception. The latter source analysis methods, all based on inverse solution approach, are able to locate multiple sources, but with a lower spatial resolution compared to fMRI. Another approach is based on Equivalent Current Dipole (ECD) source models as implemented in BESA® and as applied by, for example, Lewis and co-workers (Lewis et al., 2003) and Sprengelmeyer and Jentzsch during emotional face perception (Sprengelmeyer and Jentzsch, 2006). They compared electrophysiological responses of static expressions of disgust and happiness to neutral faces. However, they used an emotion and gender discrimination task, respectively (Lewis et al., 2003; Sprengelmeyer and Jentzsch, 2006), whereas the present EEG study applied a passive viewing task. A limitation of the latter studies might be that they have reported one symmetrical pair of dipoles (Sprengelmeyer and Jentzsch, 2006), and one single dipole (Lewis et al., 2003) located in the FuG or adjacent visual areas. However, fitting a larger number of dipoles to a source model might be a more appropriate approach in order to be able to explain the time course of the complex network of brain regions which has been reported to be involved in emotion processing (Adolphs, 2002).

A combined approach of EEG and fMRI activations has recently captured increased attention in the neuroscientific community. Recent methodological discussions about different source analysis approaches have suggested using multiple source models based on previous knowledge of anatomy and physiology or based on activation patterns recorded by fMRI (Hopfinger et al., 2005; Scherg and Berg, 1991). One of the advanced works using this approach has been recently published by Bledowski and co-workers and Wibral and co-

workers (Bledowski et al., 2006; Wibral et al., 2008). They have used different working memory tasks applying fMRI activation patterns for seeding their discrete multiple source models. A similar approach has been reported by Sabatinelli and colleagues (2007). It is important to mention that Sabatinelli and colleagues (Sabatinelli et al., 2007) used IAPS stimuli, and not emotional facial expressions as applied in the present study. Besides, they limited their analysis to the late positive potential component between 400 and 900 ms after stimulus onset. Consequently, the time course of possible sources of early processing stages was not considered, but would be of interest.

To the author's knowledge, there has been no study investigating emotion perception with an fMRI constrained approach applying complex and multiple source models with more than two dipoles or regional sources. The present study intends to investigate emotional face perception with such a complex approach to present one possible approach to fill this gap.

3.1.6 Dynamic facial expressions and ERPs

All of the reported EEG studies of the present thesis have used static stimuli to investigate the temporal dynamics of emotion perception. To the author's knowledge, there has not been a single EEG study examining the perception of static and dynamic facial expressions of happiness and disgust. The aspect of motion in emotional expressions seemed to have been neglected for a long time in electrophysiological research. In contrast, work groups have started to apply dynamic facial expressions applying fMRI because dynamic faces are supposed to convey a more ecological approach to study emotion perception (Kilts et al., 2003; LaBar et al., 2003; Sato et al., 2004; see also Chapter 1.5, 2.2, and 2.4.3 for further details). These fMRI studies have confirmed stronger and more widespread activations in a large network of brain regions involved in emotion and face perception, such as, for example, amygdala, superior temporal gyrus, inferior frontal gyrus, parahippocampal and posterior cingulated cortex, visual cortices (Kilts et al., 2003; LaBar et al., 2003; Sato et al., 2004). The latter results could be supported by the fMRI study of the present (see Chapters 2.2 and 2.4.3 for a more detailed description).

The latter results highlight the importance of examining the spatio-temporal time course of dynamic face perception.

3.1.7 Hypotheses and goals of the present EEG study

The present study entered "virgin soil" with respect to several aspects indicating the goals of the present EEG study:

Firstly, because of the fact that the present thesis applied a new stimulus database to examine static and dynamic face perception, one of the major goals was to characterize emotional modulation of ERPs and regional source models and to compare and integrate those results with fMRI data presented in Chapter 2.

Secondly, the present EEG study was the first one, to date, applying dynamic facial expressions. Thus, ERPs and source models were studied in order to reveal the spatio-temporal processing of perception of dynamic faces.

Thirdly, this was the first study examining facial expressions of static and dynamic modality in an fMRI constrained multiple regional source model.

Based on these statements the following hypotheses were formulated:

For static faces, emotional modulation of P1 was not expected because happiness and disgust, but not fear, were examined (Vuilleumier and Pourtois, 2007). Further typical ERP components were expected for the static modality: an emotional modulation of the:

- N170, as a face-specific global component associated with the structural analysis of features of a face and simultaneously extracting typical identity features and emotional content (Batty and Taylor, 2003; Bentin et al., 1996),
- early posterior negativity (EPN) component especially for disgust as suggested by Ashley and colleagues (2004), and
- late posterior positivity (LPP) over centro-parietal electrode sites for sustained evaluation of the emotional, motivationally relevant faces as suggested by Schupp and colleagues (2004b).

For dynamic facial expressions, the onset of the video showing neutral expression (for detailed stimulus description see Chapter 2.4.3 and Fig. 3 A) was expected to induce an early visual-perceptive P1 component (for early visual feature analysis of, e.g., luminance of stimuli; see also Allison et al., 1999) and a face-specific N170 in posterior regions at the beginning of the presentation of the video (Bentin et al., 1996). Those latter components were not expected to be emotionally modulated because actresses displayed an initial neutral expression by looking to the left or right before turning to the front. Therefore, no P100 and N170 deflection were expected for the analyzed time window of dynamic stimuli (development of the dynamic emotional expression) because it was preceded by the turn of the actress' face.

However, for the time window of the videos, which include the beginning and development of the emotional expression, emotion-specific components were expected for dynamic emotional versus neutral stimuli as reflected by sustained LPP over centro-parietal electrodes. In

comparison to static stimuli, LPP was expected to be more pronounced, to be distributed over broader regions, and to be more sustained because dynamic stimuli were expected to recruit, similar to fMRI results (Chapter 2), a larger and more consistent network of brain regions.
A multiple source analysis model based on the different activations found in the above described fMRI study was performed. The models were expanded by sequential fitting strategies to reveal the spatio-temporal dynamics of additionally interacting brain regions. Since there has been no study investigating emotional face perception with multiple source models, the analysis was of explorative nature.

3.2 Material and methods: EEG study

3.2.1 Participants

Twenty one female university students met the inclusion criteria of the study (no history of neurological or psychiatric illness, no drug abuse, no current psychotropic medication, right handedness). Two participants were excluded from the study due to (1) noisy data and (2) technical problems. The remaining 19 participants (range 18-28 years, mean age 21.37 years, SD 3.13) were right-handed according to a modified version of the Edinburgh Handedness Inventory Questionnaire (Oldfield, 1971; Laterality Quotient: mean 95.79%, SD: 14.27, range 40 to 100) and gave informed and written consent to participate in the present study. All individuals were native Spanish speakers (except for one female who was native Hungarian, but spoke Spanish fluently) with eleven to 20 years of education (mean 14.63, SD 2.31 years) and had normal hearing and normal or corrected to normal visual acuity.
As discussed in Chapter 2.4.1, previous fMRI-studies (Wager et al., 2003) and EEG-studies (Marinkovic and Halgren, 1998; Proverbio et al., 2006) reported gender differences in emotion perception controversially. To avoid gender effects solely females were included in the study design.

3.2.2 Data protection, data security and legal framework

The study protocol was approved by the local ethic committee of the University of Barcelona where the study was conducted according to the Code of Ethics of the World Medical Association (Declaration of Helsinki, 1964/2004).
Participants were informed about data collection, data protection and data security, about general and specific risks of the experimental equipment, and about the recordings of the electroencephalogram (EEG; see Appendix C.1).

According to this information and their right to quit the experiment during the entire course of the examination, participants gave written and informed consent for their participation prior to the beginning of the experiments (see Appendix C.1). Furthermore, they were naïve to both the working hypothesis of the study and the stimulus material.

3.2.3 Experimental procedure: study design and strategies of data analyses

3.2.3.1 Stimuli

Identical stimulus material and trial specifications was applied as described in Chapter 2.4.3 (see also Figure 3).

3.2.3.2 Trials and sequence

Dynamic and static stimuli (40 stimuli per emotional valence [neutral, happiness, disgust] and per modality [static and dynamic]) were presented in a pseudo-randomized non-stationary probabilistic sequence (Friston et al., 1999c; see also Fig. 4) and in two separate counterbalanced runs. For a detailed illustration of the experimental design see Chapter 2.4.3 and Figures 3 and 4 of the present thesis.

A hitpoint analysis for each single video (for detailed explanation, see Chapter 2.4.3.2) yielded an average duration of 1.5 sec from the maximum of the emotional expression to the end of the video. In order to keep presentation duration of the emotional expressions alike for both modalities, a presentation duration of 1.5 sec was also chosen for static faces (see above, Chapter 2.4.3).

Participants were asked to watch the faces carefully on a screen (distance 120 cm, size H 15 x W 18.33 cm., vertical and horizontal visual angle of 7.1° and 8.7°, respectively) and to "empathize" the presented expressions. Note that the visual angle of the current study was approximately half of the visual angle in fMRI study. No button press was recorded during face viewing to avoid motion-related confounding with brain activation during emotion perception (Balconi and Lucchiari, 2007).

3.2.4 Behavioral measures: rating of stimulus material

After the EEG recordings, electrodes were detached before participants rated the complete stimulus material which was presented in the same sequence as during the EEG recordings. All participants rated both the videos and the photos on 2 scales: arousal (0 not arousing – 10 highly arousing), and valence (neutral, disgust or smile) by mouse click with right index

finger (see Chapter 2.4.3 and Fig. 3 for details).

Nonparametric one-sample Kolmogorov-Smirnov tests were calculated for each variable to test for normal distribution properties justifying the following parametric statistical approach by ANOVAs using SPSS® (SPSS®, Inc., Chicago, USA). General linear models (GLM) repeated measures ANOVAs were performed on behavioral data (between subject factor: MODALITY [MOD, 2 levels: begin with static / dynamic stimuli], within subject factor EMOTION [EMO, 3 levels: neutral, happiness, disgust] and SEQUENCE [SEQ, 2 levels: static or dynamic stimuli first]) for arousal and valence (percent of correct categorization of stimuli) separately applying Greenhouse Geisser (GG) correction where appropriate. Post hoc analyses (Fisher's LSD, least significant difference tests and paired sample t-tests) were calculated according to significant and trend to significance main effects and interaction effects ($p<.05$, $p<.1$, respectively).

3.2.5 ERPs and source models

3.2.5.1 Data acquisition

Multichannel EEG was recorded in an electrically and sound shielded room from 62 Ag/AgCl scalp electrodes placed according to international 10-10-system (AF3, AF4, AF7, AF8, AFZ, C1, C2, C3, C4, C5, C6, CP1, CP2, CP3, CP4, CP5, CP6, CPZ, CZ, F1, F2, F3, F4, F5, F6, F7, F8, FC1, FC2, FC3, FC4, FC5, FC6, FCZ, FP1, FP2, FT7, FT8, FZ, M1 [=TP9], M2 [=TP10], O1, O2, OZ, P1, P2, P3, P4, P5, P6, P7, P8, PO3, PO4, PO7, PO8, POZ, PZ, T7, T8, TP7, TP8, see Fig. 9, gain: 22bits. 71nV/bit., A/D-rate 512 Hz x oversampling [each channel as an amplifier], analog filter: 15 KHz pre-sampling, digital filter: 0.27 Fsample, antialiasing, CMRratio [common rejection mode]: 50Hz/90dB, no saturation seen online, safety voltage limitation included, mounted on an easycap, average reference; ANT Software B.V., Enschede, Netherlands) including horizontal and vertical electro-occulogram (HEOG/VEOG) attached to the right canthus and below the right eye of the participant and ground electrode placed on the chest of each participant. Impedances were kept below 15 kohms and were checked repeatedly between runs.

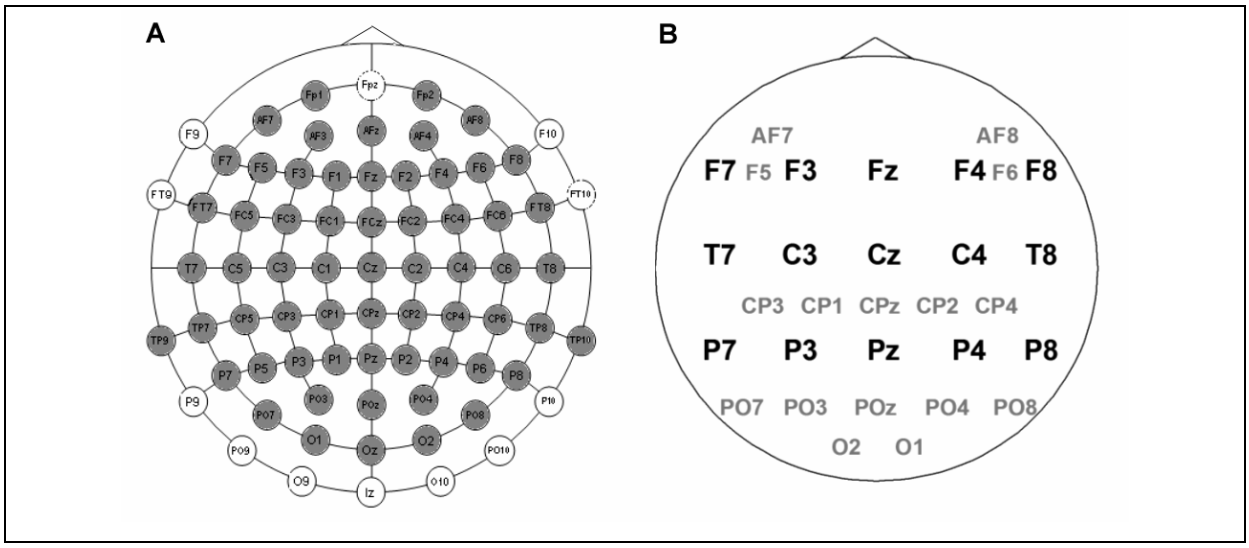

Figure 9: (A) Complete electrode setup of 62 electrodes. (B) Setup of 15 equidistant electrodes (black) and 16 additional electrode sites of interest (gray).

3.2.5.2 ERPs: data and statistical analysis

EEG data were analyzed with BESA® 5.1.8.10 (www.besa.de, MEGIS Software, Munich, Germany) for ERP averaging and equivalent regional source analysis, and with Matlab® Tools (version 6.5.1, MathWorks Inc.; Aachen, Germany) to calculate mean amplitude values and differences of source strength waveforms. FP1, FP2, TP9 (M1) and TP10 (M2) were excluded for source analysis purposes and were not further considered for ERP analysis.

ERP data analysis

Data of each single subject for each modality (static and dynamic) were visually inspected for artifacts and drifts. Channels including drifts were corrected before averaging by spherical spline interpolation algorithm implemented in BESA®. Table 3 displays the interpolated channels for several participants. The number of interpolated channels was kept below 5% (Picton et al., 2000) of the complete channel set up (maximally excluded channels: 3, equals 4.7%, see Table 3).

participants	channels - static modality	participants	channels - dynamic modality
ff003	PO7	mf000	Fz, P2
ff006	Oz	mf002	FC5
ff008	F3, C4	mf008	AF7, F3, C4
ff012	P4	mf012	FC3, P2
		mf014	O2

Table 3: Spherical spline interpolated channels for the static (left column, ff = static modality) and the dynamic modality (right column; mf = dynamic modality).

For stimulus-locked analyses, initial visual inspection of data indicated that data were low on

blink, saccade (which was not surprising because participants were asked to fixate a dot on the center of the screen), and muscle artifacts. Therefore, the data were analyzed using the artifact scan tool and automatic averaging tool implemented in BESA® including sweeps with amplitudes below 100 μV. Since eye blinks usually show amplitudes much larger than spontaneous and evoked activity, the artifact scan tool validly detects and excludes blinks, but also other artifact contaminated trials which show amplitudes larger than 100μV, from further analysis. Furthermore, artifact scan results were visually inspected on single sweep basis. The amplitude threshold of the data of 15 participants for static (amplitude mean: 76.11 μV, SD: 14,19 μV, range 61 – 100 μV) and of 17 participants for dynamic stimuli (amplitude mean: 67.05 μV, SD: 17.45, range 51.8 – 100 μV) was reduced after visual inspection single sweeps (artifact scan tool). Thus, the experimenter of the present study ensured that the data for free of artifacts for subsequent automatic averaging of ERP data. Amplitude thresholds did not differ significantly between static and dynamic modality (repeated-measures ANOVA, factor MODALITY [2], F [1, 18] = 3.4, p=.08). Consequently, automatic averaging tool was applied for 16 participants for the static and in 15 participants for the dynamic modality. Data of 3 individuals for static and 4 individuals for dynamic modality were analyzed by visual inspection on single sweep level. Artifact free ERP data included an average of 33.7 sweeps for static (SD 4.6, 84.2% of sweeps, range 24 – 40; 34.2, SD 4.3 for neutral, 33.7, SD 4.5 for smile, 33.1, SD 5.0 for disgust) and 34.8 sweeps (SD 2.6, 87.2% of all sweeps, range 29 – 40; 35.32, SD 2.5 for neutral, 34.2, SD 2.5 for smile, 35.2, SD 2.5 for disgust) for dynamic stimuli.

Data were high-pass filtered for averaging (0,1 Hz, 6 db/octave, forward, applying an indirect baseline correction), with a default epoch of -100 ms (baseline) to 1000 ms locked to stimulus begin for static facial expressions and to the beginning of the emotional expression for dynamic faces (hitpoint: begin of emotional expression, see above, Chapter 2.4.3, Fig. 3).

A low-pass filter (LPF) of 30 Hz on individual level after averaging and before grand averaging was applied. The ERP data of 19 participants were entered in a grand average analysis for each static and dynamic modality.

Analysis of onset of videos

The onset of videos was analyzed with an automatic algorithm implemented in EEprobe (version: 3.3.116, http://www.ant-neuro.com/; ANT - Advanced Neuro Technology). This analysis was applied to check whether the onset of the videos also similar evoked face-specific components, but without showing an emotional modulation. The following parameters were applied for averaging data of remaining 17 individuals (2 additional

participants were excluded due to a low number of averaged sweeps): digital filter before averaging on single subject level: high pass filter (HPF) 0.1 Hz (fourrier series, 3001 time points, sampling rate 512 Hz), rejection by trial (-100 and 100 V for all of the electrodes), FC5 was excluded in one participant because of too much noise, digital LPF of 30 Hz (fourrier series, 3001 time points, sampling rate 512 Hz) after averaging on single subject level, averaging on single subject level with an automatic algorithm (-100 to 1000 ms epoch, baseline: -100ms to 0 ms (baseline correction: on) which resulted in 25-40 averages per condition and subject, visual inspection of single subject level to check for bad channels (noise, drifts), interpolation of between 1 and 7 channels was applied when necessary (e.g., FP 1/2, AFs, Fs and/or T7/8 were interpolated).

ERP statistical analysis

After grand averaging the ERP data, evoked potentials of both modalities were visually inspected and selected time windows were determined based on previous findings and revealed peaks. Mean amplitudes of the selected time windows were calculated separately for the static and the dynamic modality. For static faces, maximum deflections of the P100 (110 ms ± 20 ms), the N170 (165 ms ± 25 ms), EPN (250-350 ms), and LPP (600-800 ms) were included for further statistical analyses.

Extracting time windows was not as obvious for dynamic as for static facial stimuli. Averaged ERPs of dynamic emotional stimuli showed a rather slow and sustained positivity especially over centro-parietal electrode positions in contrast to the above mentioned early ERP components as in static modality (e.g., P1, N170 etc.) because the onset of the emotional expression was modeled and not the onset per se of the video (see also Chapter 3.1.7). For that reason, seven 100 ms time windows (100-800 ms) were chosen by visual inspection for further exploration of the data by calculating mean amplitudes of the selected time windows.

Nonparametric one-sample Kolmogorov-Smirnov tests were calculated for each variable to test for normal distribution properties justifying the following parametric statistical approach by ANOVAs using SPSS® (SPSS®, Inc., Chicago, USA).

GLM repeated-measures ANOVAs were performed on mean amplitude values (separately for static and dynamic modality) of different time windows including within-subject factors ANTERIOR-POSTERIOR (AP, 3 levels: frontal, central and posterior electrode positions), LATERALITY (LAT, 5 levels: from right to left electrode sites), and EMOTION (EMO, 3 levels: neutral, happiness, disgust) for topographical analysis of ERP data using SPSS® (SPSS®, Inc., Chicago, USA) and including the following electrode positions: F7, F3, Fz, F4, F8, T7, C3, Cz, C4, T8, P7, P3, Pz, P4 and P8 (see Fig. 9 B, black electrode sites). Because of

their equidistance the latter electrodes are appropriate for topographical analysis (see also Fehr et al., 2006). Main effects and significant interactions were Greenhouse Geisser (GG) corrected where appropriate and sphericity was not assumed. Significant three-way interactions justified exploration of single electrodes by paired-sample t-tests. Main effects or two-way interaction effects ($p<.05$ and $p<.1$) including the factor EMOTION were further explored with ANOVAs for each single electrode site. In case of significance ($p<.05$) or trend to significance ($p<.1$), post hoc analyses (paired sample t-tests) were calculated.

Mean amplitudes of additional electrodes of regions of interest were analyzed by repeated-measurement ANOVAs (within subject factor EMO, three levels: neutral, happiness, disgust) and paired sample t-tests for the above mentioned time windows (for additional electrode set up for static and dynamic faces, see Fig. 9 B, gray electrode sites).

Choosing the latter threshold emphasizes the explorative nature of the study which applied the described stimulus material for the first time in an electrophysiological study design.

For the analysis of the onset of the videos, identical statistical procedures were applied.

3.2.5.3 FMRI constrained source models: data and statistical analysis

While one generator of neural activation in the brain can only have a unique topography, the same topography can yield many different combinations of generators called the inverse problem (see Chapter 1.6.2). This inverse problem was approached by applying fMRI constrained source localizations and an additional sequentially fit multiple regional source model (for further definitions see Chapter 1.6).

Regional sources (RS) instead of dipoles were applied for a multiple discrete source model (for definition of RS see below). Regional source activity was analyzed separately for dynamic and static facial expressions to study the differences of time course of the activities of the modeled brain regions for the different emotional conditions (Scherg and Von Cramon, 1986).

FMRI constrained source analysis: data analysis

The procedure is mainly based on an approach recently described by Bledowski and colleagues (2006) and Wibral and colleagues (2008). There were two major differences of the latter to the present study:

Firstly, the seeded regional source locations were derived from activation clusters of a different sample of individuals (see Study 1, Chapter 2).

Secondly, further regional sources were added to complement the model in order to improve

the variance explanation of the source model because several mismatches have been reported between EEG generators and fMRI activations (Im, 2007; for further discussion, see Chapter 4.2).

Source waveforms were computed using a four-shell spherical head model which takes into account individual conductance characteristics of brain, bone, cerebrospinal fluid, and scalp (Scherg and Berg, 1996), and a regularization constant of 1% for the inverse operator. Digitized individual electrode positions were not available for single participants; therefore, a standard spherical head model was used.

Regional sources (RS) consist of three equivalent current dipoles at the same location with mutually orthogonal orientations (Scherg and Berg, 1996; Scherg and Von Cramon, 1986). Consequently, RS represent neuronal current flow of arbitrary directions within the close range of the modeled brain region. Since RS activities are hardly susceptible to small differences between the modeled location of active brain regions and individual anatomical location (Scherg and Berg, 1996; Scherg and Picton, 1991), rather robust source waveforms could be obtained for the fMRI seeding technique despite anatomical differences between participants of study one (fMRI study, Chapter 2) and participants of study two (EEG, Chapter 3).

Since the perception of static and dynamic facial expressions has differed with regard to a more widespread network of brain regions which have been shown to be stronger activated compared to static ones (see Chapter 2), two separate multiple source models were calculated.

A discrete multiple source model was created based on peak activations of the above described fMRI contrasts on the master grand average over all conditions (neutral, happiness, disgust, separately for static and dynamic modality) and all individuals (N=19) in order to achieve a maximal signal-to-noise ratio. The fMRI contrasts disgust > neutral and happiness > neutral (see Table 1, Fig. 7) resulted in seven (four by disgust, three by happiness) for static stimuli and in 33 (17 peaks for disgust and 16 peaks for dynamic happiness) peak locations for dynamic stimuli. For both, but especially for the dynamic modality and its 33 peak locations, the effect of mutual interaction, also referred to as “crosstalk”, of RS needed to be controlled (Bledowski et al., 2006; Wibral et al., 2008) because the more RS are included in a multiple source model, the more decreases their mutual distance to each other and hence, the larger becomes the “crosstalk” of RSs (Bledowski et al., 2006). “Crosstalk” is based on the fact that part of the variance in a source waveform is explained by activity generated at the location of all other sources (Vanni et al., 2004), which becomes especially enhanced with an increasing number of RS. In order to avoid crosstalk between adjacent regional cluster

activations, Talairach coordinates of peak activations being less than 30 mm apart from each other were averaged according to the nearest neighbor method. Thus, closest pairs of Talairach coordinates were averaged first (distance < 30 mm), as long as they were anatomically related to each other (e.g., cerebellar peaks were not pooled with temporal regions, see below for more detailed explanations). Then the distance to the original and adjacent coordinates were checked. If the averaged coordinates were less than 20 mm from its original coordinates and more than 30 mm from adjacent coordinates apart, they were conjoined to one new coordinate. If it was less than 30 mm apart from a third peak coordinate, the latter was pooled and averaged with the initial, original two coordinates. Again, the distance to the original location and other coordinates was tested according to the mentioned constraints. Summarized, new averaged coordinates were maximally 20 mm apart from their original fMRI peak location. As described in previous studies, this approach is appropriate because RS waveforms are insensitive towards errors in equivalent center location of up to 20 mm. The sole obligation was that the distances between different sources should be larger than 20 mm (Bledowski et al., 2006; Scherg and Berg, 1991; Wibral et al., 2008). This aspect was controlled in the current study because all RS had a minimal distance of 30 mm to each other. Pooling coordinates resulted in five RS for the static and 15 RS for the dynamic modality (see Table 1, respectively).

Two exceptions were applied during the described procedure. Firstly, cerebellar (right tonsil) activation (contrast dynamic: disgust > neutral, see Table 1) was not pooled with cortical, here inferior temporal activation patterns (right Fusiform Gyrus, RS6, distance 29.73 mm, see Table 1) because its role during complex cognitive and emotional perception is not clear yet. Hence, the cerebellum is presumably functionally distinct from inferior temporal regions like the fusiform gyrus (Turner et al., 2007). Secondly, even though left medial frontal gyrus activation for the contrasts happiness > neutral and disgust > neutral for the dynamic modality was more than 30 mm apart from each other (30.68 mm), they were pooled to one new coordinate assuming similar functional specialization.

Furthermore, source sensitivity (see BESA® help, definition source sensitivity: “The 'Source sensitivity' function displays the sensitivity of the selected source in the current source model to activity in other brain regions. Sensitivity is defined as the fraction of power at the scanned brain location that is mapped onto the selected source.”) was calculated to study the interdependence of different sources to each other (see also Sabatinelli et al., 2007).

Sources lying deeper than eccentricity (ecc) < .55 Polar/US were excluded from further analysis (see Table 4 and 5, lower part). While the signal sensitivity is relatively independent

of the depth of a brain region in fMRI (except for areas being prone to susceptibility artifacts), deep brain regions produce rather small signals in EEG or sum up in a way that source waveform activity results in invalidly high amplitudes of source waveforms compared to more superficial RS. That is why exclusively brain regions with a value of eccentricity of larger than ecc. < 0.55 Polar/US were included in the source model resulting in four RSs for the static and eleven RSs for the dynamic modality. For that reason and to avoid errors for additionally fitted RSs, limbic and posterior cingulate regions were excluded from the source model - even though they substantially contributed to the emotion-specific differences of the above described fMRI study (see Table 4 and 5, lower rows).

static stimuli				
contrast activity	**(x, y, z)**	**RS**	**brain region**	**(x, y, z)**
L superior frontal gyrus	(-2, 5, 51)	RS1	L superior frontal gyrus	(-1, 4, 58)
L superior frontal gyrus	(-2, 5, 53)			
L superior frontal gyrus	(0, 3, 70)			
L precentral gyrus	(-40, -5, 61)	RS2	L precentral gyrus	(-40, -5, 61)
R cerebellar tonsil	(26, -56, -38)	RS3	L inferior frontal gyrus	(-46, 24, 17)
L putamen	(-20, 4, 0)	RS4	R cerebellar tonsil	(26, -56, -38)
		additional RS		
		RS5	L middle occipital gyrus	(-30, -91,2)
		RS6	R insula	(40, 5, 12)
		RS7	R fusiform gyrus	(39, -63, -9)
		RS8	L inferior temporal gyrus	(-49, -51, -11)
		RS9	above eyes	(4, 73, 6)
excluded brain regions		***eccentricity values***		
L putamen	*(-20, 4, 0)*	*ecc=.32*	*L putamen*	*(-20, 4, 0)*

Table 4: Talairach coordinates (x,y,z [in millimeters]) of significant fMRI activation clusters and of the resulting pooled regional sources (RS) for static stimuli are presented. The lower part *(italic)* displays excluded brain areas due to eccentricity (ecc) values of ecc<.55. RS 9 is presented (in grayscale) even though it was located outside of the brain. RS9 was excluded from further analysis. L = left; R = right.

The fMRI constrained source model was seeded on the poststimulius interval (1000ms, LPF also 30 Hz) of the master grand average. The master grand average is defined as the average of all conditions (neutral, happiness, disgust) and of all individuals, but separately for static and dynamic stimuli. In contrast to Bledowski and colleagues (2006), no spatial component for eyeblink artifacts representing the averaged blink topography across individuals was added because, in the present study, exclusively artifact free data were included into the averages of single individuals. However, additional sources were included in the model. The advantage of EEG is the very accurate temporal resolution, thus, there might be generators in the brain that could not have been modeled by fMRI, but with EEG (Im, 2007; Michel et al., 2004).

Furthermore, the following constraints were considered for additional sequential RS fitting: Firstly, exclusively sources with an eccentricity of at least 0.55 (Polar/US) were included in the model. Secondly, RSs were excluded from the model when they lied outside of the head. Thirdly, the models should explain at least 95 % of the variance.

dynamic stimuli				
contrast activity	**(x, y, z)**	**RS**	**brain region**	**(x, y, z)**
R lingual gyrus	(16, -90, -4)	RS1	R middle occipital gyrus, cuneus	(13, -90, 12)
R cuneus	(14, -95, 19)			
R cuneus	(10, -84, 30)			
L middle occipital gyrus	(-26, -97, 10)	RS2	L cuneus	(-25, -88, 25)
L cuneus	(-18, -92, 27)			
L precuneus	(-32, -74, 37)			
L supramarginal gyrus	(-53, -41, 35)	RS3	L superior temporal gyrus	(-49, -56, 29)
L superior temporal gyrus	(-50, -53, 21)			
L angular gyrus	(-44, -74, 31)			
R middle temporal gyrus	(55, -66, 3)	RS4	R superior temporal sulcus	(55, -52, 8)
R superior temporal gyrus	(67, -44, 13)			
R superior temporal gyrus	(46, -35, 5)			
R middle temporal gyrus	(51, -62, 12)			
R fusiform gyrus	(46, -67, -17)	RS5	R fusiform gyrus	(46, -67, -17)
L fusiform gyrus	(-42, -43, -15)	RS6	L fusiform gyrus	(-42, -59, -15)
L fusiform gyrus	(-42, -78, -15)			
L fusiform gyrus	(-42, -57, -16)			
R superior frontal gyrus	(6, 15, 62)	RS7	R superior frontal gyrus	(5, 18, 63)
R superior frontal gyrus	(4, 21, 63)			
L inferior frontal gyrus	(-55, 18, 6)	RS8	L precentral gyrus	(-42, 18, 7)
L extra-nuclear/claustrum	(-28, 18, 8)			
L medial frontal gyrus	(-10, 44, 25)	RS9	L medial frontal gyrus	(-7, 48, 11)
L medial frontal gyrus	(-4, 52, -4)			
R middle frontal gyrus	(59, 12, 36)	RS10	R inferior frontal gyrus	(61, 11, 26)
R inferior frontal gyrus	(63, 9, 16)			
R tuber (no GM)	(24, -38, -29)	RS11	R tuber (no GM)	(24, -38, -29)
		additional RS		
		RS12	R medial frontal gyrus	(11, -27, 57)
excluded brain regions		***eccentricity values***		
R uncus	*(18, 1, -20)*	*ecc=.26*	*R parahippocampal gyrus*	*(14, -8, -15)*
R parahippocampal gyrus	*(20, -12, -13)*			
R mammillary body	*(4, -12, -11)*			
R posterior cingulate	*(0, -54, 12)*	*ecc=.36*	*R posterior cingulate cortex*	*(9, -49, 8)*
R parahippocampal gyrus	*(18, -43, 4)*			
L uncus	*(-24, 4, -34)*	*ecc=.53*	*L uncus*	*(-24, 4, -34)*
R hippocampus	*(-28, -29, -7)*	*ecc=.38*	*R hippocampus*	*(-28, -29, -7)*

Table 5: Talairach coordinates (x,y,z [in millimeters]) of significant fMRI activation clusters and of the resulting pooled regional sources (RS) for dynamic stimuli are presented. One additional RS (RS 12) was seeded for the dynamic source model. The lower part *(italic)* displays excluded brain areas due to eccentricity (ecc) values of ecc<.55. L = left; R = right.

A sequential fitting procedure (as described in BESA® Tutorial, Chapter 3: tutorial of EEG reaction time experiment) was applied in order to improve the residual variance of the fMRI constrained source model (explained 95.7 % of the variance). Visual inspection of the residual

variance (and best fit) and the comparison of the Global field power curve reflected three epochs including residual variance:

- early epoch (52-113ms, onset to peak, 2 RS),
- later epoch (191-462ms, two RS),
- whole epoch (68-996ms, 1 RS).

Since the last RS (68-996ms) was located outside of the head, anterior to the medial frontal cortex (above the eyes), it was excluded from further analysis (see constraints above).Thus, the seeded model for the static modality resulted in a model including 8 discrete RS explaining a variance of 99.3 % indicating an excellent explanation of the data variance (see Table 4, Fig. 16).

For the dynamic modality the seeded source model already included 11 RS explaining 96.7 % of variance. Thus, simply one additional source was added to the model over almost the complete epoch (95-951ms) because this epoch included residual variance over almost the whole poststimulus interval. The attempt to fit additional sources resulted in source locations lying outside of the head, which was an exclusion criterion. Thus, the seeded model for the dynamic modality resulted in a model including 12 discrete RS (see Table 5 and Fig. 17) explaining a variance of 97.6% representing a very good fit to the data.

FMRI constrained source analysis: statistical analysis

The root mean square (RMS) of each RS (calculate the square root of the mean of the added and squared power [in nAm, nanoamperemeter] of 3 mutually orthogonal dipoles) was extracted by BESA® for each condition (neutral, happiness, disgust) and each participant. To examine the time course differences of different source waveforms between emotional categories the mean of root-mean-square values was calculated for 50 ms time windows for each RS and each subject in order to examine the temporal and spatial changes of source activity (see also Table 6 and 7).

Nonparametric one-sample Kolmogorov-Smirnov tests were calculated for each RS to test for normal distribution properties justifying the following parametric statistical approach by ANOVAs using SPSS® (SPSS®, Inc., Chicago, USA).

GLM repeated measures ANOVAs were performed on source strength values (separately for static and dynamic modality) of different time windows including within-subject factors EMOTION (EMO: 3 levels: neutral, happiness, disgust) for each RS separately. Main effects and significant interactions were Greenhouse Geisser (GG) adjusted where appropriate. Post hoc analyses (paired sample t-tests) were calculated according to significant main effects ($p <$

.05) and to statistical trends ($p < .1$).

3.3 Results

3.3.1 Behavioral data

Post hoc evaluation of the facial expression stimuli revealed a categorization rate for the static faces of 93.7 % percent (SD 4.6) for neutral, 96.7 % (SD 4.3) for happiness, and 95.7 % (SD 3.1) for disgust, and for the dynamic faces of 92.1 % (SD 12.7) for neutral, 98.0% (SD 3.5) for happy, and 96.2% (SD 3.9) for disgusted expressions.

An EMOTION (EMO, 3 levels: neutral, smile, and disgust) x MODALITY (MOD, 2 levels: static and dynamic) x SEQUENCE (SEQ, 2 levels: start with static or start with dynamic stimuli) repeated measurement ANOVA, separately conducted for the category and arousal ratings, revealed a trend for EMO x MOD ($F_{[1.5, 26]}$ =2.8, p=.099, GG-corrected) for category. No posthoc comparisons reached statistical significance (see Fig. 10 A).

Arousal showed a main effect for EMO ($F_{[2, 34]}$=22.2, p<.001) resulting in higher arousal rates for emotional compared to neutral facial expressions (posthoc Fisher's LSD, both p<.001) independent from motion and for MOD ($F_{[1, 17]}$=7.2, p=.02) yielding higher arousal rates for static compared to dynamic stimuli independent of emotion (posthoc Fisher's LSD, both p=.02) standing in contrast to previous evaluations of the stimulus material. The EMOTION x MODALITY interaction ($F_{[2, 34]}$ = 3.8, p=.03) yielded a significantly higher arousal for static compared to dynamic emotional stimuli (paired sample t-tests: p=.03 for happiness, p=.001 for disgust; see Fig. 10 B).

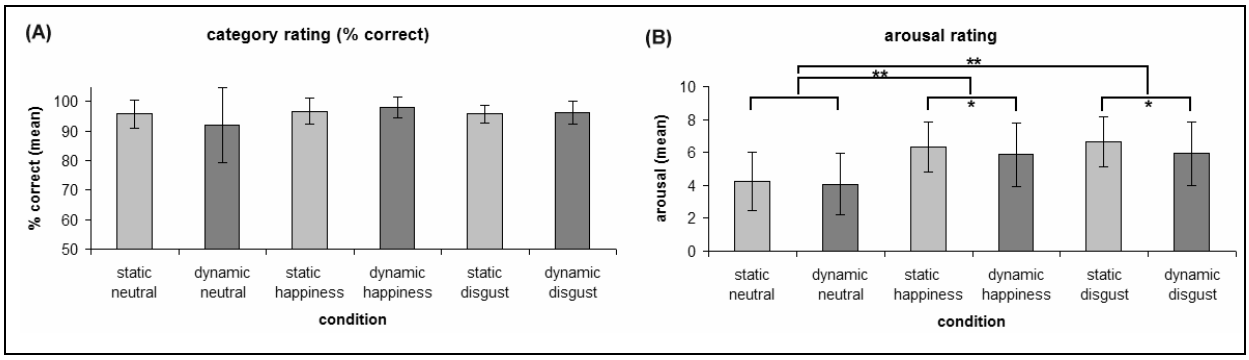

Figure 10: Rating after EEG-recordings (N=19, mean ± SD) displayed for static (light gray) and dynamic (dark gray) stimuli. (A) Correct percent categorization accuracy (y-axis). (B) Arousal ratings for neutral, happiness, and disgust (x-axis) on a scale from 0 (nothing) to 10 (highly arousing; y-axis). Posthoc comparisons: * p<.05, ** p<.001.

3.3.2 ERP data

ERP data for all conditions (neutral, happiness, disgust) are presented for all 62 electrode sites in Appendix D.1 and D.2 of static and dynamic stimuli, respectively. Tables of significant or trend to significant main and interaction effects of repeated measurement ANOVAs including within-subject factors ANTERIOR-POSTERIOR (AP, 3 levels: frontal, central and posterior electrode positions), LATERALITY (LAT, 5 levels: from right to left electrode sites), and EMOTION (EMO, 3 levels: neutral, happiness, disgust) for four different time windows for static and for seven different time windows for dynamic stimuli are displayed in Appendix E.1 and Appendix E.4, respectively. Significant posthoc comparisons ($p<.05$) are displayed in Figure 12 A and Figure 14 A for each static and dynamic stimuli, next to topographical maps of EEG-voltage maps (based on spherical spline interpolation) for selected time points of difference waves of disgust minus neutral and happiness minus neutral (Fig. 12 B and Fig. 14 B). ERP waveforms of selected electrodes are displayed in Fig. 11 and Fig. 13 for static and dynamic stimuli separately.

3.3.2.1 Static stimuli

ERPs of static stimuli showed four deflections starting with the P1, followed by the N170, and EPN, predominantly over lateral occipito-temporal regions, and by a sustained slow wave over parietal electrode sites (LPP; for ERP waveforms, see Fig. 11). Posthoc tests for selected electrodes and voltage maps for four analyzed time windows are displayed in Figure 12 (A and B, respectively). Main effects or interactions including the factor emotion did not reach significance for the early time window (90-130ms) indicating no emotional modulation of this early deflection.

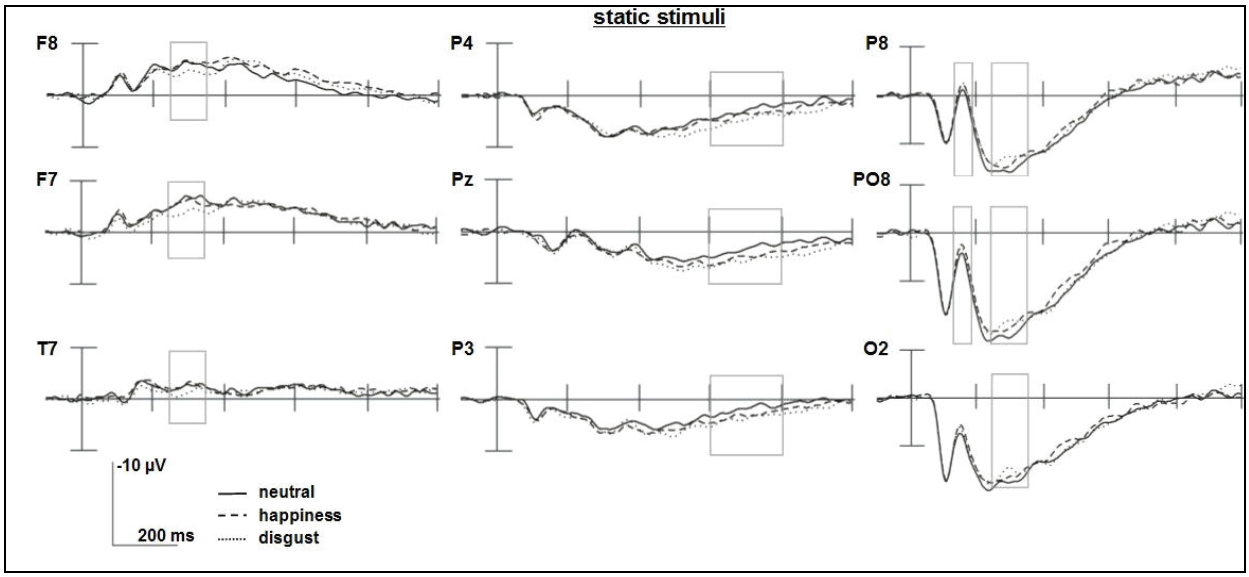

Figure 11: ERPs of selected electrodes (F8, F7, T7, P4, Pz, P3, P8, PO8, O2) for static stimuli for all conditions (solid line = neutral, dotted line = disgust, dashed line = happiness) are displayed. Gray boxes represent time window of significant differences between conditions as revealed by posthoc comparisons.

For the following time windows, three-way interactions (APxLATxEMO) reached trend to significance (140-190ms, referred to as N170; $F_{[6.6,\ 116.4]} = 2.03$, $p<.1$, GG-corrected) and significance (250-350ms, referred to as EPN, $F_{[6.2,\ 111.6]} = 3.5$, $p<.01$, GG-corrected, and 600-800ms, referred to as LPP, $F_{[7.8,\ 140.6]} = 2.0$, $p<.01$, GG-corrected; see Appendix E.1). The second pronounced deflection, with its peak around 160-165 ms, also known as the face-specific N170 or N160 component (Eimer, 2000; Halgren et al., 2000), yielded a significantly stronger negative mean amplitude for disgust compared to neutral in P8, and for happiness compared to neutral facial expressions in PO8 (see Fig. 11 and 12, see also Appendix E.3). Topographic voltage maps showed right hemisphere dominance for happiness and disgust which was less pronounced for disgust showing a rather bilateral scalp distribution of negative voltage (Fig. 12 B).

Between 250 and 350 ms, post-hoc tests revealed a relative negative peak for disgust compared to neutral in posterior temporo-occipital electrodes representing the EPN component (P8, PO8, O2; see Fig. 11 and 12, for further significant posthoc comparisons). This finding was evident in voltage maps (Fig. 12 B) showing a negative scalp distribution over temporo-occipital regions for disgust compared to neutral facial expressions.

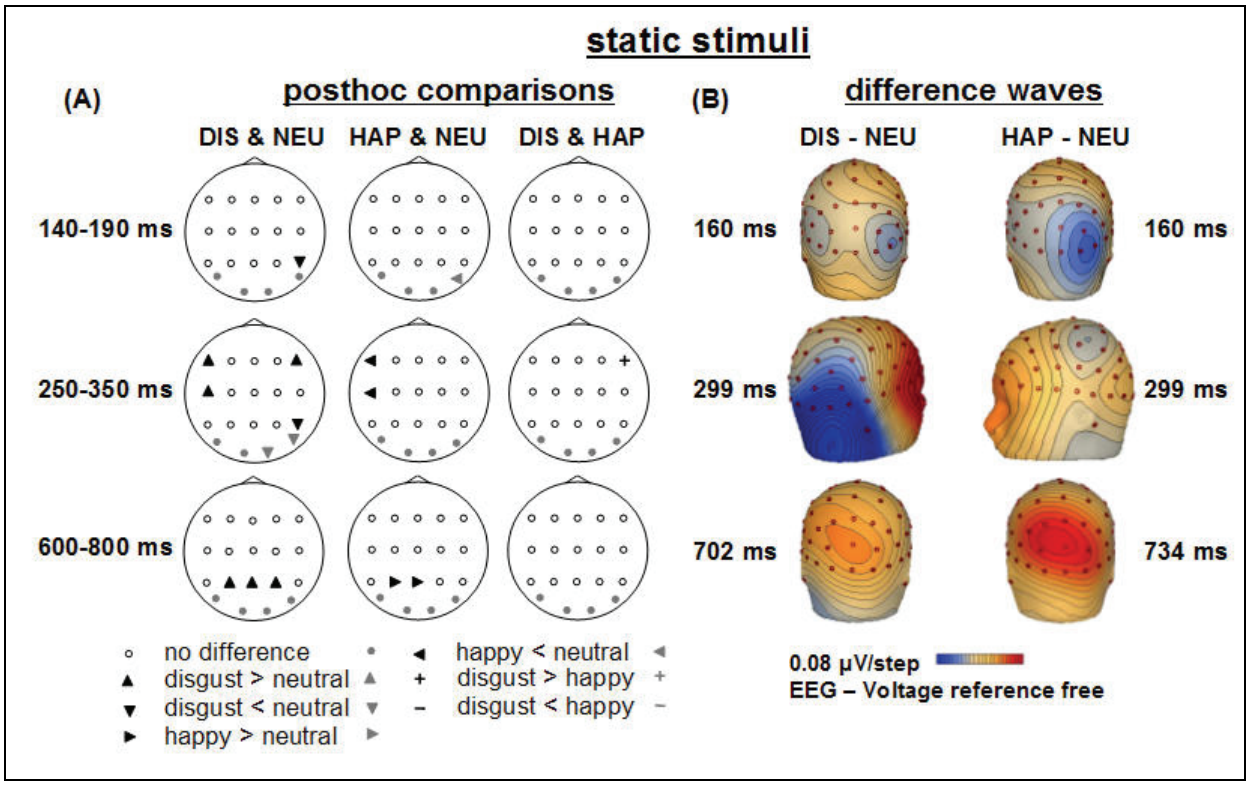

Figure 12: Static stimuli. (A) Significant differences of mean amplitudes (in µV): posthoc comparisons for 15 equidistant (black) plus four electrodes of interest positions (gray) between disgust (DIS) and neutral (NEU), happiness (HAP) and NEU, and - for the matter of completeness - DIS and HAP for three different time windows (left column). Symbols below represent the direction of significant posthoc comparisons (paired sample t-tests, $p<.05$) for equidistant electrodes (left column) in black and further channels of interest (right column) in grayscale. (B) Spherical spline maps (EEG-voltage, reference free, 0.08µV/step) displaying difference waves for static faces for left column disgust minus neutral (DIS - NEU), and right column happy minus neutral (HAP - NEU) for 3 selected time points (in rows) in milliseconds (ms).

Enhanced positive mean amplitudes for disgust (bilateral, P3, Pz, P4) and happiness (lateralized to the left, P3, Pz) compared to neutral at parietal electrodes sites was shown to be associated with the LPP (see Fig. 11, 12). Voltage maps also showed an enhancement over midline parietal regions (Fig. 12 B)

3.3.2.2 Dynamic stimuli

Since ERP data of dynamic stimuli showed sustained amplitude differences instead of typical early deflections revealed by static faces (see above, N170, EPN, LPP), seven short time windows of 100 ms were chosen to examine differences between emotional and neutral facial expressions (see Fig. 14). ERPs for selected centro-parietal electrode sites and corresponding voltage maps are displayed in Figure 13 B and 14 B, respectively.

Main effects or interactions including the factor EMO were discovered for all seven time windows (see Appendix E.4 to E.6 for statistical results). Differences were found in both disgust and positive compared to neutral stimuli over centro-parietal and parieto-occipital electrodes (CPs, POs, Ps). These started to reach significance after 200 ms left lateralized for

disgust versus neutral showing enhanced positive mean amplitudes, and 100 ms later also for smile versus neutral. This enhanced positivity remained stable for both smile and disgust from 300 to 800 ms over bilateral centro-parietal, parietal, and parieto-occipital electrodes (Fig. 13, for ERPs, and 14, for posthoc comparisons and voltage maps).

The 100 ms earlier start of significantly enhanced positivity between disgust and neutral also became evident over parieto-occipital electrodes when compared to happy instead of neutral stimuli (right column: disgust and happy, Fig. 13 and 14 A). More specifically, significantly enhanced positivity for smile compared to neutral facial expressions was revealed for central electrode sites from 300 ms (left lateralized, Cz and C3) to 500 ms (bilateral, C3, Cz, C4) to 800 ms (600-800ms, right lateralized, C4). Disgust yielded enhanced positive mean amplitudes compared to neutral stimuli over right lateralized central electrode (only C4) starting 100 ms later than happiness, but also lasting until 800 ms.

Emotional stimuli evoked more positive mean amplitudes over occipital electrode sites bilaterally for disgust versus neutral (600-800 ms) and right lateralized for smile vs. neutral (500-600ms).

Lateral frontal (F6, F8, F7, AF7, AF8) regions showed a sustained negative potential for both emotional conditions compared to neutral stimuli between 300 and 800 ms (Fig. 14 A and B, and 15,), predominantly bilateral for disgust vs. neutral and predominantly right-lateralized (300-400ms and 700-800ms), but also bilateral (400-700ms) for happy versus neutral.

The mutual comparison of both emotional valences was displayed for the matter of completeness in Figure 14 (A; right column), but will not be further discussed below. Disgust showed more positive mean amplitude values than smile over parieto-occipital and occipital areas from 200-300ms and 700-800 ms, respectively. Happiness showed enhanced positivity over centro-parietal and parietal electrodes between 300 and 800 ms (see Fig.14 A, right column).

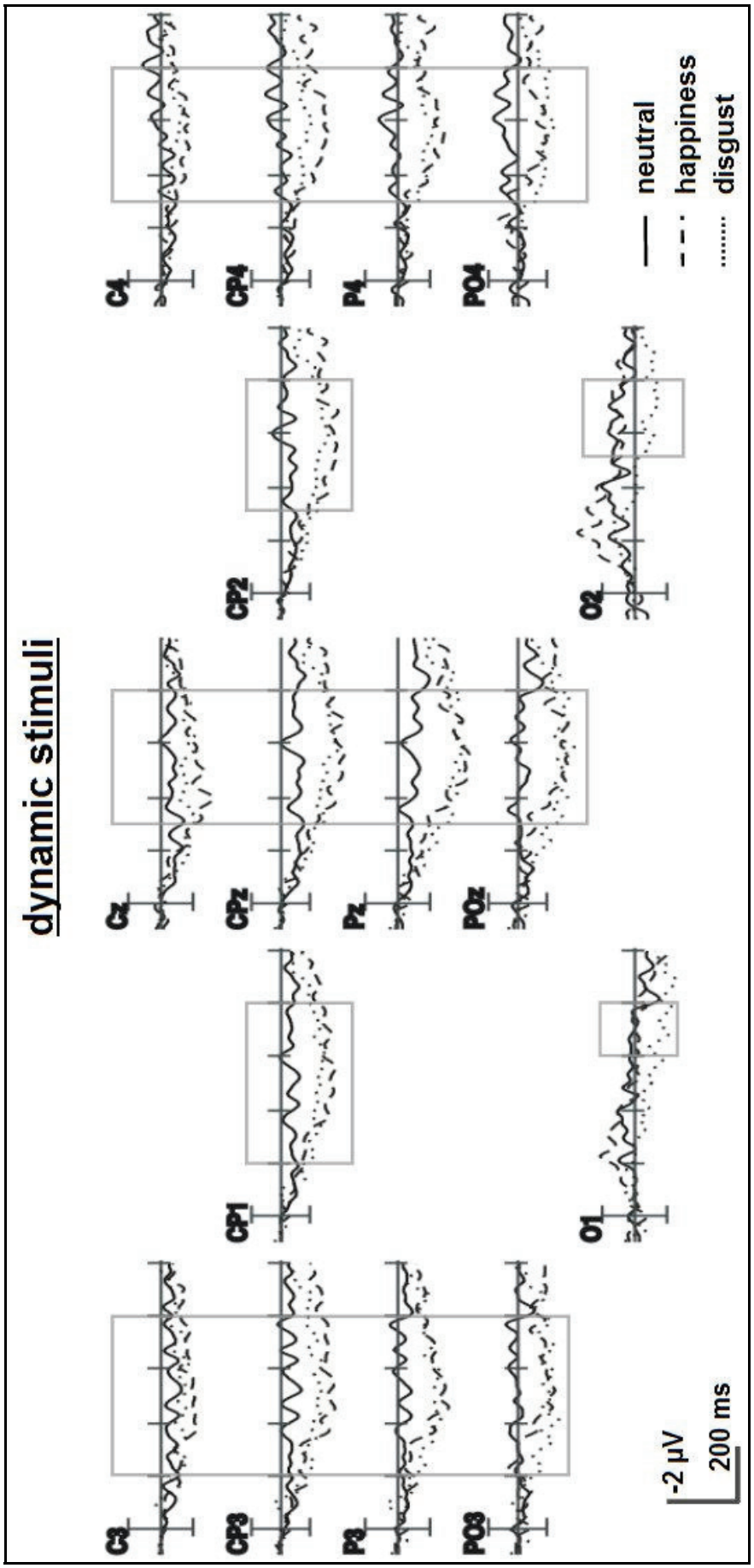
dynamic stimuli
C3
CP3
P3
PO3
CP1
O1
Cz
CPz
Pz
POz
CP2
O2
C4
CP4
P4
PO4
neutral
happiness
disgust
-2 µV
200 ms

Figure 13: ERPs for dynamic stimuli for selected central, centro-parietal, parietal and occipital electrode sites. Gray boxes indicate time windows showing significant t-tests among conditions (solid line = neutral, dashed line = happiness, dotted line = disgust).

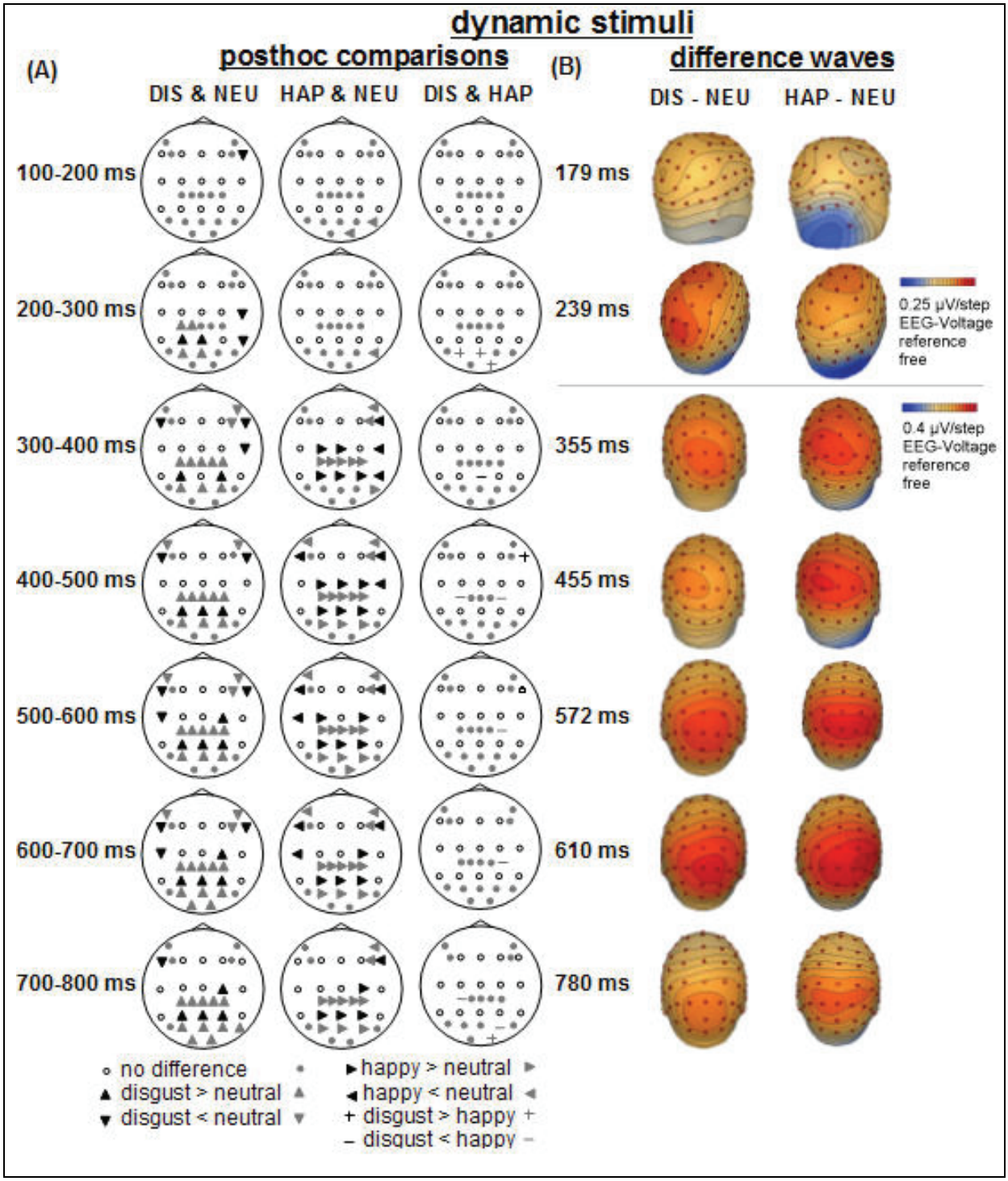

Figure 14: Dynamic stimuli. (A) Significant differences of mean amplitudes in µV: posthoc comparisons of 15 equidistant (black) plus 16 additional electrodes of interest positions (in grayscale) between disgust (DIS) and neutral (NEU), happiness (HAP) and NEU, and DIS and HAP for seven different time windows (left column). Symbols on the bottom of column (A) represent the direction of significant posthoc comparisons (paired sample t-tests, $p<.05$) for equidistant electrodes (left column) in black and further channels of interest (right column) in grayscale. (B) Spherical spline maps (EEG-voltage, reference free, 0.25µV/step [first two rows] / 0.4 µV/step [row three to seven]) displaying difference waves for dynamic faces for left column disgust minus neutral (DIS - NEU), and right column happy minus neutral [HAP - NEU]) for seven different time points (in rows) in milliseconds (ms).

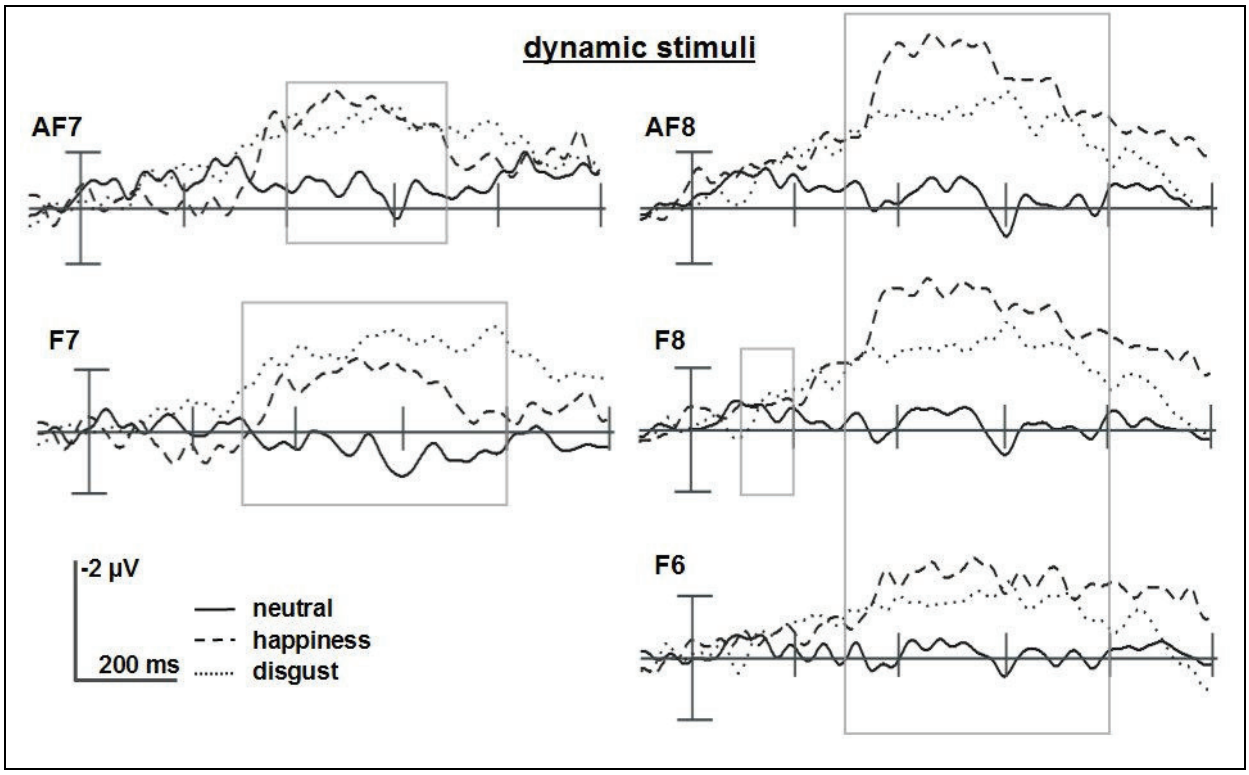

Figure 15: ERPs for selected frontal electrode sites for dynamic faces during the perception of neutral (solid line), happiness (dashed line), and disgust (dotted line). Gray boxes indicate time windows representing significant differences calculated by t-tests ($p<.05$) among emotions.

Onset of dynamic emotional facial expressions

The analysis of ERPs evoked by the onset of the video was performed for similar time windows as applied to static stimuli (see Chapter 3.2.5.2 and 3.3.2.1) because they also resulted in similar components. The analyzed time windows for the P1, N170, EPN, and LPP did not show any significant main effects or three-way interaction effects including the factor EMOTION (see Appendix F.1 an overview of ERPs and F.2 for statistic Tables). Therefore, physiological data did not indicate an emotional modulation of the processing of the onset of the video as expected in the hypotheses because actresses looked to the left or right neutrally. The results of the onset of the video will not be further discussed in the present thesis because they were supposed to serve as a proof that actresses did not convey an emotional facial expression at the beginning of the video.

3.3.3 Source analysis data

Trend to significant and significant main effects of repeated measurement ANOVAs including within-subject factor EMOTION (EMO, 3 levels: neutral, happiness, disgust) for 20 different time windows (each covering a range of 50 ms) are displayed in Appendix G.1 and for static and G.3 for dynamic stimulus material. Seeded and additionally fitted regional

sources (RS) are presented in Figure 16 for static and Figure 17 for dynamic facial expressions. Figures include (A) source sensitivity maps and Talairach coordinates (Fig. 16 A and 17 A, left column), (B) the master grand average ERP over all conditions (Fig. 16 B and 17 B, upper row), the global field power (GFP) and rest-variance (RV) of the model (Fig. 16 B and 17 B, middle row), and the source waveforms (in nAm, nanoamperemeter, Fig. 16 B and 17 B, lower row) for the fitted model, and (C) the two-dimensional representation of seeded sources from six different points of views (Fig. 16 C and 17 C, right column). Source sensitivity (Fig. 16 and 17, each column (A)) was calculated to check for independence of RS (see also Sabatinelli et al., 2007).

Significant posthoc comparisons are displayed in Table 6 and Table 7 for static and dynamic stimuli, respectively, separately for conditions happiness versus neutral (upper part), disgust versus neutral (middle part), and disgust versus happiness (lower part). This type of visualization was chosen in order to present the time course of different RS among different conditions. Selected source waveforms of those comparisons are displayed in Appendix G.2 and G.4 for static and dynamic stimuli, respectively.

3.3.3.1 Static stimuli

Two different discrete source models were calculated for the static modality, but the present study focuses on the model with four instead of five additional seeded sources because (1) both models showed a relatively similar time course of emotion-specific differences among conditions and (2) one of the adhoc constraints was to exclude sources lying outside of the skull which was the case for the last added source of the model. Sources for static facial expressions encompassed superior, inferior frontal, and precentral gyrus, cerebellar tonsil as revealed by fMRI, and middle occipital areas, insula, and inferior temporal areas including the FuG as additionally fitted (Fig. 16). Progressions of source waveforms for all conditions for selected RS are presented in Appendix G.2.

Source sensitivity was given for all but the cerebellar source (see Fig. 16 A) indicating their mutual independence. This might mean that the cerebellar source might explain activation from surrounding sources.

Source waveforms of cerebellar tonsil, left middle occipital gyrus (MOG), insula (INS), right fusiform gyrus (FuG), and left inferior temporal gyrus (RS five to eight) showed large, transient, and distinct curve progressions in early time windows, but also sustained in later time windows. In contrast, the first three RS (superior, inferior and precentral gyrus), predominantly the precentral source (RS 2), showed less intense and distinct contribution to

the source model.

Static facial expressions showed stronger source strength as early as 50-100 ms in left MOG followed by a recruitment of left inferior temporal gyrus (100-150ms) and right cerebellar tonsil, followed by an increased source strength in left MOG (350-400 ms) for happy compared to neutral facial expressions. Furthermore, right FuG (600-650 ms) showed sustained stronger source power in for happy compared to neutral stimuli (Table 6, upper part). Comparing happy to neutral stimuli yields alternating activation of RS in MOG, cerebellar tonsil, and FuG implicating a possible, enhanced connection among those areas during the perception of happy facial expressions (Table 6, upper part).

Early enhanced source power for disgust compared to neutral (100-150 ms) was shown for left inferior temporal gyrus (p=.05) which was also shown before for the processing of happy facial expressions, followed by enhanced source strength in the insula (300-350ms) and simultaneously, left MOG (350-400ms, and 450-500ms) and right FuG (350-500ms, and later 550-750 ms) activation. Left MOG and right FuG were reactivated transiently between 450-500 ms and 550-750 ms, respectively (Table 6, middle part).

Neutral compared to happy stimuli showed enhanced source strength early in the right FuG (50-100ms), followed by right cerebellar tonsil activation (100-250ms), continuing to the right FuG (200-250ms, 300-350ms) and to the left inferior frontal gyrus (700-750ms; Table 6, upper part). Neutral stimuli evoked stronger source moments in right cerebellar tonsil compared to disgust (Table 6, middle part).Comparing the two emotional conditions to each other revealed significantly higher source strength for disgusted compared to happy expressions in the following brain regions: right cerebellar tonsil (early, 150-200ms), left inferior frontal gyrus (350-450ms), right fusiform gyrus (sustained between 350-500ms) and left MOG (450-500ms). Happiness showed no stronger moment values compared to disgust in static modality (Table 6, lower part). The results of reverse contrasts are not further discussed in the present thesis.

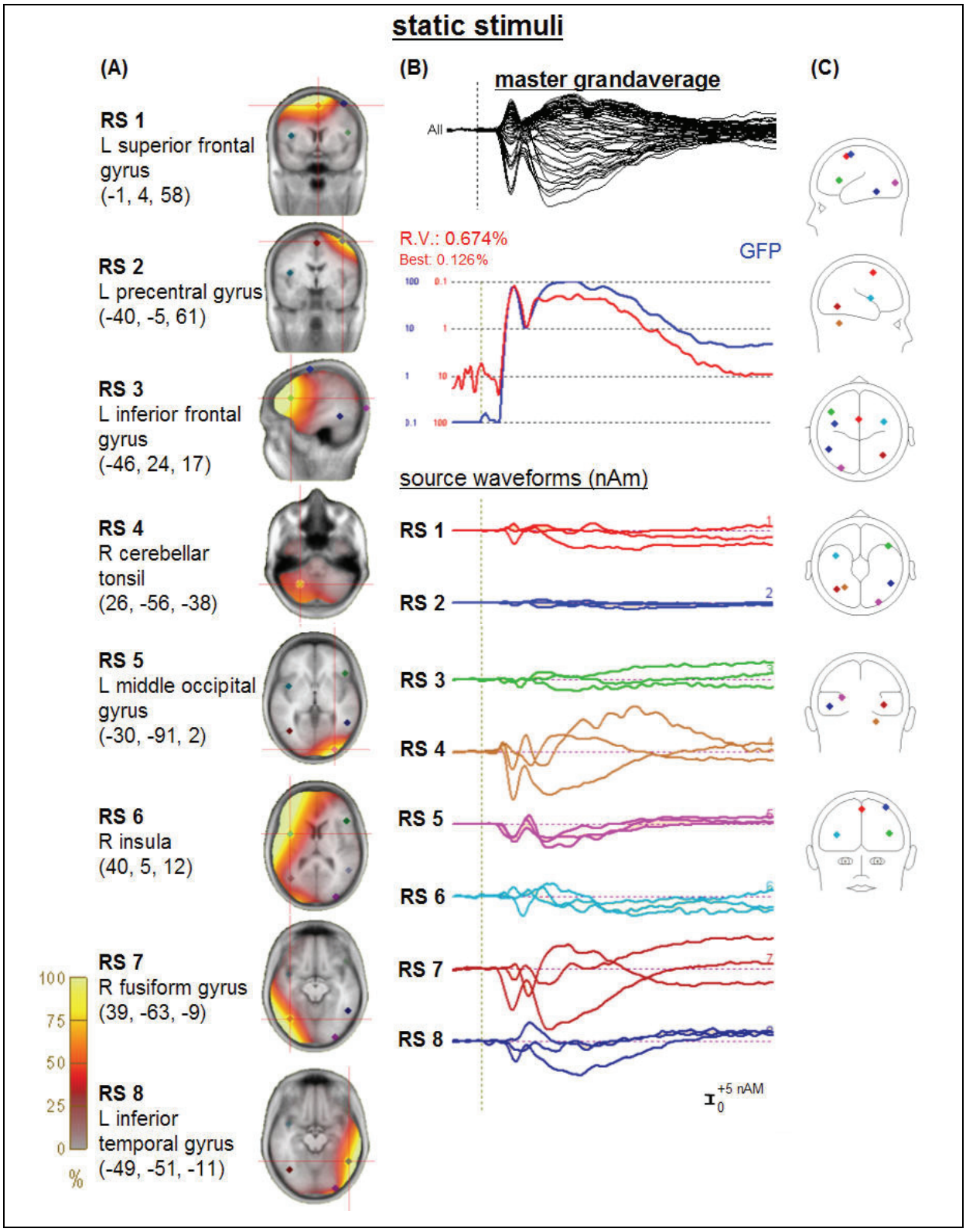

Figure 16: Source model of static stimuli. (A) Source sensitivity in percent (color bar on the left from 0-100%; higher values and brighter colors indicate increasing independency of RS to surrounding RSs) of eight RSs and related Talairach coordinates (x, y, z, in mm). (B) Upper graph represents the master grand average over all electrodes and all conditions (-100-1000ms), middle graph represents the global field power curve (GFP; blue curve) and explained variance of the model (residual variance [RV] and best fit; red curve), lower graph represents the source waveforms (in nAm) for RS one to eight, each represented in its individual color. (C) Eight RS (each in individual color) projected onto a 4-shell spherical model displayed from six different perspectives (saggital [left, right], transversal [above, below], coronal [back, front]). Note: RS one to four were seeded based on fMRI activations and RS five to eight were added by sequential fitting procedures (for more details, see methods Chapter 3.2.5.3)

static stimuli

#	brain region	tal	0-50 in ms	50-100	100-150	150-200	200-250	250-300	300-350	350-400	400-450	450-500	500-550	550-600	600-650	650-700	700-750	750-800	800-850	850-900	900-950	950-999
RS1	L superior frontal gyrus	(-1, 4, 58)																				
RS2	L precentral gyrus	(-40, -5, 61)																				
RS3	L inferior frontal gyrus	(-46, 24, 17)															hap>neu					
RS4	R cerebellar tonsil	(26, -56, -38)			hap>neu	hap>neu	hap>neu			hap>neu												
RS5	L middle occipital gyrus	(-30, -91,2)		hap>neu						hap>neu												
RS6	R insula	(40, 5, 12)																				
RS7	R fusiform gyrus	(39, -63, -9)		hap>neu			hap>neu		hap>neu						hap>neu	hap>neu	hap>neu					
RS8	L inferior temporal gyrus	(-49, -51, -11)			hap>neu																	
#	brain region	tal	-50	-100	-150	-200	-250	-300	-350	-400	-450	-500	-550	-600	-650	-700	-750	-800	-850	-900	-950	-999
RS1	L superior frontal gyrus	(-1, 4, 58)																				
RS2	L precentral gyrus	(-40, -5, 61)																				
RS3	L inferior frontal gyrus	(-46, 24, 17)																				
RS4	R cerebellar tonsil	(26, -56, -38)					dis<neu															
RS5	L middle occipital gyrus	(-30, -91,2)								dis>neu		dis>neu										
RS6	R insula	(40, 5, 12)							dis>neu													
RS7	R fusiform gyrus	(39, -63, -9)								dis>neu	dis>neu	dis>neu		dis>neu		dis>neu	dis>neu					
RS8	L inferior temporal gyrus	(-49, -51, -11)			hap>neu																	
#	brain region	tal	-50	-100	-150	-200	-250	-300	-350	-400	-450	-500	-550	-600	-650	-700	-750	-800	-850	-900	-950	-999
RS1	L superior frontal gyrus	(-1, 4, 58)																				
RS2	L precentral gyrus	(-40, -5, 61)																				
RS3	L inferior frontal gyrus	(-46, 24, 17)								dis>hap	dis>hap											
RS4	R cerebellar tonsil	(26, -56, -38)				dis>hap																
RS5	L middle occipital gyrus	(-30, -91,2)										dis>hap										
RS6	R insula	(40, 5, 12)																				
RS7	R fusiform gyrus	(39, -63, -9)								dis>hap	dis>hap	dis>hap	dis>hap									
RS8	L inferior temporal gyrus	(-49, -51, -11)																				

hap>neu
hap<neu
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Table 6: Table displays significant posthoc paired sample t-tests for eight different brain regions (eight RS) for 20 different time windows (each 50 ms long) comparing happiness (hap) versus neutral (neu) condition (upper part), disgust (dis) versus neutral condition (middle part), and disgust versus happiness (lower part). Different shades represent direction of posthoc comparisons between conditions (see legend on the bottom right of the table).

3.3.3.2 Dynamic Stimuli

The source model dedicated to the dynamic modality is based on twelve RS of which eleven are derived from the fMRI study and one additional RS was fitted to the model (Fig. 17). RS locations refer to occipital areas, STS, FuG, superior frontal, precentral, medial, and inferior frontal areas, and tuber (Fig. 17). Furthermore, significant main effects, selected source waveforms and posthoc comparisons between each two conditions (emotions) are displayed in Appendix G.3, Appendix G.4, and Table 7, respectively.

Source sensitivity was given for all RS (see Fig. 17 A) indicating their mutual independence.

Happy compared to neutral stimuli showed enhanced source strength in right tuber (150-200ms, p=.05, continuing through 250 ms), followed by a simultaneous recruitment of left cuneus, and left precentral gyrus (both 200-250 ms), and left FuG and right inferior frontal gyrus (250-300 ms). Besides, left medial frontal gyrus showed a sustained increase of source power from 350-500ms. Further, happy stimuli evoked larger responses in several transient time windows, e.g., in right medial frontal gyrus (400-450 ms, 550-600 ms, 700-750 ms), left cuneus (500-550 ms, 900-950 ms, p=.05), and right superior frontal gyrus (550-600 ms, 600-650 ms; Table 7, upper part).

The perception of disgust compared to neutral stimuli evoked stronger source strength in left superior temporal gyrus (150-200 ms), followed by activation in left precentral gyrus (200-250ms), medial frontal gyrus (200-300ms), and right inferior frontal gyrus (250-300ms). Further transiently enhanced source power was shown for left precentral gyrus and right medial frontal gyrus (both between 350-400ms), followed by right inferior frontal gyrus (400-450ms), and again right medial frontal gyrus (450-500ms, 700-750ms; Table 7, middle part).

Reverse contrasts (neutral > emotional) and the comparison of happiness and disgust are shortly presented, but are not further discussed in the present thesis because it would be beyond the scope of the study. Neutral stimuli resulted in stronger source power than disgusted faces in right tuber (early: 0-50 ms, and later, sustained: 500-650ms) and right superior frontal gyrus (100-150ms; Table 7, middle part). Comparing the two emotional conditions to each other revealed significantly higher power for happy compared to disgusted expressions in right tuber (100-250ms, 600-650ms), left fusiform gyrus (250-300ms), left medial frontal gyrus (sustained: 250-500ms), and right superior frontal gyrus (500-550ms).

Disgust showed enhanced source strength in left STG (50-100ms) and left precentral gyrus (550-600ms; Table 7, lower part).

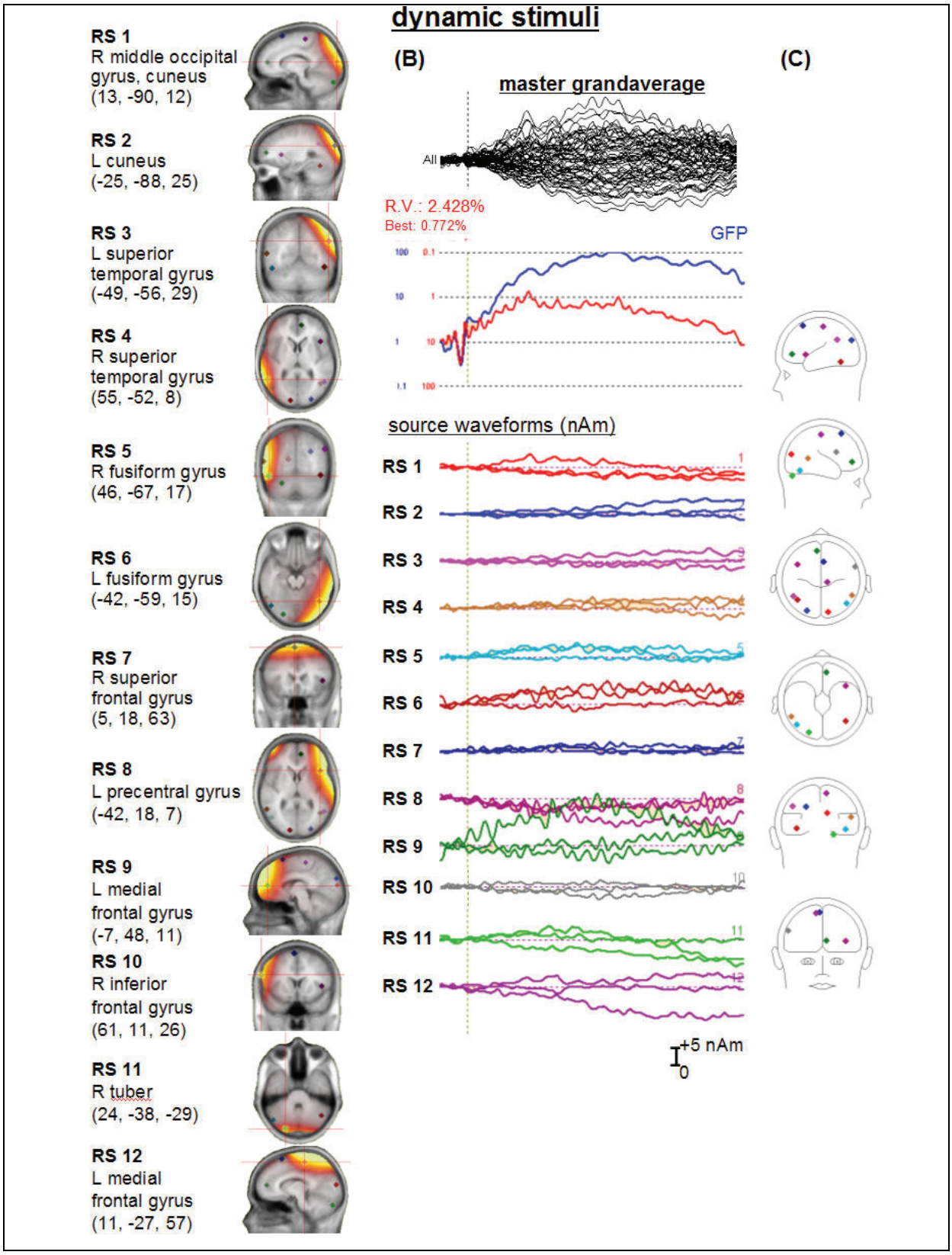

Figure 17: Source model of dynamic stimuli. (A) Source sensitivity of twelve RS (color bar on the left from 0-100%; higher values and brighter colors indicate increasing independency of RS to surrounding RSs) and related Talairach coordinates (x, y, z, in mm). (B) Upper graph represents the master grandaverage over all electrodes and all conditions (-100-1000ms), middle graph represents the global field power curve (GFP; blue curve) and explained variance of the model (residual variance [RV] and best fit; red curve), lower graph represents the source waveforms (in nAm) for regional sources one to twelve, each represented in its individual color. (C) Twelve RS (each with individual color) projected onto a 4-shell spherical model displayed from six different perspectives (saggital [left, right], transversal [above, below], coronal [back, front]). Note: RS one to eleven were seeded based on fMRI activations and RS twelve was added by sequential fitting procedure (for more details, see methods Chapter 3.2.5.3).

dynamic stimuli

#	brain region	tal	in ms	50-100	100-150	150-200	200-250	250-300	300-350	350-400	400-450	450-500	500-550	550-600	600-650	650-700	700-750	750-800	800-850	850-900	900-950	950-999
RS1	R middle occipital gyrus, cuneus	(13, -90, 12)																				
RS2	L cuneus	(-25, -88, 25)																			05	
RS3	L superior temporal gyrus	(-49, -56, 29)																				
RS4	R superior temporal gyrus	(55, -52, 8)																				
RS5	R fusiform gyrus	(46, -67, -17)																				
RS6	L fusiform gyrus	(-42, -59, -15)																				
RS7	R superior frontal gyrus	(5, 18, 63)																				
RS8	L precentral gyrus	(-42, 18, 7)																				
RS9	L medial frontal gyrus	(-7, 48, 11)																				
RS10	R inferior frontal gyrus	(61, 11, 26)																				
RS11	R tuber (no GM)	(24, -38, -29)				05																
RS12	R medial frontal gyrus	(11, -27, 57)																				
#	brain region	tal	-50	-100	-150	-200	-250	-300	-350	-400	-450	-500	-550	-600	-650	-700	-750	-800	-850	-900	-950	-999
RS1	R middle occipital gyrus, cuneus	(13, -90, 12)																				
RS2	L cuneus	(-25, -88, 25)																				
RS3	L superior temporal gyrus	(-49, -56, 29)																				
RS4	R superior temporal gyrus	(55, -52, 8)																				
RS5	R fusiform gyrus	(46, -67, -17)																				
RS6	L fusiform gyrus	(-42, -59, -15)																				
RS7	R superior frontal gyrus	(5, 18, 63)																				
RS8	L precentral gyrus	(-42, 18, 7)																				
RS9	L medial frontal gyrus	(-7, 48, 11)																				
RS10	R inferior frontal gyrus	(61, 11, 26)																				
RS11	R tuber (no GM)	(24, -38, -29)																				
RS12	R medial frontal gyrus	(11, -27, 57)																				
#	brain region	tal	-50	-100	-150	-200	-250	-300	-350	-400	-450	-500	-550	-600	-650	-700	-750	-800	-850	-900	-950	-999
RS1	R middle occipital gyrus, cuneus	(13, -90, 12)																				
RS2	L cuneus	(-25, -88, 25)																				
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RS6	L fusiform gyrus	(-42, -59, -15)																				
RS7	R superior frontal gyrus	(5, 18, 63)																				
RS8	L precentral gyrus	(-42, 18, 7)																				
RS9	L medial frontal gyrus	(-7, 48, 11)			05																	
RS10	R inferior frontal gyrus	(61, 11, 26)																				
RS11	R tuber (no GM)	(24, -38, -29)					05															
RS12	R medial frontal gyrus	(11, -27, 57)																				

hap>neu
hap<neu
dis>neu
dis<neu
dis>hap
hap>dis

Table 7: Table displays significant posthoc paired sample t-tests for brain regions (12 RS) for 20 different time windows (each 50 ms long) comparing happiness (hap) versus neutral (neu; upper part), disgust (dis) versus neutral (middle part), and disgust versus happiness (lower part). Different shades represent direction of posthoc comparisons between conditions (see legend on the bottom right of the table).

3.4 General Discussion of EEG data

The following section discusses behavioral results, ERP results, and results of the fMRI constrained and extended source analysis.

3.4.1 Behavioral data

Recognition accuracy of 95.4% for both static and dynamic stimuli (mean over all emotional categories) actually supported the common notion that facial expressions are universal and can be recognized even across different cultures (here German and Spanish) (Ekman et al., 1972; Ekman et al., 1987). Unlike hypothesized in the introduction, however, dynamic stimuli did not yield a significantly better recognition accuracy or higher arousal rates than static stimuli.

Just like reported in the Chapter 2 (fMRI study), significantly higher arousal ratings for dynamic compared to static faces could again not be confirmed for the present sample. These results are in contrast to previous studies (Biele and Grabowska, 2006; Simons et al., 1999) which reported higher arousal ratings for dynamic compared to static facial expressions. There are two possible explanations for this effect:

Firstly, during the rating, the videos disappeared from the screen as soon as they had been shown once, whereas static faces remained on the screen until participants made their choice (arousal and valence). Thus, participants might have had more time to explore the facial expression and might have experienced the latter more intensively, even though participants were asked to decide spontaneously. But since this effect was not found for the German sample (Chapter 2, fMRI study), this explanation seems to be rather unrealistic.

Secondly, since arousal ratings were significantly lower compared to the sample from the first study for dynamic happy and neutral expressions[3], cultural differences might account for this effect because the rating task consisted of faces displaying a different cultural background. Spanish women (Hispanics) participated in the current EEG study. However, the applied stimulus material showed exclusively German actresses (Caucasian). After finishing the

[3] Independent t-tests indicated a lower arousal for dynamic happy compared to static happy expressions ($t(29.12) = 1.81$; $p<.1$), and for dynamic compared to static neutral expressions ($t(33) = 1.74$, $p<.1$).

rating some of the Spanish participants mentioned that they were aware of the fact that stimuli had come from a different country and hence, that it was partly difficult to both accurately classify the displayed emotional valence (happiness, disgust, or neutral) and to rate their arousal. All in all, recognition accuracy was generally spoken very high with an average of 95.4 % for static and dynamic faces, though, supporting the universality of emotion recognition. However, dynamic faces did not show an advantage for recognition accuracy like hypothesized in the introduction and shown in the fMRI study with German participants. Arousal rates were actually lower for dynamic compared to static faces in contrast to the hypothesis. This could be related to previous findings by Ekman and colleagues (1987). They showed that assessing faces from different cultures can result in lower arousal rates for the foreign facial expressions because of less experience with the outer appearance and the interpretation of facial expressions of other cultures.

In how far this effect might have an impact on ERP amplitudes and source strengths remains unknown at this point. One study addressing this topic during the perception of IAPS pictures (Hot et al., 2006) has revealed attenuated LPP amplitudes for Japanese compared to French participants attributing this effect to a lower general emotionality of Japanese compared to French people. Studying emotional face perception across cultures by applying neuroimaging and electrophysiological methods would be an interesting approach for future research.

3.4.2 ERP data

The following chapters address the results of the electrophysiological data. According to the introductorily reported hypotheses of the EEG present study, emotional modulation was not expected for the P100, but was expected for the N170, the EPN, and the LPP. By and large, those hypotheses could be confirmed by the data of the present study which will be discussed in more detail in the following sections.

3.4.2.1 P1

As introductorily hypothesized, the present study did not confirm an affective modulation of P1 in static faces. This is in line with previous studies which also did not confirm enhanced positivity after about 100ms in posterior regions (Eimer et al., 2003; Krolak-Salmon et al., 2001; Leppanen et al., 2007). Ashley and colleagues (2004), who studied emotion perception with upright and inverted happy, fearful, disgusted and neutral faces, have also not found affective P1 modulation in emotional faces.

However, for an early emotion-specific modulation, there is a body of evidence reporting

early emotion-specific positive deflection after approximately 120 ms over centro-frontal regions (Eimer and Holmes, 2002; Pizzagalli et al., 2002) and after approximately 100ms in occipito-temporal regions (Batty and Taylor, 2003; Pizzagalli et al., 1999; Pourtois et al., 2005). The authors of the latter studies suggested a cooperation of fronto-central and posterior regions with the amygdala and related this effect to a coarse early extraction of emotional feature before the face is actually perceived as a whole (see also Vuilleumier et al., 2003).

One of the reasons for the lack of this effect in the present study might be related to the fact that emotional modulation was predominantly found in studies during the perception of fearful (Eimer and Holmes, 2002), but not in disgusted faces (Ashley et al., 2004; Sprengelmeyer and Jentzsch, 2006). The processing of fear is represented by a stronger evolutionary anchored meaning (Ohman and Mineka, 2001), by faster sympathetic physiological reaction as measured by SCR compared to disgust (Williams et al., 2005), and possibly by the fast subcortical route encompassing colliculo-pulvinar-amygdala pathways (LeDoux, 1996) which has not been evidenced for the processing of disgust yet (Sprengelmeyer and Jentzsch, 2006). However, this does not mean that the amygdala is not involved in the processing of disgusted or happy facial expressions, as Winston et al. (2003) have recently emphasized its contribution to emotion processing per se in a recent fMRI study. They suggested that one of the main reasons for the involvement of the amygdala is the *salience* of presented stimuli which is generally given in emotional facial expressions independent of emotional valence. Thus, the amygdala might be involved in the processing of disgust and possibly happiness in later stages of perception. Moreover, in contrast to the theory of early processing of fearful stimuli stands one study by Krolak-Salmon and colleagues (2004) who examined the perception of fearful stimuli in patients suffering from temporal lobe epilepsy (TLE) with intracerebral electrodes in the amygdala. They showed the first significant emotional difference between fearful and neutral faces after 200 ms. However, this result needs to be considered with care as well because firstly, they examined a small sample of only four patients with intact amygdalae (intact meant that amygdala did not show epileptic activity in that region) and secondly, differences in ERP waveforms could be seen from approximately 50 ms on, but the latter apparently did not reach significance. This result was not surprising, though, considering the small sample size.

Hence, the present results might simply imply that either the present stimulus material has not conveyed similar evolutionary intensity compared to previous studies of fear perception, or that emotional modulation with a possible contribution of the amygdala starts in later processing stages, like the N170, EPN or LPP for disgust and happiness. The author of the

present study agrees with the latter aspect.
In summary, the present study showed a positive deflection after approximately after 100 ms in posterior regions probably reflecting early sensory and perceptual visual analysis of the stimuli (Allison et al., 1999).

3.4.2.2 Emotional modulation of the N170

The emotional modulation of the N170 has been controversially discussed in the past. While the present study has confirmed a higher right lateralized amplitude of the N170 in lateral occipito-temporal regions for both happy and disgusted facial expressions, many EEG studies examining emotion perception have not confirmed this modulation. The following paragraph intends to discuss the possible (1) Cons and (2) Pros of emotional N170 modulation and its possible relation to the amygdala.

Cons and Pros of N170 emotional modulation

One of the most persisting argument contra emotional modulation of the N170 is based on the face perception model from Bruce and Young (1986) and Haxby and co-workers (2000) suggesting the sequential processing of the encoding of facial structure followed by the processing of identity and emotional expression recognition. These assumptions were based on previous EEG studies which showed the lack of emotional modulation of the N170 (Eimer and Holmes, 2002; Halgren et al., 2000; Herrmann et al., 2002; Holmes et al., 2003; Krolak-Salmon et al., 2001; Münte et al., 1998; Sato et al., 2001; Streit et al., 2000), the lack of modulation by familiarity (Bentin and Deouell, 2000) and the lack of modulation by other identification characteristics (e.g., race; see also Caldara et al., 2003). Therefore, it was presumed that the latter aspects were processed in stages following the N170 time window.
The N170 has been reported to be especially enhanced during the perception of human faces compared to monkey faces and to non-face objects in both EEG (Bentin et al., 1996) and MEG (Halgren et al., 2000) studies and has consequently been related to the holistic processing of general features of the face independently of identity and emotion (Eimer and Holmes, 2002). Identity and emotion are supposedly processed in a next step of deeper cognitive evaluation of the stimuli from about 250 ms on as reflected by occipito-temporal early posterior negativity (EPN) and (Eimer et al., 2003; Marinkovic and Halgren, 1998) and the late posterior positivity (LPP) over centro-parietal regions (Ashley et al., 2004; Eimer and Holmes, 2002; Krolak-Salmon et al., 2001; Orozco and Ehlers, 1998; Schupp et al., 2004b). Thus, one of the most persistent contra argument of emotional modulation of the N170 refers

to the presumed sequential instead of parallel processing of structural characteristics and emotional content of the displayed faces.

On the other hand, there is a large body of evidence arguing that emotional modulation of the N170 occurs. The following paragraphs discuss some of those possible Pros of this modulation.

In the present study, exclusively female participants were examined. Previous studies examining the gender effects of emotional processing with electrophysiological methods found a higher emotional susceptibility of females towards emotional stimuli, here aversive ones (Schupp et al., 2004a), resulting in generally increased amplitudes in females compared to male participants (see also Orozco and Ehlers, 1998). Most of the times, both sexes were examined in EEG emotional perception studies. However, gender differences have often been ignored or were simply not addressed by the authors (e.g., Blau et al., 2007). Therefore, the author of the present thesis believes that perception of emotions in females might be stronger and better to "catch" with EEG methods, hence resulting in an emotional modulation of the N170.

Another important aspect contributing to the emotional modulation of the N170 might be that participants are naïve to the stimulus material and watch the faces passively without evaluating and categorizing emotions. Most of the studies reporting emotional modulation of the N170 applied a passive viewing task of emotional stimuli (Pizzagalli et al., 2002; Williams et al., 2006) or participants were instructed to attend to other than emotional aspects of the stimuli (Batty and Taylor, 2003; Blau et al., 2007). Blau and colleagues (2007) found enhanced N170 amplitude for fearful compared to neutral facial expressions. They also reported topographies of emotional versus neutral stimuli which were similar to those reflecting the processing of facial structure. Furthermore, they suggested that the face-specific N170 component might be modulated by a parallel (1) structural encoding process and (2) emotional encoding system resulting in enhanced amplitude in inferior posterior lateral electrode sites. However, the aspect of a passive viewing task is contradicted by the results from Caharel and colleagues (2005). They showed an enhanced N170 for disgust compared to happy and neutral faces during an emotion categorization and a familiarity categorization task.

Schupp et al. (2004b) instructed their participants to passively watch faces of happy, threatening, and neutral valence and found a slight, but not reliably consistent effect. The question arises whether this effect would have been stronger if they had included a larger number of participants into their study per gender, i.e., instead of 10 per sex, 20 per sex, as in

the present study. The present study has measured 20 participants of the same sex and detected the emotional modulation of the N170. Thus, sample size might have an effect as well.

A further explanation of N170 emotional modulation should be considered: the speculative influence of the AMG in emotion perception.

Influence of the amygdala on the N170 and other ERP components

Emotional modulation of the N170 has been related to findings from the above described fMRI and previous fMRI studies reporting fusiform gyrus (FuG) and amygdala activation during emotion perception (fear, disgust, happiness). AMG activation was related to rapid perceptual and coarse processing of emotionally salient and relevant stimuli (Hariri et al., 2003; Winston et al., 2003). Furthermore, it was explained by anatomical reentrant feedback projections of the amydala to all stages of the ventral stream of the visual pathway including primary visual and associated occipital and temporal cortices (Amaral et al., 2003).

Parallel processing of visual structural information and emotional aspects of stimuli might account for the emotional modulation of the N170. At this early latency, modulation might be associated with coarse evaluation of affect possibly enhanced by parallel amygdala activity. This can only be indirectly assumed because it is difficult to investigate AMG activity with EEG (Anderson et al., 2003; Eimer and Holmes, 2007; Eimer et al., 2003; Vuilleumier and Pourtois, 2007). Measuring amygdala activation with EEG is difficult (that is also the reason why subcortical structures with an eccentricity <.55 were excluded from further source analysis) because it is situated deep in the brain and is - because of its nuclear structure - not as regularly aligned as the cortex. The amygdala represents a “closed field” structure (Eimer and Holmes, 2007). Closed field cells (also pyramidal cells) are characterized by stellar, radial symmetrical configuration of dendrites of the cell body. They produce electrical potential within the region of the dendrites, thus, resulting dipoles do not summate, but cancel themselves out. Many subcortical regions, like, e.g. the amygdala, include closed field cells which, hence, do not result in an extracranially measurable voltage difference. Thus, signal on the scalp surface might not be directly measurable on the scalp, but possibly indirectly by being relayed through various brain structures to the neocortex (Eimer and Holmes, 2007). This is the reason why the involvement of the amygdala could only be indirectly presumed.

LeDoux (1996) has reported a fast subcortical route predominantly during the perception of fear or threat including brainstem-collicopulvinar-thalamo-amygdala connections which hold strong connections to all levels of the visual processing stream (Amaral et al., 2003; Amaral et al., 1992). Extrastriate visual regions have been shown to be enhanced in emotional

processing with increasing emotional arousal (Lane et al., 1999; Lang et al., 1998). Both fMRI and EEG studies have suggested the parallel processing of the cortical slower and subcortically faster processing route (Batty and Taylor, 2003; Morris et al., 1996). The subcortical visual processing path (collicopulvinar-thalamo-amygdala) assigns emotional arousal or saliency of the stimulus per se, sends feedback information to the ventral visual pathway after first evaluation, and recruits resources to enhance activation in those regions to boost further and more elaborate emotion processing. Sprengelmeyer and Jentzsch (2006) have argued that there has not been evidence for a subcortical route for disgust yet.

The author of the present thesis, however, assumes that the involvement of the amygdala and its projections to the ventral visual stream could be realistic, but also speculative, for the following reasons: firstly, referring to the results of the present fMRI study (Chapter 2), amygdala activation has been confirmed for the perception of disgust in the dynamic modality which has been in line with previous research stating the involvement of the amygdala in disgust perception, at least in static pictures (Gorno-Tempini et al., 2001). Secondly, the amygdala has been shown to be activated due to salience of stimuli independent of emotional valence and intensity (Winston et al., 2003) due to a high degree of automaticity in responding to emotive stimuli, independent of task, attention, or awareness (Dolan, 2002; Vuilleumier et al., 2001). In the present study this aspect is covered by the use of *unknown* facial expressions per se which represent a high social and salient sign for communication (Adolphs, 2003). The latter point could also explain the finding of enhanced N170 for happy faces.

There is a large disagreement about the role of the AMG in face processing. Some scientists believe that the AMG is solely involved during the perception of potential threat (LaBar et al., 2003; Pessoa et al., 2002; Phan et al., 2002), whereas others support the hypothesis that the AMG processes non-specific, affectively ambiguous stimuli and appraises salient events. Winston and colleagues (2003) examined the perception of happy, disgusted, fearful, sad, and neutral facial expressions, all resulting in prefrontal, somatosensory area, and AMG activation when compared to a low-level baseline. This supported the notion, that AMG might be involved in processing of salient information per se, being important for the interpretation of social cues. Thus, the AMG is considered to process a broader category of socially salient and relevant stimuli, not solely fearful or negative events (Fitzgerald et al., 2006; Sander et al., 2003). Since the above mentioned fMRI study revealed AMG activation for disgust and was related to the processing of negative emotional stimuli per se, it is possible at exclusively this early perceptual processing stage, that the AMG might be engaged in the detection of

generally arousing and salient facial stimuli independent of emotional valence. Consequently, amygdala either repeatedly tags the stimulus for further, more elaborate processing as revealed by enhanced EPN for disgust (see below) or refrains from further processing as revealed by similar waveforms for happiness and neutrality during the EPN time window. Thus, short and transient activation of the amygdala for happy facial expressions might not be detected by fMRI (Im, 2007; see also Chapter 4.2, for more detailed discussion), and possibly could not have been detected in the present fMRI study either (see Chapter 2). Hence, the amygdala might continuously enhance posterior regions via feedback projections when continuous processing is necessary for more deeper stimulus evaluation during the perception of potential threat (Ohman and Mineka, 2001). However, also this speculation needs further investigations.

In summary, the present study confirmed an emotional modulation of the N170 represented by enhanced mean amplitudes in right lateralized posterior electrode sites for happy and disgusted (electrode PO8, P8, respectively) static faces. It was suggested that activation of the AMG might speculatively be one of the responsible brain regions enhancing the modulation of the N170 for happy and disgusted faces. Modulation of emotional compared to neutral static faces have further been related to the parallel processing of visual input of the stimulus and its emotional arousal and salience which results in an enhancement of mean amplitudes around approximately 170 ms (Batty and Taylor, 2003; Blau et al., 2007; Caharel et al., 2005; Pizzagalli et al., 2002; Sprengelmeyer and Jentzsch, 2006).

3.4.2.3 Emotional modulation of EPN (Early Posterior Negativity)

As introductorily expected in the hypotheses, EPN was confirmed for static disgusted faces between 250 and 350 ms over occipito-temporal electrode sites.

In recent studies, salient and intense, possibly socially and evolutionarily relevant stimuli (including both IAPS scenes and facial expressions) evoked larger EPN amplitudes independent of differing task requirements which covered passively viewing of threatening faces (Schupp et al., 2004b), one-back tasks attending to identity and ignoring emotional content (Ashley et al., 2004), gender discrimination tasks (Sato et al., 2001; Sprengelmeyer and Jentzsch, 2006), emotional face (Eimer et al., 2003; Leppanen et al., 2007) or IAPS picture categorization tasks (Schupp et al., 2003, 2004a). The latter aspects emphasize (1) the possibility of non-face-specificity of this component and (2) the automatic and reflexive enhancement of this component. EPN has been modulated by the passive and attentive perception of disgust in both fronto-temporal (also for happiness, and also found by

(Sprengelmeyer and Jentzsch, 2006) specific for disgust, but not for anger and fear between 350 to 400 ms) and in right occipito-temporal regions between 350 and 400 ms. Likewise, Ashley and co-workers (2004) have recently argued that the EPN in posterior sites is unique to disgust perception. The results of the present study confirmed the latter results by showing an EPN exclusively for disgust in right occipito-temporal electrode sites solely for disgust, but not for happiness. However, the present study did not study further negatively valenced emotions, so the exclusiveness of the EPN to disgust perception should be handled with care. This is also addressed by recent studies which have given rise to the assumption that the EPN might not be unique to disgust, as recently suggested by Ashley and colleagues (2004) and might be a component which is modulated automatically and reflexively by salient, especially negative stimuli including threat and fear (Eimer et al., 2003; Schupp et al., 2004b).

However, the perception of both fearful and happy facial expressions has also yielded an enhanced negative shift after about 300 ms. Sato et al. (2001) studied individuals with an implicit emotion perception task and asked them to discriminate between gender. The N270 component over occipito-temporal regions showed enhanced negative amplitude and a more negative topography in those areas for fearful and happy compared to neutral stimuli. Synchronized midline specific positivity as detected by Independent Component Analysis (ICA) was interpreted as an engagement of the limbic system and its interaction with lateral posterior temporal regions (Sato et al., 2001).

Considering the involvement of subcortical and limbic structures, especially of the amygdala, to emotion perception as reported in fMRI studies (for review see Adolphs, 2002; Phan et al., 2002) and in the above described fMRI study, enhanced EPN has also been related, just like the N170, to reentrant amygdalar pathways to occipito-temporal regions. These pathways probably project back to the ventral path of higher level visual regions (Leppanen et al., 2007; Sato et al., 2001; Schupp et al., 2004b) which are involved in the recruitment of attentional resources and followed by more elaborate processing of emotions (Schupp et al., 2004a). This could explain differences over lateral posterior sites.

In the present study, perception of happiness has not revealed an enhanced EPN. This result is in line with previous studies reporting enhanced EPN in occipto-temporal regions and midline LPP solely for threatening compared to positive and neutral faces (Schupp et al., 2004b). The author of the present thesis agrees with the suggestion by Schupp and colleagues (2004b) that EPN might represent the tagging of the emotional stimulus of threat which might again facilitate and enhance the following sustained more elaborate perceptual processing of threat. It is assumed that positive facial expressions were possibly detected by the amygdala in early

perceptual processing stages of emotion processing as reflected by an increased N170 (see above). Amygdala might have been transiently engaged at this stage, but not in later stages of the EPN. Thus, a deeper elaborate evaluation of the stimulus might not have been necessary for the following reason. It is proposed that, at this processing stage, happiness is processed more independently of subcortical sources than disgust because happy faces do not provide threat and have been shown to be processed very fast in behavioral experiments (Leppanen and Hietanen, 2004). Therefore, the processing of happiness might yield a temporal advantage for the processing of positive faces. Consequently, it is assumed that the recruitment of attentional and cognitive resources might be lower in the perception of happiness compared to the perception of disgust because humans have more experience with positive compared to threatening faces. Processing disgust might be related to the processing of aversive emotions and threat and therefore, possibly needs deeper cognitive evaluation due to less experience in everyday life with disgust compared to happiness (for further discussion, see also Chapter 2.4.5 of the present thesis) resulting in increased EPN.

In summary, the amplitude of the EPN was found to be modulated by disgust, but not by happiness, between 250 and 350 ms over lateral occipito-temporal regions. This might yield the tagging of the negative stimuli for the following more elaborate processing of evolutionary relevant stimuli of threat. It would be interesting in the future to examine whether dynamic stimuli which are considered to be ecologically more valid, also show an enhanced EPN and, moreover, show an increased EPN compared to static stimuli.

3.4.2.4 Emotional modulation of LPP (Late Positive Potential)

In the present study, significantly enlarged LPP (Late Positive Potential) were found for both static and dynamic facial expressions for both emotional valences (happiness and disgust). While the perception of static facial expressions showed enhanced positivity over parietal electrodes between 600 and 800 ms after stimulus onset, dynamic stimuli revealed stronger and more sustained effects of LPP for several hundred milliseconds. Firstly, dynamic stimuli evoked a larger positive potential from approximately 200 ms for disgust, and approximately 300 ms for happiness in centro-parietal electrode sites spreading to central and parietal sites and being sustained until 800 ms after first subjective recognition of facial expressions. Secondly, enlarged negativity (inversed polarity) in lateral frontal electrodes has been described in dynamic stimuli for happiness and disgust which has not been expected in apriori defined hypotheses. Before discussing the expected effects, the unexpected results of enhanced amplitudes in lateral frontal electrodes are addressed.

Fronto-temporal negativity

Even though not expected, an increased negativity was shown for lateral frontal electrodes in the present EEG study. Similar findings have been reported before. During a gender discrimination task, Sprengelmeyer and colleagues (2006) discovered enhanced negative amplitudes for the perception of disgust compared to anger and fear in fronto-temporal electrodes (FT7 and FT8) between 350 and 400ms. Krolak-Salmon and co-workers (2001) found similar effects specifically for disgust after 700-950 ms in right lateral front-temporal regions during an attention to emotion task (counting surprised faces). Intracranial electrodes implanted in the anterior insula (INS) have shown increased negativity between approximately 300 and 500 ms during an attention to emotion task for disgust compared to happiness, fear, and surprise in three of four patients with temporal lobe epilepsy (Krolak-Salmon et al., 2003). Thus a "late negative potential" which might be the frontal complement to the LPP over centro-parietal regions, has been repeatedly reported for disgust, and has been related to the processing of faces of disgust in the underlying INS.

The present study revealed this effect for both emotions in dynamic modality from 300 ms on for several hundreds of milliseconds. Relating the present results to previous fMRI studies, it could be assumed that the inferior frontal cortex and possibly the anterior temporal pole might be responsible for this effect. However, underlying generators can better be determined by the fMRI constrained source analysis approach as described in the next chapter (Chapter 3.4.3). If the assumption were correct, however, in fMRI studies, temporal pole activations have been associated with mentalizing and attributing thoughts to others – the so-called theory of mind (Baron-Cohen et al., 2000). Furthermore, inferior frontal regions have been linked to the mirror neuron system (Buccino et al., 2001; Leslie et al., 2004; Rizzolatti et al., 2001). This is a very speculative interpretation because the exact neural generators are not known. However, speculations are supported by results of the seeded source analysis (Chapter 3.3.3). Stronger source strength was revealed for inferior frontal regions for happiness and disgust after about 250-300 ms and 400-450 ms and are discussed in more detail below (see Chapter 3.3.3 for results and Chapter 3.4.3 for discussion).

LPP and arousal

A further approach to interpret enhanced LPP is to consider its correlation with increased arousal of perceived emotional stimuli. Higher arousal ratings have previously been shown to be in accordance with increased amplitudes of the EPN and LPP representing facilitated and more detailed processing of emotional stimuli as reported by various working groups (Schupp

et al., 2003; Schupp et al., 2004b; Schupp et al., 2007). The influence of larger arousal could be supported by the point that emotional threatening faces or pleasant and unpleasant pictures incorporate a certain motivational relevance, presumably based on evolutionary significance of facial expressions, possibly triggering the so-called "natural selective attention to evolutionary significant stimuli in the environment." (Lang et al., 1997, in Schupp et al., 2004b, pp. 198). Schupp et al (2007) emphasized that the LPP amplitude almost doubled when attention was allocated to the emotional content of presented IAPS pictures. Therefore arousal has been related to the potential activation of the appetitive or defensive motivational system and their associated pleasant or unpleasant affects (Schupp et al., 2004b) resulting in enhanced LPP and presumably a more detailed elaboration of emotional stimuli.

In the present study, participants showed higher arousal ratings for happy and disgusted compared to neutral faces independent of modality. Therefore, increased arousal might imply that both emotions reflect the engagement of the motivational system. Hence, emotional stimuli capture and focus attention selectively to emotional faces and furthermore, possibly initiating rapid learning for motivationally relevant stimuli (LaBar and Cabeza, 2006).

The LPP was supposed to represent sustained processing of threatening faces (LPP) and the transfer to working memory (Schupp et al., 2004b) or even to long term memory as suggested by Dolcos and Cabeza (2002). Dolcos and Cabeza (2002) investigated enhanced memory effects of emotionally arousing pictures (IAPS). However, associating those findings with the results of the present thesis, it needs to be emphasized that this interpretation needs to be handled with care because subsequent memory effects have not been subject of the present study. Nevertheless, the author of the present work suggests that LPP was increased for both emotional valences due to a higher arousal in emotional compared to neutral faces as evidenced by behavioral data.

Valence and LPP in other studies

As described in the introduction (Chapter 3.1.4), there have been few studies finding enhanced LPP for both positively and negatively valenced static facial expressions during attention allocation to emotion (Eimer et al., 2003; Werheid et al., 2005) and no study examining dynamic emotional expressions per se. The question arises whether LPP is modulated by arousal (Werheid et al., 2005), as discussed above, or by valence.

The majority of emotional face perception studies have reported an enhanced LPP in emotional categorization tasks, passive viewing, and passive attention to emotion tasks for negative (fear, sad, threatening) faces compared to positive or neutral faces (Eimer and Holmes, 2002; Leppanen et al., 2007; Orozco and Ehlers, 1998; Williams et al., 2006).

Possible interpretation approaches suggested that a potential danger detection module is involved in the continuous, sustained elaboration of the negative stimuli which is partially reactivated after an initial early processing stage for more detailed stimulus elaboration and context elaboration (Williams et al., 2006).

In contrast, enhanced LPP has also been shown for positive and negative facial expressions. Eimer and co-workers (2003) reported that neocortical processing of positive and negative emotional expressions strongly depends on selective and focal attention reflected by the LPP enhancement over midline frontal, central, and parietal electrodes for the following reason: LPP modulation could be confirmed for an emotion discrimination task, but not for a complex line decision task, in which participants directed their attention away from emotional stimuli. Enlarged late positivity consequently facilitates emotional intensity evaluation, independent of valence. This finding might also be accordant with the notion, that attention is captured rather automatically at early perceptual processing stages (e.g., EPN), and is sustained during later - beyond perceptual - processing stages (LPP) (Vuilleumier and Pourtois, 2007). Besides, Werheid and colleagues (2005) asked participants to quickly categorize the presented happy and angry faces preceded by the same (primed) or different (unprimed) emotion. LPP was enhanced in both emotions for the unprimed condition and was also associated with selective attention to motivationally relevant faces (i.e., emotional expressions; Schupp et al., 2004b) and their high task-relevance (categorization reflected the task-relevance of the stimulus material). The latter paragraphs supported the opinion that enhanced LPP might rather depend on arousal and a certain amount of allocated attention to the emotional facial expressions instead of valence per se. Increased LPP might therefore be involved in continued elaboration of emotional facial expressions.

The present results of enhanced LPP for both emotions might support the notion, that emotional stimuli are salient social signs, capture attention independent of their valence, and are consequently processed continuously and elaborately. Furthermore, the next paragraphs address the finding of more sustained enhanced LPP for dynamic faces compared to static ones.

LPP and enhancement in dynamic faces

Increased LPP for both opposing valences has been repeatedly described in studies applying IAPS pictures instead of facial expressions (Cuthbert et al., 2000; Schupp et al., 2007), but rarely in emotional *face* perception studies (Ashley et al., 2004; Eimer et al., 2003; Werheid et al., 2005) which applied either passive viewing or emotional categorization tasks. One of the aspects to be addressed is whether IAPS and facial expressions differ in intensity of stimuli or

in arousal ratings. If this was the case, it could explain the lacking enhancement of LPP in positive facial expressions in many previous studies (Eimer and Holmes, 2002; Leppanen et al., 2007; Orozco and Ehlers, 1998; Williams et al., 2006). Supporting the latter assumption, Britton and colleagues (2006) reported significantly lower arousal ratings for faces of happiness, sadness, anger, fear, compared to pleasant and unpleasant IAPS pictures. In the present study, the reason for finding enhanced LPP for both emotional valences, especially for dynamic faces, might be due to the fact that dynamic faces capture attention more intensively compared to static faces. This argument would be in line with the above proposed interpretation. This finding might be explained by two reasons.

Firstly, dynamic stimuli have been shown to convey a more natural concept of emotional facial expressions compared to static emotional faces (Harwood et al., 1999; Sato et al., 2004; see also Chapter 2.4.3). Even though cognitive judgment of arousal of stimuli have not always yielded larger arousal for dynamic compared to static faces in the present two studies in contrast to other behavioral studies examining arousal for static and dynamic faces (Biele and Grabowska, 2006), the higher ecological validity of moving faces might have triggered the relatively larger LPP amplitude for dynamic stimuli. Moving faces are part of one's everyday social life whereas static photographs of faces often appear unrealistic. Furthermore, emotional facial expressions have been discussed to possess an evolutionary relevance being important for survival (Schupp et al., 2004b).

Secondly, dynamic stimuli enrich emotional perception of facial expressions (Biele and Grabowska, 2006) due to the additional temporal information conveyed by a moving face. In everyday life, humans are used to be able to compare the development from one facial expression to the next during social communication and interaction.

In the present study, the onset of the first subjective recognition of facial expressions of happiness and disgust evolved to the maximum within a few hundred milliseconds for dynamic stimuli. This development was suggested to further boost the capturing of attention, the sustained evaluation of the face because of the continued comparison of the developing expressions, and the enhanced transfer to working memory.

3.4.2.5 Summary and conclusions: ERP data

Introducing a new stimulus database, three ERP components could be shown to be modulated by emotion. The N170 yielded increased negative amplitude over lateral occipito-temporal regions for both happiness and disgust. This suggested that the perception of emotions were possibly processed parallelly, and not sequentially to structural face perception. Furthermore,

the amygdala might have enhanced the N170 via feedback projections by presumably a first and coarse processing of the motivationally significant stimuli.
The EPN could be shown to be enhanced exclusively for disgust supporting previous studies by finding the enhancement exclusively for disgust and other negative emotions as, for example, fear. These results implied the tagging of the processed stimulus possibly via reentrant projections of the amygdala. This could be found especially for negative faces due to a higher evolutionary significance for continued and more elaborate processing.
Enhanced LPP was shown to be modulated by both emotions. It was related to the increased arousal conveyed by the emotional faces which hence, captured attention, maintained a sustained and continuous evaluation of emotional faces, and enabled a possible transfer to working memory. The more pronounced positive slow wave for dynamic faces could be related to a higher ecological validity of the stimulus set compared to static ones.

3.4.3 Source analysis

To date, there has been little to no evidence of studies investigating emotion perception with a combined approach of fMRI, ERPs, and multiple fMRI constrained source analysis extended by additionally fitted sources (except for Sabatinelli et al., 2007). That is why it is important to emphasize, that the current thesis is a first approach to study spatio-temporal dynamics combining those three methodological approaches for static and dynamic perception of happiness and disgust. Therefore, results will have to be replicated in the future with a similar experimental setup and approach of analysis.
It is furthermore important to mention that to date there has been no study investigating *dynamic* emotional face perception with discrete multiple source models including additional sources.
By investigating emotion perception by fMRI, wide emotion specific networks could be determined with an excellent spatial resolution for dynamic and static emotional facial expressions (study 1, see Chapter 2 of the present thesis). ERPs, in contrast, yield a high temporal resolution in the range of milliseconds, but a low spatial resolution (Hopfinger et al., 2005). The advantage of fMRI constrained source analysis is the combination of both temporal and spatial dynamics within the brain incorporating prior knowledge which is supposed to improve the validity of the model (Hopfinger et al., 2005; Michel et al., 2004; Scherg and Berg, 1991). In the present EEG study, brain regions, which were shown in the fMRI study applying identical stimulus design (Chapter 2), were seeded into the source model. In addition, further sources, which might have been invisible to fMRI, were fitted (for

further detailed explanations why additional sources have been fitted, see Chapter 4.2 and (Im, 2007)). Therefore, four additional sources have been added to the seeded model for static faces, and one additional source for dynamic faces (see also Chapter 3.2.5.3).
In the following paragraph, emotional differences of happiness and disgust compared to neutral faces in both static and dynamic modality are discussed.

3.4.3.1 Static faces

As discussed in Chapter 2.4.4, static face perception has been reported to activate similar brain regions compared to dynamic faces, but in a less widespread network and less consistently. This finding has been related to the diminished authenticity, complexity, and social relevance of static emotional expressions (see also Chapter 3.4.4).
In the present study, predominantly additionally fitted regional sources showed enhanced source strength for static emotional compared to neutral facial expressions. Static faces of happiness activated sources in posterior inferior occipito-temporal regions starting between 50 and 100 ms in left middle occipital gyrus (MOG), followed by left inferior temporal gyrus (100-150 ms), reactivating left MOG (350-400ms) and simultaneously activating right cerebellar tonsil (350-400 ms) followed by right fusiform gyrus (FuG, 600-750 ms). For disgust, first significant differences compared to static neutral faces started in left inferior temporal gyrus (100-150 ms) like for happiness, followed by INS (300-350ms), and then by left MOG and right FuG being transiently reactivated until up to 750 ms.

Activation of posterior brain areas

Similar activated brain regions and their time course during emotion perception for happy and disgusted static faces have shown alternating reactivations of inferior temporal regions, FuG, and MOG starting between 100 and 150ms and continuing in later time-windows (approximately 350 - 400 ms, and 550 - 600 ms). Reentrant projections of those areas might be associated with continuous elaboration and context evaluation of the static faces as suggested by Williams and co-workers during the perception of fearful facial expressions during a passive observation task (Williams et al., 2006; see also Chapter 3.4.2).
Especially inferior temporal and FuG areas have been shown to be part of the emotion perception process. Pizzagalli and colleagues (2002) have reported the FuG and lateral occipital regions as possible generators for the N170 as revealed by LORETA for liked compared to disliked faces. In a recent MEG study, Lewis and coworkers (2003) fitted a single FuG dipole (right lateralized for five, and left lateralized for one participant) within the

time window of the N170 (127-161 ms) during an emotion discrimination task. Therefore, they demonstrated enhanced source strength in the FuG for both happy and disgusted faces compared to the control conditions. Considering the ERP and source analysis results, the results of the present thesis could confirm previous studies (Lewis et al., 2003; Pizzagalli et al., 2002; Sprengelmeyer and Jentzsch, 2006) and the emotional modulation of inferior temporo-occipital regions on the temporal and spatio-temporal level (source analysis) in this early time window. Furthermore, enhanced source strength in occipito-temporal regions was associated with the early extraction of structural and emotional features as suggested above (Chapter 3.4.3).

It is important to mention that the N170 was right lateralized and source analysis revealed predominantly left lateralized increased source strength. At first glance, these results appear to be controversial. However, voltage topographies for difference waves of disgust and happiness versus neutral revealed a different pattern descriptively. Static disgusted faces showed increased negativity over right and left inferior occipito-temporal regions (see Fig. 12 B). Voltage topographies for happiness showed largest differences over the right hemisphere which spread to left inferior occipito-temporal regions. Thus, the revealed difference in source strength in left inferior temporal regions could not be detected by simple comparisons of ERP mean amplitudes.

Furthermore, and in contrast to the above mentioned studies, dipoles located in middle and superior temporal gyrus have also yielded emotional enhanced source strength within the P1 and N170 time windows (Batty and Taylor, 2003; Streit et al., 1999). Those regions have been shown to be reactivated also in later processing stages (~210-240 ms and ~350 ms) (Streit et al., 1999). Superior and middle temporal areas could not be supported by the present results of static emotional face perception, but were shown for perception of dynamic stimuli of disgust perception (see Chapter 3.4.3.2).

Also in later time windows, extrastriate and inferior temporal regions have been shown to be modulated by emotional content in previous studies. For example, in a gender discrimination task during the presentation of angry, disgusted, and fearful faces, Sprengelmeyer and Jentzsch (2006) have fitted a symmetrical pair of dipoles in inferior occipito-temporal regions (BA19/37) between approximately 200 and 300 ms. A similar spatio-temporal relation has been reported during a passive emotional face viewing between 250 and 350 ms as revealed by LORETA in inferior temporal regions (Williams et al., 2006). This time window is equivalent to the EPN found in the present study between 250 and 350 ms for disgust in right inferior occipito-temporal electrodes. However, source waveforms of the present study

showed emotion-specific differences in later time-windows starting approximately 350 ms which has been rather related to the LPP.

Sabatinelli and co-workers (2007) have reported the involvement of lateral occipital, inferior temporal and parietal regional sources as furthermore confirmed by fMRI during a passive viewing task of IAPS pictures between 400 and 900 ms. This effect has been related to the LPP over centro-parietal electrode sites. For static faces of the current study, inferior occipito-temporal sources have been transiently reactivated. This might indicate a relation to the LPP and a possible sustained elaboration and evaluation of both happy and disgusted facial expressions which has been associated with processes beyond 250 ms (Eimer and Holmes, 2002; Williams et al., 2006).

The basic difference of the perception of happiness and disgust within the static modality is the modulation of the cerebellar tonsil for happiness, and the INS for disgust perception. This will be discussed below.

Insula:

One of the main differences to the fMRI study is that increased source strength was exclusively revealed for static disgust compared to neutral after 300-350 ms in the insula (INS).

In humans, the cytoarchitectonic structure of the insula is less well described than in the macaque monkey. In the monkey, the insula has been shown to be involved in autonomic, olfactory, and gustatory processes (Mesulam and Mufson, 1982) and to have connections to the superior temporal sulcus area. It is furthermore involved in the discrimination of facial features (Hasselmo et al., 1989). The latter connections might also be involved in face processing in humans (Krolak-Salmon et al., 2003). Even though some fMRI studies have questioned the emotion-specific role of the insula for disgust perception in IAPS pictures, odors and facial expressions (Stark et al., 2003; Wicker et al., 2003), the insula has been repeatedly associated with the perception and evaluation of disgusted static faces in fMRI studies (Anderson et al., 2003; Phillips et al., 1998; Phillips et al., 1997; Sprengelmeyer et al., 1998), in lesion studies (Calder et al., 2000), and in Huntington disease (Sprengelmeyer et al., 1996).

Sprengelmeyer and Jentzsch (2006) found enhanced negative signal between 350 and 400 ms in fronto-temporal electrode sites for disgusted compared to angry and fearful faces. They associated these results to activations in the insula. This inference, however, should be handled with great care, because especially in EEG, inferences from the topography to underlying sources should be avoided due to the inverse problem (Hopfinger et al., 2005; see

also Chapter 1.6.2).

Krolak-Salmon and co-workers (2003) have recently supported the role of the insula in emotional face processing. They examined patients with intracranial electrodes implanted in the right anterior insula and asked them to either attend to gender or emotion (disgust, fear, happiness, surprise, and neutral) of displayed faces. Amplitudes of insula electrodes showed a disgust-specific enhancement between 300 and 500 ms for disgust, but not for happiness, surprise, neutral, and fear during the attention to emotion task. The authors have highlighted the sustained evaluation of disgusted faces during this time window and the importance of detecting disgust in humans in general as reflected by enhanced insula activation (Krolak-Salmon et al., 2003). They ascribed it to both detection and feeling of disgust (Krolak-Salmon et al., 2003). The author of the present thesis agrees with the suggestion that insula is involved in the detection of disgust. However, she disagrees with Krolak-Salmon and coworkers regarding the actual feeling of disgust because insula was activated shortly instead of continuously.

In summary, the author of the present thesis assumes firstly that because of the short time window, INS activation might have been invisible to fMRI and secondly, insula is related to explicit detection and categorization of disgust rather than to actual feeling of disgust.

Cerebellum:

Interestingly, just like in the fMRI study (Chapter 2, Table 1), activation of the right cerebellar tonsil was revealed when comparing smile to neutral faces between 350 and 400 ms. The cerebellum has been mainly neglected in previous imaging studies of emotion perception although activations have been found.

Turner and co-workers (2007) have addressed this topic in a previous PET-study examining six patients with cerebellar stroke and nine healthy age-, education-, and IQ-matched controls. Lesions of the stroke patients partly covered cerebellar tonsils. Participants passively watched pleasant, unpleasant, and neutral IAPS pictures in blocks of 30 stimuli, rated their subjective emotional experience after each of those blocks, and objectively rated each stimulus at the end of the PET-scan session. Neural responses, subjective and objective ratings were analyzed. Patients with cerebellar lesions showed decreased subjective experience during the passive viewing of pleasant pictures, but a similar objective appraisal of positive stimuli compared to the healthy control group. Turner and colleagues (2007) therefore supposed that due to the lesions of the cerebellum and its connections to - among various other brain regions - the reward system of the nucleus accumbens and the PFC, reward processing was diminished. This was consequently related to a diminished experience of pleasant - in context of

rewarding - stimuli.

The present study supports the finding of Turner and colleagues (2007) because cerebellar tonsil activation was shown between 350 and 400 ms during the perception of smiling compared to neutral faces. During this time window, higher order processing stages begin. One possible explanation would be that due to the task instructions (participants were asked to empathize with the displayed emotion) participants subjectively experienced what they saw which was again reflected by increased source strength in the right cerebellar tonsil. This new finding expands previous findings of cerebellar activations described with fMRI by adding the temporal aspect. However, results should be considered carefully because the cerebellar source was less independent from surrounding sources than other sources (see Chapter 3.3.3.1) as revealed by source sensitivity calculations. This might indicate that the cerebellar source incorporates explained variance by surrounding regional sources of, e.g., inferior temporal gyrus. On the other hand, this aspect was controlled for during the averaging process of original Talairach coordinates (see Chapter 3.2.5.3). Therefore, the author of the present thesis emphasizes the need to replicate this finding in the future.

Summary and conclusion of source analysis results for static face perception

In summary, most of the static emotional face processing occurred in posterior inferior occipito-temporal regions. This could be related to parallel processing of structural and emotional facial features (see also discussion in Chapter 3.4.2.2) (Sprengelmeyer and Jentzsch, 2006; Vuilleumier and Pourtois, 2007; Williams et al., 2006) and its continuous elaboration due to mutual reentrant feedback projections and increased arousal conveyed by facial expressions and as reported in relation to LPP (Schupp et al., 2004b). The latter aspects of reentrant feedback projections can be predominantly related to previous studies using fMRI.

On the one hand, increased activation of visual processing regions was detected in several fMRI studies. This was associated with increased emotional arousal caused by motivationally relevant stimuli (e.g., emotional facial expressions), and with reentrant feedback projections from subcortical or higher order processing structures (Breiter et al., 1996; Lang et al., 1998). Studies of the visual processing stream of the macaque monkey revealed connections of the amygdala to all stages of the visual processing stream (Amaral et al., 2003).

On the other hand, there is a large body of evidence suggesting that increased FuG activation was related to the perception of static, unchangeable features of a faces and to the recognition of identity of the face (Hoffman and Haxby, 2000; Kanwisher et al., 1997). For the present results, emotional modulation of early inferior temporal changes of source strength might be

related to the rather sensory perception of the facial structure, whereas emotional modulation of later differences might be associated to the sustained elaboration and judgment of the perceived identity and emotional expression.

These results also need further investigations in the future because the stimulus material was used for the first time. The following chapter will discuss differences revealed by source analysis for dynamic faces.

3.4.3.2 Dynamic faces

FMRI constrained source analysis of dynamic facial expressions yielded a more widespread network of interacting brain areas compared to the static modality as already revealed in the fMRI study described in Chapter 2. Besides, while four additional sources were added to the model of the static stimuli, one additional regional source has been added to the model. Therefore, fMRI, due to the much higher number of seeded sources, could either model the recorded EEG data better in the first place, or fMRI could reveal underlying sources for dynamic stimulus material more appropriately. The author of the present study agrees with the latter argument because the model for dynamic faces included similar regions as additionally fitted to the static source model (see Chapter 3.3.3.1).

Since there has been no EEG study examining dynamic facial expression with source analysis, the interpretation of the present results is limited to previous studies investigating static facial expressions. Furthermore, the author of the present thesis would like to mention that many different source analysis approaches make comparisons among studies even more difficult. Previous source analysis approaches have applied MFT analysis (Streit et al., 1999), LORETA (Esslen et al., 2004; Pizzagalli et al., 2002), LAURA (Batty and Taylor, 2003) and equivalent current dipole source analysis (Lewis et al., 2003; Sprengelmeyer and Jentzsch, 2006). Therefore, the results need to be regarded with great care and require further investigations and replications with similar methodological approaches in the future.

Dynamic disgusted compared to neutral faces yielded an early modulation of the left superior temporal gyrus (150-200ms) followed by left precentral gyrus and right medial frontal gyrus (200-250ms and 200-300 ms, respectively). The two latter sources were re-activated in later time windows (350-400 ms, and 350-400, 450-500, and 700-750ms, respectively). Furthermore, right inferior frontal gyrus showed enhanced source strength after 250 ms, and again after 400 ms.

Dynamic happy compared to neutral faces yielded a complex network of interacting regional sources starting with right tuber (150-250 ms), followed by left cuneus (200-250ms) and left

precentral gyrus (200-250 ms). Right inferior frontal areas (250-300ms) and left FuG (250-300ms) were followed by left ventromedial frontal gyrus (sustained 350-500ms), cuneus (500-550, 900-950 ms), and medially located medial (400-450ms, 550-600 ms, 700-750ms) and superior frontal gyrus (500-550ms, 600-650ms). All of these structures showed consistent reactivations.

To date, the only study integrating fMRI and EEG has been published by Sabatinelli and co-workers (2007). They applied IAPS pictures though and constrained their analysis to the time window of the LPP and their accompanying inferior temporal, occipital and parietal generators.

In contrast to the study by Sabatinelli, the results of the present study have shown a wide network of interacting regional sources which is described in the following paragraphs.

The MNS revealed by source analysis in disgust and happiness

Medial and lateral prefrontal differences in dynamic face processing have been shown to be similar for happiness and disgust and therefore, will be discussed together. An exception to this was the increased source strength for left ventromedial frontal regions (only happiness) which will be discussed separately below.

Inferior frontal activations have been reported during emotional face judgment tasks (Streit et al., 1999), passive viewing and empathizing the emotional expression tasks (Batty and Taylor, 2003; Esslen et al., 2004). On the one hand, due to the development of the facial expressions over time in the presently used videos the transient reactivation of inferior prefrontal areas might be related to continuous updating, elaboration, and judgment of incoming emotionally salient information (Streit et al., 1999) and its transfer to working memory (Fuster, 2001; Schupp et al., 2004b), especially in higher order stages of processing. On the other hand, those regions could be related to the “mirror neuron system” (MNS) (for review, see Rizzolatti et al., 2001). Single cell recording studies with non-human primates reported activation in inferior frontal regions (F5) during both the execution (hence imitation) of the observed movement and the passive viewing of hand and mouth movement (for review, see Ferrari et al., 2003; Rizzolatti et al., 2001) which was associated with the “mirror neuron system” (MNS). The human homologue to F5 is the premotor area (PMA) spreading ventrally to the Broca area (BA44/45; Rizzolatti et al., 2002), furthermore encompassing the SMA and parietal regions. Various human fMRI studies have consistently reported ventral precentral, inferior frontal regions covering Broca’s area, and medial wall structures like the middle frontal and superior frontal areas including the supplementary motor area (SMA) during the following experimental designs:

- passive observation of mouth, arm, food (Buccino et al., 2001), and hand movement (Leslie et al., 2004)
- passive observation of human dynamic body expression of fear (Grezes et al., 2007),
- and passive observation of facial expressions of anger and happiness (Leslie et al., 2004), happiness (Hennenlotter et al., 2005), and happiness and fear (Sato et al., 2004).

Thus, inferior frontal cortex and the PMA activations of the present study could be related to the MNS and might reflect an internal reconstruction of the observed actions. They could "mirror" or simulate internal representations of the observed action without actually executing the observed action (Iacoboni et al., 1999; Rizzolatti et al., 2002). Consequently, the MNS might facilitate the understanding of observed action, or, as in the present study, the displayed emotional expression. It might also play a critical role in higher order cognitive processes such as empathy (Carr et al., 2003), and might be impaired in autism spectrum disorder (Oberman et al., 2005).

It is striking that the above cited studies have mainly applied fMRI to examine the MNS. There has been hardly any evidence from studies applying ERPs or source analysis until now. No results were found when searching for "ERP" and "mirror neuron system" in the online-database "pubmed" (www.pubmed.com, searching for [A] "source analysis" and "mirror neuron system" and [B] "EEG" and the "mirror neuron system" resulted in [A] one and [B] 21 found articles, respectively, on June 15 th, 2008). There is, however, a vast amount of EEG and MEG studies focusing on the suppression of alpha-like oscillations, e.g., mu-rhythms suppression (8 - 13 Hz) over central electrode sites. The suppression of the latter rhythms have been related to activations in motor and somatosensory cortices (Pineda, 2005) and have been shown to be diminished in humans with autism spectrum disorder compared to healthy individuals (Oberman et al., 2005). Reviewing the vast amount of literature studying mu suppression during action observation would be beyond the scope of the study though, but it is important to mention this line of research. Thus, until now, the relation of the MNS and emotion perception has not been directly studied by ERPs and source analysis the way the present thesis has.

ERP results yielded larger LPP over central electrodes (see Chapter 3.3.2 and 3.4.2.4), and evidence from fMRI studies have shown similar, hence related to the MNS, regions to be activated during emotion perception (Kilts et al., 2003; LaBar et al., 2003; Sato et al., 2004; see also fMRI study of the present thesis). In the present study, firstly, participants were asked to carefully watch and empathize the displayed facial expressions. Secondly, fMRI

constrained sources yielded enhanced source strength in typical MNS brain regions. Therefore, the author of the present work interprets the present results as followed:

- On the one hand, the present results yield an alternating, and transient elaboration of dynamic facial expressions which are possibly transferred to working memory reflected by PFC activation of the source analysis and increased LPP (see above).
- On the other hand, enhanced activation of lateral inferior frontal regions possibly reflect the mirroring of the displayed expressions for the dynamic modality due to continuous reactivations of those areas.

It is assumed that the present dynamic facial expressions possibly provided more complex temporal and three-dimensional information (Knight and Johnston, 1997), were probably easier to recognize, and might have appeared to be more realistic (Harwood et al., 1999) than static faces because actresses turned towards the viewer and then started developing the emotions. Consequently and practically automatically, it feels like one is forced to attend to the evolving emotional face, and one automatically starts mirroring the displayed expression. This is at least what the author of the present thesis has experienced many times during the presentation of those stimuli to, for example, students of her seminars.

3 major emotion-specific differences between happiness and disgust

There were three major differences during the perception of dynamic facial expressions of disgust and happiness.

Firstly, increased source strength in left cuneus could be shown exclusively for dynamic happiness in both early (200-250 ms) and later processing stages (reactivation after 500-550ms, 900-950ms) and for left fusiform gyrus (FuG, 250-300ms) and right tuber which is located closely to inferior temporal regions (150-200ms) as above reported for the fMRI study. For the processing of static emotional stimuli, it was suggested that increased arousal, as it was probably experienced by participants during the perception of positive videos and as reflected by increased arousal ratings (Chapter 3.3.1), might have enhanced selective attention (Lane et al., 1999; Lang et al., 1998) in extrastriate and inferior occipito-temporal areas for happiness. Since smiling faces might have been more rewarding and more attractive to watch (O'Doherty et al., 2003), they might have captured attention more strongly and activated occipital regions more consistently compared to disgusted faces. The latter showed an emotional modulation of the superior temporal gyrus (STG, 150-200ms), but not in other posterior visual processing area. The reactivation of especially the cuneus to up to 950 ms after first onset of the developing smile underlines the possibility, that stimulus features are continuously processed possibly via feedback projections of higher order visual regions to

enhance face perception.

Secondly, as suggested in the fMRI study of the present thesis (see Chapter 2.4.1), increased source strengths in ventromedial frontal gyrus was shown exclusively for happy facial expressions. These results are in line with a previous study by Esslen and colleagues (2004). They asked their participants to carefully watch facial expressions (disgust, happiness, fear, sadness, anger) and to empathize with the displayed expressions (no response recorded), a very similar experimental task to the one used in the present study. Esslen and co-workers (2004) calculated topographic analyses and LORETA source analysis in a time window between 70 and 500 ms. For happiness, they showed early right frontal pole source activity compared to neutral faces, bilateral ventromedial PFC (350 and 500 ms), inferior middle temporal gyrus (MTG), anterior STG, and right parietal activation between 244 and 290 ms, and between 361 and 467 ms, anterior cingulate cortex covering the PMA and a trend in right inferior frontal regions.

The results of the present study confirmed increased source strength in ventromedial frontal regions for dynamic happy faces during approximately the same time windows. While Esslen and colleagues (2004) have related orbitofrontal cortex (OFC) and ventromedial PFC (vmPFC) to general emotion processing, as suggested by Fuster (2001), the OFC and vmPFC have been related more specifically to pleasant stimuli associated with social reward processing (Gorno-Tempini et al., 2001; O'Doherty et al., 2003). Since this source was exclusively active during the perception of happiness in the present study, it is presumed that happy faces conveyed increased attractiveness compared to neutral faces. Therefore, they possibly represented a more salient social signal incorporating a tremendous stimulus-reward value which has been associated with the OFC (O'Doherty et al., 2003).

Thirdly, left superior temporal gyrus (STG) showed enhanced source strength exclusively for disgust between 150-200 ms after the first recognizable frame of disgust. Interestingly, STG was already activated more widespread and more consistently for dynamic disgust compared to dynamic happy compared to neutral expressions (see Chapter 2.4.1 and 2.4.3).

The involvement of the STS area in face processing has been highlighted in a recent EEG study (Itier and Taylor, 2004). Aside from sources located within the FuG during the time window of the N170 (Deffke et al., 2007; Rossion et al., 2003), findings from patients with implanted electrodes have been supported by a previous face perception study locating sources in the superior temporal gyrus (Allison et al., 1999).

With regards to emotional face perception studies, enhanced source strength in middle temporal gyrus during the perception of emotional versus neutral faces was reported

approximately 140-170 ms and 210-240 ms after stimulus onset in a recent MEG study (Streit et al., 1999). A previous EEG study applying LAURA algorithms revealed most prominent source strength within the time windows of the N170 and P1, lasting for approximately 300 ms, in superior and middle temporal gyri for disgust, happiness, sadness, anger, surprise, and fear (Batty and Taylor, 2003). These results were linked to early sensory processing stages of the N170.

Although the results of the present study are in line with previous findings, the author of the present thesis would like to remind the reader that sensory processes might have been completed by the time the data were averaged. This was the case because the video stimulation had begun way before the emotional expression developed, namely already when the actress looked to the left/right for one second, and then turned to the front. Not until then, the actresses started executing the actual emotional expression. The emotional expression evolved to the maximum over a time course of approximately 500 ms after averaging onset (see Chapter 2.2.3 for description of stimulus material and stimulus presentation). Therefore, despite similar time windows, early differences between emotional and neutral videos in the present study could not be related to sensory processes of the N170, as suggested by the above mentioned studies, but rather to later, higher order processing stages like e.g., the LPP. Thus, it is suggested that STG source strength is related to the continuous updating of the developing emotional expressions until the maximum characteristic of the target expression had developed yielding the processing of biological motion.

The STG has been generally named the STS area covering the middle temporal gyrus, STG, superior temporal sulcus, and angular gyrus (for review, see Allison et al., 2000). In previous human fMRI and EEG studies, the STS area has been shown to be engaged in the perception of social interactions, social face processing (for review, see Adolphs, 2002; Allison et al., 2000; Puce and Perrett, 2003), biological motion like body movement (Grezes et al., 2007), facial movement (Leslie et al., 2004; Puce et al., 2003; Sato et al., 2004), lip reading, and eye gaze (Pelphrey et al., 2003). It has been furthermore suggested to be associated with the processing of changeable features of, e.g., emotional dynamic faces (Kilts et al., 2003; LaBar et al., 2003; Sato et al., 2004). While facial structural and hence invariant features have been shown to be processed by inferior temporal gyrus and fusiform gyrus, the STS area has been related to changeable information regarding like e.g., eye gaze and facial expressions (Haxby et al., 2000; Hoffman and Haxby, 2000; Kanwisher et al., 1997). Previous monkey studies revealing projections from the amygdala to the STS area (Amaral et al., 2003) led scientists to believe that increased STS activation was related to reentrant feedback projections from the

amygdala to visual areas, i.e., also the STS area, especially during the perception of negative faces (Pessoa et al., 2002; Sato et al., 2004).

The present results support the hypothesis that STG might have received input by the amygdala for further, more elaborate processing of dynamic disgusted stimuli. STG was probably enhanced because of the dynamic features of the disgusted faces which again facilitated emotional face recognition and social perception (Allison et al., 2000).

In summary, the author of the present thesis did not find support for the hypothesis that these three major differences during the perception of dynamic happy and disgusted faces, or the presently discussed differences actually support evidence for emotion-specific networks. Activated neural networks were comparable between different emotions. As already mentioned in Chapter 2.4.5, the author of the present thesis assumes that all of the revealed areas might act in concert, but with different temporal on- and offsets, and oscillating interactions of those involved brain regions, and hence, are part of a complex neuronal network of emotion perception (Basar, 2006; Fuster, 2006). Thus, exclusively those differences between emotions might have become significant, which were highly consistent among individuals and over trials.

3.4.3.3 Summary and conclusions: source analysis

Introducing a new stimulus database, different networks were shown to be involved in static and dynamic emotional face perception. Static facial expressions of disgust and happiness showed an involvement of predominantly occipito-temporal regions. The processing of disgust resulted in insula activation at approximately 300 ms indicating the detection and deeper evaluation of disgust. Furthermore, inferior temporal and fusiform gyrus areas have been shown to be activated in early and later processing stages for both emotional valences. This was suggested to indicate a parallel processing of structure, identity and emotion in early stages, and more elaborate processing of displayed emotional expressions regarding structure in later processing stages. Dynamic stimuli resulted in an emotional modulation of both occipito-temporal and prefrontal regions. These results suggested (1) an elaborate structural analysis of the displayed dynamic faces including the analysis of biological motion on the one hand, and (2) the involvement of the mirror neuron system and reward system (only happiness) on the other hand.

Consequently, on a descriptive level, comparing both modalities, static and dynamic faces showed different dominance of participating brain regions. While the former predominantly showed inferior temporo-occipital activations, the latter showed a more widespread network

of participating brain regions in both inferior and temporo-occipital and lateral and medial prefrontal areas.

In conclusion, the data of the present EEG study support the above mentioned arguments by showing firstly a more consistent and more widespread emotional modulation of the LPP over centro-parietal electrode sites for dynamic faces, and secondly, a larger and more widespread network of involved regional sources in dynamic compared to static modality comparable to the more widespread and more consistent BOLD activation patterns of fMRI study (Chapter 2.2.6 and 2.4.3).

The following chapter addresses multiple aspects which could be potentially responsible for differently engaged networks for dynamic and static face perception in more detail.

3.4.4 Ecological validity of dynamic facial expressions

The question arises how processing differences between static and dynamic facial expressions could be explained. There might be various answers to this question. Functional aspects of the brain and physical characteristics and features of the stimuli might responsible. An alternative explanation could be methodological differences between EEG and fMRI which might cause differences in involved brain regions. The current chapter focuses on the first explanation, while the second argument will be discussed more thoroughly in Chapter 4.2.

In the present study, inferior temporal (including the FuG) and middle occipital sources have been shown to be recruited in very early (hence, sensory) and later higher order processing stages, reflected by enhanced N170 (predominantly over lateral occipito-temporal regions) and LPP (predominantly over lateral occipito-temporal and centro-parietal regions), respectively. This was also demonstrated by voltage topographies (Fig. 12), and by the transiently reactivation in both emotions in later processing stages in posterior regions (Table 6). Thus, static faces showed an early and a later recruitment of posterior brain region. Those regions have predominantly been related to the structural analysis of the face (Bentin et al., 1996; Kanwisher et al., 1997). Moreover, they have been shown to be modulated by emotion in both EEG studies (in sensory processing stages as reflected by the N170) (Blau et al., 2007; Sprengelmeyer and Jentzsch, 2006; Williams et al., 2006) and fMRI studies (Narumoto et al., 2001; Pessoa et al., 2002; Vuilleumier et al., 2001). The latter results could be confirmed already in Chapter 2.4.1 and could also be supported by the present ERP and source analysis results revealing the temporal time course.

For dynamic facial expression, similar regions were reported in inferior occipito-temporal, but also, and that was the major difference compared to static faces, in superior temporal regions,

which was related to biological motion processing (Allison et al., 2000), and prefrontal regions. The lateral PFC has been predominantly discussed in the context of updating information, allocation of attentional resources and transfer to working memory (Davidson and Irwin, 1999; Fuster, 2001; Schupp et al., 2004b) which would be in line with the requirement of continuously updating the watched dynamic and hence, changing facial expressions. Furthermore, ventromedial prefrontal areas have been linked to reward processing and social reward for especially positive faces (Gorno-Tempini et al., 2001; Kim et al., 2003; O'Doherty et al., 2003), and inferior prefrontal, and premotor and supplementary motor areas have been associated with the mirror neuron system (Leslie et al., 2004; Rizzolatti et al., 2001). Relating previous findings to the current source analysis results for dynamic faces, the latter aspects lead to the assumption, that dynamic stimuli might be mirrored more easily and might even evoke empathy with the perceived emotional expression. Hence, dynamic faces might have evoked a more elaborated concept of the stimuli and thus, made it easier for the viewer to actually "empathize".

As discussed in Chapter 2.4.3 and 2.4.4, the more widespread activation patterns revealed by fMRI for emotional dynamic faces were associated with higher ecological validity of dynamic faces in previous behavioral (Biele and Grabowska, 2006), fMRI (Kilts et al., 2003; LaBar et al., 2003; Sato et al., 2004) and agnostic, mentally retarded, and autistic patient studies (Gepner et al., 2001; Harwood et al., 1999; Humphreys et al., 1993). Summarized, better recognition accuracy was ascribed to dynamic facial expressions. This was because they have showed to be more complex by conveying structural, complex, rapid changing information of facial muscles which resulted in different mimics and which enhanced and enriched emotion perception (Biele and Grabowska, 2006) and recognition. Furthermore, dynamic facial expressions capture the liveliness and realistic form of changing facial expression (Harwood et al., 1999), and they are encountered every day in social situations which result in a large amount of experience with moving faces.

In contrast, static faces are encountered in different context in everyday life. Humans are usually not required to attend, and continuously update changing facial expressions, or actually mirror the static facial expression. Therefore, static faces might be perceived as less intense and less arousing, although behavioral data did not support this line of argumentation. Static faces are usually not part of conversations, movies, or social interactions which represent a large part of everyday life. They rather reflect a "snapshot" of a person's face that one might see for just a second when turning around on the street, or that is presented on private holiday pictures or on advertisement boards, and thus appear unrealistic.

Consequently, a structural analysis by the viewer of static facial expressions might suffice. Static faces, or "snapshots", are usually not part of social interactions and therefore, one does not have to actually focus attention towards, mirror and empathize with the perceived expression. But still, in case of a potential threat, structural analysis can be enhanced by feedback projections from subcortical areas like the amygdala (Amaral et al., 2003) as previously shown in fMRI studies applying static fearful faces (e.g., Breiter et al., 1996). So these posterior regions of the brain might be recruited in a first step to simply analyze the presented static expressions structurally. In contrast, the author of the present thesis hypothesizes that experience with moving faces is more prominent, which was shown by widespread neural networks in the present study, compared to static facial expressions because they represent a large part of everyday life. Furthermore, experience with facial expressions shapes and improves steadily from birth until it reaches adult level by adolescence and has recently been requested to be studied also with dynamic faces (Herba and Phillips, 2004).

However, does this imply that participants did not follow instructions? Not necessarily. Significant transient or sustained re-activations of posterior regions have been shown up to 750 ms and could be related to transient re-evaluation and recognition of emotional features. Yet, due to the possible less realistic and less ecological valid representation of static emotions, it might not have been as easy and as fast as during the perception of dynamic faces to actually mirror the seen expressions within the first second of picture presentation (see discussion in Chapter 2.4.3). Since static faces are still and do not show temporal changes which can be related to each other, it might be more difficult to actually categorize them and to empathize them. Therefore, the seeded prefrontal fMRI sources of static stimuli which had been apparent in the fMRI study might be associated with later processing. These sources could not be detected with EEG because only the first second after picture onset was analyzed. However, fMRI revealed prefrontal areas possibly due to the fact that fMRI integrates information over time (Im, 2007; see also Chapter 4.2). Another explanation could refer to different samples of participants examined in the two different studies.

In summary, differences during the perception of static and dynamic facial expressions were based predominantly on the different physical characteristics of static and dynamic stimuli. Furthermore, the author of the present thesis reported support for the assumption that static and dynamic faces are encountered in different social contexts ("snapshot" versus "social interaction") and consequently, were related to two different processing strategies of the brain at least within the presently analyzed time window. These results support the fMRI results

and corroborate the line of arguments that dynamic faces are more complex and more ecologically valid.

4 General discussion and integration of fMRI and EEG data

For the present design specifications and the present stimulus material, the above described two studies of the present thesis are a first approach of corroborating different activation patterns for different emotions (here happy and disgusted faces compared to neutral ones), and for static and dynamic modality of emotions. Furthermore, this thesis is an explorative approach of combining the advantages of two different methods to reveal the spatio-temporal information of fMRI based source localization which were extended by additionally fitted sources.

4.1 Limitations

4.1.1 Limitations of the combination of the two studies of the present thesis

There are two predominant limitations of the two studies: the sample of the second study was not the same as in the fMRI study and neither was the culture of the second sample (Chapter 2.2.1 and 3.2.1).

State of the art technique with regards to combining EEG and fMRI is to use the same sample of participants in both sessions in order to be able to coregistrate anatomical landmarks in fMRI and EEG source analysis approaches (Michel et al., 2004). One main limitation of this combined approach in the present thesis therefore, is the different sample of participants. In the future the latter aspect should be controlled by including the same sample of participants in a counterbalanced fMRI and EEG design. However, the current approach is still appropriate for a seeded source model because the study design for the above described fMRI study and the EEG study were exactly identical. Hopfinger, Khoe, and Song (Hopfinger et al., 2005) have accumulated a general framework including four major aspects for combining the two methods. They claimed that (1) the data should be based on an identical experimental frame including the timing, the instructions, response requirements and expectations of participants which the present study covered. The study also covered (2) the identical sensory frame including the same stimuli, and (3) the spatial reference using Talairach coordinates in both experiments. The only frame which was not covered was (4) the biological reference, i.e. identical sample of participants. However, comprising three out of four frames justified the present analysis approach.

As a consequence of the different samples the preciseness of anatomical localization of additional and fMRI constrained fitted sources could be improved in the future by recording

structural anatomy in addition to brain activity of participants during the emotion perception task and by coregistering the individual brain with the seeded source models. Therefore, in future studies the same set of participants should be studied.

While gender effects were controlled, one of the confounding factors was the different cultures (German and Spanish) of the two samples. However, as discussed in Chapter 3.4.1, basic emotional expressions have been shown to be universally recognized across cultures. Only differences in arousal ratings have been reported (Ekman et al., 1987). The question is whether ERP differences might be similar across cultures. This question cannot be answered by the present studies. The present results indicated enlarged LPP (Late Positive Potential) waves for emotional stimuli, which in turn showed higher arousal than neutral faces. The author of the present thesis speculates that these differences would have been even more differentiated and enhanced if the Spanish participants had watched emotional facial expressions from their own culture. Indeed, this needs to be explored in future studies.

Hot and co-workers (2006) addressed the problem of differing LPP to emotional pictures (IAPS) in participants from France compared to Japanese people. They have revealed similar behavioral arousal ratings and similar early ERP components. However, they reported attenuated LPP amplitudes during the perception of IAPS pictures for Japanese compared to French participants. They attributed this effect to a lower general emotionality of Japanese compared to French people. Besides, the author of the present thesis speculates that since IAPS scenes were developed in the United States they might more specifically target the emotionality of Caucasians instead of Asian populations. It remains to be explored how cultural differences of emotional face perception influence EEG amplitudes in German (Caucasian) and Spanish (Hispanic) people because folk concepts of both cultures differ in temperament. Besides, it would be interesting to examine whether lower arousal rates for culturally different emotional expressions (Ekman et al., 1987) - as discussed in Chapter 3.4.1 - could also be reflected on electrophysiological basis or whether the extent of the emotion effect would be stable inter-culturally.

Another methodological limitation of the chosen source analysis approach is the exclusion of subcortical brain regions (amygdala, parahippocampal gyrus, posterior cingulated gyrus; see also Chapter 3.2.5.3) which could be shown in the fMRI study (Chapter 2) to play an important role in emotional face processing. This aspect could be improved by continuously developing advanced methods to find a solution for the “illposedness” of EEG, i.e., the inverse problem, probably one of the most challenging problems in biosignal analysis.

4.1.2 Methodological considerations among studies per se

One of the major problems in the current vast amount of EEG, and also fMRI literature is that despite the heterogeneity of stimuli and task designs the results are compared to each other. The following paragraph lists a few parameters which differ among studies without the claim of completeness:

- A variety of different task instructions have been applied like, e.g., passive viewing (Sato et al., 2004; Williams et al., 2006), gender discrimination (Anderson et al., 2003; Sato et al., 2001), emotion discrimination (Lewis et al., 2003), and one-back tasks (Ashley et al., 2004). They all represent different cognitive demands. To study emotion perception it is suggested to chose a task which does not require the preparation of a cognitive-decisional motor response by button press (Balconi and Lucchiari, 2007; Esslen et al., 2004).
- One reason for not finding, e.g., insula activation during disgust processing could be the difference in presentation duration, as suggested in the second chapter of the present thesis. Many fMRI studies used presentation durations of 2.5 sec 3 sec or even longer (Gorno-Tempini et al., 2001; Phillips et al., 1998; Phillips et al., 1997; Sprengelmeyer et al., 1998; Williams et al., 2005) compared to 1.5 sec in the present studies. In EEG studies, the presentation time varied from 100 ms (Blau et al., 2007) to 6 seconds (Cuthbert et al., 2000).
- The chosen sample of participants often did not differentiate between males and females even though gender differences in emotion perception have been reported many times (for review, see Wager et al., 2003).
- In some studies the age range of participants was so tremendous that even the authors argued that the age range might be the reason for not finding, e.g., an emotional modulation of the P1 component. This was recently described by Ashley and colleagues (2004) studying participants aged 27 to 77 years.
- The sequence of stimulus presentation varied from block design (e.g., Phillips et al., 1997), to pseudo-randomized (e.g., Glascher et al., 2004), and randomized design (Balconi and Lucchiari, 2007; Batty and Taylor, 2003). The latter has been predominantly used in EEG studies.
- Other methodological differences included different analysis approaches (EOG correction, filtering before averaging, no filtering, etc.).

The mentioned arguments do not in general “forbid” the comparison of different designs per se. Interestingly, similar results can be obtained by different task designs in regard to neuronal

activation patterns (Kilts et al., 2003; Sato et al., 2004; e.g., PET and emotional judgment versus fMRI and passive viewing, respectively; both reported similar brain regions activated during the perception of dynamic emotional stimuli), ERP components (Eimer et al., 2003; Schupp et al., 2004b; both reported EPN and LPP during an emotional discrimination task and a passive viewing task, respectively), and generators as revealed by different source analysis approaches (Batty and Taylor, 2003; Streit et al., 1999; STG activation revealed by LAURA during an object detection task versus MFT analysis and facial recognition task, respectively). However, those aspects are supposed to shed light on the possibility that comparison of results from different task designs should be handled with care, but are possible. That is the reason why in the two present studies, the following aspects were controlled:

- Only female participants were examined to avoid gender differences.
- Identical stimuli, pseudo-randomized non-stationary probabilistic sequence, and presentation time for both modalities (dynamic and static) were applied with two different methods (fMRI and EEG) to enable the comparison between different methodological approaches.
- The sample of participants were matched according to a relatively homogenous age (age range: fMRI study: 19 - 27 years (21.6 ± 2.3 years), EEG study: 18 - 28 years, (21.37 ± 3.13 years), and educational background (fMRI: study 14 - 18 years (15.1 ± 1.5 years), EEG study: 11 - 20 years (mean 14.63, SD 2.31 years)).

In summary, future studies should be conceptualized in cooperation with different laboratories examining samples matched for age, gender, handedness and education, and using the same experimental design with a decent amount of participants, 100 percent identical parameters in, e.g., EEG and fMRI recordings and analysis strategies. The author of the present dissertation suggests that this might be the only way to externally validate different experimental designs and procedures.

4.2 Critical review of the integration of fMRI and EEG

A first integration of source model results and fMRI activation patterns was discussed in Chapter 3.4.3, and also in Chapter 3.4.4 with regards to the ecological validity of the stimulus material and the involvement of differential networks during the processing of static and dynamic facial expressions. In the following paragraphs, methodological aspects are discussed for the combination of fMRI and EEG.

In the present thesis, activation patterns as revealed by fMRI have been fed into a seeded regional source model which was complemented with additional sources. One might claim

that this was not an appropriate approach because either one chooses an fMRI constrained model or a free, sequentially fitted model. This approach has not been reported in emotional perception studies before. The reasons for choosing this approach will be discussed in the following paragraphs.

Theoretical implications for the combination of fMRI and EEG

The appropriateness of the current approach seems to be supported by the described significant changes in source strength in the static modality for especially posterior regional sources (RS). This indicates that the seeded fMRI source model itself did not fully explain the data during the perception of static faces and could be improved by additionally fitted RSs.
The reason why a multiple seeded source model based on fMRI and additionally fitted constraints was calculated is simple due to the following two reasons:

- Constraints improve the explanation of the model of the recorded data, especially when based on *a priori* knowledge (Hopfinger et al., 2005; Michel et al., 2004; Scherg and Berg, 1991). One of the shortcoming of equivalent current dipole analysis is that experimenter needs to decide subjectively on the number and orientation of dipoles fitted to the model. Choosing the wrong number of sources can increase the probability of an incorrect solution (Luck, 2005b). By seeding sources based on prior knowledge the source analysis becomes more objective (Bledowski et al., 2006).
- Several authors have addressed the need that source models can even be improved by additionally fitted sources because of possible mismatches between fMRI and EEG with regards to underlying activation patterns (see, e.g., Im, 2007; and Michel et al., 2004).

The following paragraph embraces those explanations in more detail and integrates theoretical aspects with the reported data of the fMRI and EEG study.
Importantly, the reason for differences of localizations of activation patterns in fMRI and generators in EEG might be related to the aspect that fMRI and EEG are two methodological approaches to measure brain activity which are based on different principles. FMRI is based on blood flow changes coupled to brain activity, to the so-called hemodynamic response which is a rather indirect and temporally delayed measure of brain activity (Hopfinger et al., 2005; Huettel et al., 2004; see also Chapter 1.6.1). EEG is related to electrophysiological processes which are directly coupled to postsynaptic activity of neuronal assemblies and which are only attenuated by the different conductivities of the skull (Hopfinger et al., 2005; Im, 2007; Michel et al., 2004; see also Chapter 1.6.2). Besides, fMRI possesses a high spatial (in millimeter), but low temporal resolution whereas EEG has a low spatial, but high temporal

resolution (in milliseconds). Therefore, it is possible to find mismatching generators in EEG and fMRI.

Furthermore, it is important to mention that the correlation between hemodynamic response and electrophysiological measures is still far from being completely understood. Therefore, the two methods and the underlying generators they reveal cannot be considered to be completely identical (Arthurs, 2002). Recent studies have examined the correlation of different ERP components and BOLD response in different brain regions reporting controversial results. On the one hand, simple sensory processes, assessed by visual stimulation applying checkerboard stimuli resulting in visual evoked potentials (VEP; Singh et al., 2003) or by median nerve electrical stimulation resulting in somatosensory evoked potentials (SEP; Arthurs et al., 2000), have revealed a linear correlation of BOLD and electrophysiological signals. In contrast, in a more complex cognitive task, Foucher and colleagues (2003) acquired interleaved fMRI and EEG data applying an oddball paradigm in order to examine the P3 for targets and rare distractors. They found an increased P3 for rare distractors, but the opposite effect in fMRI yielding increased activation for targets in fMRI (Foucher et al., 2003), which indicated a low correlation between ERPs and fMRI activation patterns. In addition, Foucher and co-workers (2003) correlated oscillatory brain activity parameters with fMRI contrasts. The latter correlation was reported to be acceptable. Therefore, the authors questioned the linear correlation between fMRI and electophysiological approaches and suggested further exploration in the future.

However, previous pioneering work by Logothetis and co-workers (2001) have revealed a strong correlation between fMRI BOLD responses and simultaneously recorded local field potential measures which are known to reflect the synchronized input of neural assemblies. For that reason, the correlation between EEG and fMRI was presumed in the present thesis, but possible mismatches needed to be and have been taken into account. Emotion perception of static and dynamic stimuli is a rather complex task that is why possible mismatches in EEG and fMRI were considered.

Im (2007) has critically discussed three different kinds of mismatches between fMRI and EEG recently, which were regarded in the present study context.

1. FMRI might reveal additional sources which are invisible to EEG due to the depth of the generators or generators which represent closed field activations (see also Chapter 3.4.2.2).
2. Some sources are invisible to fMRI due to the transient and very fast processes in certain brain region. Hence, fMRI cannot detect those generators because it rather

integrates brain activation over time.

3. Since EEG and fMRI are based on electrophysiological and hemodynamic changes respectively, “discrepant” sources in EEG and fMRI were expected in the studies of the present thesis.

Therefore, possible differences between EEG and fMRI have been taken into account, and additional sources were added to the constrained source model to complement the model by sources which were not reliably detected by fMRI in the first study (Chapter 2).

Activation patterns revealed by fMRI, but not by EEG

Considering the first aspect reported by Im (2007), fMRI is able to detect regions in ‘closed field’ areas like, e.g., the amygdala or other regions, which are located deep within the brain (Michel et al., 2004).

As described in fMRI study of the present thesis (Chapter 2.3.2), subcortical activations have been reported in the amygdala, the parahippocampal gyrus, and the posterior cingulated gyrus. Their functional association is described in detail in Chapter 2.4.1. They were excluded from the analysis because deep brain regions produce either small signals in EEG or sum up in a way that source waveform activity results in invalidly high amplitudes of source waveforms compared to more superficial RS (see Chapter 3.2.5.3). This highlights the benefit of applying fMRI because it is insensitive to the depths of sources in contrast to EEG. However, one shortcoming is that the time course of emotion perception in those deeply located brain areas can only be assumed (see Chapter 3.4.2.2, discussion of emotional modulation of the N170) or can be discussed in studies examining patients with intracranial electrodes (e.g., Krolak-Salmon et al., 2003; Krolak-Salmon et al., 2004). The problem is, though, that the use of intracranial electrodes is exclusively ethically justified in clinical patients with, for example, epilepsy. Besides, the spatial resolution is mostly restricted to lesioned brain tissue, again limiting the transfer of results from the clinical to the healthy population. Furthermore, a high density array of electrodes would be necessary to be able to reach a relatively fair spatial resolution which would in turn pose the problem of crosstalk among electrodes. All in all, further research is necessary to solve this problem, at least for ECD (Equivalent Current Dipole) approaches.

Further sources of brain activation detected by fMRI, but not by EEG in the present studies, refer to prefrontal sources during the perception of static faces. Even though these sources were seeded in the model of the static modality, they did not yield any significant differences between emotional and neutral facial expressions within the modeled time window (1000 ms after stimulus onset). One possible explanation for this could be that - within the modeled

time window - mainly structural features of the displayed stimuli were processed. This was suggested to be the reason for not finding regions which were associated with the MNS (Mirror Neuron System) and prefrontal areas because static faces usually do not appear in social interaction context (see also Chapter 3.4.4) and might therefore be more difficult to empathize and mirror. However, since participants were asked to empathize with the displayed expressions, they might have cognitively and consciously recruited those brain regions in later processing stages which could not be detected in the current EEG analysis because the time window was limited to 1000 ms after stimulus onset. This explanation might be appropriate considering the notion that fMRI integrates information over time (Im, 2007).

Generators found by EEG, but not by fMRI

Especially the second argument suggested by Im (2007), which highlights the invisibility of very fast and transient sources in fMRI, justified the extension of the fMRI constrained source models. Besides, it has been claimed in previous works to improve the validity of source models (Im, 2007). This procedure was critically important for the static modality due to the limited activations found in the fMRI study (for discussion, see Chapter 2.4.4) because it tremendously decreased the residual variance of the source model. Adding further sources to the constrained model is, therefore, a very fruitful and appropriate approach. In case of the present studies, even though additionally fitted sources for static faces were close to the ones revealed by dynamic emotional face perception in fMRI (<30 mm), anatomically different regions have been revealed by the sequential fit for static faces (insula), and for dynamic faces (right medial frontal gyrus, see Chapter 3.3.3).

The insula was not evident in the fMRI study (see Chapter 2.4.2 for discussion). Since an increase in source strength in the INS was exclusively evident for a short epoch (300 - 350 ms) one of the reasons why it might have been “invisible” to fMRI, could be the very fast processing within this area (Im, 2007). The author assumes that in this case, insula is quickly activated for a fast the detection and evaluation (categorization) of disgust, but not for actually feeling disgust per se (see Chapter 3.4.3.1). This would also be in line with the lack of BOLD signal in the fMRI study in that area because detection and structural analysis is a rather fast than sustained and prolonged process (Im, 2007). This aspect would also agree with the explanations provided in Chapter 2.4.2 arguing that the actual feeling of disgust might take longer taken into account the delayed autonomic response in disgust compared to fear (Williams et al., 2005). For future investigations, the relations between emotion perception of disgust in EEG and autonomic responses like, e.g., the skin conductance response and heart rate should be examining more closely. Furthermore, for posterior regions for static faces and

for right medial frontal regions for dynamic faces, a similar line of argumentation might be convenient because those sources all showed rather rapid and transient instead of sustained changes. Besides, inferior frontal areas ascribed to the MNS were not activated for the perception of happy faces in the dynamic modality in the above described fMRI study, but in the EEG study (see Chapter 3.3.3.2 and 3.4.3). Again, just like suggested for the insula above, one interpretation approach might be related to previous findings which suggested that positive expressions are processed and recognized faster (Leppanen and Hietanen, 2004) so that fMRI was not able to detect this kind of transient activation (Im, 2007). Thus, EEG is apparently more sensitive to early, fast, and transiently activated regions reflected by significant 50 ms epochs in the present EEG study before differences in adjacent areas became significant.

In conclusion, the present studies showed that mismatches existed between fMRI activation patterns and EEG generators. Adding additional sources to the model improved the solution of the source models especially for the perception of static emotional faces. This approach seems to be an appropriate and mutually complementing approach for the combination of the two methods. Because of their explorative nature, the author of the present thesis suggests that the present results should be replicated in the future and that they might represent a first approach to demonstrate temporo-spatial information of static and dynamic emotional face processing.

4.3 Integration of the results of the present thesis with the emotional face perception model from Adolphs (2002)

Haxby and colleagues have claimed that their modified model of face perception should be extended by the temporal dimension (Haxby et al., 2000; see Fig. 1 for reprinted version). Many EEG studies met their demands and examined the temporal specifics of emotion perception in static facial expressions. In an extensive review by Adolphs (2002), the model by Haxby and colleagues was modified and extended by the temporal information to extend the understanding of temporo-spatial dynamics of emotion perception (see also Fig. 2).

Summarizing, the present fMRI data obtained during the processing of dynamic facial expressions and the EEG data of both static and dynamic stimuli corroborates Adolphs' (2002) model with a few exceptions, like thalamus, brain stem regions, and hypothalamus. The latter regions have been predominantly been ascribed to the fast early perceptual processing within the first 120 to 300 ms. As argued in Chapter 4.2, due to the fast and transient activation of those regions, they might have been involved in emotional face

processing, but fMRI could not detect neural activation there (Im, 2007). Besides, those regions lied too deep to be revealed during the sequential fitting procedure of the EEG data.
The fMRI study (Chapter 2) has revealed a wide network of brain regions involved in emotion perception, for example, the amygdala, the striate and extrastriate areas, the FFA, the STS area, the OFC, and SMA and PMA. These brain regions were mainly in line with the brain regions suggested by the emotion perception model by Adolphs (2002). The EEG study (Chapter 3) reported in the present thesis complemented the spatial information of the fMRI study by adding the temporal dimension. Thus spatio-temporal information might be integrated in the emotion perception model suggested by Adolphs (2002) as follows:

- P1 was reported for general fast sensory perceptual processing and N170 for structural encoding of face specific features enhanced by emotional content. Both components reflect the "core system" and were furthermore supported by increased source strength in inferior temporal regions for static happy and disgusted faces and middle occipital regions in happy faces. Results of the fMRI study yielded activations in similar regions, but only for dynamic faces. Furthermore, subcortical regions like the amygdala might be involved. The temporal dimension could only be assumed, but not directly shown by ERP and source analysis because of the amygdala's "closed field" location within the brain. Since N170 was enhanced for both emotional valences, it might be assumed that the amygdala plays a general role in the processing of salient stimuli as suggested by Winston and colleagues (2003) across various early stages of perception. Amygdala might be rather transiently activated for salient stimuli per se. Furthermore, the amygdala might be activated again at various later processing stages to more elaborately tag and process predominantly threatening stimuli (Adolphs, 2002) because negative stimuli pose an evolutionary significant potential threat (Ohman and Mineka, 2001; Phan et al., 2002). This could explain why the amygdala might not have been detected in fMRI for positively valenced faces (Im, 2007).
- Processes of the "extended system" and the "recognition modules" follow those early encoding processes and were reflected by early posterior negativity (EPN) in the present thesis (static faces) at occipito-temporal electrode sites. This was predominantly the case for static faces of disgust between 250 and 350 ms. EPN was related to a more detailed perception of the displayed negative emotion. Presumably, this component was enhanced by reentrant amygdala feedback projections because a previous study examining patients with intracranial electrodes in the amygdala has reported the involvement of the amygdala in fearful face perception after around 200

ms (Krolak-Salmon et al., 2004). Furthermore, the model suggests that somatic and automatic responses to the stimuli are evoked. However, it was not aim of the present study to reveal intercorrelations between emotion perception and somatic changes, as measured by SCR (skin conductance response) or changes in heart rate (Williams et al., 2005).

- From 300 ms on, various further cognitive processes occur according to Adolphs (2002). These include the actual recognition of the emotional valence, the continuous evaluation of the stimuli and the link to previous memories and conceptual knowledge of the displayed emotion. ERP results showed increased LPP amplitudes over centro-parietal electrodes, which were probably correlated with continuous activation of regional sources in more posterior regions. In addition, significantly stronger source strength for disgust was associated with the insula. The author of the present thesis assumed that these activations were related to continuous elaboration and structural processing for static stimuli. It is important to mention that the time course for dynamic face processing could not be compartmentalized into early sensory and later stages, like more detailed perceptual recognition and conceptualizing stages, because emotional facial expressions were preceded by a turn before developing the actual emotion. Hence, the present results reported for dynamic stimuli can solely support the later stage of Adolphs' model (2002) by showing enhanced LPP over centro-parietal electrodes. This might be related to transient and partly sustained activations of lateral inferior occipito-temporal regions, the STS area, and lateral inferior frontal and medial superior and middle frontal regions (PMA, SMA) possibly reflecting elaborate evaluation, recognition of structural features, biological motion, memory encoding, and mirror neuron system processes.

Cerebellar activation was not considered in Adolphs' model even though cerebellum has been repeatedly reported and was usually neglected in the interpretation of emotion perception studies (Turner et al., 2007). Adolphs (2002) addressed the problem of the lack of the cerebellum (and brain nuclei) as part of the emotion perception model, but did not give any suggestions of interpretative approaches of this kind of activity. The present fMRI and EEG study support the assumption that the cerebellum plays a role in subjective experience of positive emotions as previously reported by Turner and co-workers (2007) within the "cognitive module" of Adolphs' (2002) model. Future research of the role of the cerebellum as part of the emotional network during emotion perception could help to elucidate further evidence for that assumption.

In summary, the results of the two present studies mutually complemented each other on the temporal and spatial dimension and supported the suggested model by Adolphs (2002) for the most part.

4.4 Networks in dynamic and static emotional face perception

Summarizing EEG and fMRI results reported in the present thesis, activated neuronal networks of emotion processing yielded similar networks for both emotional static and dynamic faces, but with different temporal dynamics. This was specifically evident when applying the fMRI constrained source analysis approach because only few locations of regional sources (RS) differed between emotional conditions. The question is: is emotion perception functional-neuroanatomically organized in a modular fashion or rather in distributed cortical networks simply varying with regard to temporal dynamics?

Recently, the topic of "modern phrenology" and modularity of brain functions has been addressed by several authors (Basar, 2006; Esslen et al., 2004; Fuster, 2006). Esslen et al. (2004), e.g., addressed the aspect that emotion-specific processing networks would not exist. Emotion processing is engaged in various cognitive functions, like memory, attention, association, perception, and processing of internal states or external stimuli. There is rather a network of brain regions interacting with varying dynamics (Esslen et al., 2004). This approach was also discussed and enhanced by Fuster (2006) who argued that the modular way of making single brain regions responsible for higher order cognitive functions has become "old fashioned". He hypothesized that cognitive functions are represented in distributed, interactive, and overlapping networks of neurons which are engaged in, e.g., perception, memory, and attention. Those networks represent the so-called cognits (networks representing different stages of cognitive processing) which form the basis of perception-action-cycles. Cognits can be divided in:

(1) Perceptual cognits represented by neurons in posterior primary and secondary association cortices, which process sensory, lower-level information and which are engaged in automatic and well-learned behavior.

(2) Executive cognits represented by neurons in heteromodal prefrontal, parietal, and temporal cortices, which are engaged in integrating sensory input with at a higher conceptual level and in, e.g., planning of action or of behavior.

Cognits are hypothesized to be hierarchically organized (from (1) to (2) with increasing complexity). They range from low-level cognits which were suggested to be engaged in simple sensory perception or primary, well-learned motor acts to more widespread, and

higher-level cognits. The latter process and integrate more complex perceptual and executive features in secondary parieto-temporal and in prefrontal cortex, respectively. Thus, cognits are supposed to profit of their mutual interconnections by various anatomical feedforward and feedback connections between the perceptual and executive cognits (Fuster, 2006). For example, environmental input might be processed in an early step by perceptual cognits which might result in the generation of motor actions at higher level cognits, and which in turn can change the primary sensory input. This perception-action cycle indicates mutual activation dynamics of sensory and executive cognits to understand the environment and plan behavior. Depending on the complexity of the perceived input, either smaller, lower-level cognits or higher order, secondary cognits are engaged. For example, novel situations or complex stimuli might engage hierarchically higher order cognits. The latter notion actually supports the results of the previous studies: static faces recruited rather posterior brain regions for predominantly structural analysis of the stimuli because they are usually encountered in "snapshot" situations instead of complex social interaction situations. Dynamic emotional faces engaged a more widespread network of posterior and anterior brain regions because they were suggested to be faced in a more complex environment. Furthermore, the importance of dynamic stimuli in social interactions and the engagement of the mirror neuron system might explain the recruitment of more complex cognits and the so-called perception-action cycle (Fuster, 2006).

In conclusion, the author of the present dissertation assumes that there might be a common network for the processing of different emotional valences. A similar network of brain regions, which were activated with varying dynamics, could be confirmed in the present thesis with varying timing and localization of revealed brain regions during emotion processing.

5 Conclusions and outlook

The present thesis is a first step to systematically study the perception of dynamic and static facial expressions of happiness and disgust by combining fMRI, EEG, and an fMRI constrained source analysis, hence taking advantage of the high spatial resolution of fMRI and the excellent temporal solution of EEG.

The goals were to discover the spatio-temporal characteristics of the perception of static and dynamic faces of happiness and disgust which were studied with a newly developed stimulus database.

The present fMRI study revealed more widespread and consistent networks for dynamic face perception in posterior regions, like striate, extrastriate, and STS regions, inferior frontal regions, SMA, ventromedial and orbitofrontal, posterior cingulate, parahippocampal regions, and in the amygdala.

Furthermore, emotionally modulated time course of different involved brain regions in emotion processing has been described by classical ERP components like the N170 (structural face and emotion processing), EPN (tagging of negative stimuli) and LPP (elaborate evaluation of emotional facial expressions). FMRI constrained source analysis has been shown to be highly sensitive for the processing of static faces. It revealed additionally fitted sources for static faces in posterior regions proposing the possible dominance for structural analysis of the face at least within the first second of stimulus onset.

Dynamic faces showed a network of occipito-temporal, superior temporal (predominantly disgust), lateral inferior prefrontal, medial prefrontal (SMA), and ventromedial frontal regions (only happiness). Thus, this more widespread network could be determined with both methods (EEG and fMRI) and was suggested - among others - to be associated with structural analysis of facial invariant features, with changing aspects of the face, with the MNS, and the reward system. Dynamic faces were therefore discussed to be more realistic because they seem to be more common in social interactions and convey more complex and more detailed information which again facilitates the recognition of emotional valences.

Furthermore, possible mismatches between analysis of EEG and fMRI data were addressed and critically discussed.

The present thesis showed that another step has been taken to reveal the extensive profundities of the brain during the perception of static and dynamic facial expressions of disgust and happiness.

In conclusion, the author of the present thesis addresses that the research of emotion

perception is “in motion”. Applying dynamic facial expression in neuroscientific research yields a promising and ecologically more valid approach than static faces because humans are experts for the processing of authentic moving faces in social interactions. This is one of the main reasons why it is suggested to examine face and emotion processing considering authentic dynamic stimuli in order to more appropriately quantify and qualify normal and impaired brain physiological processing (Gepner et al., 2001; Harwood et al., 1999; Humphreys et al., 1993).

For future investigations, it would be of interest to examine (1) the spatio-temporal dynamics of the processing of further basic emotions (e.g., anger, fear, surprise) of the present stimulus database, (2) gender differences, and (3) the neurodevelopmental perspective of emotion processing in children and adolescents applying dynamic facial expressions. Besides it would be interesting to study emotional processing (1) by investigating additional perceptual facets of emotional processing like, e.g., prosody, language, and social interaction situations, and (2) by including further methodological approaches like, e.g., analysis of oscillations or wavelets. Last, but not least, there is a need of replicating the results of the present thesis by applying identical experimental designs, and matched samples of participants for a combined EEG and fMRI approach in order to study both spatial and temporal correlates of dynamic and static emotional face perception.

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7 Appendix

(A.1) Information form of fMRI study

Informationsblatt für Probanden

Sehr geehrte Probandin, sehr geehrter Proband, vielen Dank für Ihr Interesse an einer Studie, bei der die Aktivität im Gehirn während Bewegungen der Hand und dem Lösen von Aufgaben untersucht werden soll. Wir möchten Sie zunächst über den Ablauf informieren, um Ihnen einen Überblick über die geplanten Messungen zu ermöglichen und Ihnen das Ziel der Untersuchung zu erklären. Die Untersuchungen werden mit einem Magnetresonanztomographen (kurz MRT) durchgeführt, der uns Messungen der Durchblutung im Gehirn schmerzfrei und ohne zusätzliche Gabe von Medikamenten ermöglicht. Einige Personen werden die Untersuchung schon einmal erlebt haben, wenn hochauflösende Bilder vom Kopf im Rahmen der Diagnostik durchgeführt wurden.

Ziele der Untersuchungen

Die Studie soll die Aktivität im Gehirn bei geplanten Bewegungen einzelner Körperteile (z.B. Handbewegungen) und bei dem Lösen von Aufgaben (z.B. wieviel ist 3 mal 6) bestimmen. Die Ergebnisse könnten uns Aufschlüsse über die Zusammenhänge im Gehirn erlauben und damit in der Zukunft eine bessere Einschätzung der Patienten ermöglichen. Alle bisher zur Therapie eingesetzten Verfahren sind im Rahmen von Studien entwickelt worden; die geplante Studie hat das Ziel, diese Möglichkeiten *in der Zukunft* noch weiter zu verbessern.

Was ist eine Magnetresonanztomographie?

Im Rahmen der Studie ist eine funktionelle Magnetresonanztomographie des Gehirns vorgesehen. Mit Hilfe dieser Methode ist es möglich, die Durchblutung in Ihrem Gehirn zu messen und daraus Rückschlüsse auf die bei der Aufgabe beteiligten Bereiche zu ziehen. Hierbei treffen Radiowellen, die in dem Magnetfeld erzeugt worden sind, auf den Körper, der Signale zurückschickt. Diese Echosignale werden von speziellen Antennen aufgefangen und in einem Computer ausgewertet. Ein Kontrastmittel ist nicht erforderlich. Es werden keine Röntgenstrahlen eingesetzt.

Wie läuft die Untersuchung ab?

Vor der Untersuchung werden Sie vom Untersuchungsleiter ausführlich über die für den Tag geplanten Messungen und Ziele informiert. Sie haben das Recht, ohne Angabe von Gründen die Teilnahme an der Messung abzulehnen. Auch im Verlauf der Untersuchung werden Sie vom Untersucher jederzeit gehört. Für die Untersuchung müssen Sie sich auf eine Liege legen. Im Messbereich wird eine Kopfspule angebracht. Mit der Liege werden Sie dann langsam in die Röhre des Kernspintomographen geschoben. Dort befinden Sie sich während der gesamten Untersuchung, die normalerweise 60 min dauert, in einem starken Magnetfeld, das für die Untersuchung benötigt wird. Während der eigentlichen Messung sind sehr laute Klopfgeräusche zu hören, die völlig normal sind und von elektromagnetischen Schaltungen herrühren. Das Magnetfeld selbst können Sie weder spüren noch hören. Es ist von großer Bedeutung für die Qualität der Messungen, daß Sie während der Untersuchung möglichst ruhig liegen bleiben. Um dies zu erleichtern, werden Ihr Kopf und Arme mit Polstern und anderen Hilfsmitteln schmerzfrei gelagert. Die Aufgaben, die Sie während der Untersuchung zu bearbeiten haben, werden Ihnen über einen an der Kopfspule angebrachten Spiegel dargeboten.

1

(A.1) Information form of fMRI study (*continued)*

Mögliche Risiken der Methode?

Der Kernspintomograph hält alle für die Sicherheit des Betriebes und insbesondere die Sicherheit der Probanden/Patienten erforderlichen Grenzwerte ein. Er wurde vom TÜV einer Sicherheitsprüfung unterzogen und wird darüber hinaus in den vorgeschriebenen Intervallen überprüft. Dennoch müssen folgende Punkte beachtet werden.

1. Auf Ferromagnetische Gegenstände (z.B. Gegenstände, die Eisen oder Nickel enthalten) im Bereich des Magneten (z.B. Messer, Schraubenzieher, Kugelschreiber, Münzen, Haarspangen, ..) wird eine starke Anziehungskraft ausgeübt. Dadurch werden die Gegenstände mit großer Geschwindigkeit in den Magneten gezogen und können Personen erheblich verletzten.

2. Metallkörper und andere Fremdkörper wie Geschoßteile können ebenfalls Ferromagnetisch sein, durch magnetische Kräfte ihre Position im Körper verändern und dadurch innere Verletzungen hervorrufen.

3. Kleine Metallsplitter im Auge können durch magnetische Kräfte bewegt oder gedreht werden und das Auge verletzen.

4. Personen mit Chochlea-Implantaten, Defibrillatoren oder Pumpensystemen sollten nicht einem starken Magnetfeld ausgesetzt werden, da es auch in diesen Fällen zu Risiken durch magnetische Kräfte kommen kann.

5. Herzschrittmacher können im Magnetfeld ihre Funktionsfähigkeit verlieren. Deshalb dürfen Personen mit Herzschrittmachern nicht an Untersuchungen teilnehmen.

6. Bei der Messung mit dem Kernspintomographen kommt es zur Abstrahlung von hochfrequenter elektromagnetischer Strahlung, wie sie z.B. bei Radiosendern und Funktelefonen auftritt. Dies kann zu einer geringfügigen Erwärmung des untersuchten Gewebes führen.

7. Das Schalten der Magnetfeldgradienten führt in Teilen des Gradientensystems zu mechanischen Verformungen, die Geräusche mit Lautstärken über 100 dB erzeugen können. Deshalb müssen Sie bei allen Messungen entweder Schallabsorbierende Kopfhörer oder Lärmschutzstopfen tragen, die von uns zur Verfügung gestellt werden. Bei Einhaltung dieser Vorsichtsmaßnahmen kann eine Schädigung des Hörsystems ausgeschlossen werden.

8. Manche Menschen erleben enge Räume als bedrohlich. Sie berichten über Unwohlsein z.B. in Fahrstühlen oder in großen Menschenansammlungen. Obwohl diese Angsterkrankung meist über die Anamnese ausgeschlossen werden kann, ist ein erstmaliges Auftreten während der Messung im Kernspintomographen möglich. Der Untersucher ist bei der Messung anwesend; bei dem Auftreten von Symptomen kann der Proband über Sprechkontakt bzw. über eine Notklingel jederzeit auf sich aufmerksam machen, so das eine rasche Intervention bei Symptomen gewährleistet ist.

(A.2) Consentment form of fMRI study

Einwilligungserklärung

Über die geplante kernspintomographische Untersuchung im Rahmen einer wissenschaftlichen Studie hat mich Frau/Herr Dr._____ in einem Aufklärungsgespräch ausführlich informiert.

Auch habe ich das entsprechende Informationsblatt gelesen und den Fragebogen zu möglichen
Ausschlusskriterien ausgefüllt. Ich konnte alle mir wichtig erscheinenden Fragen, z.B. über die in meinem Fall speziellen Risiken und möglichen Komplikationen und über die Neben- und
Folgemaßnahmen stellen, die zur Vorbereitung oder während der Untersuchung erforderlich sind.

Die mir erteilten Informationen habe ich inhaltlich verstanden. Mir ist bekannt, dass ich meine Einwilligung jederzeit ohne Angaben von Gründen widerrufen kann.

Ich weiß, dass die bei Untersuchungen mit mir gewonnen Daten auf der Basis elektronischer
Datenverarbeitung weiterverarbeitet und eventuell für wissenschaftliche Veröffentlichungen verwendet werden sollen. Ich bin mit der anonymisierten Verarbeitung und Veröffentlichung dieser Daten einverstanden. Auch diese Einwilligung kann ich jederzeit ohne Angabe von Gründen widerrufen.

Ich gebe hiermit meine Einwilligung, dass bei mir im Rahmen eines Forschungsvorhabens eine
Kernspintomographie des Gehirns durchgeführt wird.

_____	_____	_____
Ort, Datum	Unterschrift /Patient/Proband	Unterschrift Untersucher

(A.3) Questionaire of fMRI study

Fragebogen für Teilnehmer/innen an Kernspinresonanzuntersuchungen am Center for Advanced Imaging (CAI – Bremen)

Name:.....
Vorname:.....
Geburtsdatum:..... Geschlecht:.....
Straße/Hausnummer:.....
Wohnort:.....
Telefon:.....
Beruf:.....

Beantworten Sie bitte folgende Fragen zu möglichen Gegenanzeigen für Ihre Teilnahme an den Untersuchungen (Zutreffendes unterstreichen):

Sind Sie Träger eines Herzschrittmachers oder anderer elektrischer Geräte?	Ja	weißnicht	nein
Besitzen Sie metallische Implantate (z.B. Zahnschrauben oder metallische, mechanische Verhütungsmittel)?	ja	weiß nicht	nein
Befinden sich in Ihrem Körper andere metallische Fremdkörper?	ja	weiß nicht	nein
Wurde bei Ihnen eine Gefäßoperation durchgeführt?	ja	weiß nicht	nein
Haben Sie eine Allergie gegen Medikamente	ja	weiß nicht	nein
Haben Sie Tätowierungen oder Piercings oberhalb Ihres Bauchnabels?	ja	weiß nicht	nein
Leiden Sie unter Platzangst?	ja	weiß nicht	nein
Sind bei Ihnen oder in Ihrer Familie Anfallsleiden (Epilepsie, Fallsucht) aufgetreten?	ja	weiß nicht	nein
Besteht die Möglichkeit, dass Sie schwanger sind?	ja	weiß nicht	nein

Beantworten Sie bitte folgende für unsere Untersuchungen wichtigen Fragen:

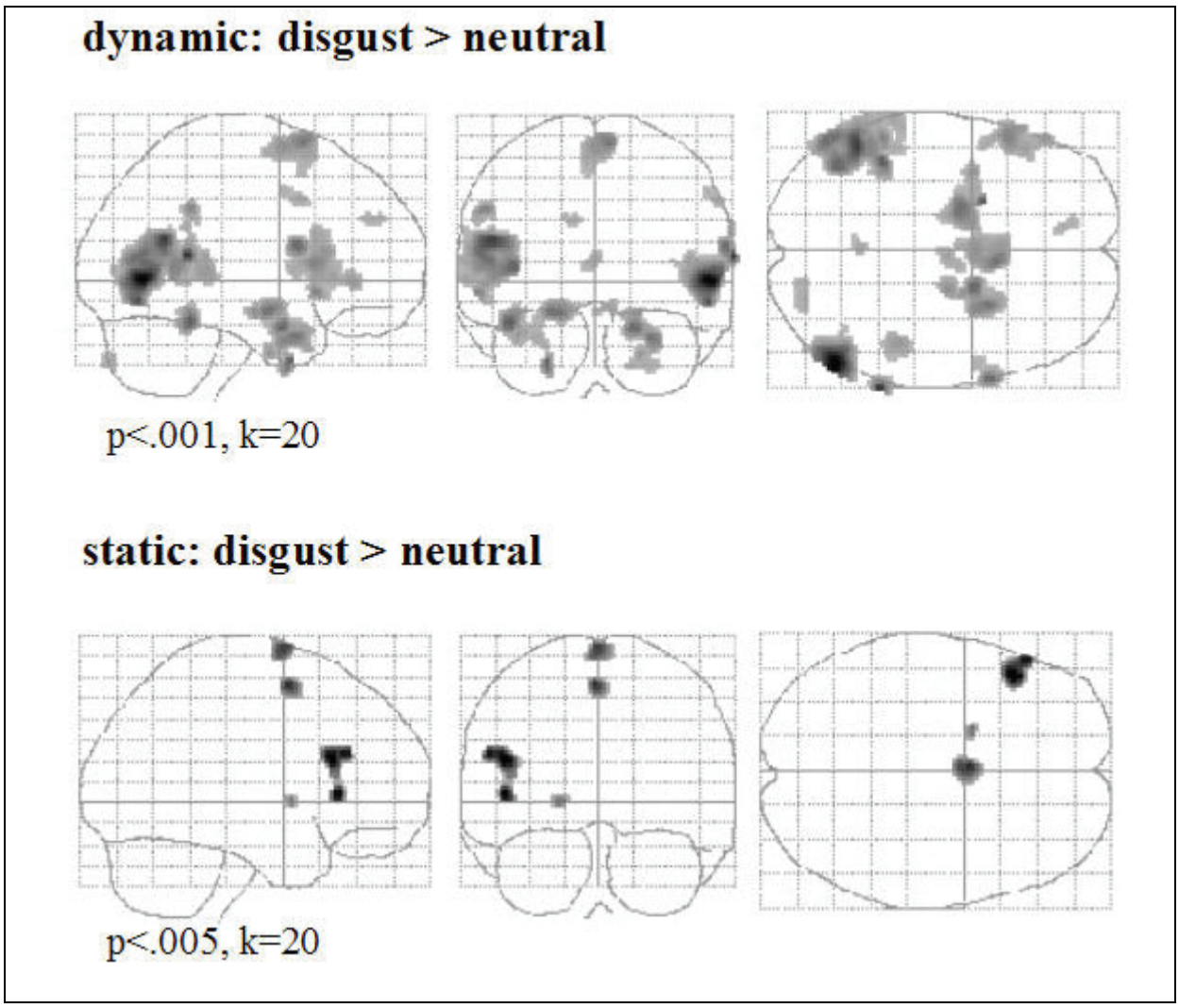
Sind Sie linkshändig oder rechtshändig?	Links	weiß	nicht rechts
Sind Sie Brillenträger/in?	ja	weiß nicht	nein
Tragen Sie Kontaktlinsen?	ja	weiß nicht	nein
Haben Sie Hörprobleme?	ja	weiß nicht	nein
Sind Sie mehrsprachig aufgewachsen?	ja	weiß nicht	nein

Ich habe alle Fragen auf dieser Seite wahrheitsgemäß und nach bestem Wissen beantwortet.

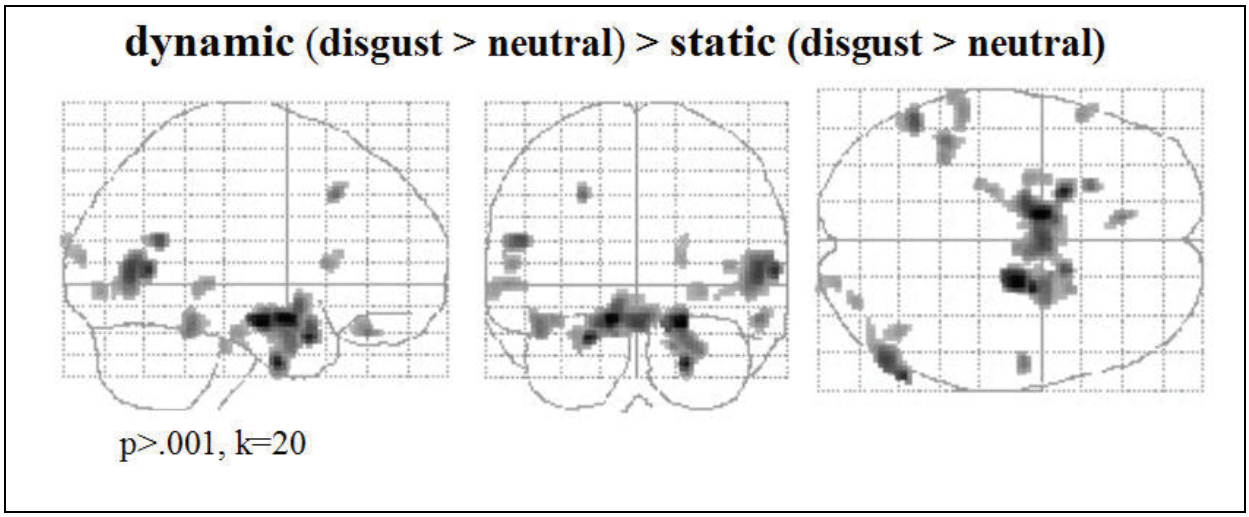
_____ _____

Ort Datum Unterschrift der Probandin/ des Probanden

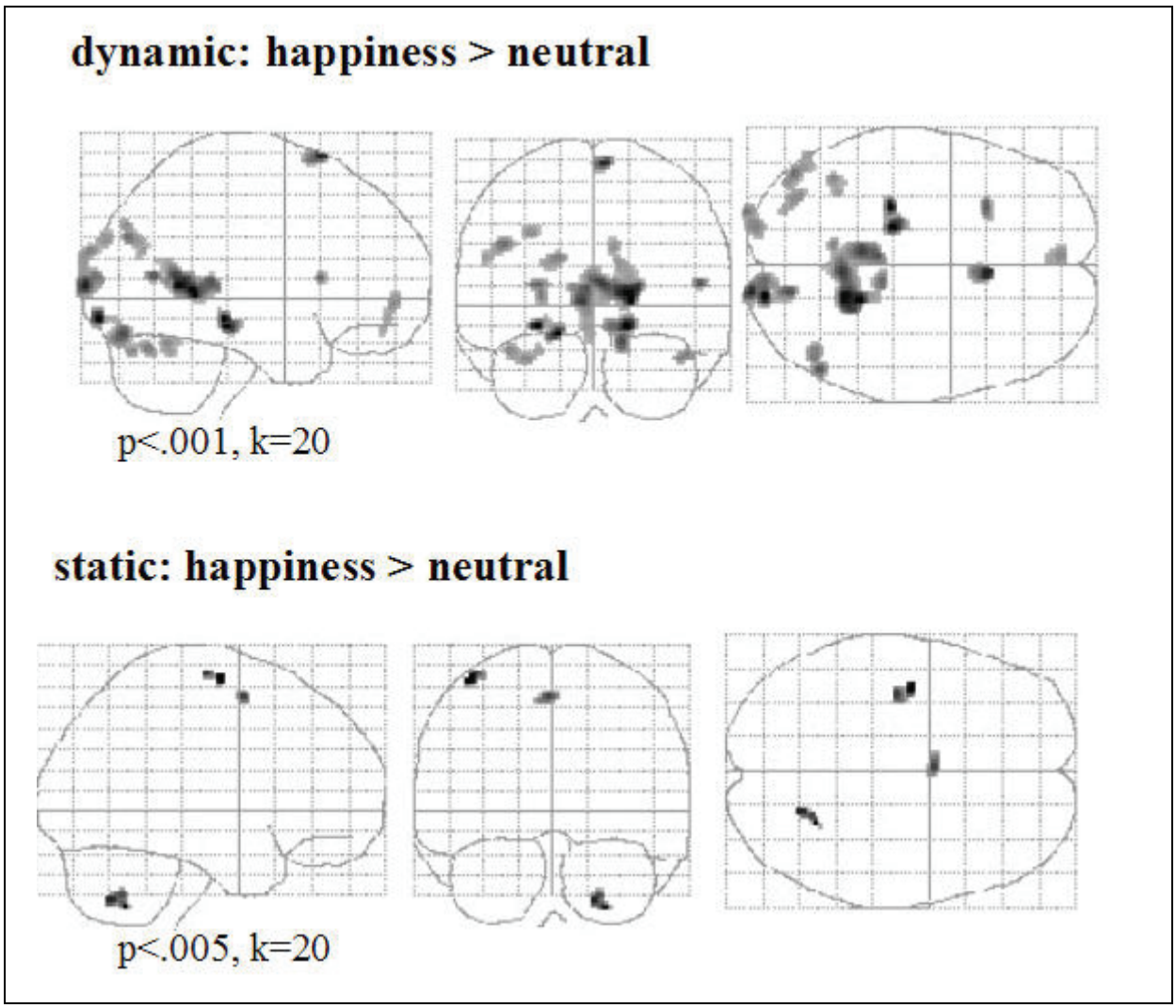
(B.1) Glassbrains of emotion effects of dynamic and static disgust



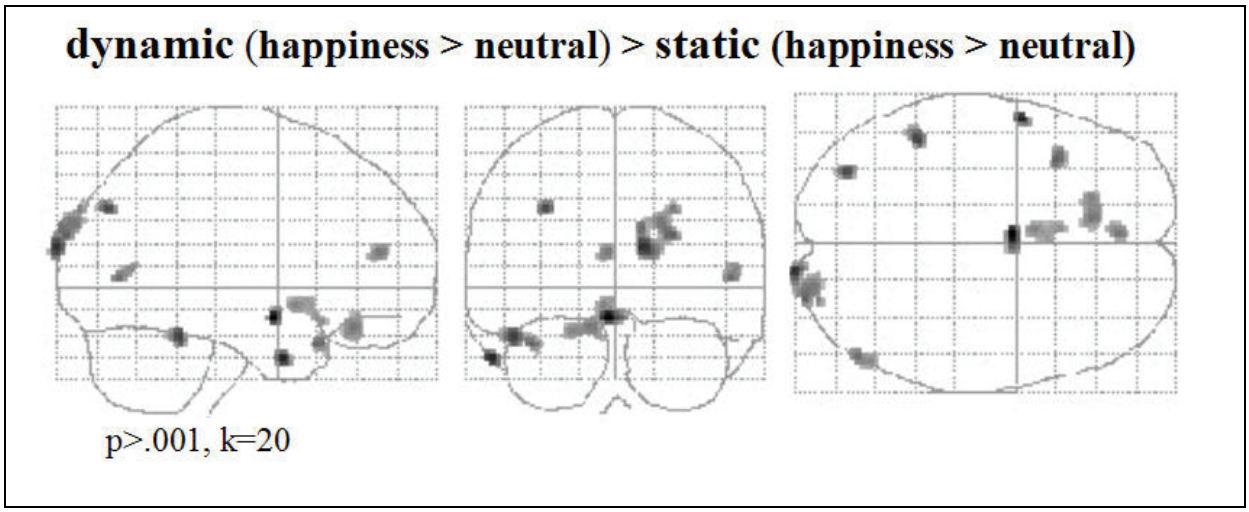
(B.2) Glassbrains of interaction effects of dynamic versus static disgust



(B.3) Glassbrains of enhanced emotion effects of dynamic versus static happiness



(B.4) Glassbrains of interaction effects of dynamic versus static happiness



(C.1) Information and consentment form of the EEG study

UNIVERSITAT DE BARCELONA

Grup de Neurociència Cognitiva. Brainlab.
Departament de Psiquiatria i Psicobiologia Clínica

Passeig de la Vall d'Hebron, 171
08035 Barcelona
Tel. 93 312 50 46
Fax 93 403 44 24
e-mail: jdominguez@ub.edu

FULL DE CONSENTIMENT

El present informe té com a objectiu primordial proporcionar-te, com a participant, tota la informació necessària per tal que puguis decidir, lliure i voluntàriament, si vols formar part d'aquest estudi. Preguem llegeixis atentament la següent informació i no dubtis en demanar qualsevol aclariment al respecte.

- **Propòsit:** l'objectiu de la present recerca és l'estudi del mecanismes cerebrals implicats en la atenció involuntària o exògena.

- **Investigador responsable:** la direcció del projecte corre a càrrec del Dr. Carles Escera i Micó, Professor Titular d'Universitat.

- **La participació en l'estudi implica:** una sessió al Laboratori del Grup de Neurociència Cognitiva (Brainlab, Departament de Psiquiatria i Psicobiologia Clínica, Universitat de Barcelona) durant la qual es realitzarà:

  1. col·locació d'elèctrodes (duració aproximada 40 min),
  2. registre de potencials evocats durant la presentació d'estímuls auditius o visuals (duració aproximada 50 min).

- **Riscs de l'estudi:** CAP, el risc personal per participar en el projecte no supera els riscos normals de la vida. L'enregistrament de l'activitat elèctrica del cervell (Electroencefalograma, EEG) és tracta d'una tècnica TOTALMENT innòcua i no invasiva.

- **Confidencialitat:** tota la informació recollida serà tractada de forma estrictament confidencial.

- **Drets:** l'exploració pot ser abandonada pel participant en qualsevol moment.

- **Deures:** els participants es comprometen a no difondre de forma oral o escrita, en cap mitjà de comunicació, qualsevol dada relacionada amb la seva participació o amb els resultats d'aquest projecte d'investigació sense prèvia autorització del director de la investigació.

- **Nota important:** durant la realització d'aquest estudi, es presentaran imatges que poden ferir la sensibilitat d'alguns participants, com ara mutilacions o fotografies eròtiques.

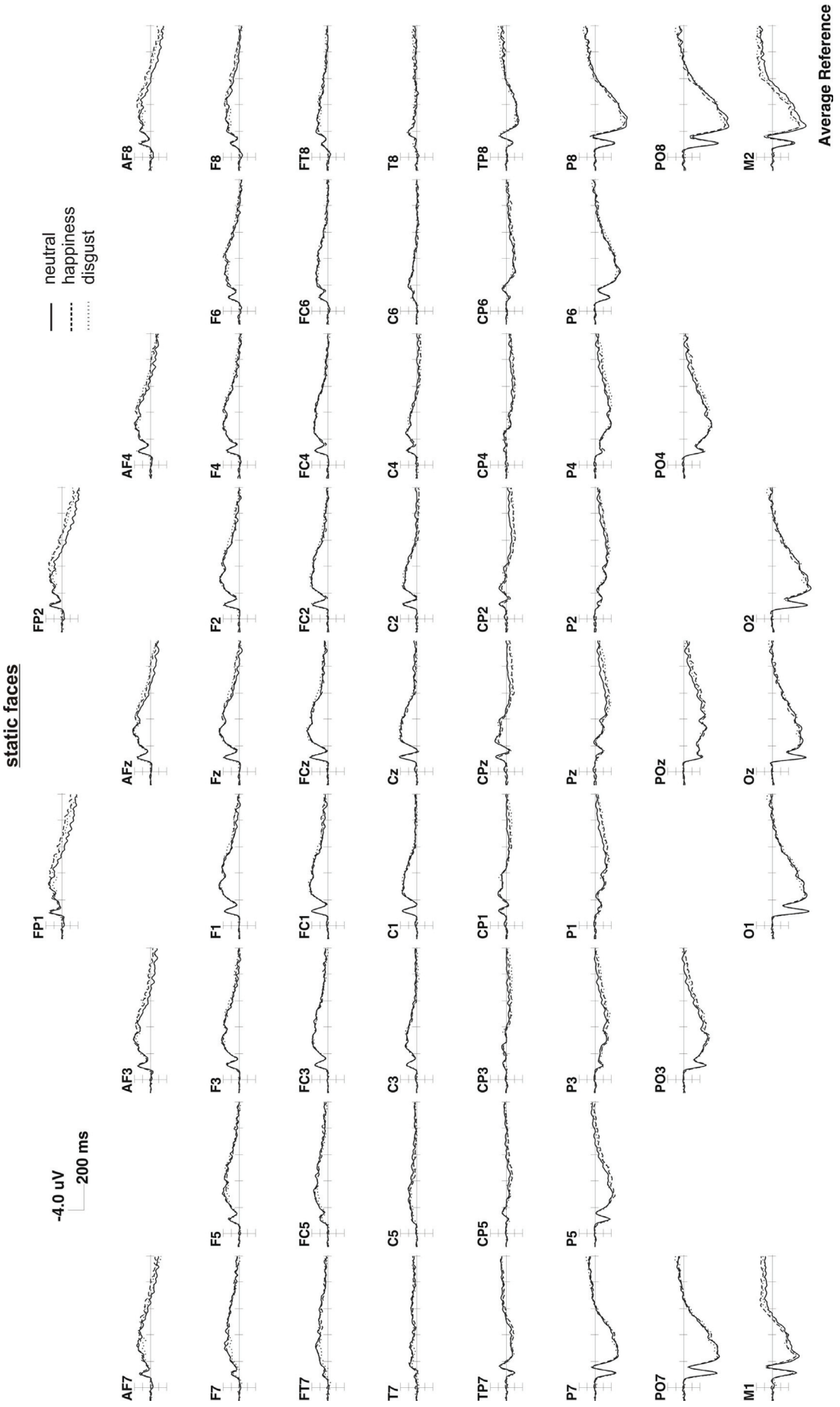
Així doncs, jo, _____ amb DNI _____
declaro haver llegit i entès les condicions de l'estudi, expressant amb la meva signatura la voluntat de participar en el present estudi.

_____ _____

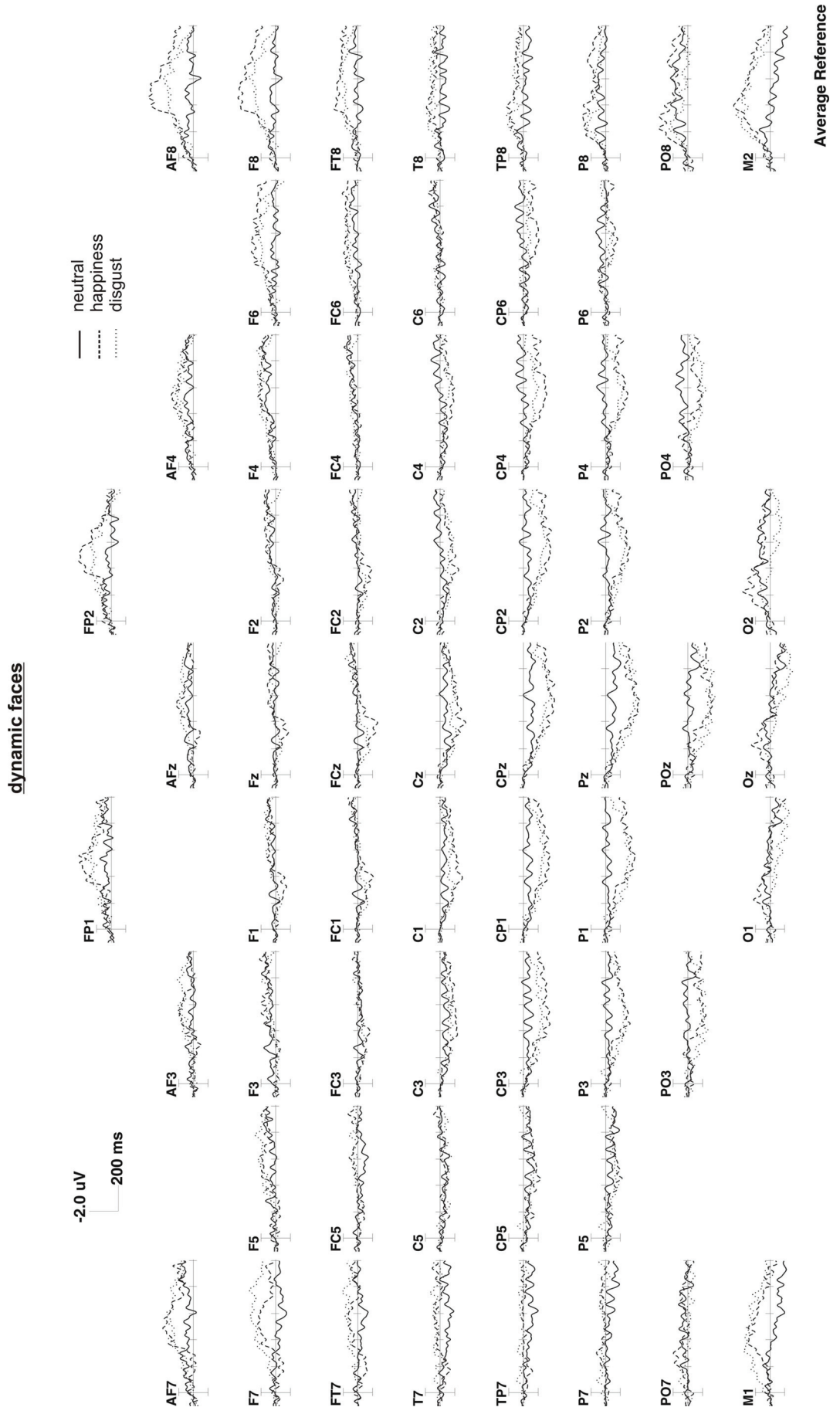
DNI i signatura del participant — Signatura de l'investigador

Barcelona, ___ de _____ del 200__

(D.1) ERPs of 62 channels for static emotional and neutral facial expressions



(D.2) ERPs of 62 channels for dynamic emotional and neutral facial expressions



(E.1) ERP statistics of 15 equidistant standard electrodes for static stimuli

Table demonstrates repeated measurement ANOVAs of static facial expressions including within-subject *factors* ANTERIOR-POSTERIOR (AP, 3 levels: frontal, central and posterior electrode positions), LATERALITY (LAT, 5 levels: from right to left electrode sites), and EMOTION (EMO, 3 levels: neutral, happiness, disgust) for four different time windows (*ms).* Degrees of freedom (*df*), F-value (*F*), significance level (*p*), Greenhouse-Geisser corrected p-value (*GG*), Huynh-Feldt corrected p-value (*HF*) are depicted. Star symbols (*) indicate that GG-correction is applied. [n.s.] = not significant.

static stimuli

ms	*factor*	*df*	*F*	*p*	*GG*	*HF*
90-130	AP	2,36	42.895	<.01	<.01 *	<.01
90-130	LAT	4, 72	22.586	<.01	<.01 *	<.01
90-130	AP * LAT	8, 144	6.489	<.01	<.01 *	<.01
140-190	AP	2,36	11.222	<.01	<.01 *	<.01
140-190	LAT	4, 72	2.122	<.1	[n.s.] *	[n.s.]
140-190	AP * LAT	8, 144	3.804	<.01	<.05 *	<.05
140-190	AP * LAT * EMO	16, 288	2,033	<.05	<.1 *	<.05
250-350	AP	2,36	76.972	<.01	<.01 *	<.01
250-350	LAT	4, 72	25.944	<.01	<.01 *	<.01
250-350	AP * LAT	8, 144	14.789	<.01	<.01 *	<.01
250-350	AP * LAT * EMO	16, 288	3.547	<.01	<.01 *	<.01
600-800	AP	2,36	9.241	<.01	<.01 *	<.01
600-800	LAT	4, 72	8.260	<.01	<.01 *	<.01
600-800	EMO	2, 36	2.526	<.1	=.1	<.1
600-800	AP * LAT	8, 144	14.425	<.01	<.01 *	<.01
600-800	AP * LAT * EMO	16, 288	1.997	<.05	<.01 *	<.05

(E.2) ERP statistics of the 15 equidistant standard electrode setup for static stimuli

Table demonstrates repeated measurement ANOVAs of single electrodes for static facial expressions including within-subject *factor* EMOTION (EMO, 3 levels: neutral, happiness, disgust) for two (out of four) different time windows (*ms*). Degrees of freedom (*df*), F-value (*F*), significance level (*p*), Greenhouse-Geisser corrected p-value (*GG*), Huynh-Feldt corrected p-value (*HF*) are depicted. Star symbols (*) indicate that GG-correction is applied.

static stimuli

ms	*electrode*	*factor*	*df*	*F*	*p*	*GG*	*HF*
250-350	F8	EMO	2, 36	3.739	<.05	<.05	<.05
250-350	F7	EMO	2, 36	5.936	<.01	<.01	<.01
250-350	T7	EMO	2, 36	2.656	<.1	<.1	<.1
250-350	P8	EMO	2, 36	2.594	<.1	<.1	<.1
600-800	P4	EMO	2, 36	3.7	<.05	<.05	<.05
600-800	Pz	EMO	2, 36	6.616	<.01	<.01	<.01
600-800	P3	EMO	2, 36	4.31	<.05	<.05	<.05

(E.3) ERP statistics of additional electrodes of interest for static stimuli

Table demonstrates repeated measurement ANOVAs of single, additional electrodes of interest for static facial expressions including within-subject *factor* EMOTION (EMO, 3 levels: neutral, happiness, disgust) for two (out of four) different time windows (*ms*). Degrees of freedom (*df*), F-value (*F*), significance level (*p*), Greenhouse-Geisser corrected p-value (*GG*), Huynh-Feldt corrected p-value (*HF*) are depicted.

static stimuli

ms	*electrode*	*factor*	*df*	*F*	*p*	*GG*	*HF*
140-190	PO8	EMO	2, 36	3.767	<.05	<.05	<.05
140-190	O2	EMO	2, 36	2.651	<.1	<.1	<.1
250-350	PO8	EMO	2, 36	3.329	<.05	=.05	<.05
250-350	O2	EMO	2, 36	2.465	<.1	.1	<.1
250-350	O1	EMO	2, 36	2.512	<.1	<.1	<.1

(E.4) ERP statistics of 15 equidistant standard electrodes for dynamic stimuli

Table demonstrates repeated measurement ANOVAs of dynamic facial expressions including within-subject *factors* ANTERIOR-POSTERIOR (AP, 3 levels: frontal, central and posterior electrode positions), LATERALITY (LAT, 5 levels: from right to left electrode sites), and EMOTION (EMO, 3 levels: neutral, happiness, disgust) for seven different time windows (*ms*). Degrees of freedom (*df*), F-value (*F*), significance level (*p*), Greenhouse-Geisser corrected p-value (*GG*), Huynh-Feldt corrected p-value (*HF*) are depicted. Star symbols (*) indicate that GG-correction is applied. [n.s.] = not significant.

Dynamic stimuli

ms	*factor*	*df*	*F*	*p*	*GG*	*HF*
100-200	AP	2, 36	7.682	<.01	<.01 *	<.01
100-200	LAT	4, 72	8.766	<.01	<.01 *	<.01
100-200	AP * LAT	8, 144	6.634	<.01	<.01	<.01
100-200	AP * LAT * EMO	16, 288	1.822	<.05	<.1 *	=.05
200-300	AP	2, 36	4.237	<.05	<.05 *	<.05
200-300	LAT	4, 72	17.662	<.01	<.01 *	<.01
200-300	AP * LAT	8, 144	6.169	<.01	<.01 *	<.01
200-300	LAT * EMO	8, 144	3.098	<.01	<.05 *	<.05
200-300	AP * LAT * EMO	16, 288	1.579	<.1	[n.s.] *	<.1
300-400	AP	2, 36	7.841	<.01	<.01 *	<.01
300-400	LAT	4, 72	22.14	<.01	<.01 *	<.01
300-400	AP * LAT	8, 144	3.353	<.01	<.05 *	<.01
300-400	LAT * EMO	8, 144	6.152	<.01	<.01 *	<.01
400-500	AP	2, 36	18.259	<.01	<.01 *	<.01
400-500	LAT	4, 72	17.621	<.01	<.01 *	<.01
400-500	EMO	2, 36	2.804	<.1	<.1	<.1
400-500	AP * LAT	8, 144	3.991	<.01	<.01 *	<.01
400-500	AP * EMO	4, 72	3.435	<.05	<.05 *	<.05
400-500	LAT * EMO	8, 144	6.086	<.01	<.01 *	<.01
500-600	AP	2, 36	18.872	<.01	<.01 *	<.01
500-600	LAT	4, 72	11.547	<.01	<.01 *	<.01
500-600	EMO	2, 36	1.515	<.01	<.01	<.01
500-600	AP * LAT	8, 144	3.883	<.01	<.01 *	<.01
500-600	AP * EMO	4, 72	7.728	<.01	<.01 *	<.01
500-600	LAT * EMO	8, 144	5.64	<.01	<.01 *	<.01
600-700	AP	2, 36	10.651	<.01	<.01 *	<.01
600-700	LAT	4, 72	7.002	<.01	<.01 *	<.01
600-700	AP * LAT	8, 144	3.281	<.01	<.01 *	<.01
600-700	AP * EMO	4, 72	6.254	<.01	<.01 *	<.01
600-700	LAT * EMO	8, 144	5.423	<.01	<.01 *	<.01
700-800	AP	2, 36	6.94	<.01	<.05 *	<.05
700-800	LAT	4, 72	4.935	<.01	<.05 *	<.05
700-800	AP * LAT	8, 144	2.945	<.01	<.05 *	<.05
700-800	AP * EMO	4, 72	4.313	<.01	<.05 *	<.05
700-800	LAT * EMO	8, 144	3.668	<.01	<.05 *	<.01

(E.5) ERP statistics of the 15 equidistant standard electrode set up for dynamic stimuli

Table demonstrates repeated measurement ANOVAs of single electrodes for dynamic facial expressions including within-subject *factor* EMOTION (EMO, 3 levels: neutral, happiness, disgust) for seven different time windows (*ms*). Degrees of freedom (*df*), F-value (*F*), significance level (*p*), Greenhouse-Geisser corrected p-value (*GG*), Huynh-Feldt corrected p-value (*HF*) are depicted. Star symbols (*) indicate that GG-correction is applied. [n.s.] = not significant.

dynamic stimuli

ms	*electrode*	*factor*	*df*	*F*	*p*	*GG*	*HF*
100-200	F8	EMO	2, 36	2.787	<.1	<.1	<.1
200-300	T8	EMO	2, 36	4.495	<.05	<.05	<.05
200-300	P8	EMO	2, 36	5.423	<.01	.01	<.01
200-300	Pz	EMO	2, 36	4.281	<.05	<.05	<.05
200-300	P3	EMO	2, 36	2.463	<.1	[n.s.]	[n.s.]
300-400	F8	EMO	2, 36	9.34	<.01	<.01	<.01
300-400	F7	EMO	2, 36	3.589	<.05	<.05	<.05
300-400	T8	EMO	2, 36	7.219	<.01	<.01	<.01
300-400	CZ	EMO	2, 36	4.078	<.05	<.05	<.05
300-400	C3	EMO	2, 36	3.312	<.1	<.1	<.1
300-400	P8	EMO	2, 36	3.887	<.05	<.05	<.05
300-400	P4	EMO	2, 36	6.487	<.01	<.01	<.01
300-400	PZ	EMO	2, 36	10.601	<.01	<.01	<.01
300-400	P3	EMO	2, 36	6.169	<.01	<.01	<.01
400-500	F8	EMO	2, 36	12.094	<.01	<.01	<.01
400-500	F7	EMO	2, 36	5.742	<.01	<.01	<.01
400-500	T8	EMO	2, 36	2.777	<.1	<.1	<.1
400-500	C4	EMO	2, 36	3.548	<.05	<.05	<.05
400-500	CZ	EMO	2, 36	3.819	<.05	<.05	<.05
400-500	C3	EMO	2, 36	4.971	<.05	<.05	<.05
400-500	P4	EMO	2, 36	12.363	<.01	<.01	<.01
400-500	PZ	EMO	2, 36	12.42	<.01	<.01	<.01
400-500	P3	EMO	2, 36	8.402	<.01	<.01	<.01
500-600	F8	EMO	2, 36	11.001	<.01	<.01	<.01
500-600	F7	EMO	2, 36	8.758	<.01	<.01	<.01
500-600	C4	EMO	2, 36	7.673	<.01	<.01	<.01
500-600	C3	EMO	2, 36	2.639	<.1	<.1	<.1
500-600	T7	EMO	2, 36	3.693	<.05	<.05	<.05
500-600	P4	EMO	2, 36	20.102	<.01	<.01	<.01
500-600	PZ.	EMO	2, 36	13.944	<.01	<.01	<.01
500-600	P3	EMO	2, 36	8.33	<.01	<.01	<.01
600-700	F8	EMO	2, 36	9.676	<.01	<.01	<.01
600-700	F7	EMO	2, 36	8.552	<.01	<.01	<.01
600-700	C4	EMO	2, 36	6.191	<.01	<.01	<.01
600-700	T7	EMO	2, 36	3.918	<.05	<.05	<.05
600-700	P4	EMO	2, 36	13.46	<.01	<.01 *	<.01
600-700	PZ	EMO	2, 36	12.64	<.01	<.01	<.01
600-700	P3	EMO	2, 36	6.701	<.01	<.01	<.01
700-800	F8	EMO	2, 36	5.637	<.01	<.01	<.01
700-800	F7	EMO	2, 36	6.417	<.01	<.01	<.01
700-800	C4	EMO	2, 36	4.854	<.05	<.05	<.05
700-800	P8	EMO	2, 36	2.647	<.1	<.1	<.1
700-800	P4	EMO	2, 36	11.236	<.01	<.01	<.01
700-800	PZ	EMO	2, 36	10.012	<.01	<.01	<.01
700-800	P3	EMO	2, 36	4.727	<.05	<.05	<.05

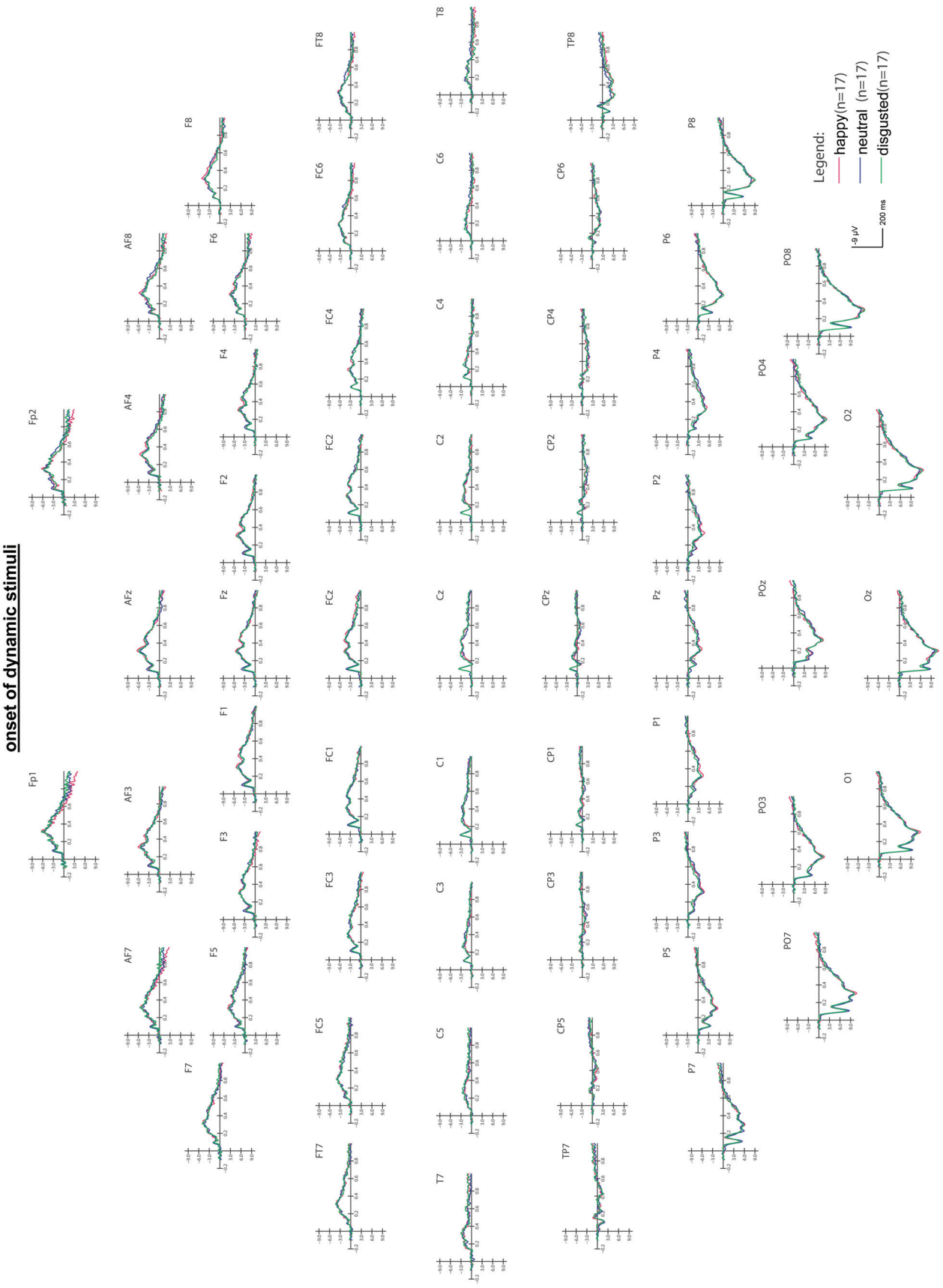
(E.6) ERP statistics of additional electrodes of interest for dynamic stimuli

Table demonstrates repeated measurement ANOVAs of single electrodes of interest for dynamic facial expressions including within-subject *factor* EMOTION (EMO, 3 levels: neutral, happiness, disgust) for six (out of seven) different time windows (*ms*). Degrees of freedom (*df*), F-value (*F*), significance level (*p*), Greenhouse-Geisser corrected p-value (*GG*), Huynh-Feldt corrected p-value (*HF*) are depicted. Star symbols (*) indicate that GG-correction is applied.

dynamic stimuli

ms	*electrode*	*factor*	*df*	*F*	*p*	*GG*	*HF*
100-200	PO8	EMO	2, 36	2.823	<.1	<.1	<.1
100-200	O2	EMO	2, 36	3.343	<.05	=.05	<.05
200-300	CP3	EMO	2, 36	2.872	<.1	<.1 *	<.1
200-300	CP1	EMO	2, 36	2.675	<.1	<.1	<.1
200-300	PO3	EMO	2, 36	3.325	<.05	<.1	.05
200-300	POz	EMO	2, 36	3.298	<.05	.05	<.05
200-300	PO8	EMO	2, 36	3.096	<.1	<.1	<.1
200-300	O2	EMO	2, 36	2.722	<.1	<.1	<.1
300-400	AF8	EMO	2, 36	5.506	<.01	<.05	<.01
300-400	F6	EMO	2, 36	3.820	<.05	<.05	<.05
300-400	CP3	EMO	2, 36	8.182	<.01	<.01 *	<.01
300-400	CP1	EMO	2, 36	6.507	<.01	<.01	<.01
300-400	CPz	EMO	2, 36	5.644	<.01	<.01	<.01
300-400	CP2	EMO	2, 36	5.875	<.01	<.01	<.01
300-400	CP4	EMO	2, 36	4.478	<.05	<.05	<.05
300-400	PO3	EMO	2, 36	5.780	<.01	<.01	<.01
300-400	POz	EMO	2, 36	5.887	<.01	<.01	<.01
300-400	PO4	EMO	2, 36	5.772	<.01	<.01	<.01
300-400	PO8	EMO	2, 36	2.727	<.1	<.1	<.1
300-400	O2	EMO	2, 36	3.492	<.05	<.05	<.05
400-500	AF7	EMO	2, 36	3.365	<.05	=.05	<.05
400-500	AF8	EMO	2, 36	9.012	<.01	<.01	<.01
400-500	F6	EMO	2, 36	4.684	<.05	<.05	<.05
400-500	CP3	EMO	2, 36	14.794	<.01	<.01 *	<.01
400-500	CP1	EMO	2, 36	10.336	<.01	<.01	<.01
400-500	CPz	EMO	2, 36	9.428	<.01	<.01	<.01
400-500	CP2	EMO	2, 36	8.619	<.01	<.01	<.01
400-500	CP4	EMO	2, 36	8.197	<.01	<.01	<.01
400-500	PO3	EMO	2, 36	4.605	<.05	<.05 *	<.05
400-500	POz	EMO	2, 36	4.702	<.05	<.05 *	<.05
400-500	PO4	EMO	2, 36	7.142	<.01	<.01	<.01
500-600	AF7	EMO	2, 36	4.334	<.05	<.05	<.05
500-600	AF8	EMO	2, 36	7.696	<.01	<.01	<.01
500-600	F6	EMO	2, 36	6.704	<.01	<.01	<.01
500-600	CP3	EMO	2, 36	11.572	<.01	<.01	<.01
500-600	CP1	EMO	2, 36	7.093	<.01	<.01	<.01
500-600	CPz	EMO	2, 36	9.774	<.01	<.01	<.01
500-600	CP2	EMO	2, 36	11.531	<.01	<.01	<.01
500-600	CP4	EMO	2, 36	16.308	<.01	<.01	<.01
500-600	PO3	EMO	2, 36	6.966	<.01	<.01	<.01
500-600	POz	EMO	2, 36	6.383	<.01	<.01	<.01
500-600	PO4	EMO	2, 36	12.150	<.01	<.01	<.01
500-600	O2	EMO	2, 36	4.133	<.05	<.05	<.05
600-700	AF7	EMO	2, 36	3.747	<.05	<.05	<.05
600-700	AF8	EMO	2, 36	5.822	<.01	<.01	<.01
600-700	F6	EMO	2, 36	5.223	<.05	<.05	<.05
600-700	CP3	EMO	2, 36	8.474	<.01	<.01	<.01
600-700	CP1	EMO	2, 36	6.249	<.01	<.01	<.01
600-700	CPz	EMO	2, 36	9.055	<.01	<.01	<.01
600-700	CP2	EMO	2, 36	11.192	<.01	<.01	<.01
600-700	CP4	EMO	2, 36	12.338	<.01	<.01	<.01
600-700	PO3	EMO	2, 36	8.943	<.01	<.01	<.01
600-700	POz	EMO	2, 36	7.528	<.01	<.01	<.01
600-700	PO4	EMO	2, 36	11.011	<.01	<.01	<.01
600-700	O2	EMO	2, 36	4.34	<.05	<.05	<.05
600-700	O1	EMO	2, 36	2.625	<.1	=.1	<.1

(F.1) ERPs of 62 channels for the onset of dynamic stimuli for emotional and neutral facial expressions for 17 participants



(F.2) ERP statistics of 15 equidistant standard electrodes for the onset of dynamic emotional stimuli

Table demonstrates repeated measurement ANOVAs of *onset* of dynamic facial expressions including within-subject *factors* ANTERIOR-POSTERIOR (AP, 3 levels: frontal, central and posterior electrode positions), LATERALITY (LAT, 5 levels: from right to left electrode sites), and EMOTION (EMO, 3 levels: neutral, happiness, disgust) for four different time windows (*ms*). These time windows are equivalent to the time windows of the static faces. Degrees of freedom (*df*), F-value (*F*), significance level (*p*), Greenhouse-Geisser corrected p-value (*GG*), Huynh-Feldt corrected p-value (*HF*) are depicted. Star symbols (*) indicate that GG-correction is applied.

dynamic stimuli - onset

ms	*factor*	*df*	*F*	*p*	*GG*	*HF*
90-130	AP	2, 32	57.033	<.01	<.01 *	<.01
90-130	LAT	4, 64	19.587	<.01	<.01 *	<.01
90-130	AP * LAT	8, 128	7.475	<.01	.01 *	<.01
140-190	AP	2, 32	35.184	<.01	<.01 *	<.01
250-350	AP	2, 32	134.533	<.01	<.01 *	<.01
250-350	LAT	4, 64	10.899	<.01	<.01 *	<.01
250-350	AP * LAT	8, 128	15.3	<.01	<.01 *	<.01
600-800	AP	2, 32	5.74	<.01	<.05*	0.02
600-800	LAT	4, 64	3.037	<.05	<0.1*	<.1
600-800	AP * LAT	8,128	2.665	<.05	<.05*	<.05

(G.1) Statistics of the fMRI constrained source model complemented by four additional regional sources (static stimuli)

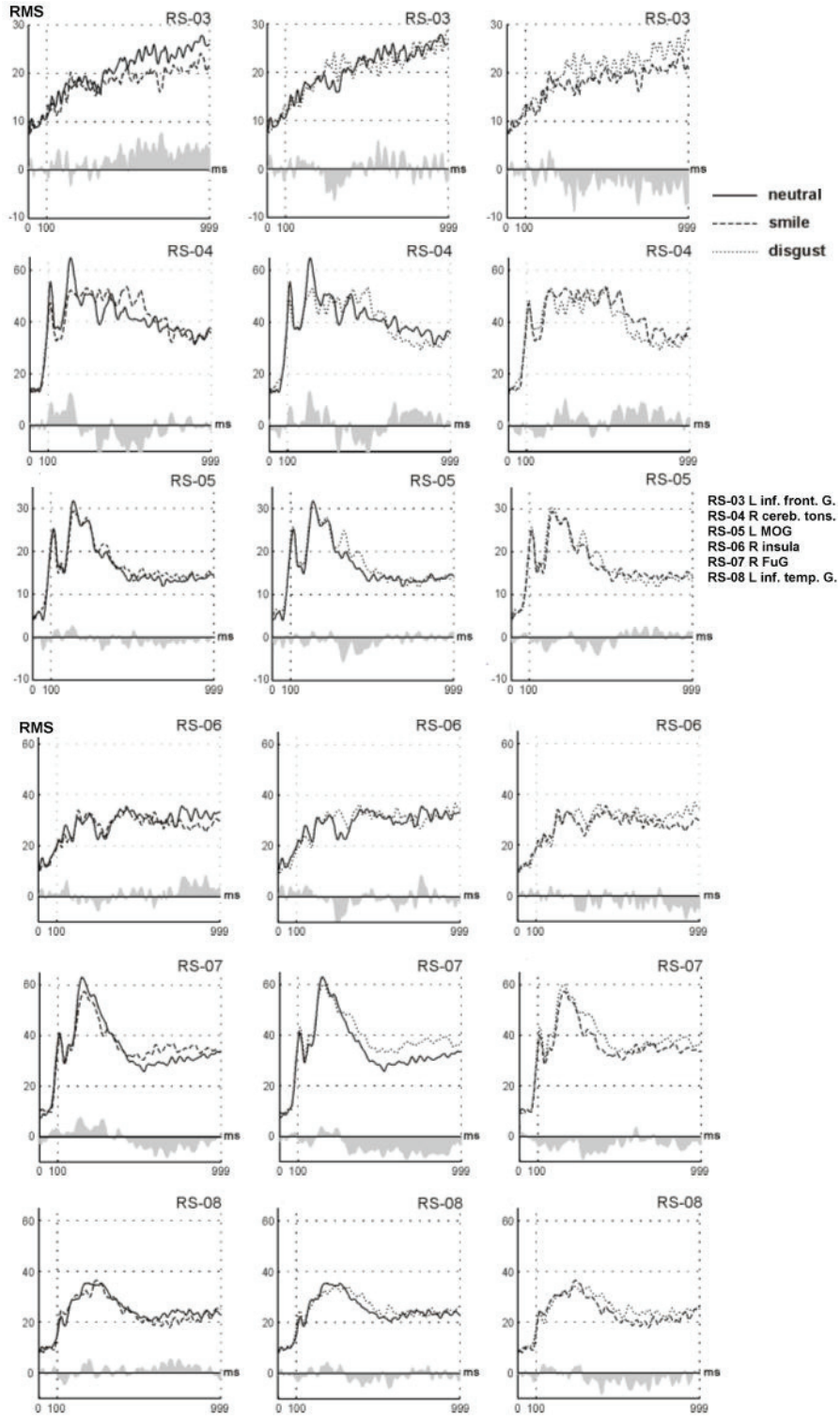
Table demonstrates repeated measurement ANOVAs of seven (out of eight) regional sources (RS) for static facial expressions including within-subject *factor* EMOTION (EMO, 3 levels: neutral, happiness, disgust) for 13 (out of 20) 50 ms time windows (ms). Degrees of freedom (*df*), F-value (*F*), significance level (*p*), Greenhouse-Geisser corrected p-value (*GG*), Huynh-Feldt corrected p-value (*HF*) are depicted. Star symbols (*) indicate that GG-correction is applied. Talairach (TAL) labels for RSs: RS-02 = left precentral gyrus, RS-03 = left inferior frontal gyrus (L inf. front. G.), RS-04 = right cerebellar tonsil (R cereb. tons.), RS-05 = left middle occipital gyrus (L MOG), RS-06 = right insula (R INS), RS-07 = right fusiform gyrus (R FuG), RS-08 = left inferior temporal gyrus (L inf. temp. G.); for TAL corrdinates and more details, see Fig. 16). [n.s.] = not significant.

static stimuli

ms	*RS*	*label (TAL)*	*factor*	*df*	*F*	*p*	*GG*	*HF*
50-100	5	L MOG	EMO	2, 36	3.01	<.1	<.1	<.1
50-100	7	R FuG	EMO	2, 36	2.461	=.1	[n.s.]	[n.s.]
100-150	4	R cereb. tons.	EMO	2, 36	2.682	<.1	<.1	<.1
100-150	8	L inf. temp. G.	EMO	2, 36	4.196	<.05	<.05	<.05
150-200	4	R cereb. tons.	EMO	2, 36	2.907	<.1	<.1	<.1
150-200	7	R FuG	EMO	2, 36	2.816	<.1	<.1	<.1
200-250	4	R cereb. tons.	EMO	2, 36	5.14	<.05	<.05	<.05
200-250	7	R FuG	EMO	2, 36	4.083	<.05	<.05	<.05
300-350	6	R INS	EMO	2, 36	5.315	<.01	<.05	.01
300-350	7	R FuG	EMO	2, 36	2.752	<.1	<.1	<.1
350-400	3	L inf. front. G.	EMO	2, 36	3.762	<.05	<.05	<.05
350-400	4	R cereb. tons.	EMO	2, 36	2.587	<.1	<.1	<.1
350-400	5	L MOG	EMO	2, 36	3.097	<.1	<.1	<.1
350-400	7	R FuG	EMO	2, 36	6.843	<.01	<.01	<.01
400-450	2	L prec. G.	EMO	2, 36	2.593	<.1	<.1	<.1
400-450	3	L inf. front. G.	EMO	2, 36	3.329	<.05	<.1	<.1
400-450	7	R FuG	EMO	2, 36	5.026	<.05	<.05*	<.05
450-500	5	L MOG	EMO	2, 36	5.17	<.05	<.05	<.05
450-500	7	R FuG	EMO	2, 36	3.724	<.05	<.05	<.05
550-600	7	R FuG	EMO	2, 36	3.937	<.05	<.05	<.05
600-650	7	R FuG	EMO	2, 36	3.482	<.05	<.05	<.05
650-700	7	R FuG	EMO	2, 36	3.477	<.05	.05	<.05
700-750	3	L inf. front. G.	EMO	2, 36	2.451	=.1	[n.s.]	=.1
700-750	7	R FuG	EMO	2, 36	3.639	<.05	.05	<.05
800-850	7	R FuG	EMO	2, 36	2.688	<.1	<.1	<.1

(G.2) Graphs represent source waveforms of selected regional sources (static stimuli)

Each graph displays strength of source waveforms (y-axis = RMS, root mean square) of two conditions (solid line = neutral, dashed line = smile/happiness, dotted line = disgust) over a time window of -100 - 999 ms (x-axis = ms). Gray shades represent difference waves of source waveforms. Each row represents source waveforms for selected RSs. Each coloumn displays comparisons between emotional conditions. L = left, R = right, inf. front. G = inferior frontal gyrus, cereb. tons. = cerebellar tonsil, MOG = middle occipital gyrus, INS = insula, FuG = fusiform gyrus, inf. temp. G. = inferior temporal gyrus.



(G.3) Statistics of the fMRI constrained source model enhanced by one additional regional source (dynamic stimuli)

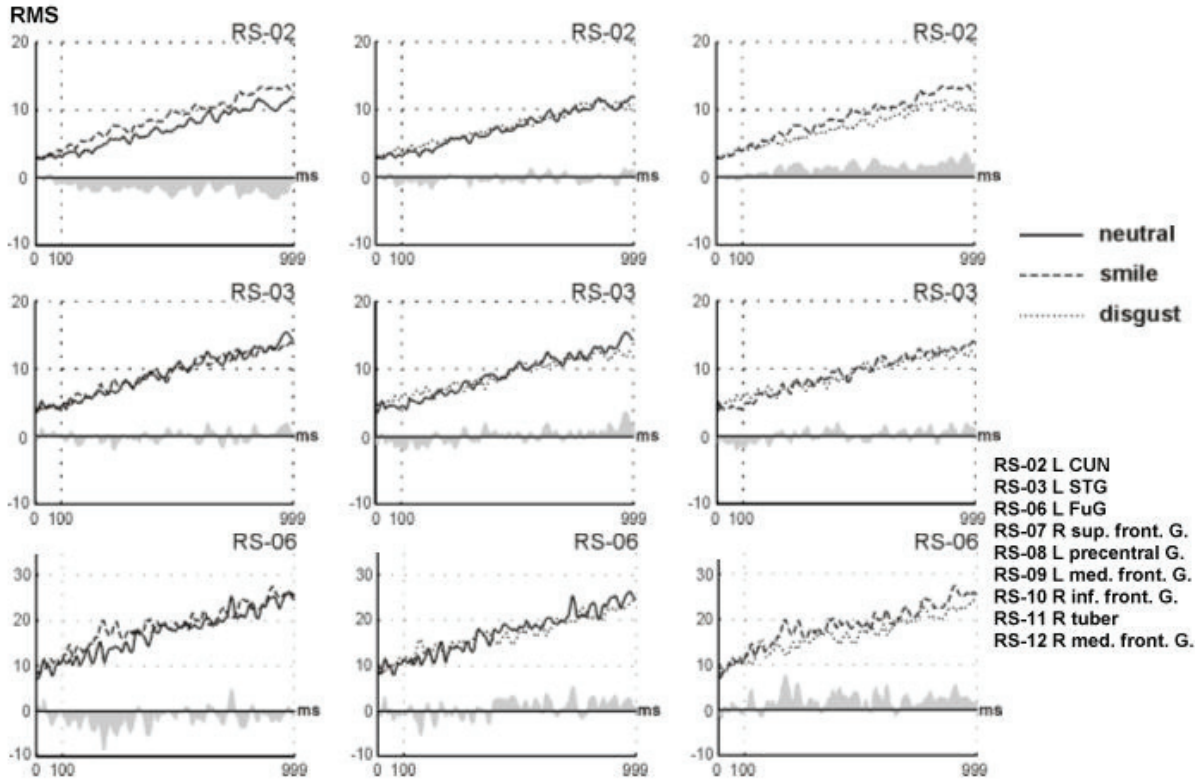
Table demonstrates repeated measurement ANOVAs of nine (out of 12) regional sources (RS) for dynamic facial expressions including within-subject *factor* EMOTION (EMO, 3 levels: neutral, happiness, disgust) for 16 (out of 20) different time windows (*ms*). Degrees of freedom (*df*), F-value (*F*), significance level (*p*), Greenhouse-Geisser corrected p-value (*GG*), Huynh-Feldt corrected p-value (*HF*) are depicted. Star symbols (*) indicate that GG-correction is applied. Talairach (TAL) labels for RSs: RS-02 = left cuneus (L CUN), RS-03 = left superior temporal gyrus (L STG), RS-04 = right superior temporal gyrus, RS-05 = right fusiform gyrus, RS-06 = left fusiform gyrus (L FuG), RS-07 = right superior frontal gyrus (R sup. front. G.), RS-08 = left precentral gyrus (L precentral G.), RS-09 = left medial frontal gyrus (L med. front. G.), RS10 = right inferior frontal gyrus (R inf. front. G.), RS11 = right tuber (R tuber), RS12 = right medial frontal gyrus (R med. front.G.); for Talairach coordinates and more details, see also fig. 17.

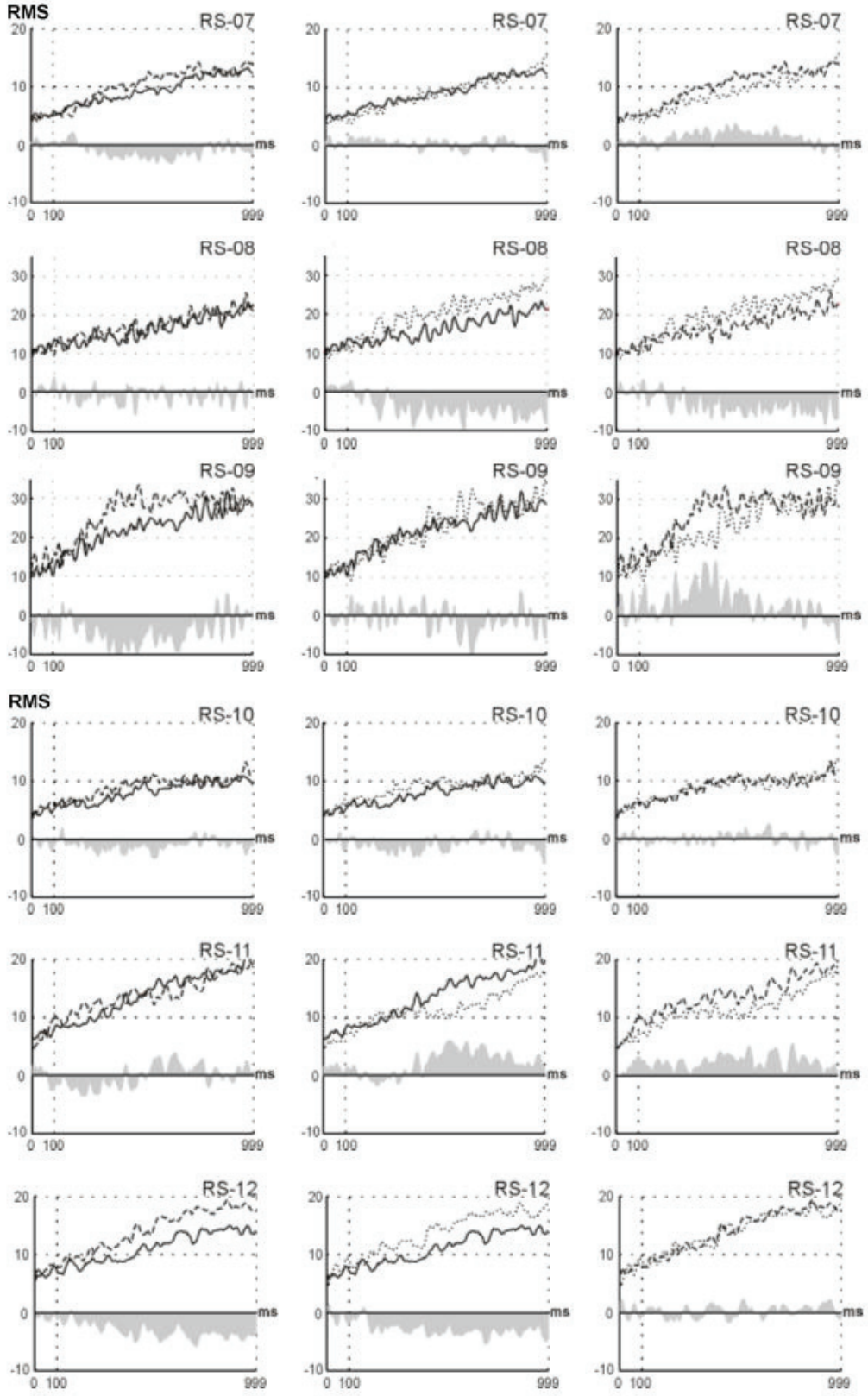
dynamic stimuli

ms	*RS*	*label (TAL)*	*factor*	*df*	*F*	*p*	*GG*	*HF*
0-50	11	R tuber	EMO	2, 36	2.894	<.1	<.1 *	<.1
50-100	3	L STG	EMO	2, 36	3.699	<.05	.05 *	<.05
50-100	11	R tuber	EMO	2, 36	3.774	<.05	<.05	<.05
100-150	7	R sup. front. G.	EMO	2, 36	2.787	<.1	<.1	<.1
100-150	9	L med. front. G.	EMO	2, 36	2.902	<.1	<.1	<.1
100-150	11	R tuber	EMO	2, 36	3.79	<.05	<.05	<.05
150-200	2	L CUN	EMO	2, 36	2.694	<.1	<.1	<.1
150-200	3	L STG	EMO	2, 36	3.847	<.05	<.05	<.05
150-200	11	R tuber	EMO	2, 36	3.036	<.1	<.1	<.1
200-250	2	L CUN	EMO	2, 36	4.47	<.05	<.05	<.05
200-250	8	L precentral G.	EMO	2, 36	3.693	<.05	<.05 *	<.05
200-250	11	R tuber	EMO	2, 36	5.26	.01	<.05	.01
200-250	12	R med. front.G.	EMO	2, 36	3.617	<.05	<.05	<.05
250-300	6	L FuG	EMO	2, 36	6.354	<.01	<.01	<.01
250-300	9	L med. front. G.	EMO	2, 36	3.515	<.05	<.1 *	<.1
250-300	10	R inf. front. G.	EMO	2, 36	6.881	<.01	<.01	<.01
250-300	12	R med. front.G.	EMO	2, 36	3.044	<.1	<.1	<.1
300-350	9	L med. front. G.	EMO	2, 36	2.913	<.1	<.1 *	<.1
350-400	8	L precentral G	EMO	2, 36	2.933	<.1	<.1	<.1
350-400	9	L med. front. G.	EMO	2, 36	8.107	<.01	<.01	<.01
350-400	12	R med. front.G.	EMO	2, 36	2.807	<.1	<.1	<.1
400-450	9	L med. front. G.	EMO	2, 36	9.56	<.01	<.01	<.01
400-450	10	R inf. front. G.	EMO	2, 36	2.751	<.1	<.1	<.1
400-450	12	R med. front.G.	EMO	2, 36	2.697	<.1	<.1	<.1
450-500	9	L med. front. G.	EMO	2, 36	4.063	<.05	<.05	<.05
450-500	12	R med. front.G.	EMO	2, 36	3.181	.05	<.01	.05
500-550	2	L CUN	EMO	2, 36	3.124	<.1	<.1	<.1
500-550	7	R sup. front. G.	EMO	2, 36	3.583	<.05	<.05	<.05
500-550	11	R tuber	EMO	2, 36	2.58	<.1	<.1	<.1
550-600	8	L precentral G	EMO	2, 36	2.545	<.1	.1	<.1
550-600	11	R tuber	EMO	2, 36	5.399	<.01	.01	<.01
550-600	12	R med. front.G.	EMO	2, 36	2.969	<.1	<.1	<.1
600-650	7	R sup. front. G.	EMO	2, 36	2.674	<.1	<.1	<.1
600-650	8	L precentral G	EMO	2, 36	2.411	.1	.11	.1
600-650	11	R tuber	EMO	2, 36	3.262	.05	<.1	<.1
650-700	9	L med. front. G.	EMO	2, 36	2.479	<.1	<.1	<.1
700-750	11	R tuber	EMO	2, 36	2.637	<.1	<.1	<.1
700-750	12	R med. front.G.	EMO	2, 36	3.779	<.05	<.05	<.05
900-950	2	L CUN	EMO	2, 36	2.593	<.1	<.1	<.1

(G.4) Graphs represent source waveforms of selected regional sources (dynamic stimuli)

Each graph displays strength of source waveforms (y-axis = RMS, root mean square) of two conditions (solid line = neutral, dashed line = smile/happiness, dotted line = disgust) over a time window of -100 - 999 ms (x-axis = ms). Gray shades represent difference waves of source waveforms. Each row represents source waveforms for selected regional sources. Each coloumn displays comparisons between emotional conditions. L = left, R = right Hemisphere, G. = gyrus, CUN = cuneus, STG = superior temporal Gyrus, FuG = Fusiform Gyrus, sup. front. G. = superior frontal gyrus, med. front. G. = medial frontal gyrus, inf. front. G. = inferior frontal gyrus.

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8 Eigenständigkeitserklärung

Hiermit versichere ich, dass ich die vorliegende Dissertation mit dem Thema

“Emotions in Motion:
Perception of Dynamic and Static Facial Expressions
of Happiness and Disgust Investigated
by FMRI and EEG”

selbständig und ohne unerlaubte fremde Hilfe angefertigt, keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt und die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen als solche kenntlich gemacht habe.

Bremen, den

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(Sina Alexa Trautmann)