CARL VON OSSIETZKY universität OLDENBURG

Master Thesis

Neurocognitive Psychology (M. Sc.)

Neuronal Correlates of Emotion. Investigating different visual affective stimuli using fMRI

submitted by

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Abstract

In neuroscience, emotions are commonly investigated using visual emotional stimuli and modern neuroimaging techniques like functional magnetic resonance imaging (fMRI). These visual stimuli frequently include images of emotional faces or emotional evocative scenes. Yet, only few researchers investigated whether these kinds of stimuli elicit similar or different patterns of activation in the brain. The main goal of the current study is to find a set of stimuli that does consistently activate emotional networks within the brain and does provide a basis for reliably studying emotions in patient populations. In this fMRI study nineteen healthy volunteers from a student population passively viewed blocks of emotional faces (Radboud Faces Database) and emotionally evocative scenes (Nencki Affective Picture System), both interleaved with a neutral baseline condition. BOLD activation patterns to both stimulus types were respectively compared to baseline and in contrast to each other. Subjective ratings of discrete emotions and arousal were examined in addition. Faces and scenes activated similar structures, containing the visual occipital cortex, fusiform gyri, and the posterior temporal cortices. Scenes additionally activated the anterior cingulate cortex, superior parietal lobe, orbital frontal cortex, bilateral inferior frontal cortex, thalamus (pulvinar), amygdala, brainstem, and the cerebellum. In accordance with recent literature on emotions, these results suggest that there are functional circuits processing different aspects of emotions rather than distinct brain regions activated during processing of discrete emotion categories. This would be supportive for the constructionists approach to defining emotion. Instead of distinguishing between discrete emotion categories, it seems more promising to consider and investigate emotions in their functional context, with regard to means of survival or social interaction. Furthermore, emotionally evocative scenes, as used in the current experiment, may produce a more stable activation pattern since they are closer related to real life experiences of emotions.

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Abbreviations of anatomical brain regions

ACC	anterior cingulate cortex
dlPFC	dorsal lateral prefrontal cortex
dmPFC	dorsal medial prefrontal cortex
IFG	inferior frontal gyrus
ITG	inferior temporal gyrus
l OFC	lateral orbitofrontal cortex
m OFC	medial orbitofrontal cortex
MFG	middle frontal gyrus
MTG	middle temporal gyrus
OFC	orbitofrontal cortex
PAG	periaqueductal grey
PCC	posterior cingulate cortex
PFC	prefrontal cortex
SFG	superior frontal gyrus
STG	superior frontal gyrus
vl PFC	ventral lateral prefrontal cortex
vm PFC	ventral medial prefrontal cortex

Other abbreviations

ACQ	Agoraphobic Cognitions Questionnaire
ANOVA	analysis of variance
BAI	Beck's anxiety inventory
BDI-II	Beck's depression inventory
BOLD	blood oxygen level dependent
BSQ	Body sensations questionnaire
EPI	echo planar imaging
FACS	facial action coding specialist
fMRI	functional magnetic resonance imaging
FoV	field of view
FSL	FMRIB software library
FWHM	full width at half maximum
GLM	general linear model
GRAPPA	generalized autocalibrating partial parallel acquisition
IAPS	international affective picture system
MI	Mobility Inventory
MNI	Montreal Neurological Institute
NAPS	Nencki affective picture system
PET	positron emission tomography
ROI	region of interest
TE	echo time
TR	repetition time
TO	temporal occipital
PD	posterior division

1 Introduction

The following sections offer a broad insight into the understanding of 'emotion' and give a short review on the current status of research in this field. First, it is attempted to explain the term 'emotion' from a very basic perspective. Subsequently, a compendium of influential theories on emotions is provided. On the basis of these theories, insights from neurosciences are included to arrive at a more profound comprehension about emotions and their neural basis. The introductory chapter, as a whole, provides the reader with necessary information about the status of emotion research and guides him/her to the actual research question, of which visual emotional stimulus material is well suited to investigate the neuronal networks, involved in processing emotions, using fMRI.

1.1 Defining Emotions

Hearing the term emotion, it is already difficult to circumscribe what it actually means. From an etymological point of view emotion stems from the Latin word "emovere". This is composed of the words "ex" which means "out" and the word "movere" that can be translated as "to move". Therefore, it may be defined as "to move out, to remove, or to agitate" (Harper, 2017 [Retrieved March 06, 2017, from http://www.etymonline.com/index.php?term=emotion]). Zimbardo and Gerrig (2004, p. 547) define emotion as "complex pattern of bodily and mental changes, including physiological arousal, cognitive processes, and behavioural reactions in response to a personally significant situation". This definition already comprises many different aspects that are associated with the term emotion. Nonetheless, it does not provide information about causal relationships of these aspects. It is not clear whether cognitive processes influence physiologic and behavioural reactions, or whether these have an impact on the cognitive feature of emotion in turn. According to Puca (2013), there is no consensus about a definition of emotions. As in the definition above, she states that emotion denotes a complex phenomenon associated with changes of different features. It can be separated into physiological reactions like sweating, or increasing cardiac frequency, a behavioural component involving mim-

ic, gestural, and vocal modulations as well as an experiential component that is usually referred to as "feelings", or "affect" (pp. 438-439). Considering a functional perspective, emotions serve three different purposes. Firstly, they may draw the focus of attention to a triggering event. Secondly, they provide important information for other functions like cognition, or unconscious appraisal processes. Lastly, they have a motivational function, since they generate goals of action, or support the prioritization of these goals (Reisenzein, 2013). Looking at these functional aspects, it is apparent, that emotions possess an actuating character. This again, attributes to the etymological origin of "moving".

There have been many different approaches to define emotions in the past and present. These attempts differ a lot regarding the features they place emphasis on, for example, whether they include bodily reactions in general as a core characteristic of emotions, or whether these are only accompanying effects of the emotions themselves (Damasio, 1994; Kringelbach & Phillips, 2014; Zimbardo & Gerrig, 2004). The following section provides an insight into theories on emotions and discusses selected theories, as most pertinent with regard to the research questions pursued in the present study.

1.2 Theories of Emotion

The science of emotions goes at least back to the early 19th century when Charles Darwin attempted to define emotional states. However, first psychological theories about emotions were developed one decade later. William James and Carl Lange developed similar ideas about the emergence of emotions. In their view, emotions are defined as the sensation of bodily changes that follow an exciting stimulus (Cornelius, 1996, pp. 65-67; Kringelbach & Phillips, 2014, pp. 27-29). Even though these theories may provide the basis for a variety of emotional theories, discussing them in detail is beyond the scope of this work. Throughout the 20th and 21st century many researchers put their focus on studying emotions from a behavioural perspective as well as in the context of their biological and neural basis. They developed different models that try to explain emotions. Some of these models can be assigned to two different positions that make considerable distinctions, determining the development and processing of emotions (Kringelbach & Philips, 2014, p. 48).

On the one hand, proponents of the locationist approach claim that emotions are basic in a sense of being uniquely valid across cultures and having distinct recognizable features like consistent behavioural patterns, and biological markers. A commonality shared between many of locationist theories is that they include anger, fear, sadness, disgust and happiness as the most reasonable basic emotions. Yet, the theories on basic emotions vary to some extent, since they label various emotions as basic and have heterogeneous underlying concepts (Ekman, Levenson & Friesen, 1983; Ekman & Cordaro, 2011; Izard, 2011; Tomkins, 1984). Ortony and Turner (1990) reviewed several studies on basic emotions and discussed the arising question whether we actually have basic emotions and how these may be characterized. They concluded, that researchers were not able to find an exclusive set of basic emotions yet. Furthermore, there are no sufficient criteria of basicness that are decent among emotion scientists.

On the other hand, proponents of the constructionist approach do not think of emotions as distinct entities with clearly distinguishable characteristics but rather as an occurrence arising from specific but collaborating systems (Barrett, 2006; Lindquist, Wager, Kober, Bliss-Moreau & Barrett, 2012; Scherer, 2005). Barrett (2006a) argues, for example, that investigations do not provide sufficient evidence for the acceptance of a basic emotion theory. According to her, neither studies of subjective experience, facial expressions, behavioural aspects, and related peripheral nervous system responses of emotions, nor research on the neural basis of emotions can reliably prove the concept of basic emotions, or, in her words, “natural-kind” emotions. Instead, she suggests consider categories of emotions as a different and independent cluster of events and to look at their common features.

Discussing the question, whether a theory of basic emotions or a constructionist model provide better explanations about the origin and definition of emotions, is not the aim of the current work. This short review on basic emotion theories is given to illustrate the complexity of the research field. It further reveals that it is favourable to treat finite statements about emotions with caution at this time. Panksepp and Watt (2011) are convinced that the ongoing debate about basic emotion or dimensional emotion models prevents emotion research from progress since both positions underlie the same core idea but are at different levels. They propose the notion of hierarchical organization of emotion regulation in the brain consisting of three levels (primary-, secondary- and tertiary-process level). The primary-process level

includes early evolutionary subcortical processes that produce states, comparable to the concept of basic emotions. At the secondary-process level, emotional learning takes place. Finally, at the tertiary level, emotions become more complex since they are cognitively affected through cortico-subcortical connections. This hierarchical view of emotional processing is more flexible and merges different theories to the same ground. It additionally puts emphasis on the study of neural circuits related to emotions, which is also elucidated in the following section. The present study is not directly based on one of the above-mentioned theories. It rather employs different aspects of these, insofar as stimuli are used that can be assigned to either distinct basic emotions (facial expressions), or to more complex patterns of emotions (emotionally charged scenes). This is described in more detail under point 2.2.

1.3 Neural mechanisms of emotions

Studying anatomical and functional aspects of the neuronal basis of emotions provided new insights in emotion research in general as well as for specific theories. The first neuroscientific investigations were already conducted at the beginning of 20th century. An early neuroscientific approach to defining neural mechanisms of emotions, for example, was proposed by James W. Papez. According to his notion, emotions are generated through a functional circuitry within the brain that consists of thalamic nuclei, hippocampus, cingulate cortex and mammillary bodies. Thus, an emotional signal is generated within the hippocampus, conveyed over the fornix to the mammillary bodies and to the anterior thalamic nuclei, and is further transferred to the cingulate cortex. The cingulate cortex, however, receives input from other regions of the cortex which is described as “emotional coloring” of the signal itself. Additionally, the cingulate cortex transfers information to the parahippocampal gyrus and closes the emotion circuit. Hence, the gyrus cingulus is, in this view, considered as the main receptive region for experiencing emotions (Papez, 1937). Approximately ten years after Papez had stated his theory about the emotion circuitry in the brain, another researcher, Paul MacLean, commented on his work. He described similar brain regions like Papez, to be active during emotional processing, and referred to these structures as the limbic system (MacLean, 1949). The term limbic system is frequently used nowadays when emotional processing is discussed with regard to its

neural correlates. This may be helpful to some extent but it does not cover the entire complexity of emotion networks in the brain (Kringelbach & Phillips, 2014, p.42).

Another influential theory on neural correlates of emotions is the 'somatic marker hypotheses'. 'Somatic markers' describe sensations of bodily changes that produce a mental picture of these. These sensations refer to bodily changes related with emotional states. In theory, their neural representations include the prefrontal cortex (PFC) as an important structure. The PFC receives input from somatosensory areas in the brain, which hold information about actual somatic changes. Furthermore, it serves situational patterns, a person has been previously engaged in. Therefore, it sends efferent signals to areas located within the brainstem and hypothalamus that lead to neurobiological and autonomous reactions (Damasio, 1994).

There is experimental evidence supporting the 'somatic marker hypotheses', suggesting some of the proposed brain regions are actually active during the subjective recall of personal emotional experience. This comprises activation of basal forebrain, orbitofrontal cortex (OFC), insula, cingulate cortex, hypothalamus, amygdala, pons and the midbrain. Researchers concluded that different activation patterns for specific emotions in these areas form complex networks producing a persons' internal state. These varying activation patterns originate from differing somatic changes and have again a descendent influence on the persons' state (Damasio et al., 2000).

More recent research on neural correlates of emotions refers to some of the emotion theories explained above. Lindquist et al. (2012) reviewed different theories on emotion, focussing on the distinction between locationist and constructionist approaches. They state that, following locationists' idea, each emotion category should be located in a single brain region. Thus, many scientists tried to find specific areas in the brain that are functionally selective for processing certain kinds of basic emotions. It is proposed that these are, for example, the amygdala (fear), the insula (disgust), the OFC (anger), and the anterior cingulate cortex (ACC) (sadness). In contrast to this view, Lindquist and colleagues favour a constructionist explanation of the neural basis of emotions. Following this perspective, emotions are not exclusively linked to specific locales within the brain. It is rather likely to assume that there are different clusters, or networks in the brain, that serve different functions, equally involved in generating various categories of emotions. Their meta-analytic results do not support a locationist assumption but they do support a constructionist view. Amygdala activity, for instance, is not restricted to the emotion category 'fear' but is

also found for other categories such as ‘disgust’. This finding also holds for other brain regions under investigation. Therefore, it seems to be more promising to consider emotions as the outcome of functional neural networks serving more basic functions in the process of generating emotions (Lindquist et al., 2012).

It is suggested that there are four to six of these functional neural networks. First, there is a network processing basic sensory input from the body, called ‘core affect’. This ‘core affect’ is processed by the second system that makes the basic sensations meaningful using information from prior learning and memory. It is called “conceptualization” because it links internal concepts with that ‘core affective states’. A third network guides the processes of ‘core affect’ and ‘conceptualization’ through enhancing or suppressing sensations or internal representations which is called ‘executive attention’. In a fourth process, language plays a critical role, since it helps labeling the abstract signals, emerging from the other networks, with “emotion words” (Barrett, 2006b; Lindquist et al., 2012). These networks include different brain regions. Lindquist and colleagues propose, based on their meta-analysis, that ‘core affect’ is represented in a network consisting of amygdala, insula, medial orbitofrontal cortex (mOFC), lateral orbitofrontal cortex (lOFC), ACC, thalamus, hypothalamus, bed nucleus of the stria terminalis, basal forebrain, and periaqueductal gray (PAG). The network, involved in ‘conceptualization’, includes the ventromedial prefrontal cortex (vmPFC), dorsomedial prefrontal cortex (dmPFC), medial temporal gyrus (MTG), and posterior cingulate cortex (PCC). ‘Executive attention’ is represented in a network comprised of the dorsolateral prefrontal cortex (dlPFC) and ventrolateral prefrontal cortex (vlPFC). “Emotion words” and language functions related to labeling are generated in vlPFC and anterior temporal lobe (Lindquist et al., 2012). Kober and colleagues (2008) provide a similar model underlying emotional processing. They introduce six functional groups of brain regions, namely the occipital/visual association group (bilateral occipital gyrus & right occipital/temporal cortex), the medial posterior group (primary visual cortex & PCC), the cognitive/motor group (cortical association routes), the lateral paralimbic group (OFC, insula, ventral striatum), the medial PFC group (ACC, dmPFC), and the core limbic group (thalamus, hypothalamus, amygdala, PAG). These groups are connected with each other in a way that sensory signals like ‘core affective states’ (visual/occipital association group, core limbic, and lateral paralimbic group) are formed into meaningful concepts (medial posterior and medial PFC group). Attention guidance and linguistic

labeling (cognitive/motor group) support these processes in creating emotional, or affective states that are conclusively perceived as 'feelings' (Kober et al., 2008, Lindquist et al., 2012).

These meta-analytic investigations yield convincing evidence for the constructionist model of emotion and challenge the view of a locationist or basic emotion approach. They show that particular brain regions are consistently active across several categories of emotion. Those brain regions can be grouped into functional networks, which facilitate the understanding of emotions since they present a more constant activation pattern for emotions in general. Another view puts emphasis on more basic evolutionary functions that are related to survival. It does not completely counter the constructionist approach but takes other functional mechanisms as a basis of emotions (LeDoux, 2012). The brain regions involved in these mechanisms, however, are comparable to those proposed in the models described before. With the idea of 'survival circuit' mechanisms it is suggested that not taking the concept of emotion into consideration is the best way to understand the same (see also Panksepp & Watt, 2011). So-called 'survival circuits' are instruments that merge sensory information and behavioural responses with the aim to obtain the most adaptive outcome in response to environmental conditions. Based on this assumption, emotional stimuli activate 'survival circuits', for example in response to danger or exposure to potential mates. These processes activate several subcortical brain regions like the amygdala, hypothalamus, and PAG that, in turn, project to cortical association areas and activate a conditioned motor or behavioural response. The conscious identification and characterization of the resulting state is then perceived as an emotion (LeDoux, 2012).

The preceding description demonstrates that there is still no integral explanation of the phenomenon 'emotion'. Neurosciences and its imaging techniques supply evidence supporting different concepts like the constructionist approach or the survival circuit theory. Nevertheless, one can not entirely rely on these concepts. According to LeDoux (2012) "[…] emotions, even so-called basic emotions, are psychological/social constructions, things created by the mind when people interact with the physical or social environment […]" (p. 654). This quotation makes clear that emotions, in the sense we use them, are only loose linguistic forms. Maybe it is more reasonable to follow the proposed models that are more flexible and reliable with regard to their neural basis but in everyday life, we still use emotion words as 'sad-

ness', 'fear', or 'disgust' to communicate about our subjective perception of affect. As also stated in the quotation above, discrete emotion categories are the basis of social and emotional interaction. Therefore, they are still accepted, even in emotion research (see chapter 4). In the current study it is investigated whether different visual emotional stimuli evoke different or similar brain activity. The paradigm includes images of faces expressing distinct basic emotions (fear, sadness, disgust) as well as images of emotionally charged scenes. The aim is to find a visual stimulation paradigm for further fMRI studies that reliably activates similar brain regions, concerning emotional processing, across subjects. Results of the fMRI analysis are discussed within the context of contemporary emotion theories. Subsequently, fMRI studies, using emotional faces and emotional scenes as a stimulus paradigm, are reviewed and the current state of literature is presented.

1.4 Emotional faces vs. emotional scenes – Insights from fMRI research

A growing body of evidence in emotion research stems from modern neuroimaging techniques like positron emission tomography (PET) or functional magnetic resonance imaging (fMRI). As discussed before, researchers in this field do not entirely agree on the question of how emotions are generated and represented in the brain. One reason is that underlying concepts of emotions differ widely. Another reason may be that tasks or paradigms, as used to evoke emotions, vary as well and produce diverse emotional states (visual, auditory, emotional recall, or expression), manifesting themselves in heterogeneous brain activity (see Phan, Wager, Taylor & Liberzon, 2002). In the visual emotional task domain, many studies investigated brain activity in response to emotional faces or emotionally evocative scenes (i.e. Blair et al., 2006; Gur et al., 2002; Kesler et al., 2001; Stark et al., 2003).

Table 1 Brain areas activated selectively for emotional faces and scenes in fMRI studies

Year	First Author	Stimuli	Activated Brain Areas
2006	Blair	Scenes (emotionally negative)	L IFG R MFG L/R amygdala L/R fusiform gyrus
2003	Stark	Scenes (disgust, fear, neutral)	L/R amygdala L/R thalamus L medial PFC L fusiform gyrus
2007	Stark	Scenes (disgust, fear, neutral)	R SFG R IFG L/R ITG L/R supramarginal gyrus L/R mid occipital gyrus L/R superior occipital gyrus L/R insula L mid cingulate gyrus
2003	Wrase	Scenes (emotionally negative)	R amygdala R IFG R MTG R fusiform gyrus L mid cingulate gyrus R ACC L/R temporo-parietal junction
2005	Schäfer	Scenes (fear, disgust, neutral)	L ITG L orbitofrontal cortex L/R MTG L/R amygdala L insula
2001	Kesler	Faces (sad, frightened, neutral)	L IFG L fusiform gyrus
2002	Gur	Faces (happy, sad, anger, fear, disgust)	L/R amygdala L/R hippocampus L parahippocampal gyrus R cingulate cortex L/R fusiform gyrus L/R thalamus L/R IFG L/R occipital lobe
2006	Fitzgerald	Faces (fear, disgust, sad, neutral)	L amygdala L/R IFG L ITG L fusiform gyrus L MFG R MTG L SFG L STG L parahippocampal gyrus
2006	Chakrabarti	Faces (sad, disgust, neutral)	mid occipital gyrus MTG STG Hypothalamus Pulvinar nucleus Claustrum Subcallosal gyrus IFG Lingual Gyrus

		Postcentral gyrus SFG Cingulate gyrus Precentral gyrus Amygdala

Columns contain year of publication, first author, kinds of stimulus material and activated brain regions detected with standard methods in fMRI analysis. *L* indicates left hemisphere. *R* indicates right hemisphere. Abbreviations of brain regions are explained in the *index of abbreviations*.

Findings from fMRI research indicate that emotional faces and emotionally evocative scenes seem to activate a similar set of brain regions. This comprises activation of the amygdala, fusiform gyrus, thalamus, cingulate gyrus as well as the occipital, temporal and frontal cortex areas (see Table 1). With regard to the previous section, these brain areas can be functionally related to networks or structures involved in the processing of emotions. Yet, there are still some differences in activation for emotional faces and scenes. As pointed out at the beginning of this section, methodological aspects and experimental paradigms, as used in fMRI studies, vary to some extent even if they contain analogous stimuli. Hence, it is difficult to directly compare these results. Some researchers, however, have tried to directly compare changes in brain activity, dependent on affective facial expressions and scenes. In a study, conducted by Hariri, Tessitore, Mattay, Fera and Weinberger (2002), the results reveal bilateral amygdala activity in response to fearful and threatening facial stimuli as well as in response to scenes. Experimental results indicate that this activity was greater for faces than for scenes. Both kinds of stimuli additionally activated bilateral posterior fusiform gyri, parahippocampal gyrus, and ventral PFC, being greater for scenes than for faces. In addition, fearful and threatening scenes activated the ACC. The authors conclude that greater amygdala activity in response to emotional facial expressions reflects a biological mechanism of detecting danger, as emanating from other humans. Furthermore, they assume that greater activity in other cortical areas for emotional scenes is related to a more complex processing of these images (Hariri et al., 2002). Another study conducted by Britton, Taylor, Sudheimer and Liberzon (2006), also comparing patterns of activation for the respective types of stimuli, yielded similar results. The authors further included positive emotional stimuli and assessed the subjective rating of valence and arousal induced by the stimulus material. They showed that both stimuli, faces and scenes, activate the amygdala, posterior hippocampus, vmPFC, and the visual cortex. Moreover, significantly greater activation in the STG, insula and ACC was found in response to faces compared to scenes. In contrast, visual cortex activity was significantly greater in response to

scenes compared to faces. It is suggested by the authors that commonalities in activation patterns for faces and scenes reflect basic emotional processes. Greater visual cortex activity for emotional scenes may reflect processes of valence and arousal, which is supported by subjective ratings. Activity in the STG, insula and the ACC is thought to be related to habituation effects since facial expressions are habituated faster compared to scenes, that differ a lot more in content and show novel features in every single image (Britton, Taylor, Sudheimer & Liberzon, 2006).

Sabatinelli et al. (2011) conducted a meta-analysis, investigating differences and commonalities in blood oxygen level dependent (BOLD) signal in response to emotional faces and scenes. Based on 100 studies, using emotional faces, and 57 studies, using emotional evocative scenes as stimulus material, they compared BOLD signal for predetermined clusters of brain regions, excluding brain areas that were active for basic visual processes (using contrasts for emotional relative to neutral stimuli). The researchers expected to find brain activity related to pure emotional arousal for both stimulus types, respectively. Results of the meta-analysis reveal that there is overlap as well as uniqueness within activated brain regions for emotional faces and scenes. Many of the brain regions, like amygdala, medial PFC, inferior frontal cortex, inferior temporal cortex, and extrastriate occipital cortex, are active across both types of stimuli, but there is considerable variability in the extent of this activation. Thus, Sabatinelli et al. (2011) conclude that the respective stimulus type significantly influences the emotional arousal. In addition to the great overlap in brain activity for these kinds of stimuli, faces activate brain regions like fusiform gyrus, STG, MTG, and inferior occipital cortex, that are thought to be related to face processing in general. Emotional scenes, in contrast, additionally activate the following brain regions: lateral occipital cortex, OFC, ACC, pulvinar nuclei, and thalamus.

All listed findings from recent literature on emotional face and scene processing show that there are common and distinct brain areas activated by these types of stimuli. Overlaps within these activated regions may reflect pure effects of emotionality. Differences in activation, however, may be caused by the functions of visual perception and aspects of visual processing of distinct image properties as well as diversity in emotional content. It is expected that emotional faces and scenes will lead to a similar activation pattern in the current study, including a great overlap in brain regions associated with emotion processing and unique effects for the stimulus types, respectively. The major goal of the current study is to answer the question, of

which of the two paradigms and stimulus materials is better applicable to further investigate emotions in healthy populations, as well as emotional dysfunctions in patient populations.

2 Method Section

The methodological section of the present study focusses on actual guidelines for reporting functional magnetic resonance imaging (fMRI) studies as developed by Poldrack, Fletcher & Henson et al. (2008). The use of these guidelines is neither obligatory nor is it uniquely valid across all kinds of functional imaging research. Poldrack et al. (2008) intended to provide a compendium of methodological criteria and aspects of data analyses that are very crucial to understanding and independently replicating fMRI studies. In a recently published review by Carp (2012) the methods reporting in a broad range of fMRI literature is discussed and analyzed. The author states that many researchers neglect to present the critical methodological aspects of their studies. Therefore it is recommended to follow integrative rules in describing a study design.

2.1 Experimental Design

The current experiment investigates neuronal activation in response to different types of emotional visual stimuli, in order to find a set of stimuli that does consistently activate emotional networks within the brain and that provides a basis for reliably studying emotions in patient populations. Since negative affect is associated with higher cerebral blood flow (Lang et al., 1998) both paradigmsonly contain negative emotional stimuli. Furthermore, it is evaluated whether the emotions, that are intended to target, really match the subjective appraisal and how the emotional scenes are rated with discrete emotion categories. Therefore, the fMRI experiments are followed by a behavioural evaluative data assessment. The fMRI measurements are further divided into two single experiments with regard to the emotional stimulus set. Both experiments are based on an experimental within subject design to assess differences in neuronal activation and connectivity as resulting from the visual stimulus set used. These different stimuli are described in the following section. There were two experimental runs for both experiments respectively resulting in a total number of four runs per subject. The stimuli were presented using a blocked design consisting of nine experimental blocks alternating with ten baseline blocks. Each block contained ten stimuli that were presented on the screen for 2000 ms with

an inter-stimulus-interval of 200 ms. Overall duration for every block was 22 s and each run lasted 7 min (Fig. 1).

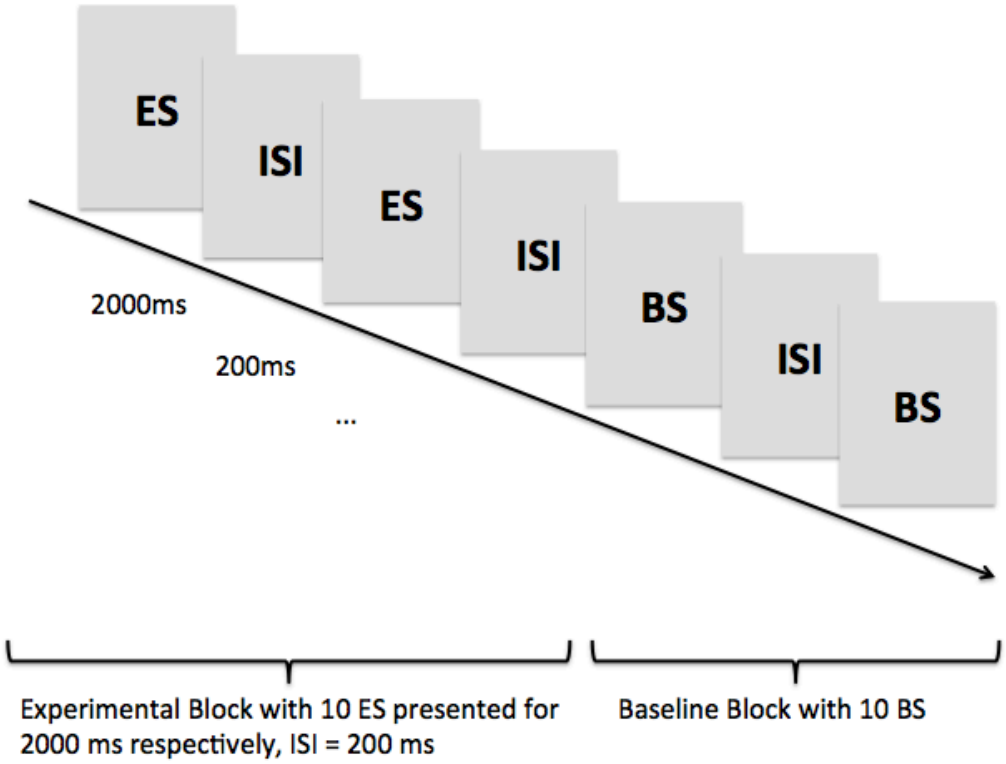


Figure 1 Time course for both experiments; ES = experimental stimulus, BS = baseline stimulus, ISI = inter-stimulus-interval, resulting in total duration of 22 s per block

Subjects were presented with the paradigm over a mirror that reflected the picture generated by a video projector located outside of the scanner room.

2.2 fMRI-experiment

2.2.1 Task and Materials

Participants were presented with two different kinds of stimuli in the respective experiment. During experiment I, named 'face-experiment' in the following text, subjects had to watch images of emotional faces taken from a database, which was developed by researchers at Radboud University in Nijmengen in the Netherlands (Langner, Dotsch & Bijlstra et al., 2010). Each experimental run comprised 90 emotional and 100 neutral stimuli alternating in blocks of ten per emotional or baseline condition. Experiment II, named 'scene-experiment' below, consisted of images of

natural environments that varied significantly with regard to content and emotional value. These images were taken from a database developed by researchers at the Nencki Institute of Experimental Biology in Poland (Marchewka, Żurawski, Jednoróg, & Grabowska, 2014). The 'scene-experiment' included 90 images of natural environments that were emotionally arousing, as well as 30 neutral environments that were repeated randomly across baseline trials. In order to maintain the participants' attention throughout the entire experiment, they had to complete a simple task in both experiments. In the 'face-experiment' subjects had to judge whether the face they watched was male or female, whereas during the 'scene-experiment' they had to decide whether the content of the image was animated or not.

2.2.2 Stimuli

As already described above, stimuli in the 'face-experiment' were taken from the *Radboud Faces Database* developed by researchers at Radboud Universtity in Nijmengen. This database contains portrait images of 39 adult Caucasian males and females expressing different emotions. The images were taken from different camera angles and with varying gaze directions. All models wore black shirts and were photographed against a white background. They had to practise the emotional expressions according to a detailed manual and were instructed by *Facial Action Coding System* (FACS) specialists throughout the entire photo shoot to obtain consistent photographs of the emotional expressions (Langner et al., 2010).

The current study included portrait images of 15 female and 15 male models expressing three different emotions (sadness, disgust, and fear) and a neutral face (for an example see Appendix A). This selection resulted in a total of 30 different images per emotional condition. Since there was only one neutral image per model in the database, neutral stimuli in the baseline condition were randomly repeated across trials.

Stimuli in the 'scene-experiment' were extracted from the *Nencki Affective Picture System* (NAPS), which can be used as an alternative database to the widely used *International Affective Picture System* (IAPS). Developers of this database state that the NAPS has several advantages over the IAPS, e.g. it contains more and higher quality images. The NAPS contains static, high quality photographs of natural environments that are emotionally charged to a varying degree. These photographs were

either taken by the researchers themselves or drawn from the non-commercial photography stock of the Polish newspaper group. They are divided into five categories, namely people, faces, animals, objects, and landscapes (Marchewka et al., 2014). Corresponding to the 'face-experiment', the 'scene-experiment' included 90 emotionally negative charged pictures from all five categories and 30 emotionally neutral pictures that were presented alternately in blocks of ten stimuli (for an example see Appendix A). As for the 'face-experiment', the neutral stimuli were randomly repeated across trials in the baseline blocks.

2.3 Behavioural Experiment

Subsequently to the fMRI session, participants had to perform a second task on a laptop computer. They were presented with the same paradigms as in the fMRI scanning session. In contrast to the first session, they were asked to rate every single picture with regard to their subjective perception of emotion and arousal in a forced-choice response format. The picture, either emotional face or emotional scene, remained on the screen until two responses had been given. In the first step participants had to indicate their experienced emotion, choosing one out of four possible options (neutral, sadness, disgust, and fear). The second step required a subjective rating of their arousal on a 7-point-Likert-scale where 1 represented very low and 7 represented very high arousal. All responses were recorded using the number pad on the keyboard.

2.4 Questionnaires

In addition to the actual experiment, all participants had to fill in five psychiatric questionnaires assessing symptoms of depression and anxiety (the Beck Depression Inventory [BDI-II], Hautzinger, Keller & Kühner, 2006; the Beck Anxiety Inventory [BAI], Margraf & Ehlers, 2007; the Body Sensations Questionnaire [BSQ], the Agoraphobic Cognitions Questionnaire [ACQ] & the Mobility Inventory [MI], Ehlers & Margraf, 2001). This assessment was conducted to possibly identify subjects with depressive symptoms or symptoms of anxiety since these psychiatric con-

ditions might have an influence on the perception and evaluation of emotions and therefore could create a bias in the fMRI-data.

2.5 Subjects

Twenty healthy subjects from a student population (9 males, 11 females; mean age = 24.3 years, SD = 3.6 years) gave written informed consent and participated in the study according to the guidelines of the medical ethics committee of the University of Oldenburg. All subjects were right-handed and did not display any neurological or psychiatric diseases. Furthermore, they did not have any other medical problems and did not receive any medical treatment related to cerebral metabolism and blood flow. One male participant had to be excluded from further analysis because of drug consumption shortly before the experiment started, which was assessed post-hoc to the measurement. Thus, 8 males and 11 females are included into analysis in total.

2.6 Data Acquisition

fMRI data acquisition was performed on a 3-T Siemens MAGNETOM Prisma MRI scanner (Siemens, Erlangen, Germany) with a 64-channel head array. Key presses were recorded with a MR-compatible response keypad (LUMITouch, Photon Control, Burnaby, BC, Canada). Visual stimuli were generated using Cogent 2000 and Cogent Graphics (http://www.vislab.ucl.ac.uk/cogent.php) toolboxes running in MATLAB (MathWorks, 2015b).

The data acquisition included seven measurement sequences that were conducted subsequently in the same order as described in the following text. First, a short "Localizer sequence" [time of repetition (TR) = 3.15 ms, time of echo (TE) = 1.37 ms, field of view (FoV) 260 × 260 mm^2, flip angle $\alpha = 8°$, slice thickness = 1.6 mm, sagittal] with low spatial resolution was performed, in order to locate the brain in relation to the head array within the scanner. Second, a high-resolution structural volume was obtained from each subject using a T_1-weighted magnetization prepared rapid acquisition gradient echo (MPRAGE) sequence (TR = 2000 ms, TE = 2.41 ms, FoV = 230 × 230 mm^2, flip angle $\alpha = 9°$, voxel size = 0.7 × 0.7 × 0.9 mm^3, slice thickness

= 0.9 mm, transversal). Third, a 2-dimensional double-echo, gradient echo field mapping sequence (TR = 400 ms, TE1 = 5.19 ms, TE2 = 7.65 ms, FoV = 192 x 192 mm^2, flip angle α = 60°, voxel size = 3.0 × 3.0 × 3.0 mm^3, slice thickness = 3.0 mm, transversal) was measured to compensate for differences in signal intensity due to artefacts. During the four subsequent functional measurements, 215 T_2*-weighted gradient echo planar imaging (EPI) volumes (TR = 2000 ms, TE = 30 ms, FoV = 192 × 192 mm^2, flip angle α = 80°, voxel size = 3.0 × 3.0 × 3.0 mm^3, slice thickness = 3.0 mm, transversal) were obtained within one session. EPI volumes as well as the structural image were acquired with parallel imaging parameters (GRAPPA, acceleration factor = 2). Volumes consisted of 36 interleaved slices (gap of 0.75 mm) covering the whole brain except for the most inferior parts of cerebellum and brain stem.

2.7 fMRI Data Analysis

fMRI data were analyzed using FMRIB Software Library (FSL) v5.0 (https://fsl.fmrib.ox.ac.uk/fsl) (Jenkinson, Beckmann, Behrens, Woolrich & Smith, 2012; Smith et al., 2004). FSL contains a great variety of analysis tools for different kinds of fMRI data. Among others, it provides the opportunity to analyse structural and functional data according to standard principles, including steps like pre-processing, registration, smoothing, and statistical modeling. Functional data, as obtained in the current experiment, were analyzed using FEAT, which is part of FSL. FEAT is based on general linear modeling (GLM), also known as multiple regression, and affords the option of single-subject and higher-level analyses. Current data were pre-processed and statistically analyzed according to standard principles of fMRI data processing. Single steps of analysis are explained in detail in the following two sections.

2.7.1 Data Pre-processing

In a first step, fMRI data for every subject were transformed from dicom (.dcm) to niffti (.nii) format using a tool called *dcm2niix* (http://www.nitrc.org/plugins/mwiki/index.php/dcm2nii:MainPage) (Li, Morgan, Ashburner, Smith & Rorden, 2016). Subsequently, structural T_1-weighted data were pre-processed using the FSL script *fsl_anat.* This tool performs several processing

steps on the structural data, including reorientation to Montreal Neurological Institute (MNI) standard space, bias-field correction, automatic cropping of the image, registration to MNI standard space, brain extraction, tissue-type segmentation, and subcortical structure segmentation.

One major advantage of the *fsl_anat* script is the bias-field correction. A bias describes artefacts that may arise from multi-coil arrays or high-field scanners and that can cause inhomogeneities in image intensity (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/fsl_anat). This, in turn, may lead to difficulties in tissue-type segmentation, making it difficult to correctly allocate brain structures to grey and white matter (Juntu, Syjbers, Van Dyck & Gielen, 2005). Following this, functional data were pre-processed, using FEAT (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FEAT/UserGuide) in FSL. The order of the pre-processing steps was as follows:

First, the first four images of every sequence were deleted, as these were initial scans ("dummy-scans"). These images served the purpose of magnetization preparation of the scanner and they had been measured before the real experiment started. Second, data were corrected for head motion, since motion within the scanner can produce strong artefacts in the BOLD signal. All images were visually scanned for head motion first, using the movie tool of FSLView (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FslView/UserGuide). Third, motion correction was performed with the tool for linear (affine) inter- and intra-model brain image registration (MCFLIRT) (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/MCFLIRT) (Jenkinson, Bannister, Brady & Smith, 2002). During the process of motion correction, the measured volumes were realigned in a process called co-registration, that means all measured volumes are superimposed onto the middle volume as a reference template, taking translational and rotational parameters of movement into account. Since none of the subjects' head movements exceeded 2 mm, all data were included into the further analysis. Fourth, a process called *B0 unwarping* was conducted. This processing step used the acquired fieldmap images (see section 2.6) to improve registration of the functional EPI data with the respective structural images.

Fifth, functional data were brain extracted, that is all non-brain voxels are removed. Furthermore, data were spatially smoothed with a 8 mm, three-dimensional, full-width-at-half-maximum (FWHM) Gaussian kernel, i.e. spatial high frequency components were removed. This reduced inter-individual anatomical differences in

the registration process (see 2.7.2) and facilitated statistical analysis on the basis of pre-defined dependencies between adjacent voxels (Jäncke, 2005). Sixth and finally, a temporal high pass filter was applied to correct for slow drifts in the BOLD signal that were not caused by changes in experimental conditions. Thus, the proportion of variance due to experimental condition could be increased.

2.7.2 Statistical Analysis of fMRI data

Statistical analysis is conducted to identify significant changes in BOLD signal that can be ascribed to manipulations in the experimental conditions. Therefore, data were first analyzed for each individual subject and experimental run (single-subject analysis), respectively. In a second step, results from these first-level analyses were integrated (higher-level analysis). The rationale of single-subject analysis is based on a regression model, called general linear model (GLM). With this procedure, data are modeled as the linear combination of different explanatory variables or regressors, correspondent to altering conditions or tasks in the fMRI experiment. Every single data acquisition point, referred to as a voxel, is measured throughout the time course of the experiment and correlates with specific stimulation conditions at different time points. That enables the researcher to infer which signal changes can be explained by which particular stimulation conditions (Jäncke, 2005; Monti, 2011).

The GLM approach for statistical fMRI data analysis is implemented in FSL FEAT (see section 2.7.1). Initially, data were modeled for both runs of every individual subject in the 'face-experiment' and in the 'scene-experiment', respectively. In both experiments the emotional stimuli (faces or scenes) were included as explanatory variables into the GLM. Contrasts were calculated for experimental condition versus baseline, so for emotional versus neutral faces and scenes ('emotional faces > neutral faces' & 'emotional scenes > neutral scenes'). Additionally, emotional faces were separated into three discrete emotion categories (sadness, disgust, and fear). These discrete emotion categories were further included as regressors into the model. Contrasts were also calculated for each of these regressors versus neutral faces ('sadness > neutral', 'disgust > neutral' & 'fear > neutral'). FILM prewhitening was applied to improve the statistic by removing temporal autocorrelations before estimating the variables in the model (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FEAT/UserGuide#Pre-Stats). As in the data

pre-processing, a temporal highpass filter was applied to exclude slow temporal drifts in signal change. The initial Z-statistic contrast images were thresholded cluster-wise with Z = 3.1 and p = .001, to correct for multiple comparisons, i.e. dependencies between estimated statistics in single data points (voxels) for a certain condition or explanatory variable (Hsu, 1996).

Before higher-level analysis could be run, data from different individuals and different measurements had to be registered to a standard brain to allow statistical group comparisons. This registration process was also carried out with FEAT in FSL. More precisely, registration incorporated certain tools, called tools for linear (affine)/non-linear inter- and intra-modal brain image registration (FLIRT & FNIRT) (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FLIRT; https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FNIRT) (Jenkinson et al., 2002; Jenkinson & Smith, 2001; Greve & Fischl, 2009). Registration in general included two steps:

First, functional data of every subject were registered to their respective T_1-weighted structural image. This was performed with FLIRT, making use of the fieldmap images (see section 2.7.1). An algorithm called boundary based registration (BBR) was used in this registration step. This algorithm applies white matter instead of grey matter boundaries for EPI to structural registration, which is more robust to confounds in the data (Greve & Fischl, 2009). Second, structural images were registered to a standard brain (in this case FSL's MNI Average152, T1 2 x 2 x 2 mm standard brain) in a non-linear registration process (using FNIRT). A combination of these registered images was then used for higher-level analysis.

Higher-level analysis was based on a mixed-effects model and was carried out with a tool for local analysis of mixed effects (FLAME 1+2) (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FEAT/UserGuide#Group_Statistics), covered in FEAT as well. Mixed-effect models take the within-session across-time variances of the single-subject analyses into account. Outliers in the data were detected and de-weighted automatically.

2.7.3 Region of Interest (ROI)-analyses

Besides the calculated Z-contrast images, ROI-analyses were conducted to investigate mean percentage signal changes in pre-defined areas of the brain. All ROIs were defined as based on the initial exploratory data analysis as well as meta-

analytic results by Sabatinelli et al. (2011) (see also section 1.4). These regions comprise bilateral amygdala, occipital cortex, extrastriate cortex as a more precise part of the occipital cortex, temporal occipital fusiform cortex, occipital fusiform cortex, OFC, temporal-occipital division of inferior and medial temporal gyrus, posterior part of superior temporal gyrus, and left and right Broca's area. Anatomical masks for these regions were created using FSLView and the *fslmaths* function (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FslView/UserGuide; https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/Fslutils). Atlas tools (including Juelich Histological Atlas, Harvard-Oxford Cortical Structural Atlas, Harvard-Oxford Subcortical Structural Atlas, MNI Structural Atlas) in FSLView were used to overlay anatomical regions on a stereotactic brain (FSL's MNI Average152, T1 2 x 2 x 2 mm). These overlaid images were saved as mask images (for an example see Appendix C) and were fed into FSL Featquery (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki/FEAT/UserGuide#Featquery_-_FEAT_Results_Interrogation). ROI-analyses were conducted on the basis of the Z-contrasts images for emotional faces and scenes versus the relative baseline, as well as for discrete emotion category contrasts. These Z-statistics were also fed into FSL Featquery. All masks were binarised before running the actual analysis. Contrast values were converted into percentage signal change values. Mean percentage signal change values were saved for every subject in the particular ROI and compared across subjects between different experimental conditions (face-contrast vs. scene-contrast, discrete emotion categories among each other). Dependent on the distribution of these mean values, both parametrical and non-parametrical, statistical tests were conducted to see which kinds of emotional stimuli evoked greater signal changes in the specified ROIs. Additionally, discrete emotion categories were included as factor levels of an independent variable in univariate analysis of variance (ANOVA).

2.8 Behavioural Data Analysis

Behavioural data were analyzed using MATLAB (MathWorks, 2015b). Individual ratings of the emotional value and arousal of the visual stimuli were recorded and considered with regard to emotion category and their potential to arouse subjects. For the 'face-experiment', mean percentage agreement of discrete emotion category with subjective rating of discrete emotion was calculated. Furthermore,

mean arousal ratings were computed for every single emotion category. For the ‘scene-experiment’ evaluation data were separated into nine blocks, corresponding to the experimental stimulus blocks. It was investigated which discrete emotion category was reported most frequently in every experimental block. Additionally, mean arousal ratings were determined for each block.

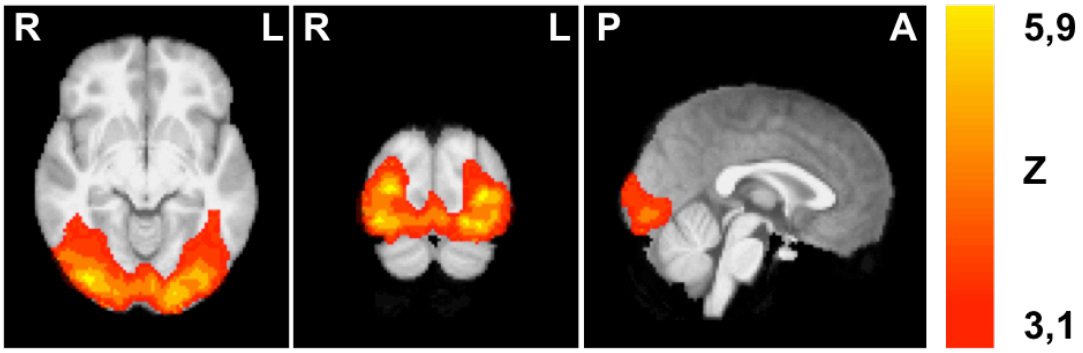
3 Results

In chapter 3 results from all statistical analyses, as described in the method section above, are reported. First, results from fMRI group analyses are presented for both experiments, separately. Then, results from ROI-analysis are shown for a detailed comparison of results from the particular group statistics. Finally, behavioural results are depicted to control for the emotional value of the stimulus material as a whole. All fMRI results are reported in MNI coordinates.

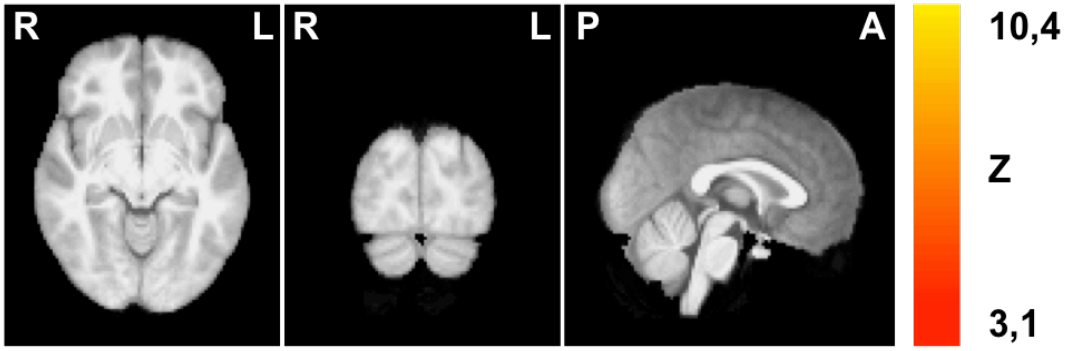
3.1 fMRI Results 'face-experiment'

Results from fMRI data analysis are illustrated and described for the 'face-experiment' first. This also includes contrast calculations for discrete emotion categories. Explorative data analysis in the 'face-experiment' reveals the following result. After correcting Z-statistic activation maps of the group contrast 'emotional faces > neutral faces' for multiple comparisons ($Z > 3.1$, $p < .001$), only one cluster of brain activation reaches significance ($p < .001$). This cluster is very large ($k = 15935$ voxels) and covers most parts of the bilateral visual cortex, the posterior parts of the left and right temporal cortices, as well as temporal and occipital parts of the fusiform gyri (Fig. 2a). Thus, emotional faces in general (sadness, disgust, and fear) evoke stronger BOLD responses in the visual cortex, parts of the temporal cortex and the fusiform cortex in comparison to neutral faces. Coordinates of peak activation are displayed in Table 2. The contrast 'sadness > neutral' does not reveal any significant clusters of brain activity (Fig. 2b). So, sad faces do not evoke stronger brain responses than neutral faces. However, for the other emotion categories, BOLD responses were stronger in relation to neutral faces. In the contrast 'disgust > neutral', there is a similar cluster of activation as in the main group contrast for the 'face-experiment', covering bilateral occipital cortex, posterior temporal cortex and parts of the fusiform cortex (Fig. 2c).

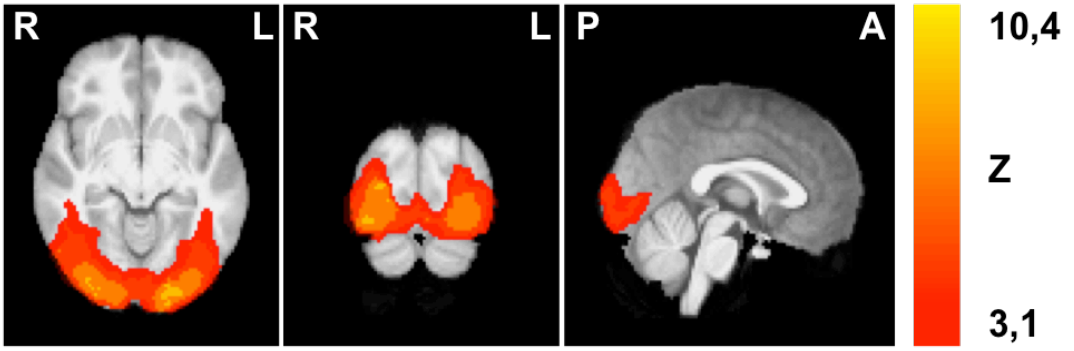
(a)



(b)



(c)



(d)

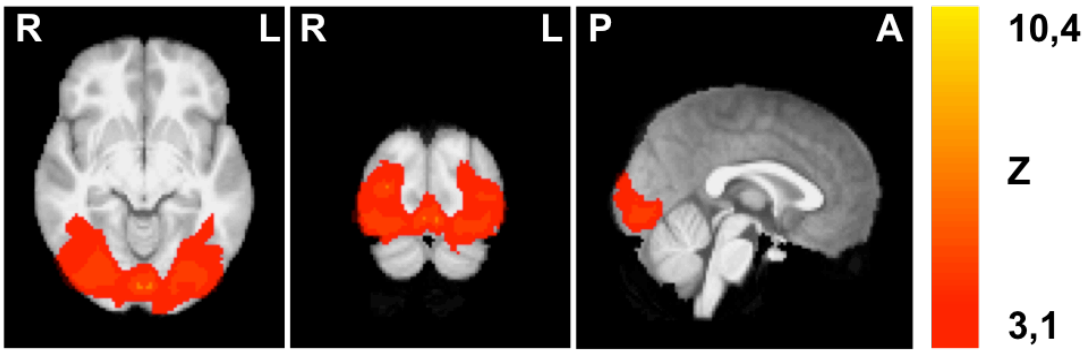


Figure 2 Group brain activation for the emotional 'face-experiment' and the respective contrasts 'emotional faces > neutral faces' (a), 'sadness > neutral' (b), 'disgust > neutral' (c), 'fear > neutral' (d). Results are displayed at [x,y,z] = [0, -86, -8].

A comparable cluster of significant brain activation is also visible for the contrast 'fear > neutral' (Fig. 2d). Peaks of activation exhibit higher Z-values for disgusted faces (Z = 10.4) in comparison to fearful faces (Z = 6.73), indicating stronger activation in an analogous set of brain regions while looking at disgusted faces compared to looking at fearful faces (see Table 3&4). Sad faces did not activate this cluster at all. The influence of these different discrete emotions on the main contrast 'emotional faces > neutral faces' is presented in detail in section 3.3.

Table 2 Coordinates of group brain activation for the contrast 'emotional faces > neutral faces'

Region of Activation	Side	x	y	z	Z
GM Visual cortex	R	30	88	10	5.9
	L	-30	-90	6	5.8
Occipital fusiform gyrus	R	30	88	-12	5.3
	L	-22	-90	-12	5.9
Temporal occipital fusiform cortex	R	44	-48	-18	4.6
	L	-38	-54	-12	4.7
Superior temporal gyrus PD	R	48	-32	6	4.6
Middle temporal gyrus TO	R	54	-38	-2	4.0
Inferior temporal gyrus TO	R	46	-46	-16	4.6
	L	-44	-46	-12	4.6

x, y, z coordinates are reported for the Z-statistic activation maps in MNI space. All reported peak activations are comprised within the same cluster (k = 15935 voxel) for Z > 3.1 and p < 0.001. GM = grey matter, PD = posterior division, TO = temporal occipital part.

Table 3 Coordinates of group brain activation for the contrast 'disgust > neutral'

Region of Activation	Side	x	y	z	Z
GM Visual cortex	R	18	-94	0	10.4
	L	-16	-100	4	10.4
Occipital fusiform gyrus	R	32	-84	-12	8.8
	L	-26	-90	-12	8.7
Temporal occipital fusiform cortex	R	44	-42	-22	7.1
	L	-38	-44	-14	7.1
Superior temporal gyrus PD	R	48	-32	6	7.1
Inferior temporal gyrus TO	R	48	-50	-12	5.3
	L	-44	-46	-12	5.3

x, y, z coordinates are reported for the Z-statistic activation maps in MNI space. All reported peak activations are comprised within the same cluster (k = 17168 voxel) for Z > 3.1 and p < 0.001. GM = grey matter, PD = posterior division, TO = temporal occipital part.

The thresholded Z-activation maps in the group statistics for disgusted and fearful faces seem to largely contribute to the overall group contrast for 'emotional faces > neutral faces', whereas sad faces do not significantly contribute to this activation. It is striking that disgusted faces activate the right superior temporal cortex (PD) and fearful faces activate the right middle temporal cortex (PD). Section 3.3 also

contains further information about direct statistical comparisons of the single discrete emotions in the 'face-experiment'. It is investigated whether the brain displays stronger activation in response to fearful or disgusted faces within specific ROIs.

Table 4 Coordinates of group brain activation for the contrast 'fear > neutral'

Region of Activation	Side	x	y	z	Z
GM Visual cortex	R	4	-86	-8	7.1
	L	-4	-86	-8	7.1
Occipital fusiform gyrus	R	28	-80	-12	7.1
	L	-32	-78	-16	7.1
Temporal occipital fusiform cortex	R	-36	-52	-16	5.5
	L	42	-48	-16	5.5
Middle temporal gyrus TO	R	58	-58	4	3.7
Inferior temporal gyrus TO	R	46	-44	-16	5.4
	L	-44	-52	-16	5.3

x, y, z coordinates are reported for the Z-statistic activation maps in MNI space. All reported peak activations are comprised within the same cluster (k = 17168 voxel) for $Z > 3.1$ and $p < 0.001$. GM = grey matter, PD = posterior division, TO = temporal occipital part.

3.2 fMRI Results "Scene-experiment"

Emotional evocative scenes activate many cortical and subcortical structures. Within the posthoc-corrected ($Z > 3.1$, $p < .001$) activation maps, two clusters reach significance. One cluster is very large (k = 107850 voxels, $p < .001$) and comprises the visual cortex, especially extrastriate visual cortex, temporal and occipital parts of the fusiform gyri, superior parietal lobe, posterior temporal cortex, thalamus, amygdala, hippocampus, insula, pallidum, putamen, superior parts of the brain stem, anterior cingulate gyrus (ACC), Broca's area, and the orbitofrontal cortex (OFC). All of these structures are activated bilaterally. The other cluster is considerably smaller (k = 638 voxels, $p = .0005$) and does only cover the left superior frontal cortex. Coordinates of peak activation can be found in Table 5. BOLD responses for emotional faces and emotionally evocative scenes are specifically compared, using pre-defined ROIs, in the following section. Fig. 3 and 4 show activation maps of the contrast 'emotional scenes > neutral scenes'. The large cluster of activation, containing many different brain structures, listed above, is clearly visible in the axial slices in Figure 4.

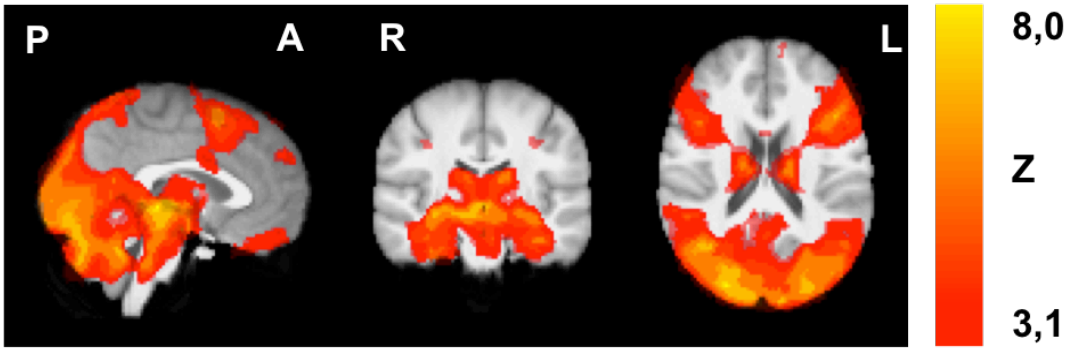


Figure 3 Group brain activation for the emotional 'scene-experiment' and the contrast 'emotional scenes > neutral scenes'. Results are displayed at [x,y,z] = [0, 0, 0].

Table 5 Coordinates of group brain activation for the contrast 'emotional scenes > neutral scenes'

Region of Activation	Side	x	y	z	Z
GM Visual cortex V4[1]	R	40	-74	-14	8.0
	L	-28	-80	-14	8.0
Occipital fusiform gyrus[1]	R	32	-80	-10	8.0
	L	-30	-76	-14	8.0
Temporal occipital fusiform cortex[1]	R	32	-54	-14	8.0
	L	-36	-60	-14	8.0
Brain stem[1]	R	4	-30	-4	8.0
Cerebellum[1]	L	-6	-78	-40	7.9
Amygdala[1]	R	24	-4	-18	6.8
	L	-24	-4	-18	5.8
Hippocampus[1]	R	34	-28	-12	5.7
	L	-28	-28	-16	5.8
Thalamus[1]	R	18	-28	4	6.9
	L	-16	-30	4	5.8
Pallidum[1]	R	20	-4	4	5.8
	L	-18	-4	4	5.8
Broca's area BA44[1]	R	50	14	24	5.7
	L	-50	12	32	6.7
Broca's area BA45[1]	L	-48	20	24	6.8
Orbitofrontal cortex[1]	R	28	26	-18	5.8
	L	-40	28	-18	5.7
Superior frontal gyrus[2]	L	-6	52	46	6.7

x, y, z coordinates are reported for the Z-statistic activation maps in MNI space. All reported peak activations are comprised within two clusters for $Z > 3.1$ and $p < .001$. 1 = cluster 1 (k = 107850 voxels). 2 = cluster 2 (k = 638 voxels). GM = grey matter, BA = Brodmann area.

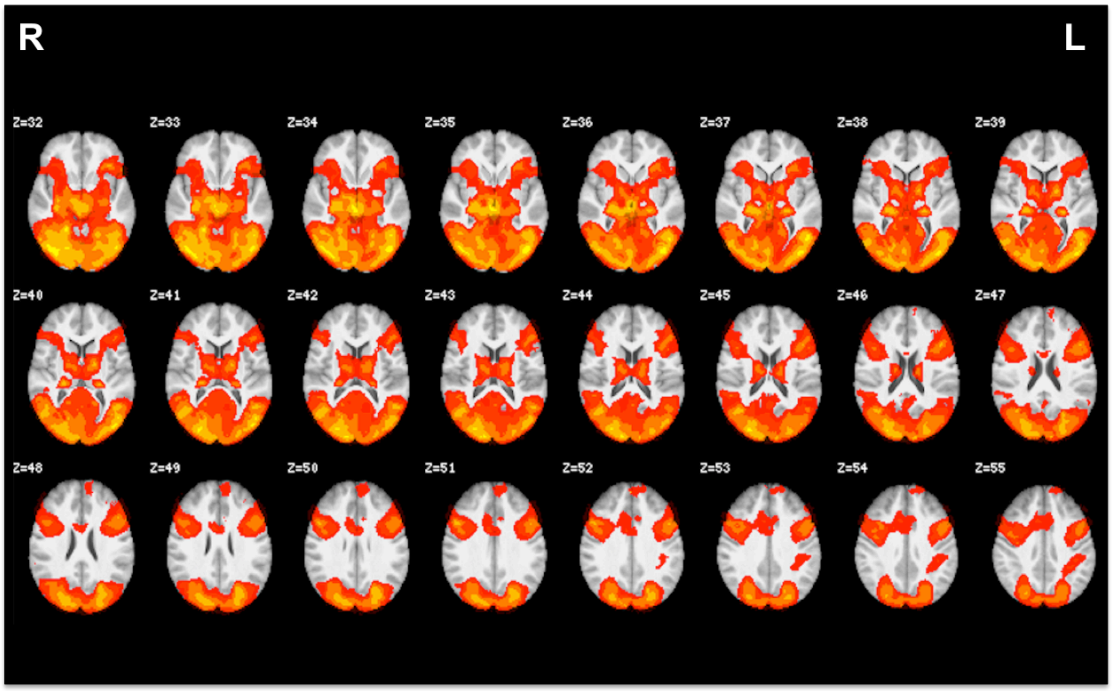


Figure 4 Group brain activation for the emotional 'scene-experiment' and the contrast 'emotional scenes > neutral scenes'. Results are displayed in axial slices.

3.3 Results Region of Interest (ROI)-analyses

ROI-analyses were conducted to compare BOLD responses for both experiments in specific brain regions. Additionally, single emotion categories in the 'face-experiment' were examined with regard to differences in brain activity. Mean percentage signal changes were calculated for thirteen ROIs in both experiments, respectively. These were again subjected to suitable statistical procedures to test whether BOLD responses were significantly stronger for one type of stimulus material.

The Shapiro-Wilk test reveals that mean percentage signal changes in three ROIs are not normally distributed. This affects amygdala, extrastriate occipital cortex and superior temporal gyrus. Therefore, a parametric test to compare signal changes between 'face-experiment' and 'scene-experiment' is not adequate. Instead of t-tests, Wilcoxon signed rank tests were conducted for data in these three ROIs. Remaining data from the other ten ROIs, were compared, using paired one-sample t-tests. The results of the Wilcoxon test reveal that mean percentage signal changes for the 'scene-experiment' are significantly greater than for the 'face-experiment' in the amygdala, $Z = -3.803$, $p < .01$ and in the extrastriate occipital cortex, $Z = -3.803$, $p < .01$. In contrast, signal changes in superior temporal gyrus for both experiments were not

significantly different from each other. Fig. 5 displays boxplots for the comparisons in these ROIs. Significances, as reported above, are visible for the first and second comparisons.

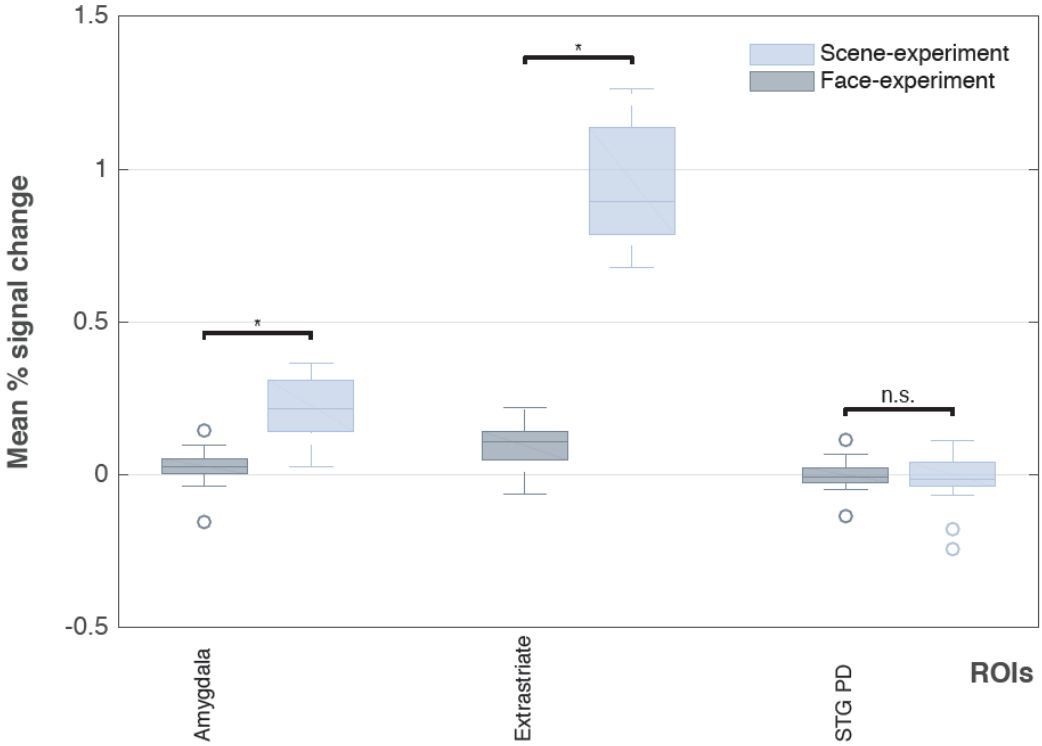


Figure 5 Boxplots showing the distributions of mean percentage signal change in three ROIs, including amygdala, extrastriate occipital cortex, and superior temporal gyrus, posterior division (STG PD). Black bars indicate results of pairwise comparisons between both experiments; * $p < .05$.

T-test results indicated significant differences for all further comparisons in the ROI, i.e. significantly greater mean percentage signal changes for the 'scene experiment' compared to the 'face-experiment' in the occipital cortex, temporal-occipital fusiform cortex, occipital fusiform cortex, OFC, temporal-occipital divisions of inferior and middle temporal gyrus, and in the left and right Broca's areas. Test statistics are provided in a table for ten ROIs (see Appendix D). Considering Fig. 6, it is observable that signal changes in all defined ROIs are greater in the 'scene-experiment', as already stated further above.

Looking at differences in signal changes with regard to discrete emotion categories in the 'face-experiment', univariate ANOVA was conducted. Preliminary test of variances revealed no significant inhomogeneities. Based on these homogeneous variances discrete emotions (sadness, disgust, and fear) were included as factor lev-

els into the ANOVA model. The effects of single emotions on mean percentage signal change in eight ROIs were examined.

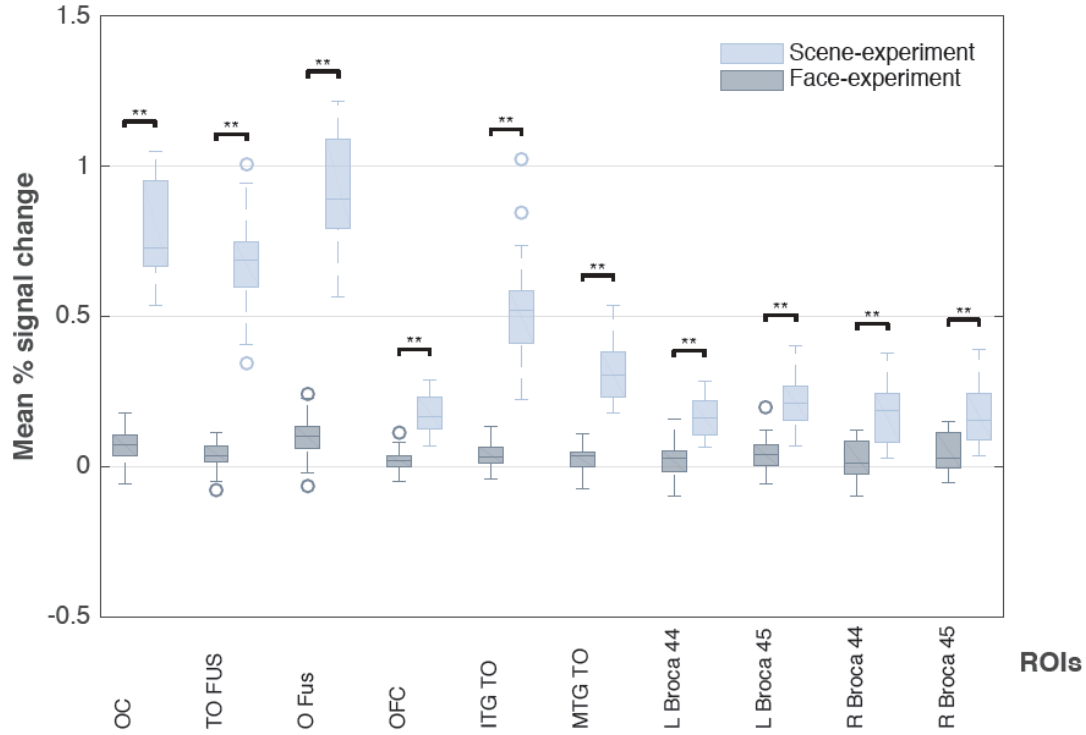


Figure 6 Boxplots showing the distributions of mean percentage signal change in ten ROIs, including occipital cortex (OC), temporal-occipital fusiform cortex (TO FUS), occipital fusiform cortex (O FUS), orbitofrontal cortex (OFC), temporal-occipital divisions of inferior and middle temporal gyrus (ITG TO, MTG TO), and left and right Broca's areas (L Broca 44, L Broca 45, R Broca 44, R Broca 45; L = left, R = right, numbers indicating different Brodmann areas). Black bars indicate results of pairwise comparisons between both experiments; ** $p < .01$.

Univariate ANOVA results indicated a significant effect of single emotions on mean percentage signal change in all ROIs, except for amygdala and STG PD. Detailed statistics are provided in Appendix D. Posthoc Bonferroni correction was additionally applied to account for multiple comparisons and to compare discrete emotion category effects with each other. In the occipital cortex, mean percentage signal change was significantly different between the emotion categories 'sadness' and 'disgust', as well as between 'sadness' and 'fear. This result was also true for the extrastriate cortex, temporal occipital fusiform cortex, occipital fusiform cortex, and the inferior temporal gyrus. In the middle temporal gyrus, mean percentage signal change was significantly different between 'sadness' and 'fear', but not between the other categories. Mean values, standard errors, p-values and confidence intervals are reported for Bonferroni pairwise comparisons in Appendix D.

Summarizing the results, it can be observed that signal changes within all ROIs, except one, are significantly greater in the 'scene-experiment' compared to the 'face-experiment'. There was no significant difference in signal change in superior temporal gyrus. Furthermore, discrete emotion categories had an effect on signal change within some ROIs, as reported above. Excluding the middle temporal gyrus, there were significant differences between sad faces and faces with other emotional content. In the middle temporal gyrus, there was only a significant difference between sad and fearful faces.

3.4 Behavioural Results

Both experiments included a behavioural follow-up, i.e. subjective ratings of image characteristics with regard to particular emotion categories and arousal were assessed. For the 'face-experiment' it was investigated whether the subjective rating of the emotion categories matched the target-emotion in the respective experimental block. For the 'scene-experiment' most frequent indication of a discrete emotion category was calculated for nine experimental blocks, respectively. Arousal ratings were examined on a 7-point Likert scale. Figures 7a-d show the results for both experiments separately.

The most frequently reported subjective emotion category within the 'scene-experiment' is 'sadness'. This discrete emotion category was indicated for blocks 1 to 7. In block 8 and 9 the most frequently reported discrete emotion was disgust (Fig. 7c). In the 'face-experiment' subjective ratings of emotional faces matched the target emotion in every category between 55-65%. Within the category 'neutral faces' agreement between rating and target category was over 90% (Fig. 7a). Mean arousal ratings in the 'face-experiment' lied between 2 and 3 for all three discrete emotions, indicating low to medium arousal. Neutral faces were rated with 1, implying very low arousal (Figure 7b). Emotionally evocative scenes were rated slightly higher with regard to the arousal level. Mean arousal ratings varied between 3 and 4 across experimental blocks, demonstrating more medium arousal. Outliers, depicted by circles in Fig. 7b&d, show that there were strikingly more single ratings within the very high arousal range for emotionally evocative scenes compared to emotional faces.

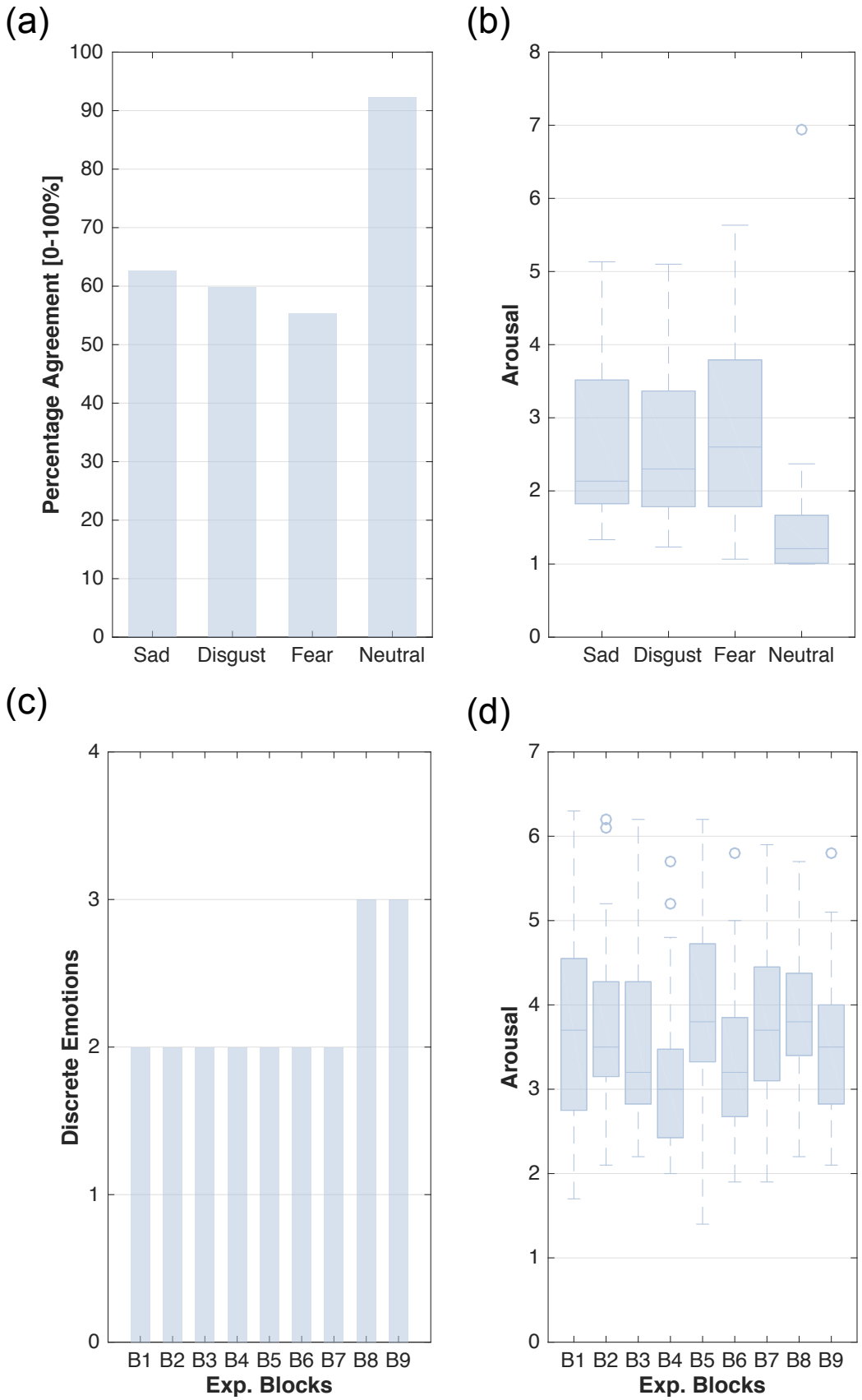


Figure 7 Emotion and arousal ratings. Faces: Percentage agreement between target emotion and subjective rating with discrete emotion category (a). Mean arousal ratings for every emotion category across several blocks (b); Scenes: Most frequently indicated emotion for every experimental block (c). 1 = neutral, 2 = sad, 3 = disgust, 4 = fear. Mean arousal ratings for every emotion category across several blocks (d), 1 indicating very low and 7 indicating very high arousal.

4 Discussion

This study produced a wealth of results, as presented in the preceding text, that are discussed in the following sections. First, the results are discussed individually for both experiments. This includes a discussion of BOLD activity and behavioural data for faces and scenes on the basis of the literature in this field. Aspects, elucidated in chapter 1, especially 1.3 and 1.4, are integrated into the discussion of the results. In a second step, the experiments are compared with each other, taking ROI-analyses into account, and the outcomes are treated, including the different perspectives on emotion, as described in section 1.2. Aim of the discussion is to arrive at a plausible conclusion regarding the different aspects of emotion and their neural representation within the brain, as related to the visual stimulus paradigms used in the present study. Finally, it is attempted to answer the research question, i.e. which of the two paradigms and stimulus materials is most suitable to further investigate emotions and related topics in patient populations.

4.1 Experiment I: Emotional Faces

The explorative data analysis in the 'face-experiment' has one main outcome: Only a single cluster appears to be significant for the contrast 'emotional faces > neutral faces'. Similar activation patterns become apparent in the contrasts 'disgust > neutral' and 'fear > neutral' but with different Z-statistics, indicating stronger BOLD responses for disgusted than for fearful faces. Sad faces, in contrast, do not significantly activate any other brain regions than neutral faces. All of these contrasts show peaks of activation in bilateral occipital cortex, fusiform gyri, and temporal occipital parts of the temporal lobes. There is one peak of activation in right STG for the contrast 'disgust > neutral' and another peak of activation in right MTG for the contrast 'fear > neutral' (see 3.1).

The results are compared to recent findings in the literature including processing of faces in general, as well as processing of facial emotions, focussing on negative emotional expressions. Face processing in general is thought to be localized in a group of brain regions, including fusiform cortex, inferior occipital cortex, and superior temporal sulcus (STS) (Haxby, Hoffman & Gobbini, 2000). Haxby et al. (2000) propose a system consisting of a part that incorporates basic visual functions,

represented in the inferior occipital regions, and of different parts that undertake several functions, such as guiding spatial attention, processing emotional content of an expression, auditory verbal comprehension of speech, and integration of biographical information about facial aspects. These functions are again represented in different regions of the brain. Processing emotional content of a facial expression, for example, is supposed to be mainly located in the amygdala and insula. Some neuroimaging studies support these assumptions, insofar as they found amygdala activity in response to fearful and also sad faces and insula activity in response to disgusted faces (see Hariri et al., 2002; Phillips et al., 1998; Sprengelmeyer, Rausch, Eyzel & Przuntek, 1998). This idea coincides partly with the locationists approach to defining emotions (see chapter 1.3). According to this idea, certain discrete emotion categories are thought to be represented by definable brain structures. However, this notion is countered by other studies that do not show activation in distinct brain regions for different emotional expressions. Winston, O'Doherty and Dolan (2003) demonstrated, for example, that different discrete facial emotions activate a similar set of brain regions containing the amygdala, extrastriate cortex, fusiform cortex, and the STS. These findings are further affirmed by studies that used other emotional stimuli, e.g. emotional scenes, searching for neural substrates of discrete emotion categories. Many of these studies show that there are no distinct neural structures, processing different discrete emotions, especially with regard to the discrete emotion categories 'disgust' and 'fear' (Schäfer, Schienle & Vaitl, 2005; Schienle et al., 2002; Stark et al., 2003). Furthermore, Schienle et al. (2002) and Stark et al. (2003) found significantly greater activity in visual cortex and occipital-temporal areas, which is in accordance with findings from the present study (see 3.1). The stronger activation of occipital cortex and occipital-temporal areas, like fusiform gyrus, in response to emotional faces compared with neutral faces is considered to be due to higher arousal, produced by the affective component of the stimulus (Lang et al., 1998). The results of the behavioural data analysis revealed higher arousal ratings for emotional in contrast to neutral faces (see 3.4), which underpins this theory. Thus, the findings support the argument that there are no brain structures selectively activated in response to discrete emotion categories. It is rather likely to assume that there is a common cluster of brain regions, spanning the entire visual cortex, fusiform cortex, and the posterior parts of temporal cortex that is activated in response to facial expressions of different negative discrete emotions (especially disgust and fear). Since

‘sad’ faces, in this study, do not significantly activate any other brain structures than ‘neutral’ faces, it can be that these emotional expression is not clearly distinguishable from the neutral expression (see Appendix A). This is discussed in detail below. A comprehensive meta-analysis by Fusar-Poli et al. (2009) concatenates both perspectives on the representation of facial expressions of different emotions in the brain. The authors found that there is common neural network active in processing emotional faces in general, including the visual cortex, fusiform cortex, and the temporal cortex. In addition, some brain structures are selectively activated by discrete facial emotions. For example, disgust significantly activated bilateral insula, whereas fear activated bilateral amygdala. The current study was not able to reproduce the latter finding as presented in this meta-analysis, but it is in accordance with the former one. Perhaps, it is possible that facial emotional stimuli in this study, drawn from the Radboud Faces Database (see 2.2.2), are not sufficiently emotionally charged to evoke differential neural responses with regard to discrete emotion categories. As already described above, ‘sad’ faces and ‘neutral’ faces do possibly not differ much. By looking at the percentage agreement of subjective emotion appraisal and target emotion in the ‘face-experiment’ (Fig. 7a), it emerges that the ratios for each discrete emotion category are located in a range between 55% and 65%. These ratios are not very high and there is a residual chance of 35-45% that emotional faces were not identified correctly leading to mixed neuronal responses across subjects. An electrophysiological study provides evidence for a differential processing of faces in general and their emotional content at slightly different time points (differences in a range of few ms). According to the authors of this study, recognition of faces occurs earlier than processing of facial expressions and the emotional content. Source analysis further revealed that processing of emotional faces could be allocated to the bilateral middle and superior temporal cortices across emotions whereas discrimination of emotional content is rather located in frontal areas of the brain (Batty & Taylor, 2003). These findings stress the importance of timing with regard to emotion processing in the brain. Since fMRI lacks in temporal resolution, discrimination processes may not be detected at all, using a block design as in the current study. In addition, Schäfer et al. (2005) considered the possibility that event-related designs might have advantages over block-designs in studying emotions using fMRI, as habituation effects could develop in blocks with similar visual stimulus material, e.g.

same facial expressions, diverting the attention from the stimulus and the emotional expressions.

Another reason that has to be discussed in this context refers to other methodological aspects including experimental paradigms and tasks, as well as methods of fMRI data analysis. An influential study by Hariri et al. (2002), cited more than 2200 times, detected amygdala activity, as well as laterality effects in this brain region, in response to fearful and threatening facial expressions (see 1.4). The results of this study are based on uncorrected statistical thresholds, as stated in their descriptions of the data analysis. The problem with uncorrected statistical methods in neuroimaging research is that Type I error, i.e. the error of accepting a hypothesis when the results may occur by chance, can be very high. In other words, it is possible to obtain significant results that are highly affected by 'false-positives' because of the multiple comparisons problem (see 2.7.2). This, in turn, can cause problematic results and misinterpretations about the questions investigated (Benett, Wolford & Miller, 2009). Eklund, Nichols and Knutsson (2016) even scrutinise the validity of a large body of fMRI research since many studies do not use proper methods to correct for 'false-positives'. Therefore, it is important to correct estimated statistics for these errors to produce valid and interpretable results. The present study includes cluster-based correction for multiple comparisons at threshold $p < .001$. Thus, the results, found in the 'face-experiment' and already discussed above, are likely to be valid and display advantages with regard to interpretability compared to the results by Hariri and colleagues (2002). Taking uncorrected statistical activation maps of the current experiment into account might provide even more evidence for this argument. When looking at the uncorrected contrast images it is evident that the amygdala is also active in response to emotional faces (Appendix E). Other authors were also not able to detect differential neural responses for discrete emotion categories, after correcting for multiple comparisons (e.g. Winston et al., 2003). Villalta-Gil et al. (2017) specifically investigated amygdala activity in response to different emotional tasks. Among others, they used emotional faces as stimuli in their paradigms. They were only able to detect amygdala activity in the face condition comparing emotional faces with geometrical shapes but not in comparison to neutral faces. Detected amygdala activity across tasks did not survive correction for multiple comparisons. Instead of amygdala activity, they found enhanced, stable visual cortex activity in response to negative affective stimuli across tasks. The findings of these studies

are consistent with the current results and support the importance of statistically correcting fMRI data for the Type I error. Moreover, it is recommended by some authors to make use of mixed-effects models in contrast to random-effects models for group analysis in fMRI research. A mixed-effects model accounts for between-subject variance by including information from first-level analyses (fixed effects), which again advances the group statistics (Thirion, Pinel, Mériaux, Roche, Dehaene & Poline, 2007). FEAT's FLAME analysis tool, as used in this study, applies a mixed-effects model to the data (see 2.7.2). Hence, the group statistics are more robust in comparison to the statistics computed in the study by Hariri et al. (2002). A further argument, also referring to methodological aspects of emotion studies, focuses on the task incorporated in a study design. Gur et al. (2002) claim that amygdala activity is likely to be induced by emotional task instead of the emotional content of the visual stimulus itself. Hence, it is possible that amygdala activity was not found in this study, since there was no emotional task, but only a simple task to maintain participants' attention during the experiment.

Comprising the discussion of the 'face-experiment', it is obvious that methodological issues play an important role in fMRI research about emotions. The ongoing question whether there are discrete emotions and whether these are represented in single entities of the brain cannot be solved with regard to this study. The results and findings from recent literature suggest that emotional faces are processed by a common cluster of brain structures, located mainly in the primary visual cortex, extrastriate areas of occipital cortex, fusiform gyri, and the posterior parts of temporal cortices. It is possible that neural effects of discrete emotions have not been detected in this study, in contrast to similar studies in this field, since these are dependent on very accurate timing effects. Therefore, discrimination between discrete emotions can possibly be studied more effectively using event-related designs. Additionally, it is questionable, whether results from other studies, especially those using uncorrected statistical computations, are ecologically valid. That again leads to the question, whether the amygdala, which is expected to be a core region in processing discrete emotions, is really involved in this process. Perhaps, it is rather active when the emotional content of a stimulus is relevant for a task implemented in a study. The suitability of the stimulus material and study design, used in the current experiment, is further discussed with regard to the 'scene-experiment' in section 4.3.

4.2 Experiment II: Emotional Scenes

In contrast to the ‚face-experiment', the ‚scene-experiment' only included one contrast within the scope of explorative data analysis. The difference in brain activity, as evoked by emotionally charged scenes in comparison to neutral scenes was investigated. Discrete emotion categories were not investigated in this part of the study. Two clusters of brain regions showed significant activation for the contrast 'emotional scenes > neutral scenes'. One cluster comprises many cortical and subcortical structures as reported in section 3.2. The other cluster does only cover the superior frontal gyrus. All detected activation patterns were still significant after cluster-wise correction ($p < .001$) for multiple comparisons.

The results of the present experiment are consistent with the results of other studies investigating brain activity in response to emotional scenes. Activated brain regions in response to emotional scenes are very similar across studies, including the visual cortex, temporal cortex, thalamus, amygdala, pulvinar, ACC, OFC and the PFC (see Sabatinelli et al., 2011) (section 1.4). An equivalent set of brain regions was also found in the present experiment. These brain regions likely reflect different functional aspects in processing the affective visual scenes and have to be discussed in detail.

Bilateral occipital cortex, especially area V4 in the extrastriate cortex, shows enhanced activation in response to emotional scenes. Neurons in extrastriate cortex area V4 are thought to be active during the guidance of spatial attention (Raftopoulos, 2014; Wolmersdorf, Bosman & Fries, 2013). Furthermore, it is proposed that area V4 is connected to other regions, like the frontal eye fields, and that it incorporates the function to shift spatial attention to certain target objects in natural scenes (Eimer, 2014). Thus, it is possible that peak activation in area V4, as present in the 'scene-experiment', is related to spatial attention processes with regard to emotional content. Since activation in V4 is greater for emotional relative to neutral scenes, guiding spatial attention to emotionally salient objects seems to strongly activate this brain region. Another region that is highly activated during the presentation of the emotional scenes is the OFC. This region is expected to play a critical role in object perception and identification through integrating affective information into early perceptual processes (Cardinal, Parkinson, Hall & Everitt, 2000; Raftopoulos, 2014). Some researchers further distinguish between medial and lateral OFC, possessing different functions. While the medial OFC is considered to use low spatial frequency

information to attribute affective relevance to an object and to influence motivation, the lateral OFC integrates sensory information as well as high spatial frequency visual information to create a more precise representation of an object (Barett & Bar, 2009). In addition to these brain areas, further peaks of activation were found in the amygdala and the thalamus. Activity in both brain structures was consistently found in response to affective visual scenes across previous fMRI studies (e.g. Schienle et al., 2002; Stark et al., 2003). Thalamus activity, or especially activity in certain nuclei of the thalamus, namely the pulvinar and the medial dorsal nucleus, seem to play an important role in guiding attention. Additionally, the pulvinar is connected to parietal and temporal cortical areas and the medial dorsal nucleus exhibits connections with frontal cortex areas (Buchsbaum, Buchsbaum, Chokron, Tang, Wei & Byne, 2006). Although both nuclei have similar functional roles, the pulvinar is especially thought to be involved in visual attention by discriminating a target object from surrounding objects in a natural scene (Michael & Desmedt, 2004; Snow, Allen, Rafal & Humphreys, 2009). The medial dorsal nucleus, in contrast, seems to have a mediating function, integrating information from frontal cortex areas into attention processes (Buchsbaum et al., 2006) (see discussion of OFC function above). Activation in the amygdala is often related to fear and threat inducing visual stimuli (e.g. Vilalta-Gil, 2017). Yet, its explicit function in processing emotional stimuli is still unclear. Sabatinelli, Lang, Bradley, Costa and Keil (2009) suggest that the amygdala is specifically responsible for differentiating between emotional and non-emotional scenes, while being highly connected to visual cortical areas. Despite the low temporal resolution of fMRI data, Frank and Sabatinelli (2014) found evidence for a functional network, comprising visual cortex, fusiform cortex areas, amygdala and thalamic nuclei, as described above, that is selectively activated during the processing of emotional visual scenes. They propose that early emotional and visual information from amygdala and fusiform gyri influence visual attention through thalamic routes having an impact on motivational behaviour. Present data in the 'scene-experiment' are highly coincident with this theory. However, it makes sense to include other brain regions like OFC and extrastriate occipital regions into this network, since these are also closely related to visual attention processes while viewing emotional scenes.

In addition to the brain areas discussed above, emotional scenes did also activate the ACC, bilateral Broca's area, and the brain stem. Activity in the ACC could

be related to the cognitive evaluation of negative emotions (Ochsner & Gross, 2005). Therefore, it is possible that consciously thinking about the emotional scenes in the current experiment, as well as judging the emotional content was reflected by ACC activity. Among others, specifically lateral inferior frontal cortex activity (especially left-lateralized) is thought to be linked to inner emotion regulation strategies, e.g. silent self-oriented speech or evaluation of affect (Morawetz, Bode, Baudewig, Jacobs & Heekeren, 2016). Since Broca's area is located in the lateral inferior frontal cortex, it is likely that the activation found in the current experiment can be associated with evaluation and appraisal functions with regard to the experienced emotions. Especially the influence of inner speech and linguistic concepts may be important in evaluating emotional scenes, reflected by activity in the Broca's area. There was another peak of activation in superior brain stem regions in response to emotional scenes as well. This activation can be due to subliminal processing of emotions, especially the processing of fear. Liddell et al. (2005) suggest that there is network consisting of the amygdala, brain stem, thalamus, and cortical regions, which is active during the unconscious perception of fear signals. They claim that this system acts very fast to respond rapidly to possible sources of danger. In accordance with the present results, activity in superior parts of the brain stem may reflect a fast neural response to threatening emotional stimuli that are perceived before being processed explicitly. Although behavioural data, as presented in section 3.4, show that emotional scenes are most frequently rated with the discrete emotion category 'sad', it is possible that images are unconsciously scanned for threatening stimuli resulting in activity of the 'brainstem-amygdala-cortical network'. Together with the theory by Frank and Sabatinelli (2014), as discussed above, it is likely that the processing of complex visual affective scenes requires at least two functional neural networks. One network is a fast acting one, consisting primarily of subcortical structures, like the brain stem, amygdala and thalamic nuclei, and that provides a survival mechanism by detecting and reacting onto potential elicitors of threat. The other network, including subcortical and cortical brain structures, like the extrastriate visual cortex, amygdala, thalamus, OFC, ACC, and the inferior frontal cortex, is responsible for the conscious perception of emotionally evocative scenes. It entails a system for guiding attention to emotional target stimuli within a natural scene and it comprises cortico-subcortical interconnections for evaluating the emotional content of an image. Therefore, it is reasonable to suppose there are distinct networks within the brain that pos-

sess different functional roles with regard to emotions and that engage different brain structures to be most adaptive in various situations. As explained in section 1.3, LeDoux (2012) suggests an emotion model that is based on so called survival circuits. Dependent on the respective situation (danger, social interaction, mating, etc.) different brain networks are active to process the emotional content of a situation and to produce the most adaptive response strategy.

Summarizing the results of the 'scene-experiment' it is most likely that different neural networks process the complex visual input. According to whether the emotional content is threatening or not, the emotional scene is either evaluated implicitly or explicitly to produce a fast behavioural response in the case of danger and a slower, more cognitively influenced response otherwise. Whether the emotional scenes, used in this study, are well suited to further investigate emotions in other populations is discussed in the following section.

4.3 Emotional Faces vs. Scenes: A comparison of the two paradigms

The separate discussion of the 'face-experiment' and the 'scene-experiment' lead to similar as well as different results in respect of the underlying neural basis for processing emotions. As discussed in section 4.1, emotional faces (disgust and fear) relative to neutral faces activate a cluster consisting of visual and temporal cortical regions, especially extrastriate and fusiform cortex. In contrast to previous studies, emotional faces did not activate brain regions like the amygdala, or the insula, which have been shown to respond to discrete emotional facial expressions before (see Fusar-Poli et al., 2009). The absence of significant activation in response to sad faces might be related to the stimulus material itself, since 'sad' faces did not differ much from 'neutral' faces. However, the general lack of differences in brain activation for distinct emotion categories can be explained when taking methodological issues into account. As also already discussed above, means of fMRI data analysis play an important role in obtaining valid results. Previous fMRI studies did often not correct their statistics for multiple comparisons (see Hariri et al., 2002), which causes problems in terms of interpretability of results (see Eklund et al., 2016).

Emotional scenes, as discussed in the previous section, evoke BOLD responses in a large cluster of brain areas, including many cortical, as well as subcortical regions. These regions are expected to be part of two functional neural networks

that process emotions, dependent on conscious or unconscious perception, and with regard to their influence on adaptive behavioural responses. This activation patterns can be related to an emotion theory from the researcher LeDoux (see section 1.3 and 4.2). Emotions are ascribed a pure functional role in his theory of 'survival circuits'. Following this theory, it is also not very useful to discriminate between single emotion categories but rather between the functional purposes of emotions. This is also in accordance with the 'constructionist approach' of explaining emotion (see 1.3). The present findings support these emotion theories, supported by similar brain responses across emotion categories in the 'face-experiment' and the likely activation of different functional neural networks with regard to emotion in the 'scene-experiment'.

Behavioural data indicate that only 55-65% of the emotional faces were identified correctly. Emotional scenes were most frequently experienced as 'sad'. Thus, it is questionable, whether emotional faces did really evoke emotional responses as proposed to be targeted. Perhaps, even discrete emotional facial expressions lead to mixed experiences of emotions, being similar across conditions. This is supported by equivalent activation patterns across emotion categories. Since emotional scenes seem to be experienced as 'sad' in most cases, it is possible that they have an influence on empathy as well. A discussion of this would be beyond the scope of the current study but it has to be kept in mind. Yet, non-conscious perception of emotional scenes may also lead to brain activity related to processing of fearful or threatening stimuli. Therefore, it is possible that scenes produce a mix of subjectively experienced emotions, even though this is not consciously evaluated. Furthermore, arousal ratings in the 'scene-experiment' were considerably higher compared to the 'face-experiment'. This is reflected by brain activity in areas involved in attention processes, like extrastriate V4, OFC, and thalamic nuclei (see 4.2).

ROI-analysis shows that signal changes in response to emotional scenes were significantly greater relative to emotional faces in all ROIs under investigation, except for STG PD. Looking at Fig. 5 and Fig. 6 it is visible that differences in activation are greatest in the visual cortex, including extrastriate areas, in the temporal and occipital fusiform gyri, and in the temporal occipital part of the inferior temporal gyrus. These higher activations in occipital temporal regions of the cortex may result from higher arousal (Lang et al., 1998), as indicated in the behavioural results. Moreover, as discussed above, perception and processing of visual affective scenes does possibly require more resources concerning higher attentional demands.

5 Conclusion

The aim of the current study was to find out whether emotional faces or emotional scenes are better suited to study emotions in further fMRI experiments. Even on the basis of the current findings, it is difficult to provide a definite answer to this question. It is rather more sensible to answer this question with regard to the specific aspects that are possibly investigated in future research. The findings from both experiments are supportive for a functional network, consisting of the primary and extrastriate visual cortex, fusiform gyri, and the posterior temporal cortices that is responsible for processing emotions in general. In addition, results from the 'scene-experiments' lead to the assumption that there is more than one functional network for processing emotions. Since already the theoretical construct 'emotion' has not been distinctly defined until now (see 1.1), it is difficult to infer, which brain areas are directly involved in the experience and processing of emotion and which brain areas are active during closely related functional processes. In everyday life we distinguish between emotion categories like sadness, disgust or fear, but it is questionable if this makes sense at all. Perhaps it is rather intuitive to distinguish emotions with regard to their functional roles in terms of social interaction or survival. This is at least supported by the findings from the 'scene-experiment' in the current study. Beyond this, results from the 'face-experiment' are not in accordance with a locationist approach to emotions, since brain activity in response to different categories of emotion is quite similar.

Implying that this perspective on explaining emotion is more reasonable, emotional scenes constitute the better-suited stimulus material for further experiments in the field of emotion research. In terms of ecological validity, emotional scenes provide a more realistic image on the presence of emotion in natural environments. Thus, related processes can be studied in greater detail.

For future research, it is necessary to combine neuropsychological methods with higher temporal information (e.g. EEG) with methods of high spatial resolution, like fMRI. Furthermore, emotional scenes should be pre-selected according to different criteria, like valence and arousal levels, perhaps again distinct emotion categories, and their potential to display realistic situations. Baring these aspects in mind, emotionally evocative scenes provide a useful stimulus material that might be better to study emotions than emotional faces.

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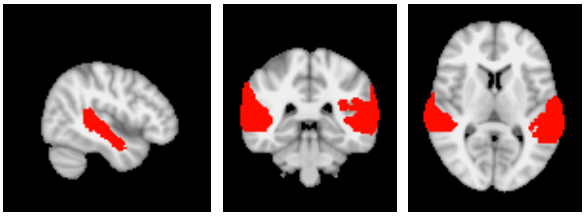
Appendix A

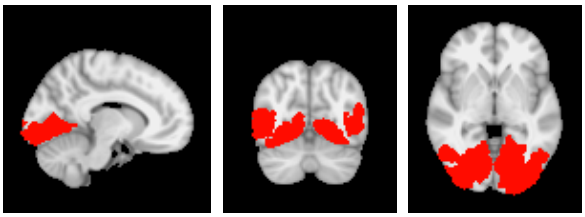
Example of the emotional stimuli in the ‚face-experiment' (female & male). From left to right: emotion categories sadness, disgust, fear, and neutral. Face stimuli were drawn from the Radboud Faces Database (Langner et al., 2010).

Example of the emotional stimuli in the ‚scene-experiment' (categories as described in section 2.2.2) (Marchewka et al., 2010).

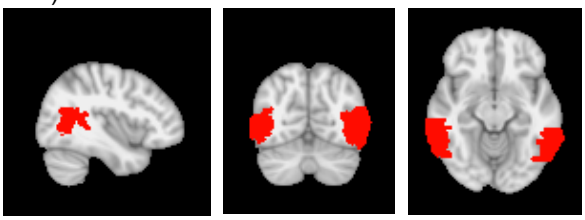
Appendix B



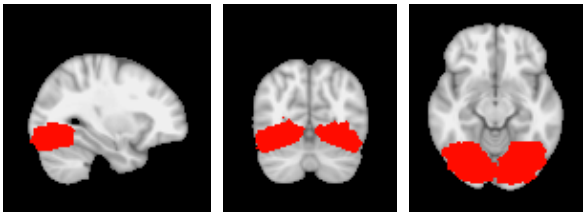
Superior temporal gyrus, posterior division (STG PD)



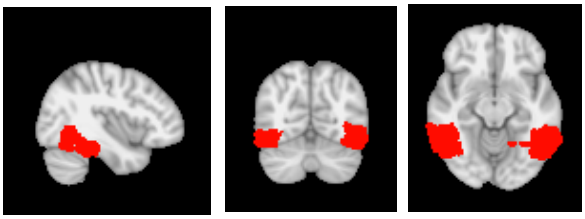
Extrastriate occipital cortex



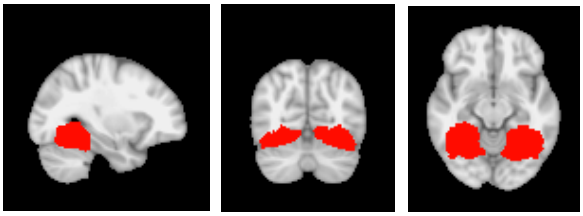
Middle temporal gyrus, posterior division (MTG PD)



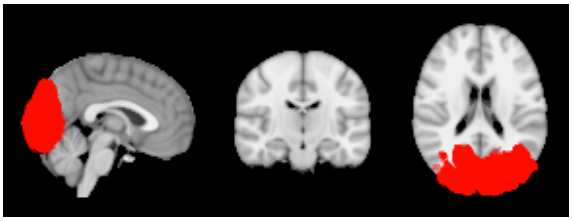
Occipital fusiform cortex (O Fus)



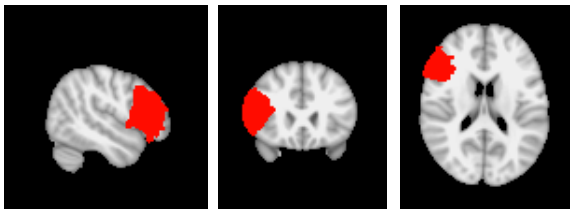
Inferior temporal gyrus, posterior division (ITG PD)



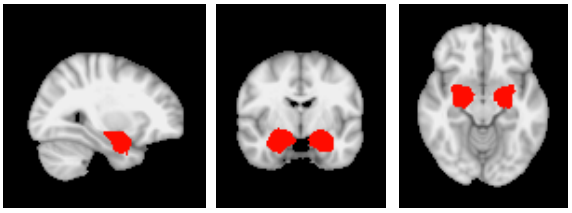
Temporal occipital fusiform cortex (TO Fus)



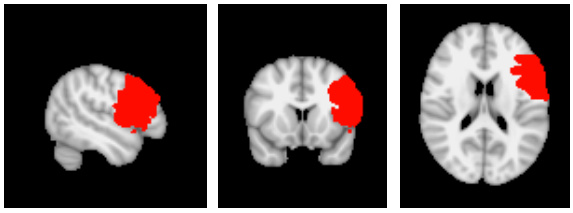
Occipital cortex (OC)



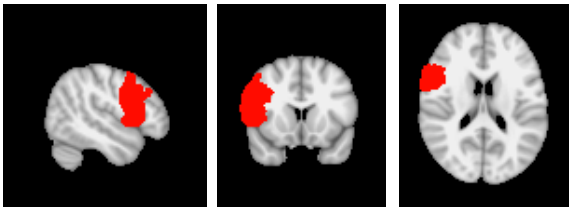
Right Broca‘s area, BA 45 (R Broca 45)



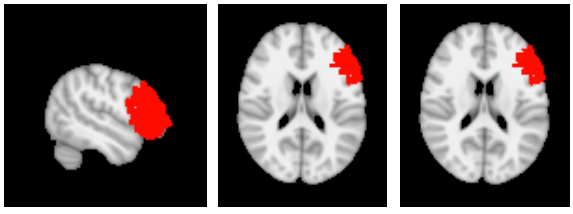
Bilateral amgdala



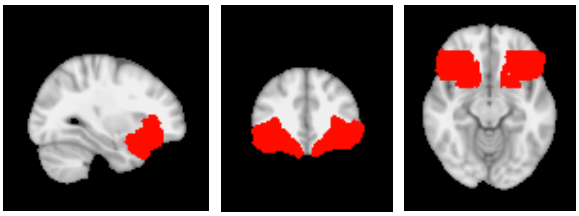
Left Broca‘s area, BA 44 (L Broca 44)



Right Broca‘s area, BA 44 (R Broca 44)



Left Broca‘s area, BA 45 (L Broca 45)



Orbital frontal cortex (OFC)

Masks images for ROI-analysis, displayed in sagittal, coronal, and axial slices. Created with FSLView using the *fslmaths* function as well as different Atlas tools (Juelich Histological Atlas, Harvard-Oxford Cortical Structural Atlas, Harvard-Oxford Subcortical Structural Atlas, MNI Structural Atlas). All masks were binarised and overlaid on a stereotactic brain (FSL's MNI Average152, T1 2 x 2 x 2 mm). Images are displayed in radiological convention.

Appendix C

Test statistics for one sample t-test, ROI

Region of Interest	t-statistic	p-value
Occipital cortex	-17.0280	.0000
Temporal occipital fusiform cortex	-16.2351	.0000
Occipital fusiform cortex	-16.9222	.0000
Orbitofrontal cortex	-9.4419	.0000
Inferior temporal gyrus, TO	-11.3589	.0000
Middle temporal gyrus, TO	-10.7279	.0000
L Broca 44	-7.3746	.0000
L Broca 45	-7.1114	.00001
R Broca 44	-5.4498	.000018
R Broca 45	-4.5429	.000126

t-statistic and p-value are reported for every single comparison between „Face-experiment“ and „Scene-experiment“. T-test were conducted on basis of $\alpha = .01$ and $df = 18$.

Test statistics for univariate ANOVA, ROI

Region of Interest	F-statistic	p-value
Occipital cortex	6.270	.004
Temporal occipital fusiform cortex	4.446	.016
Occipital fusiform cortex	7.907	.001
Superior temporal gyrus PD	1.498	.233
Inferior temporal gyrus, TO	3.669	.032
Middle temporal gyrus, TO	3.287	.045
Amygdala	2.519	.090
Extrastriate cortex	11.112	.000

F-statistic and p-value are reported for effects of discrete emotion categories on mean percentage signal change in particular ROIs for the „Face-experiment“. ANOVA was conducted on basis of $\alpha = .05$ and $df = 2$.

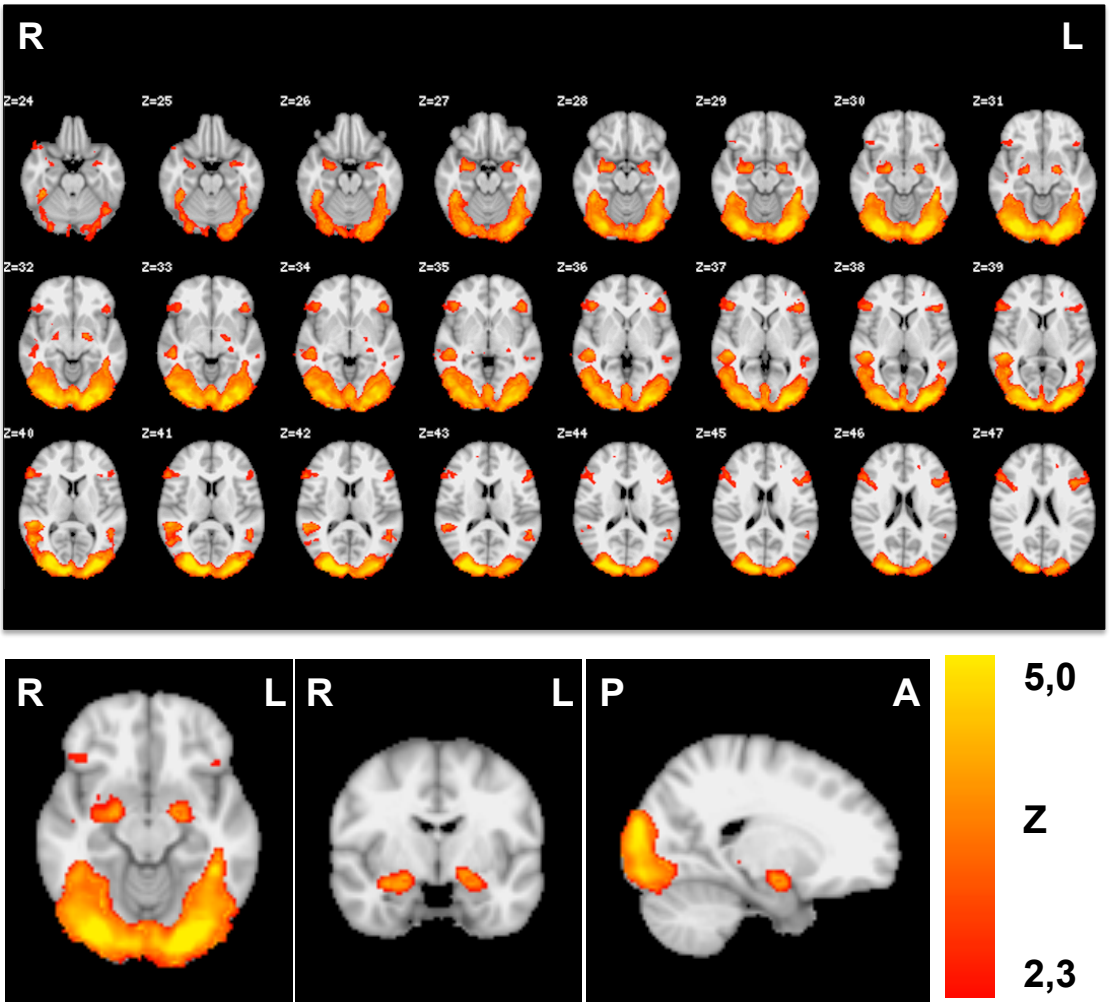
Multiple Comparisons - Bonferroni

Dependent variable	(I) 1 = sad, 2 = disgust, 3 = fear	(J) 1 = sad, 2 = disgust, 3 = fear	Mean difference (I-J)	Standard error	p	95%-Confidence Interval	
						Upper bound	Lower bound
Amygdala	1	2	-.06100	.02883	.117	-.1322	.0102
		3	-.04920	.02883	.281	-.1204	.0220
	2	1	.06100	.02883	.117	-.0102	.1322
		3	.01180	.02883	1.000	-.0594	.0830
	3	1	.04920	.02883	.281	-.0220	.1204
		2	-.01180	.02883	1.000	-.0830	.0594
OC	1	2	-.09847*	.03047	.006	-.1738	-.0232
		3	-.08745*	.03047	.018	-.1627	-.0122
	2	2	.09847*	.03047	.006	.0232	.1738
		3	.01102	.03047	1.000	-.0643	.0863
	3	1	.08745*	.03047	.018	.0122	.1627
		2	-.01102	.03047	1.000	-.0863	.0643
Extrastriate	1	2	-.15014*	.03267	.000	-.2308	-.0694
		3	-.10475*	.03267	.007	-.1855	-.0240
	2	1	.15014*	.03267	.000	.0694	.2308
		3	.04539	.03267	.511	-.0353	.1261
	3	1	.10475*	.03267	.007	.0240	.1855
		2	-.04539	.03267	.511	-.1261	.0353
TO FUS	1	2	-.06476*	.02384	.026	-.1237	-.0059
		3	-.05774	.02384	.056	-.1166	.0012
	2	1	.06476*	.02384	.026	.0059	.1237
		3	.00702	.02384	1.000	-.0519	.0659
	3	1	.05774	.02384	.056	-.0012	.1166
		2	-.00702	.02384	1.000	-.0659	.0519
O Fus	1	2	-.13436*	.03599	.001	-.2233	-.0454
		3	-.10988*	.03599	.011	-.1988	-.0210
	2	1	.13436*	.03599	.001	.0454	.2233
		3	.02448	.03599	1.000	-.0644	.1134
	3	1	.10988*	.03599	.011	.0210	.1988
		2	-.02448	.03599	1.000	-.1134	.0644
ITG_TO	1	2	-.06406	.02638	.056	-.1292	.0011
		3	-.05943	.02638	.085	-.1246	.0057
	2	1	.06406	.02638	.056	-.0011	.1292
		3	.00463	.02638	1.000	-.0605	.0698
	3	1	.05943	.02638	.085	-.0057	.1246
		2	-.00463	.02638	1.000	-.0698	.0605
MTG_TO	1	2	-.04602	.02258	.139	-.1018	.0098
		3	-.05344	.02258	.065	-.1092	.0024
	2	1	.04602	.02258	.139	-.0098	.1018

		3	-.00742	.02258	1.000	-.0632	.0484
	3	1	.05344	.02258	.065	-.0024	.1092
		2	.00742	.02258	1.000	-.0484	.0632
STG_PD	1	2	-.03668	.02435	.414	-.0968	.0235
		3	-.03634	.02435	.424	-.0965	.0238
	2	1	.03668	.02435	.414	-.0235	.0968
		3	.00034	.02435	1.000	-.0598	.0605
	3	1	.03634	.02435	.424	-.0238	.0965
		2	-.00034	.02435	1.000	-.0605	.0598

* Mean differences are significant at $\alpha < .05$.

Appendix D



Group brain activation for the emotional ‚face-experiment' and the contrast ‚emotional faces > neutral faces', displayed in axial slices (upper image) and at coordinates [x,y,z] = [20, -6, -12]. Contrast images are based on $p < .05$, uncorrected.

Eigenständigkeitserklärung

Hiermit versichere ich, dass ich diese Arbeit selbstständig verfasst und keine anderen, als die angegebenen Quellen und Hilfsmittel benutzt habe. Außerdem versichere ich, dass ich die allgemeinen Prinzipien wissenschaftlicher Arbeit und Veröffentlichung, wie sie in den Leitlinien guter wissenschaftlicher Praxis der Carl von Ossietzky Universität Oldenburg festgelegt sind, befolgt habe.

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Ort, Datum Unterschrift