Aus dem Institut für Medizinische Psychologie der
Ludwig-Maximilians-Universität München
Vorstand: Prof. Martha Merrow, PhD

The influence of mental frames on the neurocognitive processing of visual art

Dissertation
zum Erwerb des Doktorgrades der Humanbiologie
an der Medizinischen Fakultät der
Ludwig-Maximilians-Universität zu München

vorgelegt von
Sarita Silveira
aus München
2014

Mit Genehmigung der Medizinischen Fakultät
der Universität München

Berichterstatter: Prof. Dr. Ernst Pöppel

Mitberichterstatter: Prof. Dr.-Ing. Stefan Glasauer
Priv.-Doz. Dr. Peter Zill
Priv.-Doz. Dr. Angela Deutschländer

Mitbetreuung durch den promovierten Mitarbeiter: Dr. Evgeny Gutyrchik

Dekan: Prof. Dr. med. Dr. h.c. M. Reiser, FACR, FRCR

Tag der mündlichen Prüfung: 20.05.2014

Contents

1 Abstract & Deutsche Zusammenfassung

1.1 Abstract

Visual perception is characterized by two complementary processes. While properties of the visual stimulus are processed *bottom-up*, experiences and expectations of the observer that are related to stored representations of the world take *top-down* influence on the perceptual process. This doctoral thesis was devoted to investigating higher cognitive top-down processes in visual perception on a neural level using functional magnetic resonance imaging (fMRI). In the first part, neural correlates of matching expectations and sensory input are investigated. Despite the knowledge that a top-down way of processing visual stimuli is related to stored mental representations of the world, little is known about how visual stimuli are processed that do not match prior expectations because they can not occur in real life. For such a research question the use of artworks seems valuable as pictorial representations also include fantastic scenery. In a first fMRI study, the processing of surrealistic paintings was compared to the processing of naturalistic paintings. In a second project, contextual top-down influences of priming are addressed. The context chosen was an induction of mortality salience, a context of great interest for psychological research, and as visual stimuli attractive opposite-sex faces were used due to their relevance in research on death-related priming. Both experiments provide evidence for underlying neural correlates of cognitive influences in processing visual input. While the first one supports anticipatory mental operations and feedback loops between brain areas of higher and lower cognitive function, the second one suggests that human perception is malleable and sensitive to relevant changes in context.

1.2 Deutsche Zusammenfassung

Visuelle Wahrnehmung ist durch zwei komplementäre Prozesse gekennzeichnet. Während die Merkmale eines visuellen Stimulus *bottom-up* verarbeitet werden, nehmen Erfahrungen und Erwartungen *top-down* einen Einfluss auf den Wahrnehmungsprozess. Die vorliegende Doktorarbeit umfasst die Untersuchung kognitiver top-down Prozesse der visuellen Wahrnehmung auf neuronaler Ebene unter Verwendung von funktioneller Magnetresonanztomographie (fMRT). Im ersten Teil wurden neuronale Korrelate eines Abgleichs zwischen Erwartungen und sensorischen Eindrücken erhoben. Trotz des Wissens, dass top-down Wahrnehmungsprozesse mit gespeicherten mentalen Repräsentationen der Welt zusammenhängen, ist bisher wenig über die Verarbeitung visueller Stimuli bekannt, die nicht mit bestehenden Erwartungen übereinstimmen, da sie nicht in der Realität vorkommen. Um eine derartige Forschungsfrage zu operationalisieren, erscheint die Verwendung von Kunstwerken wertvoll, da künstlerische Bildwelten auch phantastische Szenen beinhalten. In einer ersten fMRT Studie wurde die Verarbeitung von surrealistischen Gemälden mit der von naturalistischen Gemälden verglichen. In einem zweiten Projekt wurden kontextuelle top-down Einflüsse durch Priming untersucht. Als Kontextmanipulation wurde die Induktion von Mortalitätssalienz gewählt, da diese in der psychologischen Forschung von Interesse ist. Attraktive gegen-geschlechtliche Gesichter dienten als visuelle Stimuli auf Grund ihrer Relevanz bei Priming mit Todesbezug. Beide Experimente liefern Einblicke in zu Grunde liegende neuronale Korrelate von kognitiven Einflüssen in der Verarbeitung visueller Eindrücke. Während die Ergebnisse der ersten Studie antizipatorische mentale Operationen und eine Rückkoppelung zwischen Arealen von höherer und solchen niedrigerer kognitiver Funktion unterstreichen, kann an Hand der zweiten Studie verdeutlicht werden, dass menschliche Wahrnehmung sensitiv gegenüber relevanten kontextuellen Veränderungen ist.

2 General introduction

2.1 Visual perception

The visual system enables human beings to perceive, interact with and relate to our physical environment by assimilating external information from the surrounding. However, visual perception is not only a translation of stimuli. Besides a bottom-up analysis of psycho-physical features, there is also a complementary top-down way of processing, which reflects a decoding of stimuli driven by experiences and expectations. In this sense, research on visual perception offers special insights into general cognitive processes. Throughout the decades, many different experimental approaches have been applied in studying visual perception. They provide insight into different levels of processing sensory stimuli. Using neuroimaging techniques is a means to study mechanisms on an implicit level of processing (Pöppel & Bao, 2011).

In the present thesis, I focus on neural correlates of top-down processes involved in visual perception. By using functional magnetic resonance imaging (fMRI), the influences of mental frames are explored. In the following subsections, theoretical underpinnings and prior empirical findings for those cognitive aspects of visual processing will be presented.

2.1.1 The creation of stability in visual perception

In processing visual stimuli, perceptual impressions are matched with cognitive expectations. This complementarity applies different levels of the perceptual process. Comparisons are made between afferent sensory signals and anticipations created by stored eye movements as proposed by the reafference principle (von Holst & Mittelstaedt, 1950) and the concept of corollary discharge (Teuber, 1960). This mechanism is relevant to perceive the world as stable even though images on the retina are never static. On a more abstract level, prior cognitive concepts are used to semantically decode visual stimuli. Supposedly, those comparisons are driven by an innate need for coherence and continuity in visual perception (Gibson, 1966; Epstein, 1985; Klinger, 1998; Heine et al., 2006; Steger et al., 2008). The invariance in the structure of objects that is expected by stored representations creates perceptual identity and stability of visual perception and might even imply a sense of reality in the surrounding world. As suggested by previous research, this stability can be controlled by attentional processes (Egeth & Yantis, 1997; Bao & Pöppel, 2007). Insofar, it has been proposed that visual attention is a means to the need for coherence and stability and that it might have evolved for this reason (Godijn & Theeuwes, 2003). Besides, perceptual identity is constrained by a temporal integration mechanism offering a time window of approximately 3 s to create or maintain stability in visual perception (Pöppel, 2009, 2010; Pöppel et al., 2011).

2.1.2 Context in visual perception

Every perceptual process is embedded within a specific mental frame, which often remains implicit (Pöppel & Bao, 2011). Contextual factors strongly influence sensory processing. The most common way to create different mental frames is by priming procedures, i.e. by artificially manipulating contexts and thereby controlling for contextual influences. Priming refers to the fact that a precedent stimulus influences the processing of a target stimulus. Underlying mechanisms have been related to spreading activation, i.e. activated nodes speed the encoding of like-valence and like-association objects (Bargh, 1997; Lerner et al., 2012), response competition (De Houwer et al., 2002; Voss et al., 2012) and associative strength (Klauer & Musch, 2002). As these priming mechanisms usually proceed on an implicit level of processing, neuroimaging techniques can be crucial in exploring in which way perception of visual stimuli is modulated by specific mental frames.

In the following sections, the above-mentioned general principals will be explicated in the case of visual arts processing. Besides, a specific case of contextual priming in psychological research will be introduced. Additional sections concerning neural correlates of processing visual stimuli provide insight into cognitive processes during visual perception in specific contexts.

2.2 Visual arts processing

In investigating basic mechanisms within the visual system on a more complex level, the use of paintings has been demonstrated to be valuable. Complementarity in visual arts processing has already been highlighted by Gustav Theodor Fechner (1871), the first and foremost experimental psychologist studying aesthetic processes. He referred to the *aesthetics from below* and the *aesthetics from above*, two ways of information processing between mind and body complementing each other. While the aesthetics from above constitute ideas and concepts of beauty that are applied to single sensory events in terms of universal standards, in the aesthetics from below perceptual experiences built a basis to form more general principles. This illustrates the complexity in processing an artwork especially with respect to search for meaning, cognitive mastering, and interpretation.

2.2.1 Mental frames in visual arts processing

Visual arts processing can be conceived of as exemplary for visual perception in general. However, it might also involve some specific processes. The act of perceiving an object as art in itself implies a specific mental frame. It is the *aboutness*, a term coined by Arthur Danto (1981), that generates expectations and knowledge and that enables to classify an object as art. The notion that a context effects a disposition for aesthetic experiences has been explained by the induction of an aesthetic attitude (Cupchick & Laszlo, 1992).

Most interestingly, pictorial representations of artworks include abstract, fantastic or surreal scenery. In this sense, artistic depictions are distinct from habits of viewing, and visual arts processing goes beyond sensory experiences accessible in every day's life. In visual arts processing, it has been demonstrated that less easily accessible paintings, which create a mismatch with prior expectations, are processed with more effort and less processing fluency (Reber et al., 2004). Aesthetic judgments turn out to be negative as a result. Thus, there is consistent evidence for aesthetic preferences for representational over abstract paintings (Vartanian & Goel, 2004).

2.2.2 Neural correlates of visual arts processing

First neuropsychological contributions to visual arts research revealed interrelations between viewer and perceptual objects. In this sense, compositional features of an artwork elicit aesthetic responses subject to biological dispositions, i.e. specifically to the functioning of the brain (Störig et al., 1983; Turner & Pöppel, 1988; Eibl-Eibesfeldt, 1988). In general, visual arts processing involves the striate and extrastriate cortex. Additionally, reward-related brain areas like the medial orbitofrontal cortex and ventral striatum are recruited (Kawabata & Zeki, 2004; Lacey et al., 2011). This highlights the reward value of artistic representations, which has been proposed for aesthetic experiences in all sensory modalities. Also parietal areas are involved in the processing of visual art, specifically when aesthetic judgments are positive (Cela-Conde et al., 2009; Cupchik et al., 2009; Kawabata & Zeki, 2004; Lutz et al., 2013). By interpretation, visuo-spatial coding and motor mapping point to embodied cognitive processes that are involved in decoding artistic representations. Recent findings suggest that also self-related operations are associated with visual arts processing. Vessel and colleagues (2012) found that the default mode network (DMN) is decisively involved in perceiving paintings, with no linear, but an incremental increase for intense aesthetic experiences. The DMN is a brain network including the cortical midline structures that are of high relevance in mental tasks related to the self (Northoff & Bermpohl, 2004). This supports the assumption that associations with episodic memory and self-related representations might be used in decoding a painting with less effort (Parsons, 1987).

2.3 The context of mortality salience

A specific case of contextual priming in psychological research is the induction of so-called *mortality salience*, i.e. the accessibility of death related ideation. Mortality salience can be induced by linguistic priming with death-related content (Arndt et al., 1997). Cognitive and emotional reactions on being reminded of the inherently finite nature of human existence have kept researchers interested during the past decades (Burke et al., 2010).

2.3.1 Mortality salience and the psychological function of specific visual stimuli

Investigating effects of mortality salience provides insight into psychological functions of presented stimuli. Finding modulations of cognition and emotion has strengthened the believe that specific stimuli can be used to overcome mortality concerns. Those stimuli are assumed to be a source of self-esteem and symbolic death-transcendence (Greenberg et al., 1992). Research provides evidence that representations of culture such as visual artworks are resources of anxiety buffering function (Sani et al., 2009). Recently it has been found that perceiving depictions of attractive opposite-sex persons is influenced by death-related priming (Kosloff et al., 2010). The role of close relationships in buffering negative affect has first been introduced by Schachter (1959): The presence of affiliated others obviously reduces anxiety. The accessibility of death-related ideation increases interest in mating and sexual reproduction as reflected in heightened birth rates after events that cause existential threat (Cohen & Cole, 2002; Florian et al., 2002; Rodgers et al., 2005; Mikulincer et al., 2003). On the basis of these results it can be argued that the visual perception of attractive opposite-sex persons is moderated by emotional and cognitive contexts that might be associated with affiliative motivation. In this sense, contextual priming procedures can offer insight into psychologically relevant stimuli by influencing the perceptual process.

Some of the effects of mortality salience can be accessed on an explicit level. For example, when presenting different types of artworks after death-related priming it has been demonstrated that subjects are more prone to prefer those paintings with a rather structured view of the world (Landau et al., 2006). However, in other parts, effects of mortality salience proceed on an implicit level. Thus, using fMRI technique is a useful means to investigate underlying mechanisms.

2.3.2 Neural correlates of mortality salience

There is first evidence provided by fMRI research that mortality salience influences blood oxygen level dependent signals in specific brain areas. The processing of death-related linguistic cues and statements is associated with neural activation in emotion regulation areas of the brain (Han et al., 2010; Quirin et al., 2012). A phylogenetically evolved anxiety-system might explain the responses on being primed with death-related content (Tritt et al., 2012). Thus, a Behavioral Inhibition System (Gray, 1982) has been suggested to be involved in processing death-related content. This is reflected in neural activation in the right hemisphere and a deactivation in frontal and prefrontal cortical regions in the left hemisphere. In investigating the processing of visual stimuli, which presumably provide self-esteem increasing qualities, Graupmann and colleagues (2013) assessed neural correlates of viewing culture related images under mortality salience. They found higher activation in the left prefrontal cortex and the temporoparietal junction after death-related compared to neutral priming. This activation can be conceived of as opposing the processing of the death-related linguistic cues, as it reflects an approach-motivated rather than a withdrawal-motivated state (McGregor et al., 2012; Tritt et al., 2012). In a further study, we could show that death-related priming also modulates the processing of paintings (Pöppel et al., 2013). This finding provides evidence that mental processes related to the self and episodic memory retrieval as indicated by activation of the precuneus (Cavanna & Trimble, 2006) are more active when viewing artworks after being primed with death-related linguistic cues.

2.4 The present work

With my doctoral research I intended to provide insight into specific cognitive aspects of visual perception on a neural level. This thesis is divided into two parts. One is addressing expectations during visual processing. As a mismatch between cognitive concepts and visual stimuli is an inherent part of art-specific experiences, I used visual artworks as sensory stimuli. In a second part, contextual influences on visual perception were addressed by exploring an effect of mortality salience on the processing of attractive opposite-sex faces.

2.4.1 Brief introduction of the thesis: Part I

The first part, published as Silveira et al. (2012), was designed to explore top-down mechanisms of visual perception in light of a need for coherence and continuity. With conceptual stability being created and maintained by a match of expectations and sensations, it remains an open question how visual stimuli are processed, which do not provide a potential match, as content cannot be expected. To answer this question it seemed valuable to use visual art. Criteria for the selection of paintings was that they either represent the world in a natural way, i.e. *naturalistic*, or include fantastic scenery that does not match physical reality and habits of viewing, i.e. *surrealistic*. Psycho-physical properties of the selected paintings were kept as equal as possible to control for comparability in bottom-up processes. Fifteen right-handed subjects participated in this fMRI study (mean age 26.32, SD 4.26 years). As a main result, a higher activation was found for processing naturalistic compared to surrealistic images in the precuneus, a part of the cortical midline structures, and in the extrastriate cortex. With respect to previously reported functions of precuneus activation and in accordance with behavioral results concerning visual arts processing, this highlights stronger episodic memory retrieval and recruitment of self-related mental processes for the perception of naturalistic paintings. Thus, habits of viewing have a great impact on visual perception, specifically on the level of higher cognitive processes and in terms of top-down modulations. Besides, the existence of both feed-forward *and* feedback loops in the perceptual process are discussed.

2.4.2 Brief introduction of the thesis: Part II

In the second part of this thesis, published as Silveira et al. (2013), contextual influences on visual perception were investigated. I chose a specific case of contextual priming, the induction of mortality salience, as it provides extensive implications for the psychological value of stimuli and, thus, for psychological research and theory. The aim was to expand and complement behavioral findings concerning a modulation of perceiving attractive opposite-sex persons under mortality salience. The use of neuroimaging technique seemed to be valuable, because to a large part those modulations proceed on an implicit level of cognitive processing. In an fMRI study 16 female (mean age 24.64, SD 3.20 years) and 16 male (mean age 24.13, SD 3.34 years) right-handed native speakers took part. To provide an ecologically valid set of stimuli in the scanner session, I used biometrically processed male and female portraits, which were rated as highly attractive in a pilot study. The portraits were presented either without or with prior priming with death-related linguistic cues. As a result for both male and female participants there was a higher activation in the left anterior insula and adjacent lateral prefrontal cortex when viewing attractive opposite-sex faces after being primed with death-related words. Together with behavioral data this activation pattern points to an enhanced approach and mating motivation under mortality salience. This finding supports the view that there is contextual influence of priming procedures on the perceptual process. This emphasizes the malleability of human perception and more specifically the impact of cognitive concepts in top-down regulating visual perception.

3 Published scientific works

3.1 Matching reality in the arts: Self-referential neural processing of naturalistic compared to surrealistic images

Perception, 2012

DOI:10.1068/p7191

Accepted: 04-Mar-2012

Published online: 25-Aug-2012

Published in print: volume 41, 569-576

Perception, 2012, volume 41, pages 569–576

doi:10.1068/p7191

Matching reality in the arts: Self-referential neural processing of naturalistic compared to surrealistic images

Sarita Silveira[1,2,5], Verena Graupmann[3], Dieter Frey[3], Janusch Blautzik[4], Thomas Meindl[4], Maximilian Reiser[4], Cheng Chen[8], Yizhou Wang[7,8], Yan Bao[2,6,7], Ernst Pöppel[1,2,5,6], Evgeny Gutyrchik[1,2,5] §
Ludwig-Maximilians-Universität [[1] Institute of Medical Psychology, [2] Human Science Center, [3] Department of Psychology, [4] Institute for Clinical Radiology], Munich, Germany; [5] Parmenides Center for Art and Science, Pullach, Germany; Peking University [[6] Department of Psychology, [7] Key Laboratory of Machine Perception, [8] National Engineering Laboratory for Video Technology], Beijing, China

Received 24 November 2011, in revised form 4 March 2012

Abstract. How are works of art that present scenes that match potential expectations processed in the brain, in contrast to such scenes that can never occur in real life because they would violate physical laws? Using functional magnetic resonance imaging, we investigated the processing of surrealistic and naturalistic images in visual artworks. Looking at naturalistic paintings leads to a significantly higher activation in the visual cortex and in the precuneus. Humans apparently own a sensitive mechanism even for artistic representations of the visual world to separate the impossible from what potentially matches physical reality. The observation reported here also suggests that sensory input corresponding to a realistic representation of the visual world elicits higher self-referential processing.

Keywords: perceptual identity, visual art, self-referential processing, cortical midline structures, reafference principle

1 Introduction

Humans have an apparently innate need for coherent and continuous perceptual experiences (Spelke 1994), usually anticipating a confirmation of what is to be expected when visual stimuli are processed (Gibson 1966; Epstein 1985; Klinger 1998; Heine et al 2006; Steger et al 2008). For a long time now, it has been hypothesised that the construction of visual stability, the search for coherent experiences, and the extraction of the meaning of visual stimuli depend on a match of expectations and sensations (Helmholtz 1896). The reafference principle (Holst 1954), or the concept of corollary discharge (Teuber 1960), has been suggested to explain why we experience the world stable even though visual input on the retina is never static; an anticipatory process takes place by comparing centrally the position of a new target (the reafference) with the efference copy of a programmed saccadic eye movement. In more general terms, stored representations of the visual world and genetically determined frames of reference constitute how we expect the world to be. Thus, unlike a sensation-based bottom–up analysis of visual information, a concept-based top–down complementary activity provides a semantic frame for what we are going to see (Zeki 1999; Pöppel 2005). These complementary processes can also be referred to in a very practical sense (Tanida and Pöppel 2006) as "surprise perception", referring to responses of stimuli that cannot be anticipated, and "support perception", referring to responses of stimuli which are expected, the latter contributing to the construction of positional and conceptual stability.

---

§ Corresponding author: e-mail: evgeny.gutyrchik@med.uni-muenchen.de

doi:10.1068/p7191

Anticipatory perception is embedded within an attentional network. As attentional processes play a functional role in predicting the location of future percepts (external) as well as in controlling top–down processing (internal) (Egeth and Yantis 1997; Bao and Pöppel 2007; Chun et al 2011), it can even be argued that attention evolved out of the need for visual stability (Godijn and Theeuwes 2003). Additionally, a temporal integration mechanism is necessary to construct perceptual identity. It has been demonstrated empirically that a pre-semantic temporal integration mechanism lasting up to approximately 3 s can serve as a temporal platform or a temporal window to create and to maintain perceptual identity (Pöppel 2009, 2010; Pöppel et al 2011).

On the basis of the invariant structure of objects (Gibson 1966), we are usually able to perceive the world as coherent and stable in a way as if reality is reflected (Gibson 1967). However, this potential match does not apply to stimuli that cannot occur in real life. Visual recognition of familiar versus unfamiliar images has been widely investigated, and functional imaging studies could provide some insights into neuroanatomy, neurophysiology, and modularity of the recognition process (Kanwisher et al 1996). To further investigate the difference in visual processing of something that is consistent with perceptual expectations and something that is perceptually impossible, we conducted a study in which we used high field functional magnetic resonance imaging (fMRI) with stimuli representing naturalistic and surrealistic paintings, determining whether this differentiation applies to artistic representations. While naturalistic paintings present the world in a habitual way, surrealistic paintings violate the expected frame of reference. Surrealistic paintings are characterised by presenting mainly recognisable objects but in constellations that do not exist in real life or that are impossible from a physical point of view. In presenting impossible scenes, these artworks prevent an effortless processing of information to come to a meaningful interpretation of the visual world. This processing fluency is proposed to be a main moderator of aesthetic experiences (Leder et al 2004; Reber et al 2004). On a behavioural level it could already be shown that surrealistic art may elicit negative reactions due to a lack of directly accessible meaning (Proulx et al 2010). We hypothesised that percepts violating an expected percept cannot be integrated effortlessly into a frame of prior experiences or expectations and therefore also lack the potential for self-reference. As it has been assumed that cortical midline structures refer to such self-representations (Han and Northoff 2008), we expected naturalistic and surrealistic paintings to have different activations in these areas.

2 Method

2.1 *Participants*

Fifteen right-handed subjects (seven male; mean age 26 ± 4 years) with normal or corrected-to-normal vision participated. The study was conducted in accordance with the Declaration of Helsinki and approved by the ethics committee. Informed consent was provided, and subjects received financial reward. All participants reported visiting an art museum less than two times per year. Thus, they were considered not to have expert knowledge of the visual arts.

2.2 *Materials*

100 surrealistic and 100 naturalistic pictures have been evaluated by twenty-five subjects in a pilot study on a 5-point Likert scale on the dimensions valence (positive or negative value), arousal (intensity of the triggered emotion), and familiarity. Extremes and pictures of high familiarity were excluded, leaving 40 pictures in each category. From these, 8 were chosen per category (naturalistic/surrealistic) matched in values on all three dimensions (see supplemental material, figure S2, at http://dx.doi.org/10.1068/p7191). Homogeneous colour fields served as control stimuli. All pictures had the same image area and were equalised in luminance.

We further compared paintings of the two conditions in several psychophysical parameters. With respect to image-luminance-related parameters, we calculated the saturation of colours, defined by a combination of light intensity and distribution across the spectrum of different wavelength, and values for colour channels in RGB colour space. Moreover, spatial-frequency-related parameters were calculated. Fourier analyses were conducted for each painting. As a measure for the overall power of Fourier components in the spatial domain, the amplitude was computed by summing all the coefficient amplitudes of each Fourier basis. To analyse the power of frequencies separately, we first divided the spatial domain into high- and low-frequency components, computed by the sum of coefficient amplitudes of the Fourier bases whose frequencies are above 73% or under 27%. Frequency components were both measured in horizontal direction (W) and in vertical direction (H). In addition, intensity gradient statistics were computed to tell the global structural information of every painting. Therefore, parameters for intensity gradient magnitude and skewness and kurtosis of pixel gradient orientations were computed by the norm of gradient at each pixel. There were no significant differences between the two painting categories (table 1).

Table 1. Statistical comparison for image characteristics of naturalistic versus surrealistic paintings.

Characteristic	M_N	SD_N	M_S	SD_S	t	p
Image-luminance-related parameters						
Luminance	116.34	22.39	104.65	21.45	1.07	0.31
Saturation	0.32	0.12	0.28	0.16	1.07	0.60
Red	125.57	30.94	112.32	26.30	0.92	0.37
Green	116.15	21.05	103.53	23.50	1.13	0.28
Blue	93.14	24.96	90.32	32.26	0.20	0.85
Spatial frequency						
Amplitude	2.79×10^9	0.77×10^9	2.19×10^9	0.73×10^9	1.62	0.13
HighW	1.06×10^5	0.29×10^5	0.85×10^5	0.26×10^5	1.52	0.15
HighH	1.06×10^5	0.30×10^5	0.87×10^5	0.26×10^5	1.36	0.19
LowW	1.17×10^5	0.30×10^5	0.95×10^5	0.25×10^5	1.63	0.13
LowH	1.20×10^5	0.31×10^5	0.95×10^5	0.27×10^5	1.70	0.11
Intensity gradient orientation and magnitude						
Magnitude	7.76	2.49	6.01	2.30	1.46	0.17
Orientation skewness	1.83	0.49	1.64	0.95	0.51	0.62
Orientation kurtosis	6.08	1.68	5.62	2.95	0.38	0.71

Note: M = mean, SD = standard deviation; subscripts: N = naturalistic, S = surrealistic. *t*-scores of *t*-test (df = 14).

2.3 *Procedure*

A block design was used with eight blocks per condition, each block comprising three pictures, ie 24 stimuli events per condition occurred. The order of stimuli and blocks was pseudo-randomised, and each picture was presented three times with different stimuli constellations per block (Presentation, Neurobehavioral Systems, USA). All pictures were framed with a black background. Subjects viewed the paintings via a mirror attached to the head-coil on an LCD screen behind the scanner. Stimuli were presented for 3500 ms, followed by a 1000 ms display of a black screen while subjects had to decide whether they were affected by the painting or not by pressing a button (LUMItouch, Photon Control, Canada). Subsequent to each block a fixation asterisk appeared on screen for 6000 ms. The subjective evaluations requested should refer to any kind of feelings about the painting ("Are you touched by the painting?").

doi:10.1068/p7191

Prior to the scanning session, detailed instructions were given and a training sequence was performed by each participant in order to guard against misunderstandings about the task.

The study was conducted with a 3T system (Philips ACHIEVA, Germany) at the University Hospital LMU Munich. For anatomical reference T1-weighted MPRAGE sequence was performed (TR = 7400 ms, TE = 3433 ms, FA = 8°, 301 sagittal slices, FOV = 240 mm × 256 mm, matrix = 227 × 227, inter-slice gap = 0.6 mm). For BOLD imaging T2*-weighted EPI sequence was used (TR = 3000 ms, TE = 35 ms, FA = 80°, 36 axial slices, slice thickness = 3.5 mm, inter-slice gap = 0 mm, ascending acquisition, FOV = 230 × 230 mm, matrix = 76 × 77, in-plane resolution = 3 × 3 mm). In total 168 functional volumes were acquired.

2.4 *Data processing and analysis*

Statistical analysis was done with MATLAB (MathWorks) and SPSS Statistics 19.0 (SPSS, USA). To analyze behavioural data, a MANOVA was computed with response type and reaction time as dependent variables. Correction for multiple comparisons was implemented by the Bonferroni procedure.

fMRI data were analysed with BrainVoyager 2.0.8 (BrainInnovations BV, The Netherlands). The first five functional volumes were discarded to avoid variable effects of blood-oxygen saturation on T1 relaxation due to instabilities of the magnetic field. All functional images were 3D motion-corrected (six-parameter rigid-body trilinear interpolation) and temporally high-pass filtered with a cutoff of two cycles in time course (removal of low frequency drifts). Functional data were subsequently aligned to the structural images, normalised (through the use of a piecewise linear transformation model) into Talairach stereotactic space to allow averaging across subjects by defining the eight landmark points of the reference system (Talairach and Tournoux 1988), resampled to 3 mm × 3 mm × 3 mm voxels and spatially smoothed to minimise noise and residual intersubject differences in anatomy (FWHM = 8 mm). Random effect general linear model was computed. Boxcar predictors were convolved with a two-gamma haemodynamic response function, and the BOLD-signal time course was normalised by z-transformation. Three contrasts were estimated—one to compare the two painting conditions and two for each painting condition against the control condition. Statistical maps for the specific contrasts were calculated as t-statistics on a voxel-wise basis and were corrected for multiple comparisons by false discovery rate $q(\mathrm{FDR}) < 0.005$. Anatomical description was done referring to the AAL (Tzourio-Mazoyer et al 2002) atlas and probability maps of the visual cortex (Amunts et al 2007) adapted for BrainVoyager.

Furthermore, bivariate correlations between behavioural and neurometabolic data were computed to control for potential concomitant effects on the different activation levels in processing naturalistic and surrealistic paintings (regions of interest analysis).

3 Results

3.1 *Behavioural results*

There were no significant differences in the affective evaluation of naturalistic or surrealistic paintings according to the behavioural data. On average, subjects indicated to be affected almost equally by naturalistic ($M = 0.53 \pm 0.17$) and surrealistic ($M = 0.48 \pm 0.23$) paintings and lower by control stimuli ($M = 0.28 \pm 0.28$). An overall significant difference in response type ($F = 8.77$; $p < 0.01$; $\eta^2 = 0.20$) was driven by the difference between both painting conditions and the control condition ($p_{\text{natural–control}} < 0.01$; $p_{\text{surreal–control}} < 0.01$). There was also a significant difference in reaction time ($F = 8.64$; $p < 0.01$; $\eta^2 = 0.20$), with reactions on naturalistic paintings ($M = 5235 \pm 392$) being of longer duration than those on surrealistic paintings ($M = 4965 \pm 52$; $p = 0.03$) and on colour fields ($M = 4730 \pm 312$; $p < 0.01$).

3.2 *Neural correlates*

A subtraction analysis comparing the naturalistic and surrealistic condition was conducted to determine potential differences in the BOLD signal levels during processing of naturalistic versus surrealistic paintings. There was a significantly higher activation in the precuneus (Brodmann area/BA 7) and medial occipital cortex (BA 17, 18, 19) with similar extent in both hemispheres and in the right-middle temporal gyrus for naturalistic pictures (figure 1 and table 2). A higher activation in these areas during the naturalistic condition could also be found in contrast to the control condition (see supplemental material, figure S1a). Even though compared to the control condition similar activation patterns showed up in both painting conditions, only the surrealistic condition contrasted to the control condition additionally resulted in a deactivation in the precuneus and parts of the medial occipital and temporal cortex (see supplemental material, figure S1 and table S1).

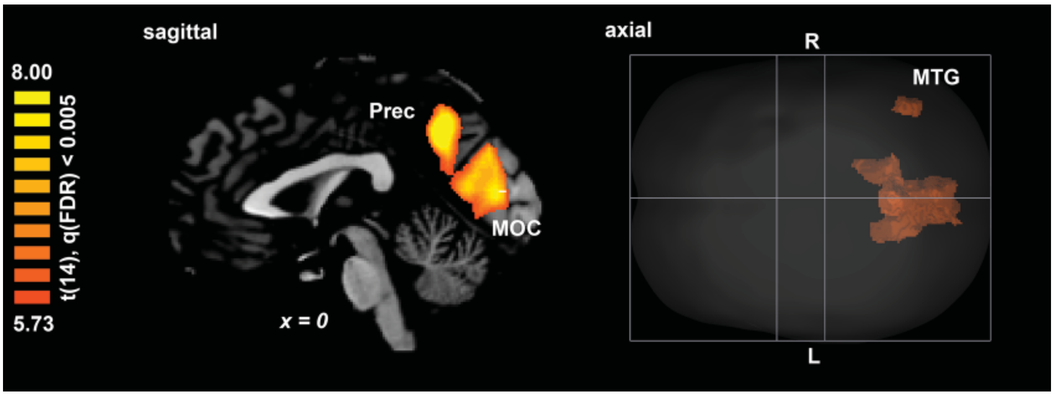

Figure 1. [In colour online, see http://dx.doi.org/10.1068/p7191] Neurometabolic level of processing for naturalistic versus surrealistic images. Sagittal section and axial glass brain view. Note: Prec = precuneus, MOC = medial occipital cortex, MTG = middle temporal gyrus, R = right, L = left.

Table 2. Brain regions with higher activation to naturalistic than surrealistic images.

Brain region	BA	Coordinates			*t*	Size in voxels
		x	*y*	*z*		
R precuneus	7	1	−55	40	10.49	58
R medial occipital cortex						
V1	17	12	−52	7	9.39	81
V2	18; 19	12	−49	4	9.03	54
R middle temporal gyrus	22; 39	45	−64	13	7.40	27
L precuneus	7	0	−55	40	11.32	72
L medial occipital cortex						
V1	17	−15	−52	4	10.67	182
V2	18; 19	−15	−52	2	10.04	91

Notes: Spatial cluster extension threshold ⩾10 voxels. Right (R) or left (L) hemisphere.
BA = Brodmann areas. The *x*, *y*, and *z* peak coordinates are in the Talairach stereotactic space.
t-scores of *t*-test (df = 14) significant by *p* (corrected for multiple comparisons) < 0.01.
Voxel size = 3 mm × 3 mm × 3 mm.

Out of the contrast between naturalistic and surrealistic paintings we anatomically defined two clusters of interest: precuneus and medial occipital cortex (together, 95% of the active clusters). Neither with subjective evaluation of the stimuli nor with reaction time were there any significant correlations for individual mean beta values ($p > 0.05$).

4 Discussion

Although subjects in this study did not show significant differences in their appraisal of emotional engagement in naturalistic and surrealistic images, there was a clear difference in the BOLD signal levels between the two presented image categories. When observing naturalistic paintings compared to surrealistic ones, subjects displayed a higher activity in striate and extrastriate areas of the visual system as well as in the precuneus. These differences in activation did not correlate with the behavioural measures.

Although we aimed to reduce concomitant factors as much as possible (see section 2), they, in principle, cannot be ruled out completely. We want to submit, however, our strong belief that the surrealistic and naturalistic paintings used in this study differ predominantly in content, not in formal criteria; this would, of course, have been different for other artistic movements like Impressionism, where paintings usually show different optical characteristics.

As all visual information has to pass the visual projection areas, the higher activity in the visual areas with the processing of naturalistic images compared to surrealistic images may indicate a feedback projection (top–down) from other central areas modulating activity on these input levels. Re-entrant projections from parietal to visual cortex could be observed (Goebel et al 2004; Koivisto and Silvanto 2012), specifically from the precuneus to the calcarine fissure (Keil et al 2009). These back-projecting modulating areas may be sensitive for the semantic content of the stimuli processed. However, it is difficult to distinguish between activations that result from recognition and those that are associated with a semantic classification and are therefore post-recognitional. A recent study has revealed that precuneus activity relates more to categorisation than to visual recognition (Schendan and Stern 2008). Thus, the higher activation in striate and extrastriate areas may be indicative of stronger feedback signals between areas of higher and lower cognitive functions, which are characteristic for top–down processing (Schmidt et al 2011). As search for meaning in paintings refers to content rather than painting style (Winston and Cupchik 1992), and as surrealistic visual information is questioning viewing habits (Proulx et al, 2010), top–down processing of surrealistic paintings may lead to a mismatch of perceived and expected representations of the visual world. The result, thus, also implies that the striate and extrastriate areas play a crucial role in a “reality check” of visual information.

The activity in the visual cortex as reported here is predominantly observed in areas corresponding to the periphery of the visual field. This is in accordance with observations of an inhomogeneity of the visual field, which is reflected, for instance, in different attentional networks corresponding to the central and peripheral area of the visual field (Bao and Pöppel 2007; Zhou et al 2010; Bao et al 2011). Thus, it can be concluded that looking at naturalistic pictures may elicit a higher attentional processing of peripheral stimuli, supporting our hypothesis that naturalistic pictures create a stronger embedding in a true-to-life context, which is not limited to the perifoveal region of just a few degrees of visual angle.

As a part of the cortical midline structures, precuneus activity has been suspected to be associated with visuo-spatial imagery, episodic memory retrieval, and even of what has been referred to as the “self” (Cavanna and Trimble 2006). Episodic memory retrieval is very likely to be associated with top–down processing (Sestieri et al 2010). However, surrealist paintings are not only unfamiliar but also disturb our sense of consistency and coherence and may therefore also hardly be related to our sense of the self. The higher activation of the precuneus in the naturalistic condition supports the hypothesis that percepts matching expectations and therefore confirming specific aspects of reality can be linked both to prior experiences and innate programmes of the representation of the visual world (Spelke 1994). The results described here furthermore support the assumption that anticipatory perception provides the formation and maintenance of conceptual stability and perceptual identity (Pöppel 2010). The artists of the presented paintings and the subjects participating in this study all share Western cultural backgrounds. As mental representations of the world influence the perception of visual information, a cultural framing effect can be assumed that is implemented on the neural level and determines implicit information processing of visual stimuli in particular and sensory stimuli in general. Thus, self-reference in the processing of visual artworks can be assumed to be associated with culture-sensitive information (Han and Northoff 2008).

Taken together, the results of this study indicate that neural processing of visual artworks corresponds to what we consider as reality. Even though a painting never shows reality as such, the visual system differentiates between paintings that correspond to reality and that are in principle possible and those that violate physical laws and psychological expectations.

Acknowledgments. We thank Marco Paolini and Anikó Sztrókay for technical assistance with the brain imaging. The study was supported by a research scholarship to SS from Hanns-Seidel-Stiftung.

References

Amunts K, Schleicher A, Zilles K, 2007 "Cytoarchitecture of the cerebral cortex—More than localization" *NeuroImage* **37** 1061–1065

Bao Y, Pöppel E, 2007 "Two spatially separated attention systems in the visual field: evidence from inhibition of return" *Cognitive Processing* **8** 37–44

Bao Y, Sander T, Trahms L, Pöppel E, Lei Q, Zhou B, 2011 "The eccentricity effect of inhibition of return is resistant to practice" *Neuroscience Letters* **500** 47–51

Cavanna A E, Trimble M R, 2006 "The precuneus: a review of its functional anatomy and behavioural correlates" *Brain* **129** 564–583

Chun M M, Golomb J D, Turk-Brown N B, 2011 "A taxonomy of external and internal attention" *Annual Review of Psychology* **62** 73–101

Egeth H E, Yantis S, 1997 "Visual attention: control, representation, and time course" *Annual Review of Psychology* **48** 267–297

Epstein S, 1985 "The implications of cognitive-experiential self theory for research in social psychology and personality" *Journal of Personality and Social Psychology* **15** 283–310

Gibson J J, 1966 *The Senses Considered as Perceptual Systems* (Boston, MA: Houghton Mifflin)

Gibson J J, 1967 "New reasons for realism" *Synthese* **17** 162–172

Godijn R, Theeuwes J, 2003 "Parallel allocation of attention prior to the execution of saccade sequences" *Journal of Experimental Psychology: Human Perception and Performance* **29** 882–896

Goebel R, Muckli L, Kim D-S, 2004 "Visual system", in *The Human Nervous System* 2nd edition, Eds G Paxinos, J K Mai (London: Elsevier Academic Press) pp 1280–1305

Han S, Northoff G, 2008 "Culture-sensitive neural substrates of human cognition" *Nature Reviews Neuroscience* **9** 646–654

Heine S J, Proulx T, Vohs K D, 2006 "Meaning maintenance model: On the coherence of social motivations" *Personality and Social Psychology Review* **10** 88–110

Helmholtz H von, 1896 *Handbuch der physiologischen Optik* 2nd edition (Hamburg and Leipzig: Verlag von Leopold Voss)

Holst E von, 1954 "Relations between the central nervous system and the peripheral organs" *British Journal of Animal Behaviour* **2** 89–94

Kanwisher N, Chun M M, Dermott J M, Ledden P J, 1996 "Functional imaging of human visual recognition" *Cognitive Brain Research* **5** 55–67

doi:10.1068/p7191

Keil A, Sabatinelli D, Ding M, Lang P J, Ihssen N, Heim S, 2009 “Re-entrant projections modulate visual cortex in affective perception: evidence from Granger causality analysis” *Human Brain Mapping* **30** 532–540

Klinger E, 1998 “The search for meaning in evolutionary perspective and its clinical implications”, in *The Human Quest for Meaning: A Handbook of Psychological Research and Clinical Application* Eds P T P Wong, P S Fry (Lincoln, NE: University of Nebraska Press) pp 137–186

Koivisto M, Silvanto J, 2012 “Visual feature binding: The critical time window of V1/V2 and parietal activity” *NeuroImage* **59** 1608–1614

Leder H, Belke B, Oeberst A, Augustin D, 2004 “A model of aesthetic appreciation and aesthetic judgments” *British Journal of Psychology* **95** 489–508

Pöppel E, 2005 “Complementarity as a generative principle in visual perception” *Visual Cognition* **12** 665–670

Pöppel E, 2009 “Pre-semantically defined temporal windows for cognitive processing” *Philosophical Transactions of the Royal Society of London B* **364** 1887–1896

Pöppel E, 2010 “Perceptual identity and personal self”, in *Personality from Biological, Cognitive, and Social Perspectives* Eds T Maruszewski, M Fajkowska, M W Eysenck (New York: Eliot Werner) pp 77–84

Pöppel E, Bao Y, Zhou B, 2011 “Temporal windows as logistical basis for cognitive processing” *Advances in Psychological Science* **19** 775–793

Proulx T, Heine S J, Vohs K D, 2010 “When is the unfamiliar the uncanny? Meaning affirmation after exposure to absurdist literature, humor, and art” *Personality and Social Psychology Bulletin* **36** 817–829

Reber R, Schwartz N, Winkelman P, 2004 “Processing fluency and aesthetic pleasure: Is beauty in the perceiver’s processing experience?” *Personality and Social Psychology Review* **8** 364–382

Schendan H E, Stern C E, 2008 “Where vision meets memory: prefrontal-posterior networks for visual object constancy during categorization and recognition” *Cerebral Cortex* **18** 1695–1711

Schmidt K E, Lomber S G, Payne B R, Galuske R A, 2011 “Pattern motion representation in primary visual cortex is mediated by transcortical feedback” *NeuroImage* **54** 474–484

Sestieri C, Shulman G L, Corbetta M, 2010 “Attention to memory and the environment: functional specialization and dynamic competition in human posterior parietal cortex” *Journal of Neuroscience* **30** 8445–8456

Spelke E S, 1994 “Initial knowledge. Six suggestions” *Cognition* **50** 443–447

Steger M F, Kashadan T B, Sullivan B A, Lorentz D, 2008 “Understanding the search for meaning in life: personality, cognitive style, and the dynamic between seeking and experiencing meaning” *Journal of Personality* **76** 199–228

Talairach J, Tournoux P, 1988 *Co-planar Stereotaxic Atlas of the Human Brain* (Stuttgart: Georg Thieme Verlag)

Tanida K, Pöppel E, 2006 “A hierarchical model of operational anticipation windows in driving an automobile” *Cognitive Processing* **8** 37–44

Teuber H-L, 1960 *Perception. Handbook of Physiology—Neurophysiology III* (Heidelberg: Springer) pp 1595–1668

Tzourio-Mazoyer N, Landeau B, Papathanassiou D, Crivello F, Etard O, Delcroix N, Mazoyer B, Joliot M, 2002 “Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain” *NeuroImage* **15** 273–289

Winston A S, Cupchik G C, 1992 “The evaluation of high art and popular art by naïve and experienced viewers” *Visual Arts Research* **18** 1–14

Zeki S, 1999 *Inner Vision* (Oxford: Oxford University Press)

Zhou B, Bao Y, Sander T, Trahms L, Pöppel E, 2010 “Dissociation of summation and peak latencies in visual processing: An MEG study on stimulus eccentricity” *Neuroscience Letters* **483** 101–104

3.2 Existential neuroscience: effects of mortality salience on the neurocognitive processing of attractive opposite-sex faces

Social Cognitive and Affective Neuroscience, 2013

DOI: 10.1093/scan/nst157

Accepted: 23-Sept-2013

Social Cognitive and Affective Neuroscience Advance Access published October 27, 2013

doi:10.1093/scan/nst157 SCAN (2013) 1 of 7

Existential neuroscience: effects of mortality salience on the neurocognitive processing of attractive opposite-sex faces

Sarita Silveira,[1,2]* Verena Graupmann,[3,2]* Maria Agthe,[4] Evgeny Gutyrchik,[1,2] Janusch Blautzik,[5] Idil Demirçapa,[6] Andrea Berndt,[6] Ernst Pöppel,[1,2] Dieter Frey,[4] Maximilian Reiser,[5] and Kristina Hennig-Fast[6,7]

[1]Institute of Medical Psychology, Ludwig-Maximilians-University, Munich, Germany, [2]Human Science Center, Ludwig-Maximilians-University, Munich, Germany, [3]Department of Psychology, DePaul University, Chicago, IL, USA, [4]Department of Psychology, Ludwig-Maximilians-University, Munich, Germany, [5]Institute of Clinical Radiology, Ludwig-Maximilians-University, Munich, Germany, [6]Institute of Psychiatry and Psychotherapy, Ludwig-Maximilians-University, Munich, Germany, and [7]Department of Psychology, University of Vienna, Austria

Being reminded of the inherently finite nature of human existence has been demonstrated to elicit strivings for sexual reproduction and the formation and maintenance of intimate relationships. Recently, it has been proposed that the perception of potential mating partners is influenced by mortality salience. Using functional magnetic resonance imaging, we investigated the neurocognitive processing of attractive opposite-sex faces after priming with death-related words for heterosexual men and women. Significant modulations of behavioral and neural responses were found when participants were requested to decide whether they would like to meet the presented person. Men were more in favor of meeting attractive women after being primed with death-related words compared to a no-prime condition. Increased neural activation could be found under mortality salience in the left anterior insula and the adjacent lateral prefrontal cortex (lPFC) for both men and women. As previously suggested, we believe that the lPFC activation reflects an approach-motivated defense mechanism to overcome concerns that are induced by being reminded of death and dying. Our results provide insight on a neurocognitive level that approach motivation in general, and mating motivation in particular is modulated by mortality salience.

Keywords: fMRI; mortality salience; terror management theory; attractiveness; lateral prefrontal cortex

INTRODUCTION

One of the challenges of human life is handling the awareness of the inherently finite nature of existence. Cognitive and emotional reactions on mortality salience have become an important topic in psychological science during the past decades (Burke *et al.*, 2010). Research on coping with mortality salience provides evidence for psychological strategies that are used to overcome feelings of anxiety or uncertainty. Such strategies include striving to maintain or recreate self-esteem (Greenberg *et al.*, 1992; Graupmann *et al.*, 2013a), and defending one's cultural worldview including cultural values and beliefs (Greenberg *et al.*, 1990). These phenomena have been explained within the framework of terror management theory (TMT, Greenberg *et al.*, 1986), which posits the reliance on symbolic immortality as a way to buffer the existential threat conveyed in notions of mortality. The idea of symbolic immortality, e.g. living on in one's progeny, can serve as a shield to buffer the psychological threat implied in the thought of death (Lifton, 1973; Florian and Mikulincer, 1998). Recent research has shown that death reminders influence human reproductive behaviors. Not only are birth rates heightened following disastrous events (Cohen and Cole, 2002; Rodgers *et al.*, 2005), but there is also an increase in desire for offspring when mortality is made salient (Wisman and Goldenberg, 2005; Fritsche *et al.*, 2007). Affiliative tendencies in regulating distress have first been shown by Schachter's fear and affiliation paradigm (Schachter, 1959). The presence of other persons seems to lower imminent threats. According to more recent results formation and maintenance of a romantic relationship appears to buffer anxiety when confronted with death reminders (Florian *et al.*, 2002; Mikulincer *et al.*, 2003). In particular, increased preference for sexually attractive opposite-sex persons has been found in heterosexual participants when reminded of death and dying (Kosloff *et al.*, 2010). Together these findings suggest that romantic and reproductive motivations are enhanced under mortality salience.

Faces offer important cues relevant for mate selection. Mating preferences for attractive faces are attributed to structural properties of the faces, which are related to health (Fink and Penton-Voak, 2002). Sexual preference and gender constellations apparently influence reactions on attractive faces, which might be explained by mating motivations and social comparisons or rivalry (Maner *et al.*, 2007; Agthe *et al.*, 2011). For heterosexual persons attractive opposite-sex faces thus serve as cues providing the possibility for sexual reproduction. The impact of attractive faces of preferred sex on attention and attraction is moderated by cognitive and motivational factors and strongly depends on mating tendencies (Maner *et al.*, 2007; Koranyi and Rothermund, 2012). Attraction to an appealing opposite-sex person also reflects basic human needs for intimacy (McAdams, 1992), affiliation (Koestner and McClelland, 1992) or belongingness (Baumeister and Leary, 1995) and has been highlighted as a source of self-esteem (Leary *et al.*, 1995; Leary, 1999). By now several studies have been conducted to investigate the underlying neural correlates of processing facial attractiveness showing predominantly heightened activations in reward-related brain regions innervated by dopaminergic pathways (Aharon *et al.*, 2001; Kampe *et al.*, 2001; O'Doherty *et al.*, 2003; Cloutier *et al.*, 2008; Chatterjee *et al.*, 2009). In particular, striatal regions (nucleus accumbens, caudate nucleus and putamen) and the orbitofrontal cortex are involved in processing attractive faces. On a neural level faces of preferred sex are processed with a higher responsiveness in regions within the reward circuitry (Kranz and Ishai, 2006). For heterosexual participants a gender difference could be found in the

Received 13 June 2013; Accepted 23 September 2013

---

*First two authors contributed equally to this work.

The study was supported by a research scholarship to S.S. from Hanns-Seidel-Stiftung

Correspondence should be addressed to Kristina Hennig-Fast, Department of Psychology, University of Vienna, Liebiggasse 5, 1010 Vienna, Austria. E-mail: kristina.hennig-fast@univie.ac.at

perception of attractive opposite-sex faces (Cloutier *et al.*, 2008; Van Hooff *et al.*, 2011): stronger neural responses were found when men viewed attractive female faces.

The first insights into neural substrates of mortality salience, which were provided by functional magnetic resonance imaging (fMRI) studies, revealed that the processing of death-related cues compared with control stimuli was related to metabolic modulations in brain areas that are relevant for emotion processing. In particular, higher activations in the left anterior cingulate cortex, right amygdala and right caudate nucleus (Quirin *et al.*, 2012) and deactivation in the insula (Han *et al.*, 2010) were found. In a more theoretical approach, a phylogenetically evolved anxiety system has been proposed to underlie the processing of death reminders (Tritt *et al.*, 2012). In this sense, mortality salience is proposed to induce activity in the behavioral inhibition system (BIS) (Gray, 1982). BIS is represented in an activated circuitry in the right hemisphere and an inhibition of frontal and prefrontal areas in the left hemisphere that are associated with approach motivation (Tucker and Federick, 1989; Harmon-Jones and Harmon-Jones, 2008). The activation pattern of processing death-related cues found by Quirin *et al.* (2012) most likely fits the BIS as a general anxiety system. The influence of mortality salience on the neural correlates of other social, cognitive and affective processes is just beginning to be understood. In an fMRI study, it has been demonstrated that after priming with death-related content brain activation in areas that are responsive to others' suffering was decreased (Luo *et al.*, 2013). In more direct connection to the defense mechanisms proposed by TMT, the processing of culture related images has been associated with activation in the lateral prefrontal cortex (lPFC) and the temporoparietal junction when death (in comparison to neutral or meaning threat content) was primed (Graupmann *et al.*, 2013b). Yet, more evidence for neural correlates of the different strategies to counteract mortality concerns like the formation and maintenance of self-esteem, worldview and symbolic immortality is needed. Such strategies can be understood as a counterpart of mortality concerns and are supposed to provide an opportunity to switch from a withdrawal-motivated to an approach-motivated state (McGregor *et al.*, 2012). Thus, it has been proposed that an alleviation of death-related concerns should be represented in a switch from the BIS to a higher activation of left frontal and prefrontal areas (Tritt *et al.*, 2012).

In our study, we investigated how mortality salience modulates the processing of attractive opposite-sex faces. Based on prior research we expected that heterosexual viewers perceive attractive opposite-sex persons with higher mating motivation under mortality salience. Using fMRI, we specifically aimed to investigate the neural correlates of viewing attractive opposite-sex persons under mortality salience. Assuming that defensive strategies to overcome mortality concerns are related to approach motivation, the depictions of potential mating partners are expected to elicit neural activation in left frontal and prefrontal brain areas. To further vary a mating-relevant frame, we used two different experimental tasks: one to assess explicit evaluations of attractiveness and one to create the prospect of meeting the presented person. We assessed both male and female observers to provide insight into potential sex differences.

MATERIALS AND METHODS

Participants

Sixteen female (age 18–35; mean = 24.64, s.d. = 3.20 years) and 16 male (age 18–35; mean = 24.13, s.d. = 3.34 years) right-handed heterosexual subjects with normal or corrected to normal vision participated. The experiment was conducted in accordance with the Declaration of Helsinki and approved by the ethics committee. Informed consent was provided, and subjects received a financial reward of 50€.

Materials

An ecologically valid selection of stimulus material being essential in the study of high-level neuroesthetic processing (e.g. Silveira *et al.*, 2012; Avram *et al.*, 2013; Lutz *et al.*, 2013), we ran a pilot study in which 93 male and 94 female gray scale portraits were evaluated by 65 subjects (31 male; age 18–35; mean = 25.60, s.d. = 2.64 years). Faces were rated on their attractiveness (1–10). Portraits with high values on attractiveness (>8) were chosen separate for male and female faces with 12 photos remaining in each category. Photos were biometrically processed and standardized in position of nose, chin and eyes (Passbild Generator 3.5a). Luminance was equalized for all pictures. Control stimuli were created by scrambling 12 portraits (half male and half female) using Adobe Photoshop. Those stimuli were added with a dot either on the left or on the right side.

We used death-related linguistic primes to induce mortality salience. Previous research has shown that words associated with death are suitable in priming concepts of death and dying (Arndt *et al.*, 1997). Primes consisted of 24 death-related word combinations and were created similar in length (mean = 11.16, s.d. = 1.81 letters) and comparable incidence rate in language use. Exemplary for those combinations is 'Todesursache' (cause of death) or 'Todeszelle' (death row). Words were chosen out of the Berlin affective word list (BAWL-R; Võ *et al.*, 2009). Every word of the BAWL is coded with an affective value ranging from –3 (very negative) through 0 (neutral) to +3 (very positive). We chose words related to death and dying with a negative value of less than −2.

Procedure

A block design was used, consisting of four blocks per portrait condition (either male or female faces) and four blocks per control condition. Each block comprised three original or scrambled portraits, which were presented either with or without a prior prime (Figure 1). Portraits and primes were displayed on a black background. The order of stimuli and blocks was pseudo-randomized, and also the order of runs and conditions was randomized between subjects. We used two different types of questions to assess both explicit and implicit reactions to the attractive faces. In the explicit condition, participants had to rate the presented faces as either attractive or not. In the implicit condition, participants were asked to decide whether they would like to meet the presented person or not. Half of the subjects first viewed the run with implicit and the other half first viewed the run with explicit questions.

Subjects viewed the stimuli via a mirror attached to the head-coil on a LCD screen behind the scanner, using stimulus delivery software (Presentation 15.1). Prior to each block a question appeared related to the presented run and condition for 1000 ms. Questions were 'meet?' (implicit; portrait conditions), 'attractive?' (explicit; portrait conditions) or 'dot?' (control condition). Primes were displayed for 400 ms. In the non-prime conditions, a black screen was presented instead. Subsequently stimuli were presented for 3600 ms, followed by 1000 ms displaying a black screen with a white question mark while subjects had to answer the respective question by pressing a button using a scanner compatible response device (LUMItouch). Subsequent to each block a black screen appeared on a screen for 4000 ms.

The study was conducted with a 3-T whole body system (ACHIEVA) at the University Hospital LMU Munich. For anatomical reference T1-weighted MPRAGE sequence was performed (TR = 7.4 ms, TE = 3.4 ms, FA = 8°, 301 sagittal slices, FOV = 240 × 256 mm, matrix = 227 × 227, inter-slice gap = 0.6 mm). For blood oxygen level dependency imaging T2*-weighted EPI sequence was used (TR = 3000 ms, TE = 35 ms, FA = 90°, 36 axial slices, slice

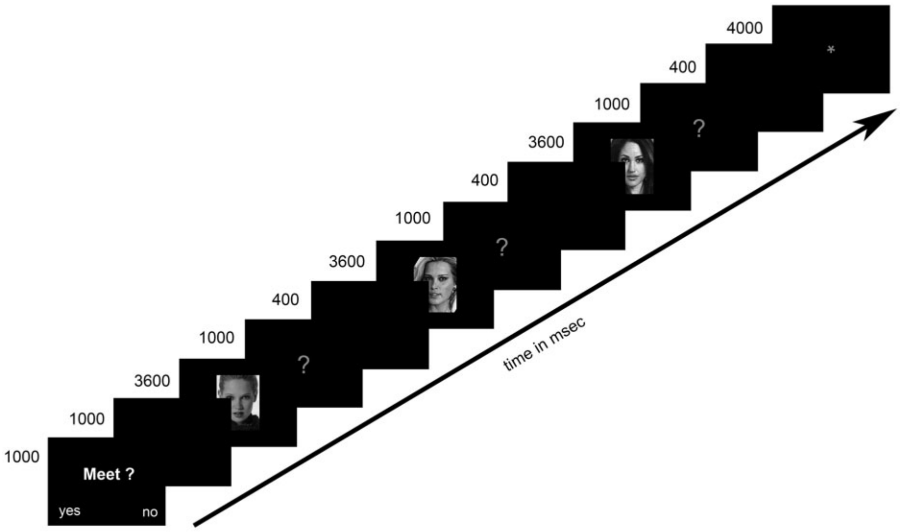

Fig. 1 Example of one block presenting attractive female faces without priming.

thickness = 3.5 mm, inter-slice gap = 0 mm, interleaved acquisition, FOV = 230 × 230 mm, matrix = 76 × 77, in-plane resolution = 3 × 3 mm). In total, 336 functional volumes were acquired.

Data processing and analysis

The preprocessing and statistical analyses of neuroimaging data were performed using Statistical Parametric Mapping software (SPM 8). In the preprocessing analysis, motion correction, realignment and spatial normalization to the T1 template (Evans *et al.*, 1993) were performed. Smoothing was executed using a Gaussian kernel of 8 mm FWHM.

There were two prime conditions (no prime and death-related prime) and two types of evaluation (implicit and explicit) for either attractive male or female faces. They were modeled by a boxcar function convolved with a hemodynamic response function. Several *t*-contrasts have been calculated for each subject, with each face–prime–question combination compared to the control condition. The individual contrast images were used for two random effect general linear models at a second level. We used a full factorial design with a 2 (gender) × 2 (prime condition) × 2 (evaluation type) matrix to calculate reactions on attractive opposite-sex faces. For all contrasts we used a significance threshold of $P < 0.01$. Contrasts were clusterwise corrected for alpha inflation errors with $P(FDR) < 0.05$. Anatomical description was done referring to the automatic anatomic labeling (Tzourio-Mazoyer *et al.*, 2002) atlas from the WFU Pickatlas (Maldjian, 2007).

For behavioral data a repeated measures analysis of variance was performed using a 2 (gender) × 2 (prime condition) × 2 (evaluation type) matrix. For one male and one female subject data could not be analyzed, so only 15 male and female subjects were included in the behavioral analyses.

All statistical analyses of variance were computed with Statistical Package for the Social Sciences (SPSS). Gaussian distribution, homogeneity of variance and covariance and sphericity could be assumed ($P > 0.05$). Corrections for multiple comparisons were done by the Bonferroni procedure.

RESULTS

Behavioral results

In the evaluation of presented attractive opposite-sex faces, there was a significant within-subjects effect of question type [F (1,28) = 9.65; $P < 0.01$; $\eta^2 = 0.26$] and significant interactions between gender and priming [F (1,28) = 4.43; $P < 0.05$; $\eta^2 = 0.14$] and between priming and question type [F (1,14) = 5.15; $P < 0.05$; $\eta^2 = 0.16$). Besides, there was a significant between-subjects main effect of gender ($F = 9.15$; $P < 0.01$; $\eta^2 = 0.25$). No significant effect of priming [F (1,14) = 0.00; $P > 0.05$] and no significant interaction between gender and question type [F (1,14) = 0.52; $P > 0.05$] could be found. Overall, the evaluations of opposite-sex persons were more positive when made by male compared with female participants. The presented faces were rated as attractive more often than average both with (male: 55 ± 7%; female: 78 ± 5%) and without (male: 62 ± 6%; female: 79 ± 5%) prior priming. For explicit attractiveness ratings there was no effect of priming. Female participants were less than average interested in meeting attractive men both with (47 ± 6%) and without (48 ± 6%) prior priming. A priming effect was found for the implicit question type only for male participants. They appeared to be more in favor of meeting an attractive woman under mortality salience (76 ± 5%) than without priming (68 ± 6%) ($\chi^2 = 14.82$; $P < 0.05$).

Neural correlates

We investigated the neural correlates of viewing attractive opposite-sex faces compared to the control 'dot' condition without priming for men and women, respectively (Table 1). In male participants, we found activations in the left fusiform gyrus, bilaterally in the striatum (caudate nucleus, putamen) and the pallidum and in the right thalamus. Activations in female participants were located in the right hemisphere. They were located in the fusiform gyrus, the striatum (putamen), the pallidum, the hippocampus and the parahippocampus. There was no significant gender difference in the neurocognitive processing of attractive opposite-sex faces without priming.

Between death-related priming *vs* no priming conditions for men and women, respectively, no significant differences in neural activation

Table 1 Neural correlates of viewing attractive opposite-sex faces

Brain region (BA)	Hemisphere	BA	Coordinates			z	Volume (mm^3)
			x	y	z		
Male observers							
Pallidum	L		−16	0	4	3.82	1176
	R		22	−6	0	3.33	1456
Putamen	L		−10	8	−4	3.22	680
	R		18	14	0	3.12	488
Caudate nucleus	L		−18	22	14	4.32	2720
	R		20	18	14	4.50	1264
Thalamus	R		10	−20	2	3.05	784
Fusiform gyrus	L	37	−26	−44	−10	2.79	872
Cerebellum	L		−14	−64	−10	2.96	872
Vermis			4	−52	−18	3.09	1120
Female observers							
Pallidum	R		16	2	2	2.55	120
Putamen	R		28	6	10	3.14	408
Hippocampus and parahippocampus	R		18	−12	−12	2.92	544
Thalamus	R		18	−8	4	2.94	1296
Fusiform gyrus	R	37	18	−38	−10	2.77	320
Cerebellum	R		8	−34	−10	2.51	120
Vermis			2	−52	−22	3.01	688

The *x*, *y* and *z* coordinates are in the MNI space.

could be found when participants had to explicitly evaluate the attractiveness of the presented opposite-sex faces. When participants had to deliberate about whether they would like to meet the presented opposite-sex persons, death-related priming modulated the neural correlates of face processing (Figure 2A; Table 2). Interestingly, in both men and women a significantly higher activation was found in the left anterior insula and the adjacent left lPFC in processing the opposite-sex faces after death-related priming compared to no priming. No significant gender differences could be found in death-related priming effects on the neurocognitive processing of attractive opposite-sex faces.

DISCUSSION

We investigated how male and female subjects respond to attractive opposite-sex faces with or without prior death-related priming. Being aware of the fact that fMRI data have to be interpreted with great caution (Bao and Pöppel, 2012), the common neural patterns we find for both male and female observers of opposite-sex faces, imply the existence of a general underlying mechanism. For both male and female participants the processing of attractive faces corresponds to neural activation located in the fusiform gyrus, an area associated with face recognition in general (Kanwisher *et al.*, 1997) and with facial attractiveness in particular (Chatterjee *et al.*, 2009). In accordance with prior studies, we found the processing of those faces to be associated with dopaminergically innervated brain areas (Aharon *et al.*, 2001; Kampe *et al.*, 2001; O'Doherty *et al.*, 2003; Cloutier *et al.*, 2008; Chatterjee *et al.*, 2009). Activation in striatal areas (putamen and caudate nucleus) points to the possible stimulus-reward value of attractive faces. While for female participants brain areas involved in the processing of facial attractiveness were located in the right hemisphere, for male participants we found a bilateral activation pattern. According to prior research, men show a stronger response to attractive opposite-sex faces than women (Van Hooff *et al.*, 2011). This can be underlined by sexual strategies theory (Buss and Schmitt, 1993), which proposes that men and women have evolved different mating strategies in that men show a higher attention to cues that suggest reproductive value like facial beauty. Our results on the behavioral level are congruent with this theory in that men rated the female faces more often as attractive than women rated the male faces as attractive, even though all presented portraits had been pre-rated as highly attractive by a sample of mixed sex. Yet, in a direct comparison of neural substrates that are related to the processing of attractive faces, we found no significant differences between male and female observers. This suggests that differences in explicit responses are potentially socialized by the cultural stereotype related to gender roles, but unmediated responses to opposite-sex stimuli are similar in nature.

An effect of death-related priming could not be found when participants were asked to explicitly evaluate facial attractiveness. Only when deliberating on whether one would like to meet the presented person, did death reminders modulate responses to the faces. Yet, on a behavioral level a gender bias occurred in the participants' statements. While for women no moderating influences could be found, the percentage of male participants willing to meet attractive women was increased significantly under mortality salience. This suggests that the motivational states aroused by death reminders lead to differential mating related behavioral expression. The finding that men indicate more interest in meeting the female stimulus person conforms to cultural norms that men are more proactive in pursuing mating strategies than are women. This is in accordance with evolutionary theory regarding the asynchrony of mating strategies in men and women. Sexual strategies theory (Buss and Schmitt, 1993) suggests that men are more concerned with missing a mating opportunity. This might be especially true when confronted with the idea of having limited time via mortality salience. On the other hand women are more concerned with avoiding costly mating situation with someone who is not a committed partner. Therefore, perceived time limitation through mortality salience should not be an issue for women to the same degree.

Again, however, there was no sex difference in the neural response to mortality salience. We found a significantly higher activation in the left anterior insula and adjacent lPFC after death-related compared to no priming for both men and women. As a part of the left frontal and prefrontal network associated with approach motivation (Tucker and Federick, 1989; Harmon-Jones and Harmon-Jones, 2008; Tritt *et al.*, 2012), recruitment of lPFC is congruent with our hypothesis and supports the idea that approach motivation is associated with viewing attractive opposite-sex faces under mortality salience. In addition, this finding is consistent with findings for lPFC activation when culture content was presented after death has been primed (Graupmann *et al.*, 2013b), providing converging evidence for a specific processing style associated with mortality salience proposed by TMT. In particular, the association of the lPFC with emotion regulation and self-distraction from pain (Kalisch *et al.* 2006) gives weight to this interpretation. However, this effect was limited to the prospect of meeting the presented person. Prior research has shown that physical attractiveness in opposite-sex constellations has a specific impact when the other person is indexed as a potential mating partner (Maner *et al.*, 2007). Together with our behavioral results, which revealed a main effect of question type, it can be assumed that the prospect of meeting the person created a stronger mating-relevant impact than an observed facial attractiveness *per se*.

The insula is divided into a posterior and an anterior part. The latter is playing a pivotal role in processing emotions such as anger, fear, disgust, happiness, sexual arousal, empathy, romantic love, but also craving and addiction, interoception and consciousness (for review, see Craig, 2009). In a nutshell, the insula has a highly integrative function, relating bodily states to cognitive and emotional processes. Due to the quantity of psychological functions we focus on interpreting insular activation on the basis of conceptual considerations and previous findings. An association of anterior insular activation and death-related priming has previously been interpreted in terms of interoception, i.e.

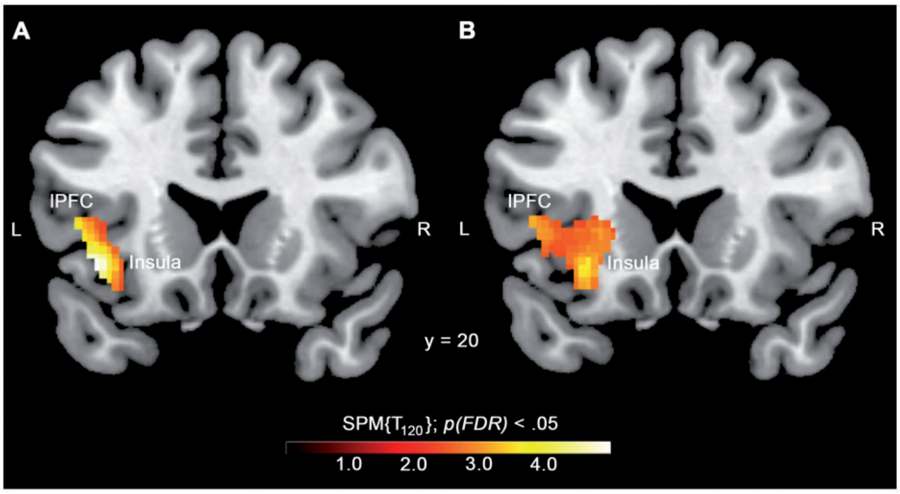

Fig. 2 Increased neural activation when viewing attractive opposite-sex faces after death-related compared with no priming in (**A**) men and (**B**) women.

Table 2 Higher activation after death-related compared with no priming

Brain region	Hemisphere	BA	Coordinates			z	Volume (mm^3)
			x	y	z		
Male observers							
LPFC	L	45, 47	−48	14	6	4.71	1296
Insula	L		−40	18	−6	5.05	1336
Female observers							
LPFC	L	45, 47	−46	18	8	3.23	1576
Insula	L		−28	22	−6	3.84	1872

BA, Brodmann areas. The *x*, *y* and *z* coordinates are in the MNI space.

awareness of internal bodily sensations, which in return decisively contributes to emotional experiences (Zaki *et al.*, 2012). Han *et al.* (2010) who found a decrease in bilateral anterior insular activation during the processing of death-related linguistic cues proposed that interoceptive tendencies are suppressed by death reminders. In contrast, we could show an increased activation in the left anterior insula when attractive opposite-sex faces are presented after death-related priming. This indicates that an awareness of bodily sensations could be even more intense under mortality salience than before. The distinctive results, however, are not necessarily contradictory. In terror management research, the connection between mortality salience and focus on the body has been examined extensively. The discrepancy between trying to ward off thoughts of finitude and the apparent finite nature of the human body is oftentimes solved by loading bodily sensations, e.g. sexuality, with meaning (Goldenberg *et al.*, 2000). In our study, the increased interest in opposite sex stimulus persons under mortality salience might therefore be an indication of directing the uncomfortable presence of bodily sensations—that resulted in a suppression of interoceptive processing in Han *et al.*'s study—into a culturally meaningful social tendency. What is more, bodily sensations are naturally involved in sexual desire, while somatic awareness might reasonably be avoided when imagining bodily decay. This might explain our finding that a higher mating motivation not necessarily was found on a level of subjective statements, i.e. self-reflective awareness. Drawing on the somatic marker hypothesis (SMH; Damasio *et al.*, 1991), which proposes that physiological signals rather than cognitive processes are triggered by certain relevant stimuli, the implicit nature of our result might be explained. According to SMH implicit responses reflect an evolutionary benefit, which is hindered by an awareness of this process. With the insula being directly connected to the amygdala, cingulate and orbitofrontal cortex it might be referred to as somatic marker stimulating approach motivation or avoidance and therefore enabling responses for genetic survival (Verdejo-García and Bechara, 2009).

Besides, the insula has previously been related to the experience of love and sexual desire (Bartels and Zeki, 2000; Cacioppo *et al.*, 2012; Diamond and Dickenson, 2012). Mating is associated with release of the hormone oxytocin (Borrow and Cameron, 2012), and oxytocin was found to increase activation in the insula and inferior frontal gyrus (Riem *et al.*, 2012). It has previously been shown that when choosing a dating partner the insula as well as adjacent lateral prefrontal areas are involved (Turk *et al.*, 2004). This activation pattern is similar to the one we found in our study when participants had to decide whether they would like to meet an attractive opposite-sex person under mortality salience. Thus, insular activation suggests an increase in mating motivation under mortality salience. This interpretation is in accordance with previous findings that mortality salience motivates the formation of romantic relationships (Florian *et al.*, 2002; Mikulincer *et al.*, 2003) and reproductive desire (Wisman and Goldenberg, 2005; Fritsche *et al.*, 2007).

In conclusion, our results provide insight into neural correlates of a defensive mechanism in the context of mortality salience. On the basis of our results we can assert that approach motivation is involved in defensive strategies to overcome mortality concerns. The neural correlates underlying a mortality salience effect on processing attractive opposite-sex faces also point to an increased mating motivation when reminded of death and dying, which has previously been found on a behavioral level. Besides, our findings match the neural correlates found for other strategies of dealing with mortality salience, providing converging evidence for some of the mechanisms proposed by TMT. Approach motivation in general and mating motivation in particular might therefore serve as a psychological strategy and probably phylogenetic relevant mechanism to overcome the existential threat that is implied in the idea of death.

REFERENCES

ACHIEVA 3T [Apparatus MRI system.]Hamburg, Germany: Philips.

Agthe, M., Spörrle, M., Maner, J.K. (2011). Does being attractive always help? Positive and negative effects of attractiveness on social decision making. *Personality and Social Psychology Bulletin*, *37*, 1042–54.

Aharon, I., Etcoff, N., Ariely, D., Chabris, C., O'Connor, E., Breiter, H. (2001). Beautiful faces have variable reward value: fMRI and behavioral evidence. *Neuron*, *32*, 537–51.

Arndt, J., Greenberg, J., Pyszczynski, T., Solomon, S. (1997). Subliminal exposure to death-related stimuli increases defense of the cultural worldview. *Psychological Science*, *8*, 379–85.

Avram, M., Gutyrchik, E., Bao, Y., Pöppel, E., Reiser, M., Blautzik, J. (2013). Neurofunctional correlates of esthetic and moral judgments. *Neuroscience Letters*, *534*, 128–32.

Bao, Y., Pöppel, E. (2012). Anthropological universals and cultural specifics: conceptual and methodological challenges in cultural neuroscience. *Neuroscience and Biobehavioral Reviews*, *36*, 2143–6.

Bartels, A., Zeki, S. (2000). The neural basis of romantic love. *NeuroReport: For Rapid Communication of Neuroscience Research*, *11*(17), 3829–34.

Baumeister, R.F., Leary, M.R. (1995). The need to belong: desire for interpersonal attachments as a fundamental human motivation. *Psychological Bulletin*, *117*, 497–529.

Borrow, A., Cameron, N. (2012). The role of oxytocin in mating and pregnancy. *Hormones and Behavior*, *61*, 266–76.

Burke, B.L., Martens, A., Faucher, E.H. (2010). Two decades of terror management theory: a meta-analysis of mortality salience research. *Personality and Social Psychology Review*, *14*, 155–95.

Buss, D., Schmitt, D. (1993). Sexual strategies theory: an evolutionary perspective on human mating. *Psychological Review*, *100*, 204–32.

Cacioppo, S., Bianchi-Demicheli, F., Frum, C., Pfaus, J., Lewis, J. (2012). The common neural bases between sexual desire and love: a multilevel kernel density fMRI analysis. *Journal of Sexual Medicine*, *9*, 1048–54.

Chatterjee, A., Thomas, A., Smith, S., Aguirre, G. (2009). The neural responses to facial attractiveness. *Neuropsychology*, *23*, 135–43.

Cloutier, J., Heatherton, T., Whalen, P., Kelley, W. (2008). Are attractive people rewarding? Sex differences in the neural substrates of facial attractiveness. *Journal of Cognitive Neuroscience*, *20*, 941–51.

Cohen, C.L., Cole, S.W. (2002). Life course transactions and natural disaster: marriage, birth, and divorce following Hurricane Hugo. *Journal of Family Psychology*, *16*, 14–25.

Craig, A.D. (2009). How do you feel—now? The anterior insula and human awareness. *Nature Reviews Neuroscience*, *10*, 59–70.

Damasio, A.R., Tranel, D., Damasio, H. (1991). Somatic markers and the guidance of behaviour: theory and preliminary testing. In: Levin, H.S., Eisenberg, H.M., Benton, A.L., editors. *Frontal Lobe Function and Dysfunction*. New York: Oxford University Press, pp. 217–29.

Diamond, L., Dickenson, J. (2012). The neuroimaging of love and desire: review and future directions. *Clinical Neuropsychiatry: Journal of Treatment Evaluation*, *9*, 39–46.

Evans, A.C., Collins, D.L., Mills, S.R., Brown, E.D., Kelly, R.L., Peters, T.M. (1993). 3D statistical neuroanatomical models from 305 MRI volumes. *Proceedings: IEEE Nuclear Science Symposium, Medical Imaging*, 1–3, 1813–7.

Fink, B., Penton-Voak, I. (2002). Evolutionary psychology of facial attractiveness. *Current Directions in Psychological Science*, *11*, 154–8.

Florian, V., Mikulincer, M. (1998). Symbolic immortality and the management of the terror of death: the moderating role of attachment style. *Journal of Personality and Social Psychology*, *74*, 725–34.

Florian, V., Mikulincer, M., Hirschberger, G. (2002). The anxiety-buffering function of close relationships: evidence that relationship commitment acts as a terror management mechanism. *Journal of Personality and Social Psychology*, *82*, 527–42.

Fritsche, I., Jonas, E., Fischer, P., Koranyi, N., Berger, N., Fleischmann, B. (2007). Mortality salience and the desire for offspring. *Journal of Experimental Social Psychology*, *43*, 753–62.

Goldenberg, J.L., Pyszczynski, T., Greenberg, J., Solomon, S. (2000). Fleeing the body: a terror management perspective on the problem of human corporeality. *Personality and Social Psychology Review*, *4*, 200–18.

Graupmann, V., Frey, D., Streicher, B. (2013a). The self-fortress: motivational responses to threats to the self. In: Hunter, B.O., Romero, T.J., editors. *Psychology of Threat*. New York: Nova Science Publishers, pp. 1–29.

Graupmann, V., Peres, I., Michaely, T., et al. (2013b). Culture and its neurofunctional correlates when death is in mind. *Neuroscience Letters*, *548*, 239–43.

Gray, J.A. (1982). *The Neuropsychology of Anxiety*. Oxford: Oxford University Press.

Greenberg, J., Pyszczynski, T., Solomon, S. (1986). The causes and consequences of a need for self-esteem: a terror management theory. In: Baumeister, R.F., editor. *Public Self and Private Self*. New York: Springer-Verlag, pp. 189–212.

Greenberg, J., Pyszczynski, T., Solomon, S., et al. (1990). Evidence for terror management theory II: the effects of mortality salience on reactions to those who threaten or bolster the cultural worldview. *Journal of Personality and Social Psychology*, *58*, 308–18.

Greenberg, J., Solomon, S., Pyszczynski, T., et al. (1992). Why do people need self-esteem? Converging evidence that self-esteem serves an anxiety-buffering function. *Journal of Personality and Social Psychology*, *63*, 913–22.

Han, S., Qin, J., Ma, Y. (2010). Neurocognitive processes of linguistic cues related to death. *Neuropsychologia*, *48*, 3436–42.

Harmon-Jones, E., Harmon-Jones, C. (2008). Action-based model of dissonance: a review of behavioral, anterior cingulate, and prefrontal cortical mechanisms. *Social and Personality Psychology Compass*, *2*, 1518–38.

Kalisch, R., Wiech, K., Herrmann, K., Dolan, R.J. (2006). Neural correlates of self-distraction from anxiety and a process model of cognitive emotion regulation. *Journal of Cognitive Neuroscience*, *18*, 1266–76.

Kampe, K., Frith, C., Dolan, R., Frith, U. (2001). Reward value of attractiveness and gaze. *Nature*, *413*, 589.

Kanwisher, N., McDermott, J., Chun, M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *17*, 4302–11.

Koestner, R., McClelland, D.C. (1992). The affiliation motive. In: Smith, C.P., editor. *Motivation and Personality: Handbook of Thematic Content Analysis*. New York: Cambridge University Press, pp. 205–10.

Koranyi, N., Rothermund, K. (2012). When the grass on the other side of the fence doesn't matter: reciprocal romantic interest neutralizes attentional bias towards attractive alternatives. *Journal of Experimental Social Psychology*, *48*, 186–91.

Kosloff, S., Greenberg, J., Sullivan, D., Weise, D. (2010). Of trophies and pillars: exploring the terror management functions of short-term and long-term relationship partners. *Personality and Social Psychology Bulletin*, *36*, 1037–51.

Kranz, F., Ishai, A. (2006). Face perception is modulated by sexual preference. *Current Biology*, *16*, 63–8.

Leary, M.R. (1999). Making sense of self-esteem. *Current Directions of Psychological Science*, *8*, 32–5.

Leary, M.R., Tambour, E.S., Terdal, S.K., Downs, D.L. (1995). Self-esteem as an interpersonal monitor: the sociometer hypothesis. *Journal of Personality and Social Psychology*, *68*, 518–30.

Lifton, R.J. (1973). The sense of immortality: on death and the continuity of life. *American Journal of Psychoanalysis*, *33*, 3–15.

LUMItouch [Apparatus]. fMRI optical response keypad Burnaby, British Columbia. Canada: Photon Control Inc.

Luo, S., Shi, Z., Yang, X., Wang, X., Han, S. (2013). Reminders of mortality decrease midcingulate activity in response to others' suffering. *Social Cognitive and Affective Neuroscience*. doi: 10.1093/scan/nst010.

Lutz, A., Nassehi, A., Bao, Y., et al. (2013). Neurocognitive processing of body representations in artistic and photographic images. *Neuroimage*, *66*, 288–92.

Maldjian, J.A. (2007). WFU Pickatlas (Version 2.4) [Computer software]. http://www.ansir.wfubmc.edu.

Maner, J.K., Gailliot, M.T., Rouby, D.A., Miller, S.L. (2007). Can't take my eyes off you: attentional adhesion to mates and rivals. *Journal of Personality and Social Psychology*, *93*, 389–401.

McAdams, D.P. (1992). The intimacy motive. In: Smith, C.P., editor. *Motivation and Personality: Handbook of Thematic Content Analysis*. New York: Cambridge University Press, pp. 224–8.

McGregor, I., Prentice, M., Nash, K. (2012). Approach relief: compensatory ideals relieve threat-induced anxiety by promoting approach-motivated states. *Social Cognition*, *30*, 689–714.

Mikulincer, M., Florian, V., Hirschberger, G. (2003). The existential function of close relationships: introducing death into the science of love. *Personality and Social Psychology Review*, *7*, 20–40.

O'Doherty, J., Winston, J., Critchley, H., Perrett, D., Burt, D., Dolan, R. (2003). Beauty in a smile: the role of medial orbitofrontal cortex in facial attractiveness. *Neuropsychologia*, *41*, 147–55.

Passbild Generator (Version 3.5a) [Computer software]. http://www.passbild-generator.de.

Presentation (Version 15.1) [Computer software]. https://www.neurobs.com.

Quirin, M., Loktyushin, A., Arndt, J., et al. (2012). Existential neuroscience: a functional magnetic resonance imaging investigation of neural responses to reminders of one's mortality. *Social Cognitive and Affective Neuroscience*, *7*, 193–8.

Riem, M., Bakermans-Kranenburg, M., Pieper, S., et al. (2012). Oxytocin modulates amygdala, insula, and inferior frontal gyrus responses to infant crying: a randomized controlled trial. *Biological Psychiatry*, *70*, 291–7.

Rodgers, J.L., St. John, C.A., Coleman, R. (2005). Did fertility go up after the Oklahoma City bombing? An analysis of births in metropolitan counties in Oklahoma, 1990–1999. *Demography*, *42*, 675–92.

Schachter, S. (1959). *The Psychology of Affiliation*. Stanford, CA: Stanford University Press.

Silveira, S., Graupmann, V., Frey, D., et al. (2012). Matching reality in the arts: self-referential neural processing of naturalistic compared to surrealistic images. *Perception*, *41*, 569–76.

SPM (Version 8) [Computer software]. http://www.fil.ion.ucl.ac.uk/spm.

Tritt, S., Inzlicht, M., Harmon-Jones, E. (2012). Toward a biological understanding of mortality salience (and other threat compensation processes). *Social Cognition*, *30*, 715–33.

Tucker, D., Federick, S. (1989). Emotion and brain lateralization. In: Wagner, H., Manstead, A., editors. *Handbook of Social Psychophysiology*. Chichester, UK: Wiley, pp. 27–70.

Turk, B., Banfield, J., Walling, B., et al. (2004). From facial cue to dinner for two: the neural substrates of personal choice. *Neuroimage*, *22*, 1281–90.

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., et al. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *Neuroimage*, *15*, 273–89.

Van Hooff, J.C., Crawford, H., van Vugt, M. (2011). The wandering mind of men: ERP evidence for gender differences in attention bias towards attractive opposite sex faces. *Social Cognitive and Affective Neuroscience*, *6*, 477–85.

Verdejo-García, A., Bechara, A. (2009). A somatic marker theory of addiction. *Neuropharmacology*, *56*, 48–62.

Võ, M.L., Conrad, M., Kuchinke, L., Urton, K., Hofmann, M.J., Jacobs, A.M. (2009). The Berlin affective word list reloaded (BAWL-R). *Behavior Research Methods*, *41*, 534–8.

Wisman, A., Goldenberg, J.L. (2005). From the grave to the cradle: evidence that mortality salience engenders a desire for offspring. *Journal of Personality and Social Psychology*, *89*, 46–61.

Zaki, J., Davis, J., Ochsner, K. (2012). Overlapping activity in the anterior insula during interoception and emotional experience. *Neuroimage*, *62*, 493–9.

4 References

Arndt, J., Greenberg, J., Pyszczynski, T., & Solomon, S. (1997). Subliminal exposure to death-related stimuli increases defense of the cultural worldview. *Psychological Science, 8*, 37985.

Bao, Y., & Pöppel, E. (2007). Two spatially separated attention systems in the visual field: evidence from inhibition of return. *Cognitive Processing, 8*, 37-44.

Bargh, J. (1997). The automaticity of everyday life. In R. S. Wyer Jr. (Ed.), *The automaticity of everyday life: Advances in social cognition, Vol. 10* (pp. 1-61). Mahwah, NJ: Erlbaum.

Burke, B. L., Martens, A., & Faucher, E. H. (2010). Two decades of terror management theory: A meta-analysis of mortality salience research. *Personality and Social Psychology Review, 14*, 155-195.

Cavanna, A. E., & Trimble, M. R. (2006). The precuneus: a review of its functional anatomy and behavioural correlates. *Brain, 129*, 564-583.

Cela-Conde, C. J., Ayala, F. J., Munar, E., Maestú, F., Nadal, M., Capò, M. A., del Rio, D., Lopez-Ibor, J. J., Ortiz, T., Mirasso, C., & Marty, G. (2009). Sex-related similarities and differences in the neural correlates of beauty. *Proceedings of the National Academy of Sciences, 106*, 3847-3852.

Cohen, C. L., & Cole, S. W. (2002). Life course transactions and natural disaster: Marriage, birth, and divorce following Hurricane Hugo. *Journal of Family Psychology, 16*, 14-25.

Cupchik, G. C., & Laszlo, J. (1992). *Emerging visions of the aesthetic process: Psychology, semiology, and philosophy.* New York: Cambridge University Press.

Cupchik, G. C., Vartanian, O., Crawley, A., & Mikulis, D. J. (2009). Viewing artworks: contributions of cognitive control and perceptual facilitation to aesthetic experience. *Brain and Cognition, 70*, 84-91.

Danto, A. C. (1981). *The transfiguration of the commonplace: A philosophy of art.* London: Harvard University Press.

De Houwer, J., Hermans, D., Rothermund, K., & Wentura, D. (2002). Affective priming of semantic categorization responses. *Cognition and Emotion, 16*, 643-666.

Egeth, H. E., & Yantis, S. (1997). Visual attention: control, representation, and time course. *Annual Review of Psychology, 48*, 267-297.

Eibl-Eibesfeldt, I. (1988). The biological foundation of aesthetics. In I. Rentschler, B. Herzberger & D. Epstein (Eds.), *Beauty and the brain: Biological aspects of aesthetics* (pp. 29-68). Basel: Birkhäuser Verlag.

Epstein, S. (1985). The implications of cognitive-experiential self theory for research in social psychology and personality. *Journal of Personality and Social Psychology, 15*, 283-310.

Fechner, G. T. (1871). *Vorschule der Ästhetik.* [Preschool of aesthetics] Hildesheim: Olms.

Florian, V., Mikulincer, M., & Hirschberger, G. (2002). The anxiety-buffering function of close relationships: Evidence that relationship commitment acts as a terror management mechanism. *Journal of Personality and Social Psychology, 82*, 527-542.

Gibson, J. J. (1966). *The senses considered as perceptual systems.* Boston, MA: Houghton Mifflin Company.

Godijn, R., & Theeuwes, J. (2003). Parallel allocation of attention prior to the execution of saccade sequences. *Journal of Experimental Psychology:*

Human Perception and Performance, 29, 882-896.

Graupmann, V., Peres, I., Michaely, T., Meindl, T, Frey, D., Fehse, K., & Gutyrchik, E. (2013). Culture and its neurofunctional correlates when death is in mind. *Neuroscience Letters, 548*, 239-243.

Gray, J. A. (1982). *The neuropsycholgy of anxiety.* Oxford: Oxford University Press.

Greenberg, J., Solomon, S., Pyszczynski, T., Rosenblatt, A., Burling, J., Lyon, D., Simon, L., & Pinel, E. (1992). Why do people need self-esteem? Converging evidence that self-esteem serves an anxiety-buffering function. *Journal of Personality and Social Psychology, 63*, 913-922.

Han, S., Qin, J., & Ma, Y. (2010) Neurocognitive processes of linguistic cues related to death. *Neuropsychologia, 48*, 3436-3442.

Heine, S. J., Proulx, T., & Vohs, K. D. (2006). Meaning maintenance model: On the coherence of social motivations. *Personality and Social Psychology Review, 10*, 88-110.

Kawabata, H., & Zeki, S. (2004). Neural correlates of beauty. *Journal of Neurophysiology, 91*, 1699-1705.

Klauer, K., & Musch, J. (2002). Goal-dependent and goal-independent effects of irrelevant evaluations. *Personality and Social Psychology Bulletin, 28*, 802-814.

Klinger, E. (1998). The search for meaning in evolutionary perspective and its clinical implications. In P. T. P. Wong & P. S. Fry (Eds.), *The human quest for meaning: A handbook of psychological research and clinical application* (pp 137-186). Lincoln, NE: University of Nebraska Press.

Kosloff, S., Greenberg, J., Sullivan, D., & Weise, D. (2010). Of trophies and pillars: Exploring the terror management functions of short-term and long-term relationship partners. *Personality and Social Psychology Bulletin, 36*, 1037-1051.

Lacey, S., Hagtvedt, H., Patrick, V., Anderson, A., Stilla, R., Deshpande, G., Hu, X., Sato, J., Reddy, S., & Sathian, K. (2011). Art for reward's sake: Visual art recruits the ventral striatum. *Neuroimage, 55*, 420-433.

Landau, M. J., Solomon, S., Pyszczynski, T., & Martens, A. (2006). Windows into nothingness: Terror management, meaninglessness, and negative reactions to modern art. *Journal of Personality and Social Psychology, 90*, 879-892.

Lerner, I., Bentin, S., & Shriki, O. (2012). Spreading activation in an attractor network with latching dynamics: Automatic semantic priming revisited. *Cognitive Science, 36*, 1339-1382.

Lutz, A., Nassehi, A., Bao, Y., Pöppel, E., Sztrókay, A., Reiser, M., Fehse, K., & Gutyrchik, E. (2013). Neurocognitive processing of body representations in artistic and photographic images. *Neuroimage, 66*, 288-292.

McGregor, I., Prentice, M., & Nash, K. (2012). Approach relief: Compensatory ideals relieve threat-induced anxiety by promoting approach-motivated states. *Social Cognition, 30*, 689-714.

Mikulincer, M., Florian, V., & Hirschberger, G. (2003). The existential function of close relationships: Introducing death into the science of love. *Personality and Social Psychology Review, 7*, 20-40.

Northoff, G., & Bermpohl, F. (2004). Cortical midline structures and the self. *Trends in Cognitive Sciences, 8*, 102-107.

Parsons, M. (1987). *How we understand art: A cognitive developmental account of aesthetic experience.* Cambridge: Cambridge University Press.

Pöppel, E. (2009). Pre-semantically defined temporal windows for cognitive processing. *Philosophical Transactions of the Royal Society B, 364*, 1887-1896.

Pöppel, E. (2010). Perceptual identity and personal self. In T. Maruszewski, M. Fajkowska & M. W. Eysenck (Eds.), *Personality from biological, cognitive, and social perspectives* (pp.77-84). New York: Eliot Werner Publications.

Pöppel, E., & Bao, Y. (2011). Three modes of knowledge as basis for intercultural cognition and communication: A theoretical perspective. In S. Han & E. Pöppel (Eds.), *Culture and neural frames of cognition and communication* (pp. 215-231). Heidelberg: Springer Verlag.

Pöppel, E., Bao, Y., & Zhou, B. (2011). Temporal windows as logistical basis for cognitive processing. *Advances in Psychological Science, 19*, 775-793.

Pöppel, E., Avram, M., Bao, Y., Graupmann, V., Gutyrchik, E., Lutz, A., Park, M., Reiser, M., Russell, E., Silveira, S., Smigielski, L., Szymanski, C., & Zaytseva, Y. (2013). Sensory processing of art as a unique window into cognitive mechanisms: Evidence from behavioral experiments and fMRI studies. *Procedia - Social and Behavioral Sciences* (in press).

Quirin, M., Loktyushin, A., Arndt, J., Küstermann, E., Lo, Y.-Y., Kuhl, J., & Eggert, L. (2012). Existential neuroscience: A functional magnetic resonance imaging investigation of neural responses to reminders of ones mortality. *Social Cognitive and Affective Neuroscience, 7*, 193-198.

Reber, R., Schwarz, N., & Winkielman, P. (2004). Processing fluency and aesthetic pleasure: Is beauty in the perceivers processing experience? *Personality and Social Psychology Review, 8*, 364-382.

Rodgers, J. L., St. John, C. A., & Coleman, R. (2005). Did fertility go up after the Oklahoma City bombing? An analysis of births in metropolitan counties in Oklahoma, 1990-1999. *Demography, 42*, 675-692.

Sani, F., Herrera, M., & Bowe, M. (2009). Perceived collective continuity and ingroup identification as defense against death awareness. *Journal of Experimental Social Psychology, 45*, 242-245.

Schachter, S. (1959). *The psychology of affiliation.* Stanford, CA: Stanford University Press.

Silveira, S., Graupmann, V., Frey, D., Blautzik, J., Meindl, T., Reiser, M., Chen, C., Wang, Y., Bao, Y., Pöppel, E., & Gutyrchik, E. (2012). Matching reality in the arts: Self-referential neural processing of naturalistic compared to surrealistic images. *Perception, 41*, 569-576.

Silveira, S., Graupmann, V., Agthe, M., Gutyrchik, E., Blautzik, J., Demircapa, I., Berndt, A., Pöppel, E., Frey, D., Reiser, M., & Hennig-Fast, K. (2013). Existential neuroscience: effects of mortality salience on the neurocognitive processing of attractive opposite-sex faces. *Social Cognitive and Affective Neuroscience.* (in press)

Steger, M. F., Kashadan, T. B., Sullivan, B. A., & Lorentz, D. (2008). Understanding the search for meaning in life: personality, cognitive style, and the dynamic between seeking and experiencing meaning. *Journal of Personality, 76*, 199-228.

Störig, P., Sütterlin, C., & Pöppel, E. (1983). Rechts und Links in Bildwerken: Ein neuropsychologischer Beitrag zum Kunstverständnis. *Umschau in Wissenschaft und Technik 83, 14*, 427-428.

Teuber, H.-L. (1960). Perception. In I. Field & H. W. Magoun (Eds.), *Handbook of Physiology - Neurophysiology* (pp. 1595-1668). Washington, DC: American Physiological Society.

Tritt, S., Inzlicht, M., & Harmon-Jones, E. (2012). Toward a biological understanding of mortality salience (and other threat compensation processes). *Social Cognition, 30*, 715-733.

Turner, F., & Pöppel, E. (1988). Metered poetry, the brain, and time. In I. Rentschler, B. Herzberger & D. Epstein (Eds.), *Beauty and the brain: Biological aspects of aesthetics* (pp. 71-90). Basel: Birkhäuser Verlag.

Vartanian, O., & Goel, V. (2004). Neuroanatomical correlates of aesthetic preference for paintings. *Neuroreport, 15*, 893-897.

Vessel, E., Starr, G., & Rubin, N. (2012). The brain on art: intense aesthetic experience activates the default mode network. *Frontiers in Human Neuroscience, 6*, doi:10.3389/fnhum.2012.00066.

Von Holst, E., & Mittelstaedt, H. (1950). Das Reafferenzprinzip. *Naturwissenschaften, 37*, 464-476.

Voss, A., Rothermund, K., Gast, A., & Wentura, D. (2012). Cognitive processes in associative and categorical priming: A diffusion model analysis. *Journal of Experimental Psychology, 142*, 536-559.

5 Acknowledgements

First I would like to thank the Hanns-Seidel-Stiftung for making this scientific pursuit possible by supporting my doctoral thesis.

My sincere thanks go to my advisor, Prof. Dr. Ernst Pöppel, not only for his tremendous scientific input, but also for his encouragement and trust, for challenging my motivation by playing the advocatus diaboli, for valuing authenticity, and for reminding me of the joy of thinking and re-thinking.

I also thank Dr. Evgeny Gutyrchik, who introduced me to the world inside the brain, and the whole cellar crew for fruitful discussions on how to explore this neuro-cosmos with all its mysteries. My sincere thanks also go to Dr. Verena Graupmann for her curiosity and inspiration that has motivated and encouraged me to build bridges between different research areas.

Last but not least I would like to thank my beloved ones - my parents, my sister and my friends, who supported me throughout the last three years.

Eidesstattliche Versicherung

Silveira, Sarita

Ich erkläre hiermit an Eides statt,

dass ich die vorliegende Dissertation mit dem Thema

The influence of mental frames

on the neurocognitive processing of visual art

selbständig verfasst, mich außer der angegebenen keiner weiteren Hilfsmittel bedient und alle Erkenntnisse, die aus dem Schrifttum ganz oder annähernd übernommen sind, als solche kenntlich gemacht und nach ihrer Herkunft unter Bezeichnung der Fundstelle einzeln nachgewiesen habe.

Ich erkläre des Weiteren, dass die hier vorliegende Dissertation nicht in gleicher oder in ähnlicher Form bei einer anderen Stelle zur Erlangung eines akademischen Grades eingereicht wurde.

Ort, Datum	Unterschrift