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

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Being reminded of the inherently finite nature of human existence have 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; Graumann 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...
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 started that after priming with death-related content brain activation just beginning to be understood. In an fMRI study, it has been demonstrated that defensive strategies to overcome mortality concerns like the formation and maintenance of self-esteem, worldview and symbolic immortality is needed. Such defensive strategies can be understood as a counterpart of mortality concerns (McGregor et al., 2012). Thus, it has been proposed that an alleviation of death-related concerns should be represented in a switch from a withdrawal-motivated to an approach-motivated state (McGregor 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 (>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; Vo 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...
thickness = 3.5 mm, inter-slice gap = 0 mm, interleaved acquisition, FOV = 230 x 230 mm, matrix = 76 x 77, in-plane resolution = 3 x 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 r-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) x 2 (prime condition) x 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 cluster-wise 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) x 2 (prime condition) x 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...
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 IFPC in processing the opposite-sex faces after death-related 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 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 studies, 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 IFPC 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 IFPC 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 IFPC 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 IFPC 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.
reflective awareness. Drawing on the somatic marker hypothesis necessarily was found on a level of subjective statements, i.e. self-awareness might reasonably be avoided when imagining bodily decay. This might explain our finding that a higher mating motivation not only tends to result in a suppression of interoceptive processing in Han et al. (2000) but also could show an increased activation in the left anterior insula under mortality salience (Han et al., 2012). The insula has previously been related to the experience of bodily sensations, e.g. sexuality, with meaning (Goldenber 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.

| Table 2 | Higher activation after death-related compared with no priming |
|------------------|------------------------|------------------|---------|
| Brain region     | Hemisphere | BA       | Coordinates | z    | Volume (mm³) | BA, Brodmann areas. The x, y and z coordinates are in the MNI space. |
| Male observers   |            |          |             |      |              |
| LPFC             | L          | 45, 47   | 48          | 14   | 6.71         | 1296 |
| Insula           | L          | 40, 18   | 18          | 8    | 5.05         | 1336 |
| Female observers |            |          |             |      |              |
| LPFC             | L          | 45, 47   | 46          | 18   | 3.23         | 1576 |
| Insula           | L          | 28, 22   | 6           | 8    | 3.84         | 1872 |

(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-Garcia 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).


