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Original Article

Mortality Salience Enhances Neural Activities Related to Guilt and Shame When Recalling the Past

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Abstract

Mortality salience (MS) influences cognition and behavior. However, its effect on emotion (especially moral emotions) and the underlying neural correlates are unclear. We investigated how MS priming modulated guilt and shame in a later recall task using functional magnetic resonance imaging. The behavioral results indicated that MS increased self-reported guilt but not shame. The neural results showed that MS strengthened neural activities related to the psychological processes of guilt and shame. Specifically, for both guilt and shame, MS increased activation in a region associated with self-referential processing (ventral medial prefrontal cortex). For guilt but not shame, MS increased the activation of regions associated with cognitive control (orbitofrontal cortex) and emotion processing (amygdala). For shame but not guilt, MS decreased brain functional connectivity related to self-referential processing. A direct comparison showed that MS more strongly decreased a functional connectivity related to self-referential processing in the shame than in the guilt condition. Additionally, the activation of insula during MS priming was partly predictive of neural activities related to guilt and shame in the subsequent recall task. Our study sheds light on the psychological and neural mechanisms of MS effects on moral emotions and provides theoretical insights for enriching terror management theory.

Key words: mortality salience; guilt; shame; functional magnetic resonance imaging; terror management theory.

Introduction

Reminders of death (mortality salience, MS) have remarkable impacts on individuals' psychological processes and behaviors (Wisman and Koole 2003; Burke et al. 2010; Zaleskiewicz et al. 2015; Hu et al. 2018). This is because humans' unique awareness of inevitable death induces existential anxiety (Becket 1973; Greenberg et al. 1986; Greenberg et al. 2003). According to terror management theory (TMT), humans have evolved two defensive strategies—proximal and distal defenses—to manage existential anxiety (Greenberg et al. 1986, 1997; Pyszczynski et al. 1999). Proximal defenses cope with conscious thoughts of death, which occur during or immediately after exposure to MS (Pyszczynski et al. 1999). They are rational attempts to remove death-related thoughts from consciousness by suppressing such thoughts with distractions, pushing them into the distant future, or denying one's vulnerability to death. It helps individuals avoid facing death-related anxiety directly. In contrast, distal defenses are responses to thoughts of death beneath consciousness, which occur after a distractor task following the MS or when MS is combined with high cognitive load. Distal defenses implicitly influence individuals' cognition, emotion, and/or behavior in a way that targets upholding individuals' cultural worldviews and boosting individuals' self-esteem (Pyszczynski et al. 1999). It enables individuals to believe that some valued aspects of themselves continue to exist symbolically after death and eliminates existential anxiety indirectly (Greenberg et al. 1986).

Previous studies have found abundant evidence to support the existence of proximal and distal defenses (Pyszczynski et al. 1999; Burke et al. 2010; Hayes et al. 2010; Hu et al. 2018). For example, in support of the existence of proximal defenses, studies have consistently shown that death-related words viewing reduces activity in the insula, which reflects a suppression of sentient self-awareness (Han et al. 2010; Shi and Han 2013; Klackl et al. 2014; Luo et al. 2019). In support of the existence of distal defenses, studies have revealed that MS modulates the neural activities underlying psychological and behavioral responses (e.g. empathy and altruistic punishment) that conform to moral norms, which may help strengthen cultural worldviews and self-esteem (Silveira et al. 2014; Li et al. 2015; Feng et al. 2017).

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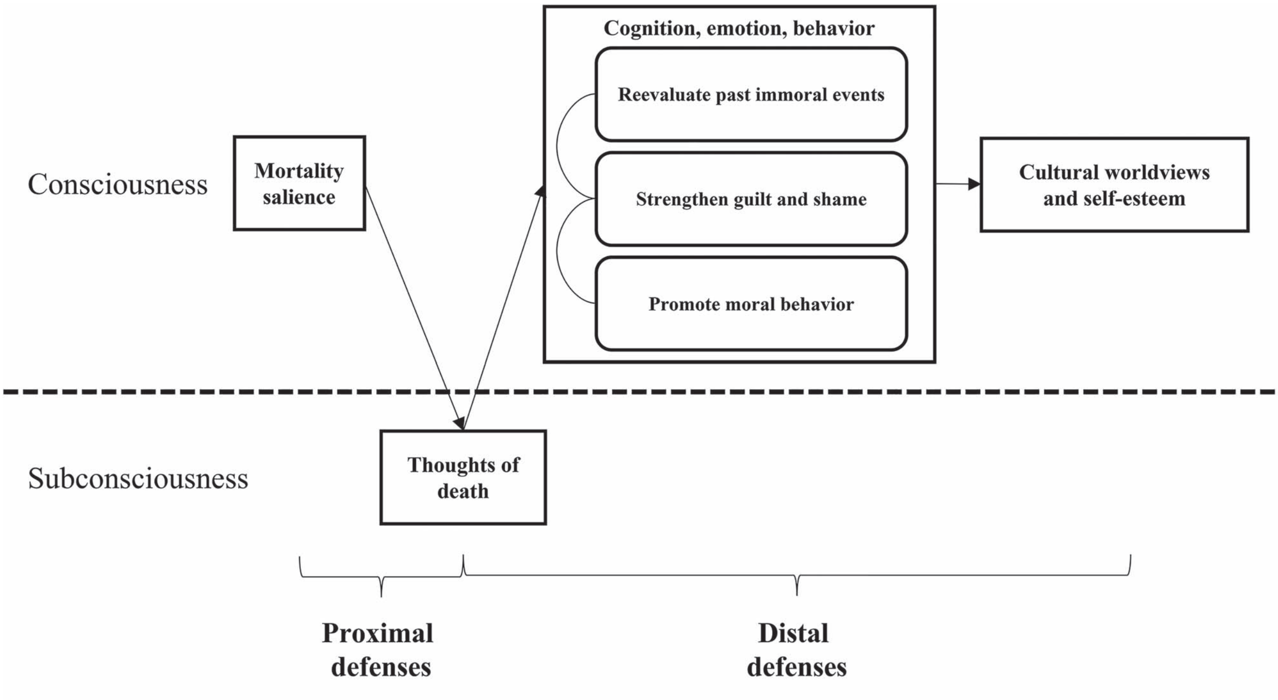

Figure 1. Theoretical construction of how guilt and shame are related to MS within the framework of TMT.

After reviewing the literature, we noticed two gaps in the currently available research. One is that compared with studies on the influence of subconscious thoughts of death on cognition and behavior, far fewer studies have investigated the effect of subconscious thoughts of death on emotion, especially moral emotions (e.g. guilt and shame) (see three reviews, Greenberg and Kosloff 2008; Niesta et al. 2008; Burke et al. 2010). Guilt and shame warn individuals of their moral transgressions, stop them from continuing moral transgressions, and encourage them to follow moral norms (Haidt 2003; Tangney et al. 2007; Chang et al. 2011; Sznycer 2019). Within the framework of TMT, guilt and shame may play such roles in distal defenses (see Fig. 1). Subconscious thoughts of death implicitly facilitate individuals to reevaluate immoral events that they have engaged in and increase individuals' guilt and shame. These two emotions prepare individuals psychologically and promote various moral behaviors (e.g. apology, compensation, or self-punishment) (Haidt 2003; Tangney et al. 2007; Zhu et al. 2017). As moral norms are vital elements of cultural worldviews that provide a sense of order and meaning (Gailliot et al. 2008; Pyszczynski and Kesebir 2012), moral behaviors can help individuals uphold cultural worldviews and maintain self-esteem in the moral aspect (e.g. Harrison and Mallett 2013). Supporting this proposition, previous studies have found that after moral behavior, guilty and ashamed individuals have fewer feelings of guilt and shame, obtain a sense of relief, and most importantly believe that they achieve purification and reparation for their sins (i.e. rebuild moral self-esteem) (Glucklich 2001; Monin and Jordan 2009; Nelissen and Zeelenberg 2009; Bastian et al. 2011). We propose that subconscious thoughts of death implicitly change individuals' evaluations of immoral events and strengthen guilt and shame; strengthened guilt and shame promote moral behavior; and guilt- and shame-promoted moral behavior (rather than guilt and shame per se) influences individuals' cultural worldviews and self-esteem. Thus, strengthened guilt and shame are an important intermediate step in the chain from morality salience to boosted cultural worldviews and self-esteem.

Although both guilt and shame are moral emotions that promote moral behaviors, they supposedly evolved for solving different social problems (Sznycer 2019). Guilt often manifests in situations where individuals harm others and individuals' interpersonal relationships are broken (Parkinson and Illingworth 2009; Sznycer 2019). Shame usually occurs in situations where individuals expose their (moral) inability and individuals' social reputations are damaged (Sznycer 2019; Scrivner et al. 2021). Thus, it is worth examining the effects of MS on guilt and shame, which provides opportunities to test the explanatory power of TMT in different social contexts (Sometimes, social situations where guilt and shame occur are not exclusive of each other. However, guilt may be more associated with situations related to direct reciprocity, while shame may be more associated with situations related to indirect reciprocity [Sznycer 2019].).

In addition to examining whether MS affects guilt and shame, it is also interesting and important to investigate how they happen (i.e. neural correlates). The way MS affects the neural correlates of guilt and shame may depend on the psychological features of guilt and shame. Three psychological processes are shared by guilt and shame. Based on self-reports, previous studies have shown that individuals in guilt and shame have negative emotional experiences (i.e. emotion processing), pay attention to others' suffering (i.e. mentalizing), and blame themselves for the suffering that occurs (i.e. self-referential processing) (Tangney and Dearing 2003; Bastin et al. 2016). Consistently, neuroimaging and brain injury studies have revealed that both guilt and shame activate brain regions associated with emotion processing (e.g. amygdala and insula) (Michl et al. 2014; Pulcu et al. 2014; Zhu, Feng, et al. 2019; Piretti et al. 2020), mentalizing (e.g. temporoparietal junction [TPJ]) (Takahashi et al. 2004; Finger et al. 2006; Moll et al. 2007; Wagner et al. 2011; Michl et al. 2014), and self-referential processing (e.g. ventral medial prefrontal cortex [vmPFC]/anterior cingulate cortex [ACC] and posterior cingulate cortex [PCC]/precuneus) (Shin et al. 2000; Yu et al. 2014, 2020; Bastin et al. 2016; Gifuni et al. 2017; Li et al. 2020).

Despite the similarities, guilt and shame have theoretical and tangible differences (Tangney 1995; Tangney et al. 1996; Tracy and Robins 2006). It is believed that in a state of guilt, individuals concentrate on what they did to victims and criticize their own behavior (e.g. "I did a bad thing"), whereas in a state of shame, individuals focus on who they are and degrade themselves (e.g. "I am a bad person") (Tangney and Dearing 2003). Consistent with this opinion, behavioral studies have revealed that guilt promotes other-oriented behaviors related to relationship reparation, including apology and compensation (Howell et al. 2012; Yu et al. 2014), whereas shame leads to self-oriented behaviors associated with self-image management, such as escape and hiding (De Hooge et al. 2010; Gausel and Leach 2011; Sznycer et al. 2016). The results from neural imaging studies suggest that guilt involves more mentalizing (e.g. indicated by the activation of TPJ) and cognitive control (e.g. indicated by the activation of orbitofrontal cortex [OFC]) than shame (Wagner et al. 2011; Zhu, Feng, et al. 2019), while shame may involve more self-referential processing (e.g. indicated by the neural activities of the dmPFC/ACC) than guilt (Zhu, Feng, et al. 2019). Given the similarities and differences between guilt and shame, the MS effects on the neural activities related to guilt and shame may not be exactly the same.

The other research gap is that few studies have examined the relationship between the two types of defenses (but see an exception, Luo et al. 2019). Behavioral studies could not quantitively measure proximal defenses (Pyszczynski et al. 1999; Greenberg et al. 2000), whereas functional magnetic resonance imaging (fMRI) studies paid attention to either neural activities during MS priming (related to proximal defenses) or neural activities during a task after MS priming (related to distal defenses). In addition, we noticed that fMRI studies revealed little interest in making theoretical contributions to proximal and distal defenses. In fact, most fMRI studies on MS did not mention the words "proximal defenses" or "distal defenses" at all.

To fill in the two research gaps above, we investigated whether and how MS modulates guilt and shame with fMRI scanning. Based on TMT (Greenberg et al. 1986; Pyszczynski et al. 1999), we predicted that MS enhances guilt and shame. According to the existing neural findings and similarity between guilt and shame (e.g. Bastin et al. 2016), we predicted that in both guilt and shame conditions, MS enhances the neural activities associated with emotion processing (i.e. amygdala and insula), mentalizing (i.e. TPJ), and/or self-referential processing (i.e. vmPFC, dmPFC, and PCC). Considering the difference between guilt and shame (Wagner et al. 2011; Zhu, Feng, et al. 2019), we also predicted that the extent to which MS modulates the neural activities associated with cognitive control (i.e. OFC), mentalizing (i.e. TPJ), and/or self-referential processing (i.e. vmPFC, dmPFC, and PCC) varies across the guilt and shame conditions.

As to fMRI data, we adopted both univariate activation and psychophysiological interaction (PPI) analyses because some psychological processes associated with guilt and shame (e.g. self-referential processing and mentalizing) rely on not only the activation of related brain regions but also the communication among them. Regarding self-referential processing, studies found that viewing or evaluating self-related stimuli activates several cortical midline structures (CMSs; i.e. vmPFC/ACC, dmPFC, and PCC/precuneus) (Northoff and Bermpohl 2004; Northoff et al. 2006; van Buuren et al. 2010). In the meantime, self-referential processing is associated with a decrease in the functional connectivity between regions within the CMS (e.g. vmPFC-PCC and vmPFC-precuneus connectivity) (van Buuren et al. 2010, 2012). Regarding mentalizing, studies have found that understanding others' thoughts and feelings activates brain regions in the mentalizing network (e.g. TPJ and superior temporal cortex) (Schurz et al. 2014) and enhances the functional connectivity between regions within the mentalizing network (e.g. functional connectivity between bilateral TPJ) (Van Overwalle et al. 2019). Thus, the use of both univariate activation and PPI analyses might enable us to identify subtle differences in the effects of MS on guilt and shame.

In addition, we explored the relationship between proximal and distal defenses. Considering that both serve to manage existential anxiety (Pyszczynski et al. 1999), we predicted that individuals with stronger proximal defenses engage in stronger distal defenses. As previous studies have consistently identified a deactivation in the insula when individuals were processing death-related information and regarded it as a suppression of sentient self-awareness (Han et al. 2010; Shi and Han 2013; Klackl et al. 2014; Luo et al. 2019), we used insula activity as an indicator of proximal defenses. We used the neural activities modulated by MS during guilt and shame experience as indicators of distal defenses.

Materials and methods

Participants

We expected a moderate to large effect of MS on guilt and shame based on a meta-analytic review of MS (effect size: $r = 0.35$/Cohen's $d = 0.75$) (Burke et al. 2010). We set the expected effect size to be Cohen's $d = 0.75$, the probability of type I error to be 0.05, and the statistical power to be 0.80, and we determined the minimum sample size to be 58 participants. Assuming 5–10% data loss, we recruited 65 right-handed college students (35 females, 30 males; 22.2 ± 2.78 years). None reported a history of psychiatric or neurological disorders and all had normal or corrected-to-normal vision. Data from three participants were excluded from analyses (two did not complete the experiment for personal reasons and one misunderstood the instruction). Thus, we had data from 62 valid participants for analysis (MS group: 32 participants, 16 females and 16 males, $M_{age} = 22.62$ years, $SD_{age} = 3.05$; NA group: 30 participants, 18 females and 12 males, $M_{age} = 21.77$ years, $SD_{age} = 2.45$). This study was approved by the Ethics Committee of the Department of Psychology at Renmin University of China. Written consent was obtained from all the participants before the experiment.

Prescanning Questionnaire

Our study elicited target emotions using an autobiographical memory paradigm, the validity of which had been demonstrated by previous research (Wagner et al. 2011). Two to three weeks before fMRI scanning, participants completed an online questionnaire. They were required to recall events from their own experience that were associated with guilty, ashamed, or neutral feelings (3 events for each type of emotion; in total: $3 \times 3 = 9$ events). The participants were asked to ensure that the recalled events met three prerequisites. The prerequisites for each type of emotion described a situation in which the target emotion typically appeared. The prerequisites for guilt and shame events came from a previous study (Wagner et al. 2011). The prerequisites for neutral events were adapted from studies in which a neutral feeling was evoked (De Hooge et al. 2008; Zhu, Xu, et al. 2019) (see the Supplementary material). For privacy protection, the participants were asked to provide several keywords for each event instead of reporting the entire event. The keywords were used as a reminder in the later emotion-reliving task to help the participants recall the specific events. After providing the keywords, the participants rated how strongly they felt several emotions (i.e. sadness, guilt, happiness, shame, pride, anger, disgust, surprise, and fear) when they experienced each event on an 11-point scale (0 = not at all to 10 = very strong).

To increase the chance of inducing the target emotion, for each type of emotional event, we selected two valid events from the three recalled events for presentation in the later emotion-reliving task. The guilt or shame events were regarded as valid when their target emotion ratings were higher than any other emotion ratings (e.g. for a valid guilt event, its guilt rating should be higher than any other emotion rating). If all three recalled events were valid, the two with higher target emotion ratings were selected. The neutral events were regarded as valid when neither their guilt nor shame rating was the highest. If all three events were valid, the two with lower mean values of all emotion ratings were selected. On average, the guilt ratings of the selected guilt events were higher than any other emotion ratings (all $F > 58.32$, $P < 0.001$, partial $\eta^2 > 0.49$); the shame ratings of the selected shame events were higher than any other emotion ratings (all $F > 17.35$, $P < 0.001$, partial $\eta^2 > 0.22$) (see Supplementary Table 1). Interestingly, the happiness ratings of the selected neutral events were higher than any other emotion ratings (all $F > 57.38$, $P < 0.001$, partial $\eta^2 > 0.49$). This may be because recalling a neutral event can be considered happy relative to recalling a guilt or shame event. The dominant emotions in the selected guilt, shame, and neutral events were guilt, shame, and happiness, respectively.

Procedure during fMRI Scanning

The participants completed three tasks during fMRI scanning. The first task was statement reading (~4 min), which has been widely used for MS priming (Han et al. 2010; Luo et al. 2014; Feng et al. 2017). The participants read some statements and indicated whether they agreed with each of the statements by pressing a button (within 7 s). The participants were randomly assigned to one of two groups. The MS group read 28 statements related to death (e.g. "My body will be cremated after my death, leaving only some bone ash"), whereas the negative affect (NA) group read 28 statements referring to negative emotions unrelated to death (e.g. "I am always discomposed about matters in life"). The statements were from a previous study on the effect of MS (Feng et al. 2017).

In the second task, the participants performed 40 calculations (~5 min). They judged whether the result of each calculation was an even or odd number by button press (e.g. 3578 + 5926) (within 7 s). This task served as a distraction (or delay) between MS or NA priming and the core-dependent measures (i.e. emotional and neural responses in the emotion-reliving task). After distraction, thoughts of death are likely to recede from consciousness but remain active in subconsciousness (Pyszczynski et al. 1999). As previous studies have shown that distal death defenses occur only when thoughts of death are subconscious, distraction is an important step for a typical MS study (Schimel et al. 2006; Burke et al. 2010; Hu et al. 2018).

In the third task, an emotion-reliving task (~8 min), the participants read the keywords they provided in the prescanning questionnaire (two sets for guilt events, guilt condition; two sets for shame events, shame condition; and two sets for neutral events, neutral condition), recalled the events, and relived the emotions

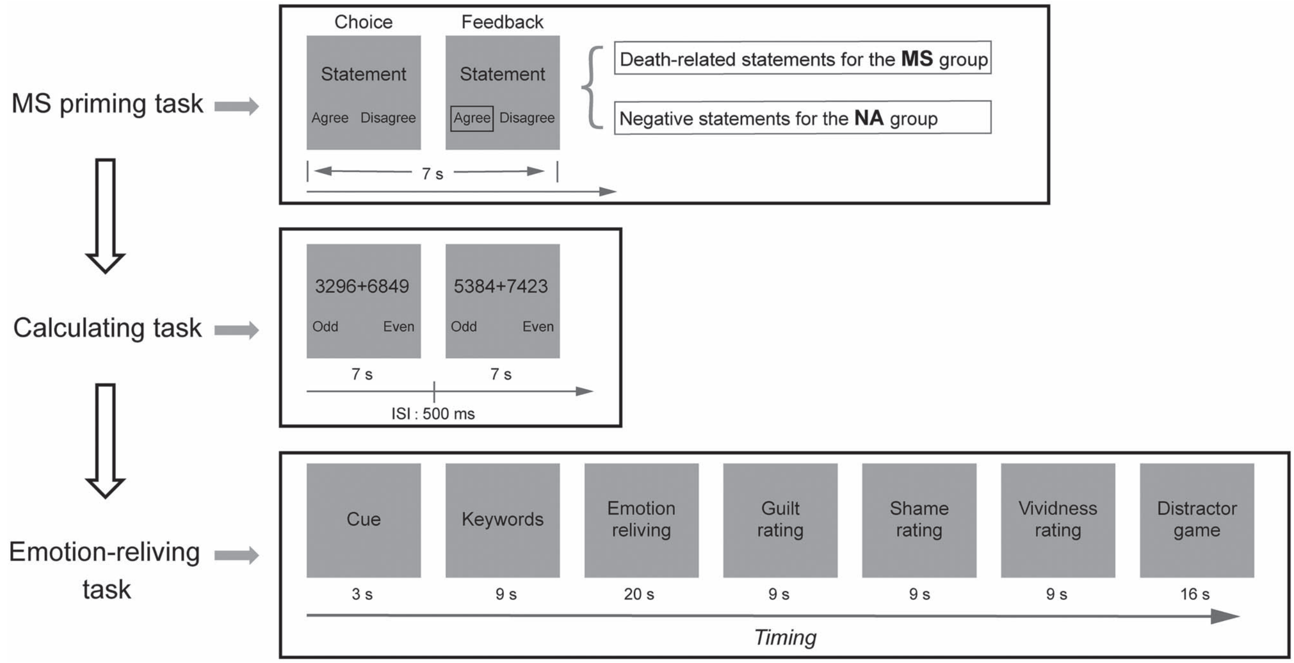

Figure 2. Illustration of the procedure with fMRI scanning. There were three tasks. The first task was an MS priming task, during which the participants read death-related statements (MS group) or negative statements (NA group) and determined whether they agreed or disagreed with each of the statements. The second task was a calculating task that served as a distracting phase, in which the participants completed 40 calculations. The third task was an emotion-reliving task. At the beginning of each trial, a cue word was presented to indicate the type of emotional event that the participants would recall. Then, the participants saw the keywords of an emotional event, relived the event and felt the emotion. Afterward, the participants rated their guilt intensity, shame intensity, and vividness of memory. At the end of the trial, a number detection game was used as a distracter to avoid the emotion of the current trial spilling over to the next trial. ISI, interstimuli interval.

(Before the participants entered the fMRI scanner, they read the keywords they provided 2–3 weeks before the fMRI experiment. All of them confirmed that they remembered the events corresponding to the keywords.). The events were recalled in a random order, with the constraint that events of the same type were not separated by events of another type. The timeline of a trial is shown in Fig. 2. Each trial began with a cue word (i.e. guilt, shame, or neutral) indicating the emotion type of the event that the participants would recall (3 s). Then, the keywords of an event were presented (9 s). After the presentation of the keywords, a reliving phase followed. In this phase, the participants recalled the event and felt the emotion (20 s). Additionally, they were asked to press a certain button if they stopped recalling before the end of the reliving phase (no participant ever pressed it). Then, the participants rated their feelings of guilt (within 9 s) and shame (within 9 s) (0 = not at all to 10 = very strong) and rated the vividness of their memories (within 9 s) (0 = not vivid at all to 10 = very vivid). After the rating, the participants participated in a distractor game (16 s) (The distractor game began with a fixation cross (3 s). Then, five single digits were successively shown on the screen, each appearing for 2 s. The participants were asked to press a button when the number "3" appeared.), which was incorporated into the task to clear the participants' minds and avoid the emotion of the current trial contaminating the next trial (Wagner et al. 2011). At the end of a trial, a fixation cross (3 s) was presented to signal the upcoming trial.

After the third task, we checked the manipulation of MS priming. The participants rated their subjective feelings of closeness to death, fear of death, and unpleasantness after the priming task on an 11-point scale (0 = not at all to 10 = very strong) (Feng et al. 2017; Luo et al. 2019). The participants also reported the time at which each event they recalled occurred (i.e. how many weeks ago did each event occur).

MRI Acquisition and Preprocessing

MRI data were acquired by a 3 Tesla magnetic resonance scanner (Siemens Magnetom Prisma) using a standard head coil at Peking University. High-resolution structural images were obtained with a $T1$-weighted sequence (repetition time [TR] = 2530 ms, echo time [TE] = 2.98 ms, and flip angle = 7°). To correct image distortions, a field map was acquired (slices = 62, slice thickness = 2.0 mm, TR = 620 ms, and voxel size = $2 \times 2 \times 2$ mm^3). Whole-brain functional images were acquired with a $T2$-weighted gradient echo planar image sequence (TR = 2000 ms, TE = 30 ms, flip angle = 90°, field of view = 224 mm, number of axial slices = 62, slice thickness = 2.0 mm, and voxel size = $2 \times 2 \times 2$ mm^3).

Neuroimaging data preprocessing and analyses were conducted using Statistical Parametric Mapping (SPM) 12 (Wellcome Department of Imaging Neuroscience; http://www.fil.ion.ucl.ac.uk/spm). Preprocessing of images followed a standard procedure in SPM 12, including geometric distortion correction (using field map images), slice timing correction, realignment for head motion correction, coregistration, spatial normalization into Montreal Neurological Institute (MNI) space (voxel size = 2 × 2 × 2 mm^3), and smoothing using a 6-mm full-width at half-maximum Gaussian kernel.

Behavioral Analysis

To check the manipulation of MS, we evaluated the ratings of closeness to death, fear of death, and unpleasantness using two-sample *t*-tests with groups (MS vs. NA) as a between-subjects factor. To test whether guilt or shame was the dominant emotion in the specific condition during the emotion-reliving task, we compared guilt and shame ratings (a within-subjects factor) in the guilt, shame, and neural conditions using paired-sample *t*-tests. To examine whether irrelevant variables were comparable between groups, we evaluated the vividness of the memory and the occurrence time of the guilt, shame, and neutral events using two-sample *t*-tests with groups (MS vs. NA) as a between-subjects factor.

To examine whether MS enhances guilt and shame feelings, we investigated the effects of MS on the changes in guilt ratings of the guilt events and the changes in shame ratings of the shame events, respectively. The changes in emotion (guilt or shame) ratings refer to the ratings the participants provided during the emotion-reliving task (after the priming task) minus the ratings provided in the prescanning questionnaire (before the priming task; as a baseline). We submitted the changes in guilt and shame ratings to two two-sample *t*-tests with groups (MS vs. NA) as a between-subjects factor, respectively. We also combined the data of the MS and NA groups and explored whether the ratings of closeness to death and fear of death were correlated with the changes in guilt and shame ratings using Pearson correlation. Although the closeness to death but not fear of death was the key psychological structure associated with MS (Pyszczynski et al. 1999), we still included the ratings of fear of death in the analysis for completeness.

In addition, we directly compared the effects of MS on guilt and shame (We note that these were exploratory analyses, and no prediction could be made based on terror management theory.). Specifically, we submitted the changes in emotion ratings to a two-way analysis of variance (ANOVA) with groups (MS vs. NA) as a between-subjects factor and emotion conditions (guilt vs. shame) as a within-subjects factor. We were interested in the interaction effect of the ANOVA. Besides, we conducted Fisher *r*-to-z transformation to compare whether the correlations between the closeness to death and changes in emotion ratings were different between the guilt and shame conditions. The same analysis (i.e. Fisher *r*-to-z transformation) was also conducted on fear of death.

fMRI Data Analysis

Univariate Activation Analysis

We examined the neural responses to MS in the priming task with a two-level general linear model (GLM). At the first level, we modeled the choice stage as a regressor (duration: response time) and left the feedback stage as an implicit baseline. The regressor was convolved with the canonical hemodynamic response function. Six head-movement parameters were modeled in the GLM to control the effect of head motion. A contrast was constructed to investigate brain responses during the choice stage (compared with those at the implicit baseline). At the second level, we used the contrast images from the first level to test the group differences (MS vs. NA) with a two-sample *t*-test. As previous studies have demonstrated the association between death-related information processing and insula deactivation (Han et al. 2010; Klackl et al. 2014; Luo et al. 2019), the insula was considered a region of interest (ROI). The insula mask was initially defined based on the anatomical automatic labeling template (AAL3) (i.e. the insula mask; 1770 voxels) (Rolls et al. 2020). To test the reliability of our findings, the insula mask was also defined based on Brodmann's area template (i.e. the insula mask; 2096 voxels) (Brodmann 1909; Zilles 2018) or the meta-analysis map from Neurosynth (we searched for a meta-analysis map on Neurosynth using the term "insula", downloaded the map, specified the peak voxel coordinate of the insula [40, 20, −10], and drew a 10-mm sphere around the peak voxel; 515 voxels) (https://www.neurosynth.org; Yarkoni et al. 2011). The statistical threshold was set at voxel level $P < 0.001$ and an extent cluster level threshold of $P < 0.05$ (FWE-corrected) (whole-brain or within predefined ROI using small-volume correction). The statistical findings remained the same regardless of which way we defined the insula mask. We used the results when the insula mask was defined based on the AAL3 for the following analyses.

We tested the effect of MS on brain activation related to guilt and shame in the emotion-reliving task with a two-level GLM. At the first level, we modeled different stages separately in the GLM, including the cue (duration: 3 s), keywords (duration: 9 s), emotion reliving (duration: 20 s), guilt rating (duration: 9 s), shame rating (duration: 9 s), and vividness rating (duration: 9 s). Based on the emotion type, the emotion-reliving stage was further divided into three regressors corresponding to three conditions (i.e. guilt, shame, and neutral conditions). Six head motion parameters were included as nuisance regressors. The regressors except for the nuisance regressors were convolved with a canonical hemodynamic response function. Two contrasts (i.e. guilt vs. neutral; shame vs. neutral) were created to specify the brain activation of guilt and shame for each participant. At the second level, we used the contrast images from the first level to test the group differences (MS vs. NA) with two two-sample *t*-tests. As previous studies have found that guilt and/or shame are associated with the brain regions implicated in emotion processing (i.e. insula and amygdala) (Michl et al. 2014; Pulcu et al. 2014; Zhu, Feng, et al. 2019; Piretti et al. 2020), self-referential processing (i.e. vmPFC, dmPFC, and PCC) (Shin et al. 2000; Yu et al. 2014, 2020; Bastin et al. 2016; Gifuni et al. 2017;

Li et al. 2020), mentalizing (i.e. TPJ) (Takahashi et al. 2004; Moll et al. 2007; Wagner et al. 2011; Michl et al. 2014), and cognitive control (i.e. OFC) (Wagner et al. 2011; Zhu, Feng, et al. 2019), we considered these regions as ROIs. The insula and amygdala masks were defined as two 10-mm spheres around the coordinates reported in a meta-analysis about the neural correlates of negative emotional experience (MNI coordinates: insula, [−26, 22, −12]; amygdala, [−30, −4, −22]; Lindquist et al. 2012). The vmPFC, dmPFC, and PCC masks were defined as three 10-mm spheres centered around the coordinates reported in a meta-analysis on self-referential processing (MNI coordinates: vmPFC, [−6, 42, −12]; dmPFC, [−6, 27, 42]; PCC, [−3, −54, 18]; Northoff et al. 2006) (also see Lemogne et al. 2011). The TPJ mask was defined as a 10-mm sphere centered around the coordinates reported in a meta-analysis on mentalizing (MNI coordinates: TPJ, [62, −58, 20]; Schurz et al. 2014). The OFC mask was defined as a 10-mm sphere centered around the coordinates reported in a meta-analysis on emotion-related cognitive control (MNI coordinates: OFC, [−40, 22, −18]; Feng et al. 2018). Each 10-mm sphere contained 515 voxels. The statistical threshold was set at voxel level $P < 0.001$ and an extent cluster level threshold of $P < 0.05$ (FWE-corrected) (whole brain or within predefined ROI using small-volume correction).

In parallel with the behavioral analysis, we compared the effects of MS on brain activation between the guilt and shame conditions. We focused on the brain regions that were significantly affected by MS in the guilt (i.e. vmPFC, OFC, and amygdala) or shame condition (i.e. vmPFC [The vmPFC cluster identified in the shame condition was not overlapped with the vmPFC cluster identified in the guilt condition.]). Using these four identified clusters as masks, respectively, we extracted mean estimates from the mask in the guilt and shame conditions across the MS and NA groups. Then, we submitted these mean estimates from four clusters to four two-way ANOVAs with groups (MS vs. NA) as a between-subjects factor and emotion conditions (guilt vs. shame) as a within-subjects factor.

Functional Connectivity Analysis

Univariate activation analysis revealed that the MS group had stronger activation in four clusters than the NA group in the guilt and shame conditions. To further explore the effect of MS on functional connectivity, we conducted PPI analysis using the SPM-based generalized PPI toolbox (https://www.nitrc.org/projects/gppi; McLaren et al. 2012). Four seed regions were defined as four 10-mm spheres centered on the peaks of the two vmPFC clusters, one OFC cluster, and one amygdala cluster identified by the two contrasts in the univariate activation analysis (i.e. MS group (guilt vs. neutral) vs. NA group (guilt vs. neutral), the peak MNI coordinates of the vmPFC: [−10, 46, −20], OFC: [−40, 32, −18], and amygdala: [−34, 2, −22]; MS group (shame vs. neutral) vs. NA group (shame vs. neutral), vmPFC: [−2, 34, −14]). Mean time series were extracted from the seed regions (guilt condition: vmPFC from the guilt condition, OFC, amygdala; shame condition: vmPFC from the shame condition). Six head motion parameters were controlled to regress out any head-movement influence. For the PPI analysis, at the first level, we constructed two contrasts to examine the difference in functional connectivity between the conditions (i.e. guilt vs. neutral; shame vs. neutral). At the second level, we used the contrast images from the first level to test the group differences (MS vs. NA) with two two-sample *t*-tests. The statistical threshold was set at the voxel level $P < 0.001$ and an extent cluster level threshold of $P < 0.05$ (FWE-corrected) (whole brain).

We found that the MS group had weaker vmPFC-precuneus and vmPFC-PCC functional connectivity than the NA group in the shame condition. To compare the effects of MS on the functional connectivity between the guilt and shame conditions, we conducted an additional PPI analysis in the guilt condition using the vmPFC mask defined based on the univariate activation result in the shame condition (i.e. a 10-mm sphere centered on [−2, 34, −14]) as a seed. Then, we extracted the mean estimates of the vmPFC-precuneus and vmPFC-PCC functional connectivity in the guilt and shame conditions across the MS and NA groups. We submitted these mean estimates of those functional connectivity to two two-way ANOVAs with groups (MS vs. NA) as a between-subjects factor and emotion conditions (guilt vs. shame) as a within-subjects factor.

Dynamic Causal Modeling

PPI findings can indicate the strength of the connectivity between brain regions but cannot reveal the direction of the connectivity (Stephan et al. 2010; Stephan and Friston 2010). Inspired by the advice of an anonymous reviewer, we used dynamic causal modeling (DCM) to test whether MS affected the direction of the vmPFC-precuneus and vmPFC-PCC connectivity, which was identified by our PPI analysis. The DCM results showed that the direction of the vmPFC-precuneus and vmPFC-PCC connectivity was the same across the MS and NA groups. The analysis and results of DCM can be seen in detail in the Supplementary material.

Death-Related Ratings and Neural Activities

To further examine whether the group differences in guilt and shame-related neural activities were caused by MS, we tested whether the ratings of closeness to death were correlated with the neural activities that showed a group difference in activation or functional connectivity during the emotion-reliving task across all the participants. To conduct Pearson correlation analysis, mean estimates were extracted from the brain regions that revealed a significant group difference in neural activities. Besides, we conducted Fisher *r*-to-z transformations to compare whether the correlations between closeness to death and neural activities varied between the guilt and shame conditions. Consistent with the behavioral analysis strategy, the same set of analyses was conducted on fear of death for completeness.

Proximal and Distal Defenses

As previous studies consistently found that viewing death-related words decreased activation in the insula (Han et al. 2010; Shi and Han 2013; Klackl et al. 2014; Luo et al. 2019), we adopted the activation of the insula during the priming task as an indicator of proximal defenses. We used the neural activities modulated by MS during the emotion-reliving task as indicators of distal defenses. We examined the Pearson correlation between the proximal and distal defenses across all the participants.

Results

Manipulation Check

The MS group had higher ratings of closeness to death ($M_{(MS)} = 5.38 \pm 1.96$, $M_{(NA)} = 1.70 \pm 2.26$, $t(60) = 6.81$, $P < 0.001$, Cohen's $d = 1.73$) and fear of death ($M_{(MS)} = 3.75 \pm 2.76$, $M_{(NA)} = 2.37 \pm 2.65$, $t(60) = 2.01$, $P = 0.048$, Cohen's $d = 0.51$) than the NA group (Supplementary Table 2). In line with previous studies (Greenberg et al. 1994; Feng et al. 2017), there was no significant difference in the ratings of unpleasantness between the groups ($M_{(MS)} = 4.21 \pm 3.15$, $M_{(NA)} = 3.96 \pm 3.12$, $t(60) = 0.40$, $P = 0.69$, Cohen's $d = 0.10$) (Supplementary Table 2). These results suggest that our manipulation of MS was successful.

During the emotion-reliving task, in both the MS and NA groups, guilt ratings were higher than shame ratings in the guilt condition (MS: $t(31) = 4.81$, $P < 0.001$, Cohen's $d = 0.85$; NA: $t(29) = 5.93$, $P < 0.001$, Cohen's $d = 1.08$); shame ratings were higher than guilt ratings in the shame condition (MS: $t(31) = 5.36$, $P < 0.001$, Cohen's $d = 0.95$; NA: $t(29) = 5.27$, $P < 0.001$, Cohen's $d = 0.96$). No significant difference was found between guilt and shame ratings in the neural condition (MS: $t(31) = 1.33$, $P = 0.194$, Cohen's $d = 0.24$; NA: $t(29) = 0.79$, $P = 0.434$, Cohen's $d = 0.14$). These results confirm that guilt and shame were the dominant emotions in the guilt and shame conditions, respectively, but neither of them was dominant in the neutral condition.

No significant difference in the vividness of memory in the guilt ($t(60) = 1.61$, $P = 0.113$, Cohen's $d = 0.41$), shame ($t(60) = 0.56$, $P = 0.576$, Cohen's $d = 0.14$), or neutral ($t(60) = 1.61$, $P = 0.112$, Cohen's $d = 0.41$) condition was identified between the MS and NA groups (Supplementary Table 3). In addition, no significant difference in the occurrence time of events in the guilt ($t(60) = 0.53$, $P = 0.599$, Cohen's $d = 0.13$), shame ($t(60) = 0.23$, $P = 0.818$, *Cohen's* $d = 0.06$), or neutral ($t(60) = 1.37$, $P = 0.175$, *Cohen's* $d = 0.35$) conditions was identified between the MS and NA groups (Supplementary Table 4). The results suggest that the vividness of memory and occurrence time of events were comparable between the MS and NA groups.

MS Decreased the Activation of the Insula during The Priming Task

Consistent with previous findings (Han et al. 2010; Shi and Han 2013; Klackl et al. 2014), a small-volume-correction analysis (using the AAL3 insula template as the mask) showed that the MS group had weaker activation in the insula than the NA group during the priming task (Fig. 3 and Supplementary Table 5). The results remained when the insula mask was defined based on Brodmann's area template or the meta-analysis map from the Neurosynth database (Supplementary Table 6). In addition, a whole-brain analysis revealed that the MS group had weaker activation in the middle temporal gyrus and cerebellum than the NA group (Supplementary Table 5).

MS Strengthened the Feelings of Guilt But Not Shame

We found a significant difference in the changes in guilt ratings between the MS and NA groups in the guilt condition ($M_{(MS)} = -0.15 \pm 1.89$, $M_{(NA)} = -1.07 \pm 1.54$, $t(60) = 2.09$, $P = 0.040$, Cohen's $d = 0.52$, Fig. 4A). Although the changes in shame ratings were more positive in the MS group than in the NA group in the shame condition, the difference was not significant ($M_{(MS)} = 0.48 \pm 1.52$, $M_{(NA)} = 0.12 \pm 2.48$, $t(60) = 0.70$, $P = 0.488$, Cohen's $d = 0.08$, Fig. 4C). The results confirm the influence of MS on guilt. Additionally, the ratings of closeness to death were significantly correlated with the changes in guilt ratings in the guilt condition across all the participants ($r(62) = 0.31$, $P = 0.015$, Fig. 4B, Supplementary Table 7), whereas the correlation between the ratings of closeness to death and the changes in shame ratings in the shame condition was not significant ($r(62) = 0.15$, $P = 0.254$, Fig. 4D). The ratings of fear of death were not correlated with the changes in guilt ratings in the guilt condition or the changes in shame ratings in the shame condition (Supplementary Table 7).

In addition, the interaction effect of groups and emotion conditions on changes in emotion ratings was not significant ($F(1,60) = 0.08$, $P = 0.362$, partial $\eta^2 = 0.014$, Supplementary Fig. 1A). The difference in the correlations between the closeness to death and changes in emotion ratings between the guilt and shame conditions was not significant ($z = 1.08$, $P = 0.139$, Supplementary Fig. 1B). The difference in the correlations between the fear of death and changes in emotion ratings between the guilt and shame conditions was also not significant ($z = 0.12$ $P = 0.454$). It is implied that the influence of MS on shame is similar to that on guilt (but may have a smaller effect size).

MS Enhanced Brain Activation Related to Guilt and Shame

The small-volume-correction analysis showed that, in the guilt condition, the MS group had greater activation in the vmPFC, OFC, and amygdala than the NA group (Fig. 5A and Table 1); in the shame condition, the MS

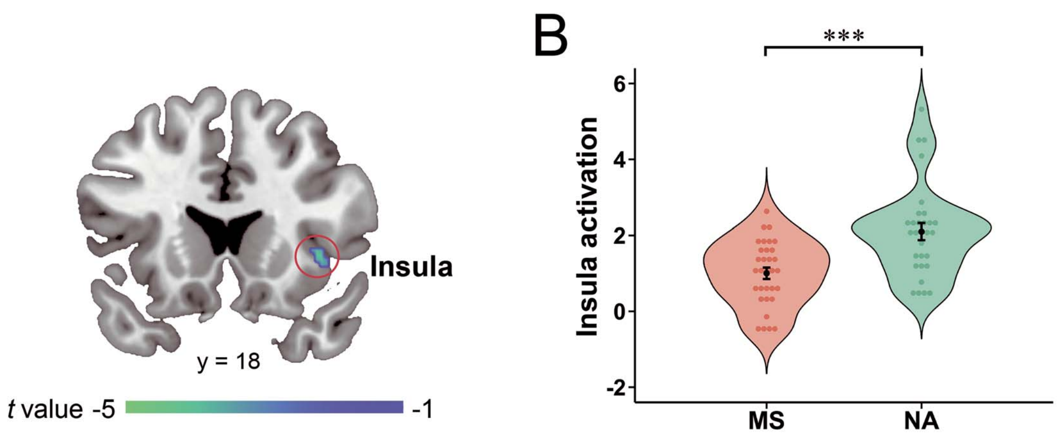

Figure 3. Brain activation during the priming task. (*A*) The activation of the insula was weaker in the MS group than in the NA group. (*B*) The mean estimates were extracted from the insula for visual display. They are shown as the mean ± standard error with overlaid dot plots. ***$P < 0.001$; MS, mortality salience group; NA, negative affect group.

Table 1. Differences in brain activation between the MS and NA groups during the emotion-reliving task

Region	MNI coordinates			t score	Voxels	P_{FWE}
	x	y	z			
MS (Guilt-Neutral) > NA (Guilt-Neutral)						
[a]vmPFC	−10	46	−20	4.07	15	0.021
[a]OFC	−40	32	−18	4.27	7	0.038
[a]Amygdala	−34	2	−22	4.55	15	0.021
MS (Shame-Neutral) > NA (Shame-Neutral)						
[a]vmPFC	−2	34	−14	3.91	11	0.028
NA (Guilt-Neutral) > MS (Guilt-Neutral)						
None	-	-	-	-	-	-
NA (Shame-Neutral) > MS (Shame-Neutral)						
None	-	-	-	-	-	-

Note: $P < 0.001$, uncorrected voxel level and $P < 0.05$, cluster level with FWE correction. [a]Small volume correction; vmPFC, ventromedial prefrontal cortex; OFC, orbitofrontal cortex; MS, mortality salience group; NA, negative affect group.

group showed stronger activation in the vmPFC than the NA group (Fig. 5*B* and Table 1). In addition, the ratings of closeness to death were positively associated with activation of the identified brain regions in the guilt and shame conditions across all the participants (Fig. 5), which further supports that these neural activities were related to the influence of morality salience. The ratings of fear of death were correlated with only vmPFC activation in the shame condition (Supplementary Table 9). The whole-brain analysis found no significant result.

The interaction effects of groups and emotion conditions on brain activation in the four clusters identified above were not significant (vmPFC cluster from the guilt condition: $F(1,60) = 2.58$, $P = 0.114$, partial $\eta^2 = 0.041$; OFC cluster: $F(1,60) = 1.50$, $P = 0.226$, partial $\eta^2 = 0.024$; amygdala cluster: $F(1,60) = 0.55$, $P = 0.463$, partial $\eta^2 = 0.009$; vmPFC cluster from the shame condition: $F(1,60) = 0.25$, $P = 0.619$, partial $\eta^2 = 0.004$; Supplementary Fig. 2*A*). The differences in the correlations between the closeness to death and mean estimates from identified clusters between the guilt and shame conditions were not significant (vmPFC cluster from the guilt condition: $z = 0.08$, $P = 0.466$; OFC cluster: $z = 1.42$, $P = 0.077$; amygdala cluster: $z = 0.55$, $P = 0.291$; vmPFC cluster from the shame condition: $z = 1.42$, $P = 0.078$; Supplementary Fig. 2*B*). The differences in the correlations between the fear of death and mean estimates from identified clusters between the guilt and shame conditions were also not significant (vmPFC cluster from the guilt condition: $z = 1.43$, $P = 0.076$; OFC cluster: $z = 1.27$, $P = 0.102$; amygdala cluster: $z = 1.15$, $P = 0.124$; vmPFC cluster from the shame condition: $z = 1.61$, $P = 0.054$). It is indicated that the influences of MS on brain activation are not fundamentally different between the guilt and shame conditions.

MS Modulated the Functional Connectivity Related to Shame

In the guilt condition, no functional connectivity was significantly different between groups. In the shame condition, the MS group had weaker vmPFC-precuneus and vmPFC-PCC functional connectivity than the NA group (whole-brain correction; Fig. 6*A*,*B* and Supplementary Table 8). The ratings of closeness to death were negatively correlated with both the vmPFC-precuneus and vmPFC-PCC connectivity across all the participants (Fig. 6*B*). The ratings of fear of death were not correlated with the vmPFC-precuneus or vmPFC-PCC connectivity (Supplementary Table 9).

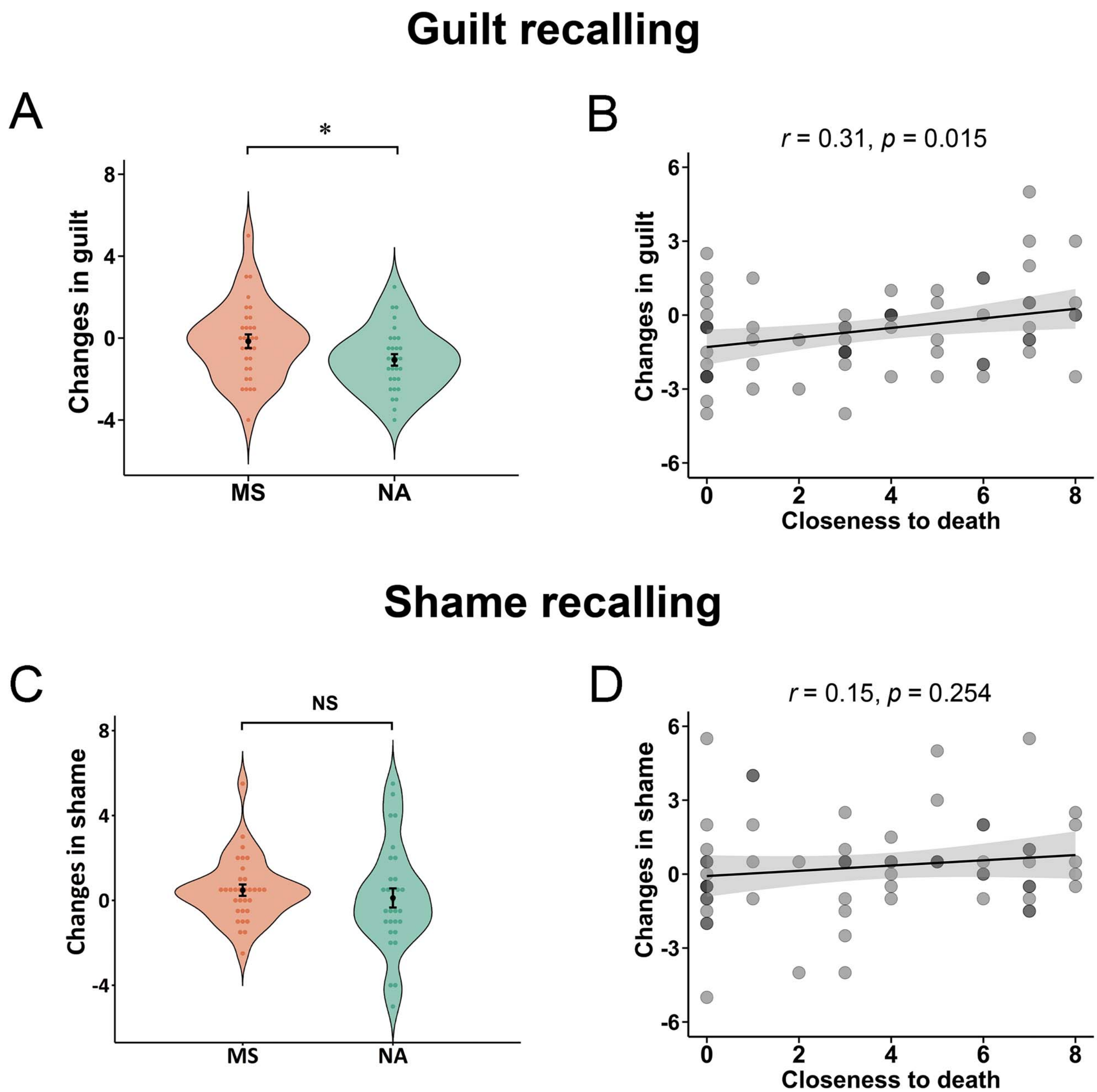

Figure 4. Guilt and shame during the emotion-reliving task. (*A*, *C*) A significant difference in the changes in guilt ratings was found between the groups, whereas there was no significant difference in the changes in shame ratings between the groups. The changes are shown as the mean ± standard error with overlaid dot plots. (*B*, *D*) The changes in guilt ratings were positively correlated with the ratings of closeness to death, whereas the changes in shame ratings were not correlated with the ratings of closeness to death. Darker dots indicate an overlap between points. The solid line represents the least squares fit, with shading showing the 95% confidence interval. *$P < 0.05$; NS, not significant; MS, mortality salience group; NA, negative affect group.

The interaction effect of groups and emotion conditions on vmPFC-PCC connectivity was significant ($F(1,60) = 6.87$, $P = 0.011$, partial $\eta^2 = 0.103$; Fig. 6C), while the interaction effect on vmPFC-precuneus connectivity was not ($F(1,60) = 1.63$, $P = 0.207$, partial $\eta^2 = 0.026$; Supplementary Fig. 3A). The difference in the correlations between the closeness to death and vmPFC-PCC connectivity between the guilt and shame conditions was significant ($z = 1.73$, $P = 0.042$, Fig. 6C), while the difference in the correlations between the closeness to death and vmPFC-precuneus connectivity between the guilt and shame conditions was not ($z = 1.26$, $P = 0.103$, Supplementary Fig. 3B). The results demonstrate a unique influence of MS on vmPFC-PCC connectivity in the shame condition. The differences in the correlations between the fear of death and vmPFC-related functional connectivity between the guilt and shame conditions were not significant (vmPFC-PCC: $z = 0.92$, $P = 0.178$; vmPFC-precuneus: $z = 0.56$, $P = 0.289$).

Proximal Defenses could Partly Predict Distal Defenses

Insula activation during the priming task was predictive of amygdala activation (but not vmPFC or OFC

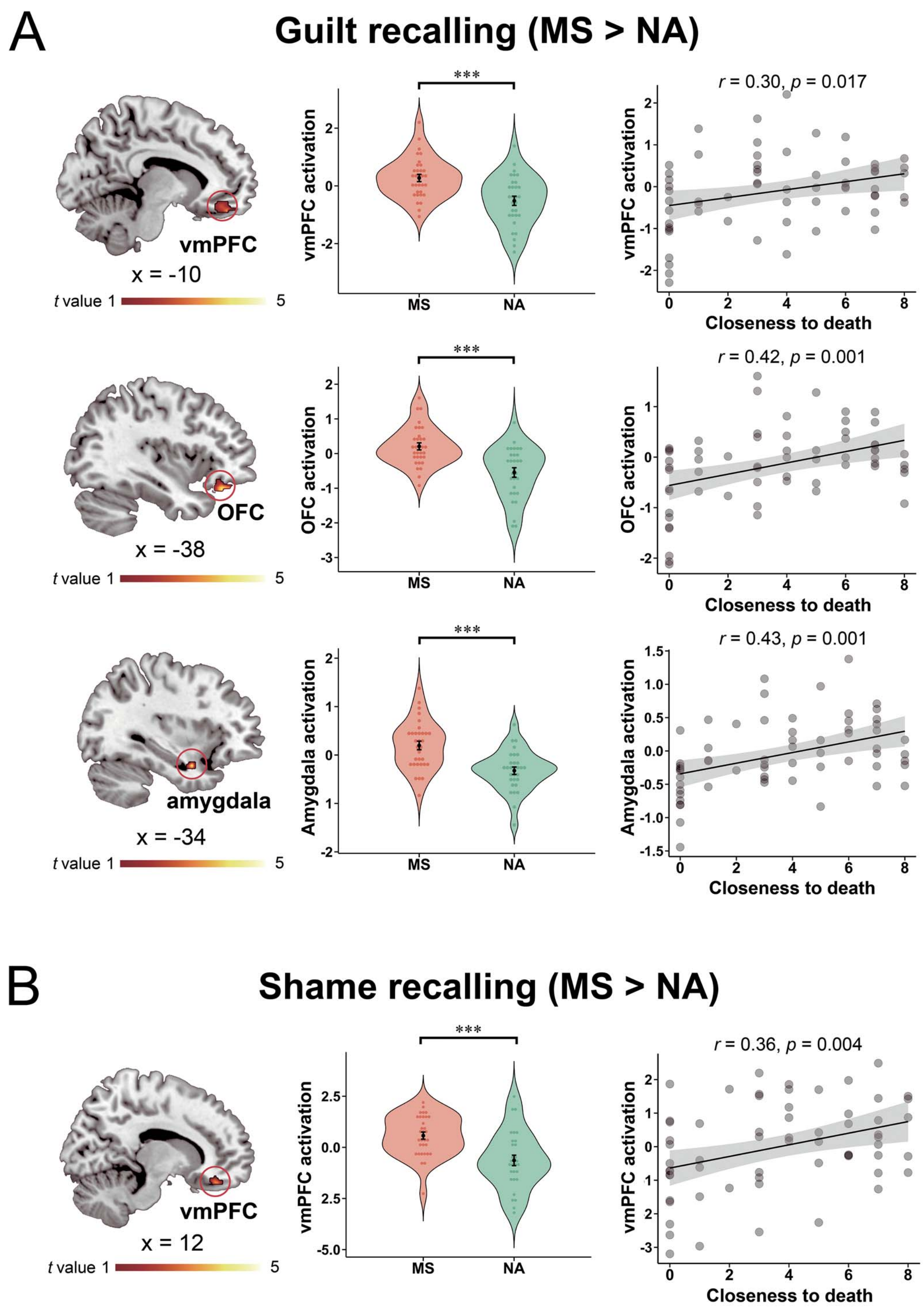

Figure 5. Brain activation during the emotion-reliving task. (*A*, left panel) When the participants were recalling guilt events (the guilt condition), the activation of the vmPFC, OFC, and amygdala was stronger in the MS group than in the NA group. (*B*, left panel) When the participants were recalling shame events (the shame condition), the activation of the vmPFC was stronger in the MS group than in the NA group. (*A*, *B*, left panel) The maps here are thresholded with $P < 0.005$ for illustrative purposes. (*A*, *B*, middle panel) For visual display, the mean estimates were extracted from the brain regions that reveal significant group differences in activation. They are shown as the mean ± standard error with overlaid dot plots. (*A*, *B*, right panel) Neural activations were positively correlated with the ratings of closeness to death across all the participants. The darker color of dots indicates an overlap between the points. The solid line represents the least squares fit, with shading showing the 95% confidence interval. ***$P < 0.001$; MS, mortality salience group; NA, negative affect group.

activation) during the emotion-reliving task in the guilt condition (Fig. 7A; Supplementary Table 10). Insula activation during the priming task was predictive of vmPFC activation and vmPFC-precuneus functional connectivity (but not vmPFC-PCC functional connectivity) during the emotion-reliving task in the shame condition (Fig. 7B; Supplementary Table 10). Given that the activation of the insula during the priming task

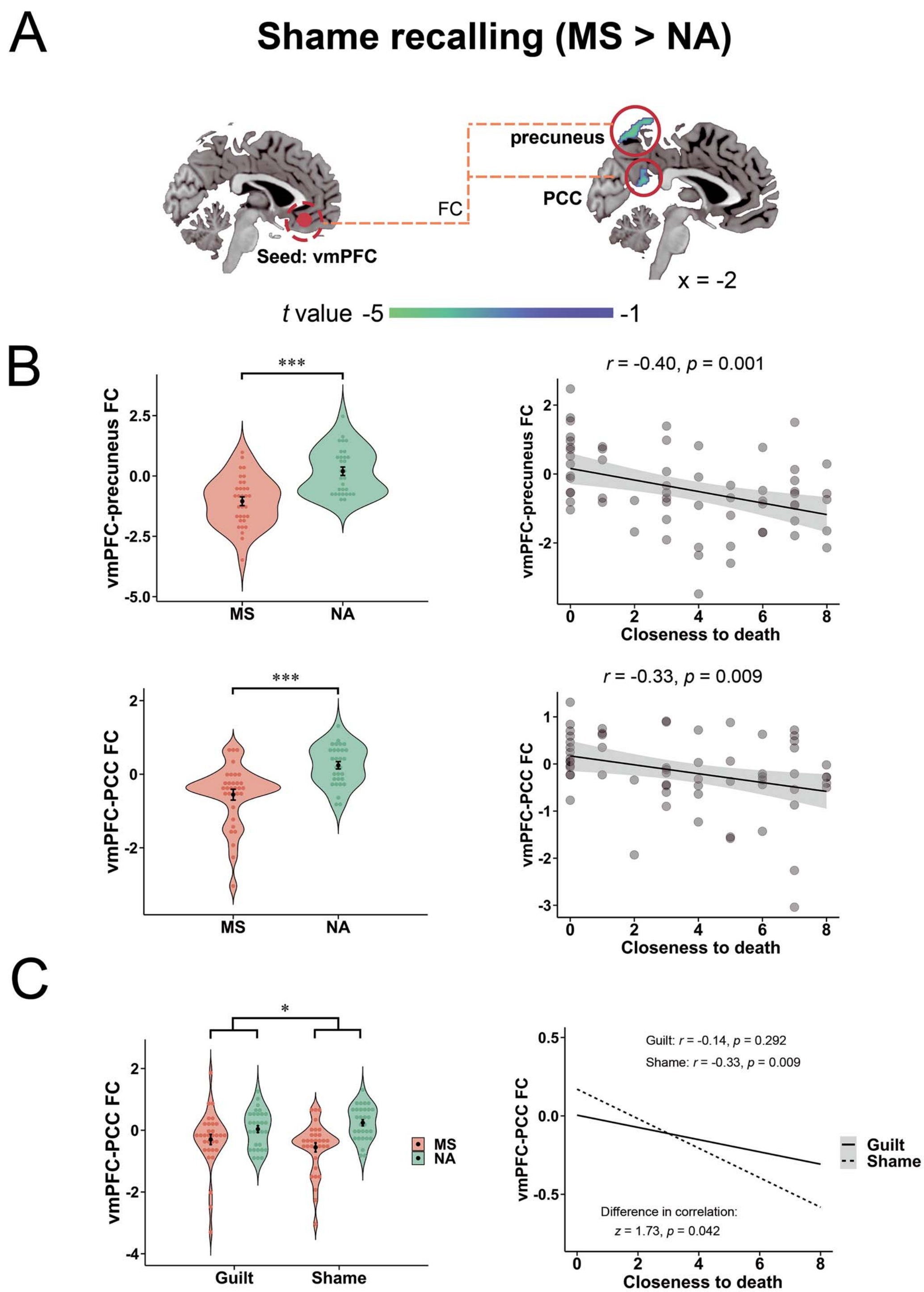

Figure 6. Functional connectivity during the emotion-reliving task. (*A*) In the shame condition, the vmPFC-precuneus and vmPFC-PCC functional connectivity was weaker in the MS group than in the NA group. (*B*, left panel) For visual display, the mean estimates of the vmPFC-precuneus and vmPFC-PCC functional connectivity in the shame condition were extracted. They are shown as the mean ± standard error with overlaid dot plots. (*B*, right panel) The vmPFC-precuneus and vmPFC-PCC functional connectivity was negatively correlated with the ratings of closeness to death in the shame condition. Darker dots indicate an overlap between the points. The solid line represents the least squares fit. (*C*, left panel) MS compared with NA more strongly decreased vmPFC-PCC functional connectivity in the shame than in the guilt condition. (*C*, right panel) The negative correlation between closeness to death and vmPFC-PCC functional connectivity was stronger in the shame than in the guilt condition. *$P < 0.05$, ***$P < 0.001$; FC, functional connectivity; MS, mortality salience group; NA, negative affect group.

is regarded as an indicator of proximal defenses and that the neural activities modulated by MS during the emotion-reliving task are regarded as indicators of distal defenses, the results show that proximal defenses are partly related to distal defenses.

Discussion

We studied the effects of MS on guilt and shame and their neural correlates. Behaviorally, MS strengthened guilt feelings in the guilt condition. This effect was closely related to closeness to death but cannot be attributed

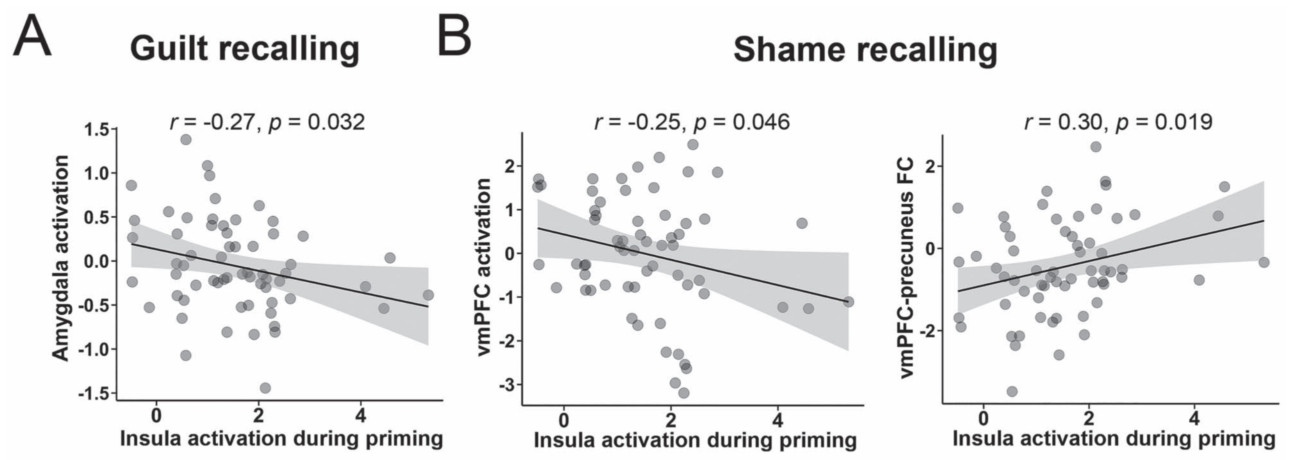

Figure 7. Correlations between activation of the insula during the priming task and brain activities during the emotion-reliving task. (*A*) Activation of the insula during the priming task was negatively correlated with amygdala activation when the participants were recalling guilt events (the guilt condition). (*B*) Activation of the insula during the priming task was negatively correlated with vmPFC activation and positively correlated with vmPFC-precuneus functional connectivity when the participants were recalling shame events (the shame condition). Darker dots indicate an overlap between the points. The solid line represents the least squares fit, with shading showing the 95% confidence interval.

to the group difference in unpleasantness, vividness of memory, or occurrence time of recalled events. Although the MS group had more intense shame feelings than the NA group in the shame condition, the difference was not significant.

Beyond the behavioral findings, MS modulated brain activation related to guilt and shame. In both guilt and shame conditions, MS, compared with NA, increased activation in a region associated with self-referential processing (i.e. vmPFC; Northoff et al. 2006). The vmPFC can be activated by reflection on one's own attributes (Kelley et al. 2002; Macrae et al. 2004; Liu et al. 2017). Many studies have found associations between the activation of the vmPFC and guilt and shame (Beer et al. 2003; Zahn et al. 2009; Morey et al. 2012; Bastin et al. 2016; Seara-Cardoso et al. 2016). Our results suggest that MS promotes self-reflection when guilt and shame events are recalled.

In the guilt but not the shame condition, MS, compared with NA, increased activation in a region associated with cognitive control (i.e. OFC; Feng et al. 2018), which is necessary to inhibit selfish impulses and maximize long-term benefits (Miller 2000; Koechlin et al. 2003; Windmann et al. 2006). Previous studies have observed that the OFC was uniquely activated in the guilt condition but not in the shame condition (Wagner et al. 2011; Zhu, Feng, et al. 2019). It is believed to be related to preparing guilty individuals to compensate the victims (i.e. inhibit selfish impulses) (Wagner et al. 2011; Zhu, Feng, et al. 2019). As ashamed individuals are more inclined to escape than to compensate after moral transgressions (Tangney and Dearing 2003), shame does not show associations with brain regions related to cognitive control (e.g. OFC) (Wagner et al. 2011). Our results therefore indicate that MS increases individuals' cognitive control when they recall guilt events, which may boost them to compensate for the immoral things they did.

In addition, in the guilt but not the shame condition, MS, compared with NA, increased activation in regions associated with emotion processing (i.e. amygdala; Lindquist et al. 2012). Studies have demonstrated the involvement of the amygdala in various emotional experiences (Phan et al. 2002; Murphy et al. 2003), including guilt and shame (e.g. Michl et al. 2014; Whittle et al. 2016; Göttlich et al. 2020). Our results confirm that MS enhances the intensity of guilt experience at the neural level.

Additionally, in the shame but not the guilt condition, MS reduced vmPFC-precuneus and vmPFC-PCC functional connectivity compared with NA. The CMSs (i.e. vmPFC/ACC, dmPFC, and PCC/precuneus) are each specialized for distinct subfunctions of self-referential processing (see a review, Northoff et al. 2006). For example, the vmPFC is associated with coding stimuli as self-referential by integrating cognitive and emotional information (Northoff and Bermpohl 2004; Schmitz and Johnson 2007; Van Overwalle et al. 2019); the PCC/precuneus is implicated in combining autobiographical memory with external information (Summerfield et al. 2009; Bahk and Choi 2018). Previous studies found a decrease in the functional connectivity between regions within the CMS during self-referential processing (van Buuren et al. 2010, 2012). This pattern of functional connectivity is important for achieving the functional specialization of self-referential processing (van Buuren et al. 2012). Our results show that MS strengthens self-referential processing in the shame condition by decreasing functional connectivity between the regions within the CMS.

We also directly compared the influence of MS on guilt and shame at the behavioral and neural levels. The effects of MS on self-reported feelings, brain activation, and some functional connectivity were not significantly different between the guilt and shame conditions.

This manifests the similarities of the MS effects on guilt and shame. Notably, MS more strongly decreased vmPFC-PCC connectivity in the shame than in the guilt condition. This shows a unique influence of MS on shame, which echoes previous findings that the self-referential processing of shame is different from that of guilt (Tangney and Dearing 2003; Zhu, Feng, et al. 2019; Zhu, Wu, et al. 2019).

The effects of MS on guilt and shame we found reflect a key part of distal defenses. Under the implicit influence of subconscious thoughts of death, individuals reevaluate past immoral events and feel stronger feelings of guilt and shame. Guilt and shame psychologically prepare individuals for moral behavior (Tangney et al. 2007; Chang et al. 2011; Sznycer et al. 2016, 2018; Sznycer 2019). As moral norms are key components of cultural worldviews, conducting moral behavior is conducive to guarding individuals' cultural worldviews and boosting their self-esteem (Gailliot et al. 2008; Kesebir and Pyszczynski 2012). Thus, we display empirical evidence at both the behavioral and neural levels for the effects of MS on moral emotions and provide a theoretical explanation of how they are related to distal defenses within the framework of TMT (Greenberg et al. 1986; Florian and Mikulincer 1997).

Individuals experiencing guilt and shame blame themselves and may have low (moral) self-esteem (Lewis and Block 1971; Tangney and Dearing 2003). Given that the function of distal defenses should be boosting self-esteem, at first glance, one may feel surprised that MS enhances guilt and shame. We note that strengthened guilt and shame are not the final step of distal defenses (see Fig. 1). Previous studies have found that guilt and shame promote various moral behaviors, such as apology, compensation, and self-punishment (Haidt 2003; Tangney et al. 2007; Zhu et al. 2017; Sznycer 2019). These moral behaviors, on the one hand, attenuate individuals' guilt and shame (Glucklich 2001; Bastian et al. 2011); on the other hand, they allow individuals to believe that they achieve purification and reparation for their sins, which helps them rebuild their moral selves (i.e. boost self-esteem) (Glucklich 2001; Monin and Jordan 2009; Nelissen and Zeelenberg 2009). Guilt- and shame-promoted moral behaviors (rather than guilt and shame per se) are conducive to upholding cultural worldviews and boosting self-esteem. We admit that we did not directly test whether guilt and shame promote moral behavior. However, this link has been demonstrated by dozens of previous studies (e.g. De Hooge et al. 2007, 2008; Ghorbani et al. 2013; Yu et al. 2014; Gao et al. 2018). Future studies may depict the full chain from MS to boosted cultural worldviews and self-esteem in one study by examining the effects of MS on both moral emotion and moral behavior.

Consistent with previous studies (Han et al. 2010; Shi and Han 2013; Klackl et al. 2014; Luo et al. 2019), we found that MS deactivated the insula in the priming stage compared with NA. It indicates a suppression of sentient self-awareness and supports the existence of proximal defenses (Northoff and Bermpohl 2004; Northoff et al. 2006; Lemogne et al. 2011). Moreover, using the activation of the insula in the priming stage as an indicator of proximal defenses, we found that proximal defenses partly predicted the distal defenses indicated by neural activities in the emotion-reliving task.

We considered the activity of the insula as a reliable indicator of proximal defenses, as previous studies consistently identified its deactivation when individuals were processing death-related information (Han et al. 2010; Shi and Han 2013; Klackl et al. 2014; Luo et al. 2019). In contrast, the findings of other regions (e.g. ACC) were contradictory (Quirin et al. 2012; Luo et al. 2019). In line with our results, Luo et al. (2019) found that brain activation during the MS priming stage was predictive of brain activation during a learning task after MS priming. Nevertheless, neither Luo et al. (2019) nor any other fMRI studies on MS discussed the theoretical association between their findings and proximal and distal defenses. We propose that brain activities during the MS priming stage and during a task after priming can be used as indicators of proximal and distal defenses, respectively. Given the difficulties behavioral studies face when they attempt to indicate proximal and distal defenses (e.g. a lack of a quantitative indicator) (Pyszczynski et al. 1999), we believe that clearly pointing out these neural indicators helps renew researchers' interest and enrich TMT. Along with the findings of Luo et al. (2019), we show that individuals who exhibit stronger proximal defenses have stronger distal defenses. In other words, one who responds more intensely in the face of death-related information is more inclined to equip themselves with cultural worldviews and self-esteem against existential anxiety later.

Many studies have demonstrated that closeness to death rather than fear of death drives terror management defenses (see a review, Pyszczynski et al. 1999). Closeness to death is the crucial indicator for checking the manipulation of MS (Feng et al. 2017; Luo et al. 2019). We found significant correlations between closeness to death and changes in guilt ratings and neural activities that revealed significant differences between the groups. They show that the significant group differences in guilt and neural activities were closely related to MS. In contrast, fear of death (possibly as a byproduct of closeness to death) was not correlated to the changes in guilt ratings and was correlated with only a few neural activities. The findings are in line with the proposition that individuals may attempt to manage their existential terror without actually feeling it (Pyszczynski et al. 1999).

Despite the effects of MS on shame-related neural activities, the difference in self-reported feelings of shame between the MS and NA groups did not reach significance. This situation often occurs in fMRI studies on high-level cognition and emotion (e.g. empathy) (Xu et al. 2009; Sheng and Han 2012; Luo et al. 2014). This implies that fMRI signals, compared with subjective ratings, are more sensitive to complex emotions (e.g. shame) (Luo et al. 2014). Another possible reason is that in our study, MS intensively enhanced the neural activities related to the cognitive component of shame (e.g. vmPFC activation; self-referential processing) but not the emotional component of shame (e.g. amygdala activation; emotional experience). Thus, MS may facilitate individuals' self-reflection but may not strongly increase their negative emotional experience in the shame condition.

We did not find a significant effect of MS on any neural activity related to mentalizing (e.g. TPJ), although mentalizing processing is an important psychological component of guilt and shame. One possible reason is that we used a recall paradigm to induce guilt and shame. The participants might extract others' thoughts and feelings from their memories instead of making a mental inference, which may have resulted in the null effect of MS on mentalizing processing. Future studies need to examine the effects of MS on guilt and shame using interpersonal paradigms (Zhu, Feng, et al. 2019; Li et al. 2020; Yu et al. 2020).

Two previous studies investigated the effect of MS on guilt (Arndt et al. 1999; Harrison and Mallett 2013). The studies found that MS increased guilt when individuals imagined that they did something different from others (i.e. engaged in creative activity) (Arndt et al. 1999) or when individuals thought that the group they belong to destroyed the ecological environment (Harrison and Mallett 2013). However, a recent fMRI study demonstrated that an imagination paradigm may be less efficient at inducing guilt than a recall paradigm (Mclatchie et al. 2016). The former might evoke only anticipatory thoughts while inducing few affective experiences of guilt (Mclatchie et al. 2016). We reexamined the effect of MS on guilt using a recall paradigm and extended the examination to the neural level. In addition, to the best of our knowledge, our study is the first to investigate the effect of MS on shame.

Moral emotions, such as guilt and shame, are closely associated with individuals' cultural environments (Bedford 2004; Wong and Tsai 2007). The effect of MS also depends on the culture to which individuals belong (Greenberg et al. 1990; Bedford and Hwang 2003; Pyszczynski and Kesebir 2012; Luo et al. 2017). Hence, cultural differences probably modulate the effects of MS on guilt and shame. Our participants came from a collectivistic society (i.e. China). Future studies should compare how individualism and collectivism influence the effects of MS on guilt and shame.

Our findings have implications for real life. Many veterans and depressive patients who feel a strong connection to death suffer from excessive guilt and shame (Kim et al. 2011; Bryan et al. 2013, 2015). Our findings provide an explanation for this phenomenon and suggest that offering additional ways of managing existential anxiety (e.g. social affiliation) (Wisman and Koole 2003) may help these groups regulate guilt and shame. On the other hand, a lack of guilt and shame causes moral violation and even crime (Tangney et al. 2011, 2014). It may be necessary to enhance moral emotions among specific groups (e.g. incarcerated recidivists). Existing studies have mainly focused on how to reduce guilt and shame (Finlay 2015; Krishnamoorthy et al. 2021). We show that MS priming is a candidate emotion-regulation intervention for increasing guilt and shame. However, it should be reiterated that the implementation of any regulation of moral emotions should be treated with caution (Finlay 2015).

A limitation of our study is that we did not measure the participants' neural response before MS or NA priming as a baseline. Thus, the fMRI results may suffer from some noise due to individual differences. To the best of our knowledge, most (if not all) existing fMRI studies on MS measured participants' neural response only after priming (Quirin et al. 2012; Luo et al. 2014; Silveira et al. 2014; Li et al. 2015; Feng et al. 2017; Shi and Han 2018; Guan et al. 2020). This decision is a result of a tradeoff between the value of the information one can obtain from baseline neural data and the cost of money and time one needs to bear. In line with previous studies, we made a similar decision. Thus, we believe that our study may meet the current standard of studying the effect of MS using fMRI. Future studies are encouraged to conduct more fMRI measures (e.g. measuring baseline neural signal) when investigating the effect of MS.

In conclusion, we show that MS enhances subjective self-reported feelings of guilt and modulates neural activities related to guilt and shame. Proximal defenses are partly predictive of distal defenses. Our study not only sheds light on the psychological and neural mechanisms of the MS effects on moral emotions but also provides new empirical evidence and theoretical insights for enriching TMT.

Supplementary Material

Supplementary material can be found at *Cerebral Cortex* online.

Notes

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