



Distinct effects of reminding mortality and physical pain on the default-mode activity and activity underlying self-reflection

Zhenhao Shi & Shihui Han

To cite this article: Zhenhao Shi & Shihui Han (2018) Distinct effects of reminding mortality and physical pain on the default-mode activity and activity underlying self-reflection, Social Neuroscience, 13:3, 372-383, DOI: [10.1080/17470919.2017.1329165](https://doi.org/10.1080/17470919.2017.1329165)

To link to this article: <https://doi.org/10.1080/17470919.2017.1329165>



Accepted author version posted online: 09 May 2017.
Published online: 15 May 2017.



Submit your article to this journal [↗](#)



Article views: 134



View Crossmark data [↗](#)



Citing articles: 1 View citing articles [↗](#)



Distinct effects of reminding mortality and physical pain on the default-mode activity and activity underlying self-reflection

Zhenhao Shi^{a,b} and Shihui Han^a

^aSchool of Psychological and Cognitive Sciences, PKU-IDG/McGovern Institute for Brain Research, Beijing Key Laboratory of Behavior and Mental Health, Peking University, Beijing, China; ^bCenter for Studies of Addiction, Department of Psychiatry, University of Pennsylvania Perelman School of Medicine, Philadelphia, PA, USA

ABSTRACT

Behavioral research suggests that reminding both mortality and negative affect influences self-related thoughts. Using functional magnetic resonance imaging (fMRI), we tested the hypothesis that reminders of mortality and physical pain decrease brain activity underlying self-related thoughts. Three groups of adults underwent priming procedures during which they answered questions pertaining to mortality, physical pain, or leisure time, respectively. Before and after priming, participants performed personality trait judgments on oneself or a celebrity, identified the font of words, or passively viewed a fixation. The default-mode activity and neural activity underlying self-reflection were identified by contrasting viewing a fixation vs. font judgment and trait judgments on oneself vs. a celebrity, respectively. The analyses of the pre-priming functional MRI (fMRI) data identified the default-mode activity in the posterior cingulate cortex (PCC), ventral medial prefrontal cortex (MPFC), and parahippocampal gyrus, and the activity underlying instructed self-reflection in both the ventral and dorsal regions of the MPFC. The analyses of the post-priming fMRI data revealed that, relative to leisure time priming, reminding mortality significantly reduced the default-mode PCC activity, and reminding physical pain significantly decreased the dorsal MPFC activity during instructed self-reflection. Our findings suggest distinct neural underpinnings of the effect of reminding morality and aversive emotion on default-mode and instructed self-reflection.

ARTICLE HISTORY

Received 17 January 2017
Revised 28 March 2017
Published online 15 May 2017

KEYWORDS

Self-reflection; mortality salience; fMRI; medial prefrontal cortex; posterior cingulate cortex

Introduction

Knowing that all men ultimately die contradicts human instinct to live. Though people routinely avoid explicit thinking of their inevitable death, death-related thoughts remain a source of existential terror and influence our behavior tremendously (Pyszczynski, Greenberg, & Solomon, 1999). Research during the past two decades has shown increasing behavioral evidence for the Terror Management Theory (TMT) that claims that, in order to alleviate the existential terror, people automatically resort to defensive buffers (Greenberg et al., 1990; Rosenblatt, Greenberg, Solomon, Pyszczynski, & Lyon, 1989). These buffers encompass a wide range of mental processes including adherence to cultural world view, pursuit of self-esteem, and reliance on intimate relationships (Hart, Shaver, & Goldenberg, 2005). One major line of empirical research supporting TMT has been focusing on testing the mortality salience (MS) hypothesis that reminders of death intensify efforts to bolster and defend faith in one's cultural world view (Burke, Martens, & Faucher, 2010). Another line

of empirical research has shown evidence that successful implementation of such buffers can effectively reduce the accessibility of subconscious death-related thoughts, whereas threatening the buffers heightens the level of terror (Hayes, Schimel, Arndt, & Faucher, 2010).

Given the profound influences of death-related thoughts on our lives, recent brain imaging research has shown increasing interests in the neural correlates of death-related thoughts. Early functional magnetic resonance imaging (fMRI) research found that making judgments on colors of words related to death or on semantic death relevance of words activated the frontoparietal attention network (Han et al., 2010; Shi & Han, 2013). Reading sentences related to death also activated the amygdala and the ventral anterior cingulate cortex (Quirin et al., 2012). Likewise, a near-infrared spectroscopy research reported greater activity in the right ventrolateral prefrontal cortex in response to the word “death” compared to “pain” (Yanagisawa et al., 2013) and an fMRI study found that self-esteem modulates the functional

connectivity between the amygdala and the ventrolateral prefrontal cortex during the processing of death-related stimuli (Yanagisawa, Abe, Kashima, & Nomura, 2016). Together, these brain imaging findings suggest the presence of emotion responses and emotion regulation during the processing of death-related stimuli/thoughts.

Death-related thoughts also induce neural activities that may not be simply attributed to the enhancement of emotional responses. For instance, Han and colleagues found that the neural activity in the insular cortex, which typically increases to emotion-laden stimuli (Craig, 2009), was decreased in response to death-related words compared to negative or neutral words (Han et al., 2010; Shi & Han, 2013). The decreased insular activity was also observed during reading sentences related to death compared to unpleasant but death-unrelated sentences (Klackl, Jonas, & Kronbichler, 2014). Event-related potential (ERP) studies revealed distinct effects of words related to death and negative emotion on brain activity by showing that an early frontal activity decreased to death-related words compared to neutral words (Liu et al., 2013). Death-related words also enlarged a long-latency positive activity over the parietal/central regions compared to neutral words (Liu et al., 2013; Klackl, Jonas, & Kronbichler, 2013).

Brain imaging studies also uncovered influences of death-related thoughts on neural correlates of other social/affective processing. For example, an ERP study reported that, relative to reminders of dental pain, thinking about one's own death or MS priming decreased the amplitude of a positive frontal activity (P2 component) but increased the amplitude of a negative frontal activity (N2 component) during judgments of facial expressions and these effects were more salient for racial in-group compared to out-group faces (Henry, Bartholow, & Arndt, 2010). Luo, Shi, Yang, Wang, and Han (2014) found that, relative to reminders of negative affect (or NA priming), MS priming decreased the anterior cingulate activity in response to perceived pain in others. Li et al. (2015) also showed both ERP and fMRI evidence that MS priming enhanced brain activity in the anterior and mid-cingulate cortex that differentiated between racial in-group and out-group members' emotional states. These findings indicate that MS priming modulate neural activities that are closely related to social behavior. However, to date, the findings only suggest that MS priming influences the neural correlates of social/affective processing in relation to others. We have known little about whether and how brain activity involved in self-related processing is modulated by MS priming.

Two lines of behavioral research have suggested a relationship between MS and self-related processing.

On the one hand, researchers found that exposure to one's own mirror reflection that increased self-awareness made people reluctant to consciously think over their mortality (Arndt, Greenberg, Simon, Pyszczynski, & Solomon, 1998, Study 1). Moreover, when the level of self-awareness was heightened by exposure to a mirror or by perceiving the self as distinctive, participants showed increased accessibility of subconscious death-related thoughts estimated in a death-relevant word completion task (Silvia, 2001). These findings suggest that existential terror may stem from one's ability to reflect on the self. On the other hand, it has been found that MS priming made participants write less in a task prompting an internal focus of attention than in a task that required external focus (Arndt et al., 1998, Study 2). In consistence with this finding, other studies have shown that MS priming facilitated behavioral index of decreased sense of selfhood and escape from identity issues (Baumeister, 1991; Wheeler, Adams, & Keating, 2001) such as increased intention to take risks (Goldenberg, Cox, Pyszczynski, Greenberg, & Solomon, 2002; Taubman-Ben-Ari, Florian, & Mikulincer, 1999), to consume unhealthy food (Ferraro, Shiv, & Bettman, 2005), and to engage in spiritual/religious activities (Jonas & Fischer, 2006). These behavioral findings suggest a causal relationship between mortality threats and avoidance of self-focus or self-reflective thinking.

Self-reflection may not be specifically affected by existential concerns, but is rather generally influenced by negative affect. For example, heightened self-reflection elevated the awareness of threatening objects (Carver, Blaney, & Scheier, 1979) and increased everyday negative mood (Moberly & Watkins, 2008), which were not necessarily death-related. Reflection on one's own negative personality traits activated the anterior insula in which the activity predicted self-report of distress (Ma, Li, et al., 2014). A meta-analysis revealed that excessive self-focus can be maladaptive and can exacerbate the symptoms of affective disorders such as depression and anxiety (Mor & Winquist, 2002). Thus, one may choose to avoid self-related processing in response to most forms of negative affect. Indeed, it has been shown that reminding one's negative personality traits led to slowed responses to one's own face (Ma & Han, 2010). People also avoided self-reflection when realizing that they were unable to achieve their goals (Silvia & Duval, 2001). However, these behavioral findings did not clarify whether reminding mortality and death-irrelevant negative affect influences different types of self-reflection in a similar vein.

Brain imaging studies have elaborated two types of self-reflection in terms of the underlying neural

substrates. One is the instructed self-reflection or self-referential processing which occurs when participants are explicitly asked to reflect on their personal attributes. It is now well known that reflection on one's own personality traits compared with thinking others' personality traits activates the ventral region of the medial prefrontal cortex (MPFC, Han et al., 2008, 2010; Kelley et al., 2002; Ma & Han, 2011; Ma, Bang, et al., 2014; Moran, Macrae, Heatherton, Wyland, & Kelley, 2006; Phan et al., 2004; Wang et al., 2012; Zhu, Zhang, Fan, & Han, 2007) and the posterior cingulate cortex (PCC, Fossati et al., 2003; Kelley et al., 2002). Another type of self-related processing occurs during a wakeful rest when individuals are immersed in task-independent thoughts about the self, which has been termed as the default mode. During the default mode, one engages in mind wandering and mental time travel, especially envisioning the future of the self (Buckner & Carroll, 2007; Smallwood, Nind, & O'Connor, 2009). The default mode brain activity is characterized by increased activity in the default-mode network consisting of the PCC as the core node and other brain regions including the ventral MPFC, the parahippocampal gyrus, and the lateral parietal cortex, when participants rest quietly (or in a resting state) compared with when they performed a specific cognitive task (Buckner, Andrews-Hanna, & Schacter, 2008; McKiernan, D'Angelo, Kaufman, & Binder, 2006; Raichle et al., 2001; Vanhaudenhuyse et al., 2011). Moreover, it was shown that the greater default-mode activity in the MPFC and PCC predicted how often an individual conducts mind wandering in the absence of external task demands (Mason et al., 2007). A direct comparison between the two types of self-related processing revealed that instructed self-referential processing preferentially recruited the MPFC whereas the default mode preferentially recruited the PCC as well as the adjacent precuneus (Whitfield-Gabrieli et al., 2011).

The previous behavioral and brain imaging findings allow us to predict that reminders of mortality and physical pain decrease brain activity underlying self-related thoughts. The current work tested this hypothesis by examining whether reminding mortality and reminding a death-irrelevant but aversive emotion (e.g., physical pain) produce distinct effects on brain activity involved in instructed self-referential processing and default-mode processing by scanning healthy adults using fMRI. Participants were first scanned when they performed personality trait judgments on oneself or a celebrity, identified the font of words, or passively viewed a fixation. The default-mode activity and neural activity underlying instructed self-referential processing was identified by contrasting viewing a fixation vs. font judgment and trait judgments on oneself vs. a celebrity, respectively. Participants were then

randomly assigned to three treatment groups who were primed with death-related thoughts (MS group), physical pain (PP), or leisure time (LT), respectively. They were then scanned again when they performed personality trait judgments on oneself or a celebrity, identified the font of words, or passively viewed a fixation. We analyzed the fMRI data in the pre-priming session to functionally define the MPFC and the PCC that were, respectively, linked to instructed self-referential processing and default-mode processing. The neural activities in the MPFC and the PCC were then extracted from the post-priming session and compared across the three subject groups in order to examine (1) whether MS and PP priming led to reduced neural activities underlying the default-mode and instructed self-referential processing compared to LT priming and (2) if so, whether MS priming and PP priming induced similar modulations of the MPFC and PCC activities that are associated with instructed self-referential and default-mode processing, respectively. Self-esteem, neuroticism, and dispositional death anxiety were monitored using questionnaires to control variations of these traits among the three priming groups.

Methods

Participants

Forty-eight healthy Chinese college students (30 female; aged between 19 and 27 years, mean \pm SD = 22.75 \pm 1.85) participated in this study as paid volunteers. All were right-handed, had normal or corrected-to-normal vision, and reported no neurological or psychiatric history. They were randomly assigned to three groups who received MS, PP, and LT priming (6 male and 10 female for each group; aged 22.75 \pm 1.98 vs. 22.69 \pm 1.54 vs. 22.81 \pm 2.10 years, $F(2,25) = 0.02$, $p > 0.9$, $\eta^2_p = 0.001$), respectively. All participants were included in fMRI data analyses though one participant from PP group and three from LT group did not complete the manipulation check due to technical failure. Informed consent was obtained before the study. This study was approved by a local ethics committee.

Stimuli and procedure

Stimuli consisted of 120 positive and 120 negative trait adjectives of 2 Chinese characters that were selected from established personality trait adjective pools (Liu, 1990). The stimuli were black on a gray background and presented through an LCD projector onto a rear-projection screen viewed with an angled mirror positioned on the head coil. The imaging procedure consisted of a

pre-priming session and a post-priming session that were intervened with priming and calculation tasks. During priming, participants were presented with 28 sentences and were asked to think over each sentence and to indicate whether they agreed with them by pressing one of the two buttons with the right index or middle finger. MS group read sentences about death (e.g., “I will feel frustrated if getting close to death”) adapted from Luo et al. (2014). PP group read sentences about physical pain (e.g., “I will be frightened if my body is pricked by a syringe needle”). LT group read sentences about neutral events related to oneself (e.g., “It is enjoyable for me to take a walk after dinner”). Each sentence was presented for 7 s and followed by a 0.5-s fixation. Immediately after the priming, participants performed a calculation task that allowed death-related thoughts to fade from focal attention. Participants performed 28 trials of arithmetic operations (e.g., $(7 + 3 \times 5) \div 2 - 7 =$) and judged whether each calculation gave an odd or even number by pressing one of the two buttons. The calculation task was self-paced, and each trial was followed by a 0.5-s fixation. Participants were not scanned while they completed the priming and calculation tasks inside the scanner. After the calculation task, they completed the two post-priming scans of trait judgments.

Both the pre-priming and post-priming sessions consisted of two functional scans. Using a box-car design, each scan consisted of six blocks of trials. The self-referential and other-referential tasks required judgments on whether an adjective can describe the self or Xiang Liu (a well-known Chinese athlete), respectively. The font judgment task required judgments on whether an adjective was bold-faced or light-faced. Each scan contained two blocks of each task, and the order of these blocks was randomized. Each block lasted 30 s, during which five positive and five negative adjectives were presented in a random order. Each trial consisted of a cue word (either “Self”, “Xiang Liu” or “Font”) above a trait adjective presented for 2 s at the center of the screen. Two successive trait adjectives were intervened by the fixation for 1 s. Participants responded by pressing one of the two buttons with the right index or middle finger. Each block of trials was followed by a 10-s resting state block during which participants passively viewed a fixation cross. Each Chinese character in the cue words and trait adjectives subtended a visual angle of $1.71^\circ \times 2.31^\circ$ (width \times height) and $2.09^\circ \times 2.82^\circ$, respectively, at a viewing distance of 80 cm. The fixation cross subtended a visual angle of $1.31^\circ \times 1.31^\circ$.

After scanning, participants completed Rosenberg Self-Esteem Scale (Rosenberg, 1965), neuroticism subscale in the short version of revised Eysenck Personality Questionnaire (Eysenck, Eysenck, & Barrett, 1985), and

Templer’s Death Anxiety Scale (Templer, 1970). Participants were also asked to answer three questions for manipulation check (“To what extent did you think of your ‘death’/‘painful feeling’/‘leisure time’ when you read sentences inside the scanner?”) on a 7-point scale (1 = not at all; 7 = very much).

fMRI data acquisition and analysis

Scanning was performed on a 3-T GE scanner with a standard head coil. Thirty-two transversal slices of functional images covering the whole brain were acquired using a gradient-echo echo-planar pulse sequence ($64 \times 64 \times 24$ matrix with spatial resolution of $3.75 \times 3.75 \times 5$ mm, TR = 2000 ms, TE = 30 ms, FOV = 24×24 cm, flip angle = 90°). Anatomical images were obtained using a 3D FSPGR T1 sequence ($256 \times 256 \times 128$ matrix with spatial resolution of $0.938 \times 0.938 \times 1.4$ mm, TR = 7.4 ms, TI = 450 ms, TE = 3.0 ms, flip angle = 20°).

SPM8 (the Wellcome Trust Centre for Neuroimaging, London, UK) was used for data analysis. Data from the pre-priming scans and the post-priming scans were processed separately. The images were slice time corrected, realigned to the first scan to correct for head movement between scans, and co-registered with each participant’s anatomical scan. Functional images were then normalized into a standard anatomical space ($3 \times 3 \times 3$ -mm isotropic voxels) using bilinear interpolation based on the Montreal Neurological Institute template. Normalized data were then spatially smoothed using a Gaussian filter with a full-width at half maximum parameter set to 8 mm.

Statistical analyses used a hierarchical random effects model with two levels. In the first level of each subject, the onsets and durations of each session were modeled using a general linear model according to stimulus conditions. All conditions were included in the model. A box-car function convolved with a canonical hemodynamic response function was used to model each condition. Effects at each voxel were estimated and regionally specific effects were compared using linear contrasts in individual participants using a fixed effects analysis. Random effect analyses were then conducted based on statistical parameter maps from each individual subject to allow population inference. GLM Flex (http://nmr.mgh.harvard.edu/harvardagingbrain/People/AaronSchultz/Aarons_Scripts.html) was used to conduct whole-brain mixed-design analyses of variance (ANOVAs). Significant activations were identified at cluster-level $p < 0.05$ corrected for false-discovery rate correction (using a combined threshold of uncorrected $p < 0.005$ and

cluster extent > 33 voxels determined by a 1000-iteration Monte-Carlo simulation; Slotnick, Moo, Segal, & Hart, 2003). This threshold is similar but more stringent than the one that was suggested to be good for balancing Type I and Type II errors (Lieberman & Cunningham, 2009).

The contrasts of self-judgment vs. other judgment and rest vs. font judgments during the pre-priming scans were calculated to define the MPFC involved in self-referential processing and the PCC involved in default mode, respectively. Region of interests (ROIs) were defined as spheres with radii of 5 mm centered at the peak activation voxels observed in the contrasts of self-judgment vs. other judgment and the contrast of rest vs. font judgments in the pre-priming session. Parameter estimates were then extracted from the ROIs using MarsBaR 0.42 (<http://marsbar.sourceforge.net>). One-way ANOVAs of the MPFC and PCC activity during the post-priming session were conducted with Priming (MS/PP/LT) as an independent between-subjects factor. Whole-brain statistical parametric mapping analyses were also conducted to estimate the interaction between Session (pre-priming/post-priming) and Priming (MS/PP/LT).

Results

Behavioral results

Questionnaire measurements showed that MS, PP, and LT groups were homogenous in self-esteem (mean \pm SD: 19.50 ± 2.48 vs. 20.25 ± 3.96 vs. 21.69 ± 2.80 , $F(2,45) = 2.06$, $p > 0.1$, $\eta^2_p = 0.08$), neuroticism (4.25 ± 2.89 vs. 4.19 ± 3.25 vs. 5.69 ± 3.00 , $F(2,45) = 1.24$, $p > 0.3$, $\eta^2_p = 0.05$), and dispositional death anxiety (4.88 ± 4.15 vs. 6.63 ± 3.91 vs. 6.50 ± 3.14 , $F(2,45) = 1.08$, $p > 0.3$, $\eta^2_p = 0.05$). Manipulation check was not successful in one participant from the PP group and three from the LT group due to technical failure. Univariate ANOVAs of manipulation check results showed that MS priming provoked more thoughts of death than PP and LT priming (3.56 ± 1.36 vs. 1.67 ± 1.45 vs. 1.07 ± 0.28 , $F(2,41) = 17.74$, $p < 0.001$, $\eta^2_p = 0.46$). PP priming provoked more thoughts of painful feeling than MS and LT priming (4.67 ± 1.68 vs. 1.75 ± 1.18 vs. 2.08 ± 1.61 , $F(2,41) = 17.21$, $p < 0.001$, $\eta^2_p = 0.46$). LT priming provoked more thoughts about leisure time than MS and PP priming (4.69 ± 2.21 vs. 2.63 ± 1.67 vs. 1.87 ± 1.19 , $F(2,41) = 10.01$, $p < 0.001$, $\eta^2_p = 0.33$).

Response accuracy during font judgments was high in both the pre-priming and post-priming sessions ($92.9 \pm 11.0\%$ vs. $99.1 \pm 2.16\%$). A three-way ANOVA on

reaction times (RTs) was conducted to examine the effects of Task (self-judgment/other/font judgments), Session (pre-/post-priming session), and Priming Type (MS/PP/LT). There was a significant main effect of Task ($F(2,90) = 218.15$, $p < 0.001$, $\eta^2_p = 0.83$) as RTs were longer during self-judgment/other judgment (1078 ± 137 vs. 1074 ± 143 ms) compared to font judgments (830 ± 118 ms; p 's < 0.001). Participants responded faster in the post-priming session than in the pre-priming session (966 ± 116 vs. 1021 ± 133 ms, $F(1,45) = 35.65$, $p < 0.001$, $\eta^2_p = 0.44$). This effect was further qualified by an interaction between Task and Session ($F(2,90) = 9.55$, $p < 0.001$, $\eta^2_p = 0.18$), suggesting greater changes of RTs to font judgments (783 ± 101 vs. 876 ± 147 ms) than self-judgments (1063 ± 146 vs. 1093 ± 142 ms) and other judgments (1053 ± 144 vs. 1094 ± 155 ms) across the pre-priming and post-priming sessions. Neither the main effect of Priming nor its interaction with the other factors was significant ($F = 0.12$ – 2.44 , p 's > 0.05, $\eta^2_p < 0.098$).

fMRI results

The whole-brain analysis of fMRI data across all participants during the pre-priming session revealed significant activation in the MPFC that covered a portion of the paracingulate cortex ($x/y/z = 12/53/13$, $Z = 4.12$, $k = 1986$; Figure 1(a)) during self-judgment vs. other judgments. The contrast of viewing a fixation vs. font judgments showed significant activation in the PCC ($x/y/z = 9/-28/34$, $Z = 6.09$, $k = 17344$; Figure 1(b)), the ventral MPFC ($x/y/z = 3/53/-5$), and the right parahippocampal gyrus (PHG; $x/y/z = 39/-4/-26$, Figure 1(b)). Whole-brain one-way ANOVAs of the pre-priming neural activities for self-judgment vs. other judgments and rest vs. font judgments with Priming (MS/PP/LT) as a between-subjects factor did not reveal any significant effect, suggesting comparable baseline neural activities across the three subject groups. We therefore defined the PCC as well as the ventral MPFC and the right PHG shown in the pre-priming session as ROIs for subsequent analyses of priming effects on default-mode processing in the post-priming session, and the MPFC shown in the pre-priming session as an ROI for subsequent analyses of priming effects on self-referential processing in the post-priming session. The whole-brain analysis also revealed that other vs. font judgments activated the dorsal MPFC ($x/y/z = -9/50/40$, $Z = 7.50$, $k = 7953$), the precuneus ($x/y/z = -6/-58/22$, $Z = 4.81$, $k = 160$), the bilateral middle temporal gyrus ($x/y/z = -48/-43/-8$ & $48/-22/-14$, $Z = 6.22$ & 5.64 , $k = 472$ & 126). Self-judgment vs. font judgment also activated the dorsal MPFC ($x/y/z = -9/41/46$, $Z = 7.56$, $k = 6402$) and the precuneus ($x/y/z = -3/-55/19$, $Z = 6.02$, $k = 281$).

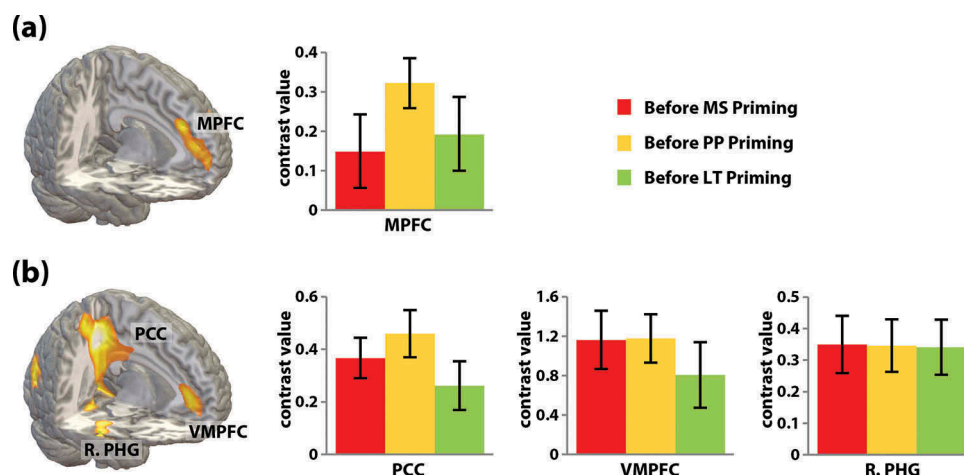


Figure 1. (a) The MPFC activation shown in the contrast of self-judgment vs. other judgment across all subjects before priming (left panel) and illustrations of the contrast values for each group before priming (right panel). (b) Activations in the PCC, the ventral MPFC, and the right PHG shown in the contrast of fixation vs. font judgments across all subjects before priming (left panel) and illustrations of the contrast values of each group before priming (right panel). The error bars represent standard errors. MPFC, medial prefrontal cortex; PCC, posterior cingulate cortex; PHG, parahippocampal gyrus; MS, mortality salience; PP, physical pain; LT, leisure time.

To assess the effect of MS/PP/LT priming on the neural activity related to the default-mode and instructed self-referential processing, we extracted the contrast values in the ROIs of the PCC ($x/y/z = 9/-28/34$), the ventral MPFC ($x/y/z = 3/53/-5$), and the right PHG ($x/y/z = 39/-4/-26$) for rest vs. font judgments from individual contrast images of the post-priming session, and the contrast values in the MPFC ROI ($x/y/z = 12/53/13$) for self-judgment vs. other judgment from individual contrast images of the post-priming session. These contrast values were then subjected to one-way ANOVAs to examine the effects of priming (MS/PP/LT). Both the MPFC underlying instructed self-reflection and the default-mode PCC activity were significantly different across the subject groups who received the MS, PP, and LT priming ($F(2,45) = 3.74$ and 5.51 , $p < 0.05$ and 0.01 , $\eta^2_p = 0.14$ and 0.20). Pairwise t -tests further confirmed that the MPFC activity

underlying instructed self-reflection was significantly decreased by the PP priming (-0.02 ± 0.43) compared to the MS priming (0.26 ± 0.26 ; $t(30) = 2.21$, $p < 0.05$, Cohen's $d = 0.78$) and the LT priming (0.35 ± 0.48 ; $t(30) = 2.32$, $p < 0.03$, Cohen's $d = 0.82$), but did not significantly differ between MS and LT priming ($t(30) = -0.66$, $p > 0.5$, Cohen's $d = 0.24$; Figure 2(a)). The default-mode PCC activity, however, was significantly reduced by the MS priming (0.06 ± 0.28) compared to PP priming (0.41 ± 0.34 ; $t(30) = 3.16$, $p < 0.005$, Cohen's $d = 1.12$) and the LT priming (0.28 ± 0.28 ; $t(30) = 2.23$, $p < 0.05$, Cohen's $d = 0.79$), but did not significantly differ between PP and LT priming ($t(30) = 1.18$, $p > 0.2$, Cohen's $d = 0.42$; Figure 2(b)). Similar analyses were also applied to the neural activity in the ventral MPFC and the right PHG ROIs. However, none of these regions showed a significant effect of Priming ($F(2,45) = 0.22$ and 0.18 , p 's > 0.8 , $\eta^2_p < 0.01$).

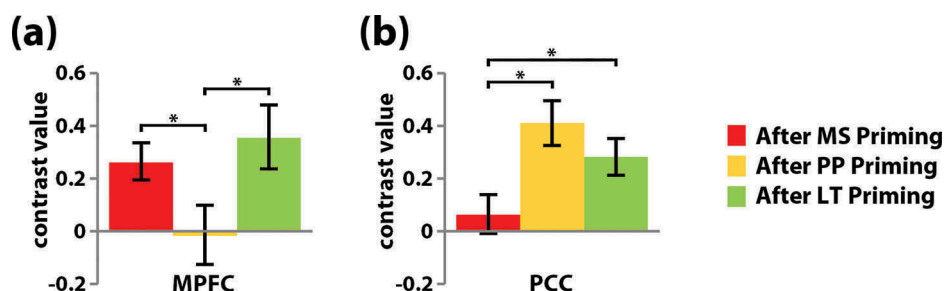


Figure 2. (a) The contrast values of the MPFC in the contrast of self-judgment vs. other judgment for each group after priming. (b) The contrast values of the PCC in the contrast of rest vs. font judgments for each group after priming. The error bars represent standard errors. MPFC, medial prefrontal cortex; PCC, posterior cingulate cortex; MS, mortality salience; PP, physical pain; LT, leisure time. Error bars represent standard errors of mean. * $p < 0.05$.

To complement the above ROI analyses and to examine whether neural activity in other brain regions were affected by MS/PP/LT priming, we conducted whole-brain ANOVAs of the contrast of self-judgment vs. other judgment with Session (pre-priming/post-priming) as a within-subjects factor and Priming (MS/PP/LT) as a between-subjects factor. This analysis revealed significant Session-by-Priming interactions in the MPFC ($x/y/z = -12/32/34$, $Z = 3.23$, $k = 114$; Figure 3(a)), the right superior frontal gyrus ($x/y/z = 12/32/46$, $Z = 3.63$, $k = 185$), the medial occipital gyrus ($x/y/z = 6/-70/22$, $Z = 3.05$, $k = 51$), and the left middle temporal gyrus ($x/y/z = -48/-70/19$, $Z = 3.21$, $k = 43$). A similar analysis of the contrast of viewing a fixation vs. font judgments revealed significant Session-by-Priming interactions in the PCC ($x/y/z = -6/-37/37$, $Z = 3.19$, $k = 41$; Figure 3(b)), the left precentral gyrus ($x/y/z = -36/-4/43$, $Z = 3.35$, $k = 82$), the thalamus ($x/y/z = 0/-25/-5$, $Z = 3.90$, $k = 61$), and the right inferior frontal gyrus ($x/y/z = 36/17/28$, $Z = 3.78$, $k = 52$). *Post hoc* analyses did not reveal any significant cross-group difference in neural activity during the pre-priming session. However, during the post-priming session, MPFC activation for self-judgment vs. other judgment was eliminated following PP priming, but retained following MS and LT priming. The PCC activation shown in the contrast of view a fixation vs. font judgments before priming was eliminated after MS priming, but retained following PP and LT priming. We also conducted whole-brain ANOVAs on the contrasts of other judgment vs. font judgment as well as self-judgment vs. font judgment. The contrast of other judgment vs. font judgment revealed significant Session-by-Priming interactions on the right ventrolateral prefrontal activity that was enlarged following the MS and PP priming compared with the

LT priming ($x/y/z = 48/28/-13$, $Z = 3.78$, $k = 51$). No significant interaction was observed for the contrast of self-judgment vs. other judgment.

Discussion

The present study examined whether and how reminders of mortality and negative affect (e.g., physical pain) influence the default-mode activity and the activity underlying instructed self-reflection on personality traits. The manipulation check confirmed that the MS and PP priming induced thoughts about mortality and negative affect, respectively. Behavioral performances during trait or font judgments were not influenced by the priming procedure and thus excluded influences arousal or task difficulty on our neuroimaging results. Consistent with the results of previous fMRI research (e.g., Fossati et al., 2003; Han et al., 2008, 2010; Kelley et al., 2002; Ma & Han, 2011; Ma, Bang, et al., 2014; McKiernan et al., 2006; Moran et al., 2006; Phan et al., 2004; Qin & Northoff, 2011; Wang et al., 2012; Whitfield-Gabrieli et al., 2011; Zhu et al., 2007), we found that instructed self-reflection on one's own (vs. a celebrity's) personality traits activated the MPFC/paracingulate cortex and the default-mode processing during viewing a fixation (vs. font judgments) engaged the PCC, the ventral MPFC, and the parahippocampal region. Moreover, we found that, relative to the LT priming, the MS priming selectively reduced the default-mode PCC activity whereas the PP priming selectively weakened the MPFC activity during instructed self-reflection. These results suggest that reminders of mortality and an aversive affect (e.g., physical pain) moderate the neural activity underlying these two types of self-referential processing, respectively.

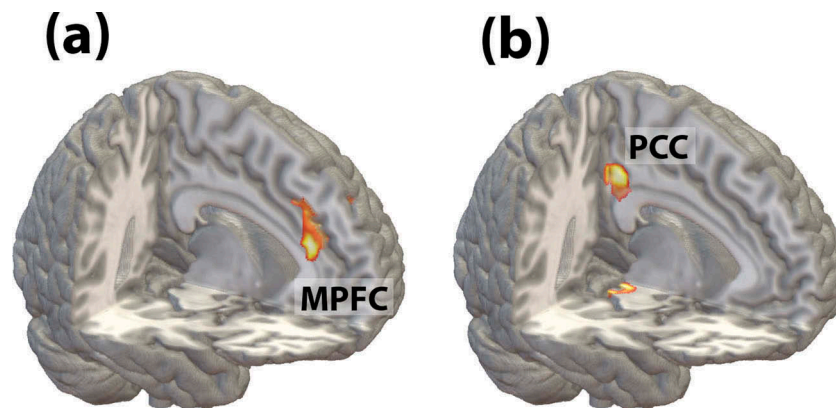


Figure 3. Whole-brain Session-by-Priming ANOVAs showed (a) significant interaction in the MPFC in the contrast of self-judgment vs. other judgment and (b) significant interaction in the PCC in the contrast of rest vs. font judgments. MPFC, medial prefrontal cortex; PCC, posterior cingulate cortex.

Both the PCC and MPFC are the key nodes of the cortical midline structure and are engaged in self-referential processing but play different roles (Northoff & Bermpohl, 2004; Northoff et al., 2006). For instance, the PCC and adjacent precuneus was activated during reflection on one's own personality traits that required the integration of self-referential stimuli in the context of personal attitudes (Fossati et al., 2003; Kelley et al., 2002; Kjaer, Nowak, & Lou, 2002) and preferentially responded to spontaneous self-reflection (Whitfield-Gabrieli et al., 2011). Autobiographical memory tasks based on the integration of self-referential cues (e.g., familiar names) also activated the PCC (Fink et al., 1996). The PCC also showed strong functional connectivity with other brain regions in the default-mode network during the resting state (Fransson & Marrelec, 2008). A greater default-mode PCC activity during the resting state was associated with high frequency of mind wandering (Mason et al., 2007) and predicted the degree of awareness and feeling of subsequent painful stimulations (Boly et al., 2007). The findings are consistent with the idea that the default-mode neural activities underlie mind wandering, which was enriched during task-independent self-reflection and mental time travel (Buckner & Carroll, 2007; Smallwood et al., 2009). These findings suggest a role for the PCC and the adjacent precuneus in integrating self-referential stimuli in the context of one's own person (Northoff & Bermpohl, 2004; Northoff et al., 2006). Given the functional role of the PCC during the resting state mentioned earlier, one may speculate that our finding of reduced default-mode PCC activity following death reminders may be concomitant with less self-related mind wandering during the resting state. The decreased PCC activity during viewing a fixation after MS priming relative to other priming conditions may also mediate MS-priming induced avoidance of exposing oneself to a mirror or the usage of less first person-pronouns (Arndt et al., 1998) because such behaviors may be concomitant with task-independent introspection or episodic memory retrieval. Therefore, the reduction of the default-mode PCC activity following death reminders further support the idea that people under MS are likely to actively suppress self-related mind wandering, and thereby avoid envisioning the future self.

Unlike the PCC and the adjacent precuneus that are preferentially engaged in spontaneous self-reflection, the MPFC activity preferentially responds to instructed self-reflection (Whitfield-Gabrieli et al., 2011) and is responsible for analytically encoding and evaluating self-related stimuli (Northoff et al., 2006). It has been shown that the MPFC activity underlying judgments of trait adjectives associated with oneself can predict later memory performance on self-related adjectives (Ma &

Han, 2011; Macrae, Moran, Heatherton, Banfield, & Kelley, 2004). In addition, there is evidence that the MPFC activation was more pronounced when one reflects on the present self than on the future self (D'Argembeau et al., 2010). Our findings that the MPFC activity underlying instructed self-reflection was not affected by MS priming but was reduced by PP priming have two implications. First, if MS priming threatens an individual's future destination rather than one's current state, it is then easy to understand why MS priming failed to modulate the MPFC activity that is more sensitive to reflection on the present self than the future self (D'Argembeau et al., 2010). This is consistent with the behavioral findings that MS priming even induced an increased motive for self-reflection when participants were explicitly instructed to conduct self-reflection (Landau et al., 2009). However, PP priming threatens one's current physical states and thus may induce avoidance of reflection of the present self by reducing the MPFC activity involved in instructed self-reflection. In consistent with our fMRI results, behavioral research has revealed that priming negative affect toward the self-deteriorated recognition of one's own face (Ma & Han, 2010) – another form of processing of the present self.

Recent research has shown increasing neuroimaging evidence for the interaction of the default-mode activity and stimulus-induced activity in both human and animals (Northoff, Qin, & Nakao, 2010). It has been shown that the level of the default-mode activity in brain regions such as the PCC/precuneus and the temporal parietal junction can predict the degree of awareness and feeling of subsequent painful stimulations (Boly et al., 2007). The level of the default-mode activity during stimulation also predicts the neuronal activity in visual and auditory cortices during the auditory and visual tasks (Greicius & Menon, 2004). These findings indicate that the default-mode activity can, to a certain degree, influence stimulus-induced activity and the associated behavioral and mental states. Together with our findings that MS priming decreased the default-mode activity in the PCC, it may be proposed that the impact of death-related thoughts on human behavior occurs through the modulation of the default-mode activity first. Such effects on the default-mode activity in turn may lead to changes of the neural activity induced by specific stimuli and tasks in multiple brain regions that are involved in sensory, perceptual, emotional, and motor processing. It may be further hypothesized that the defensive buffers, such as cultural worldview and self-esteem proposed by the TMT (Greenberg et al., 1990; Rosenblatt et al., 1989), may mitigate the existential terror by modulating the default-mode activity. This should be tested in future research.

Both behavioral and brain imaging studies have revealed novel effects of death-related thoughts on social perception and social interaction. MS enhances prosocial attitudes toward in-group members (Jonas, Schimel, Greenberg, & Pyszczynski, 2002), the need for intimate relationships (Mikulincer & Florian, 2000), and the willingness to affiliate with others (Wisman & Koole, 2003). MS also encourages punishment toward those who pose threat to one's own cultural world view (Rosenblatt et al., 1989) and induces negative evaluations of those who embrace a different religion (Greenberg et al., 1990). Neuroimaging research further showed that MS priming facilitates neural differentiation between in-group and out-group members (Henry et al., 2010) and decreases the empathic responses to others' pain in the anterior cingulate cortex (Luo et al., 2014). The current findings complement the previous research by showing evidence that the MS priming also influences the default-mode processing related to oneself.

The current work also raised other interesting questions for future research. For example, because self-esteem provides a defensive buffer against existential terror (Pyszczynski, Greenberg, Solomon, Arndt, & Schimel, 2004) and individuals with high versus low self-esteem showed stronger deactivation in the anterior insula in response to death-related sentences (Klackl et al., 2014), future research should clarify whether and how the MS priming effect on the PCC activity varies across individuals with high or low self-esteem. It is also interesting to examine whether and how the MS priming effect on the default mode activity mediates irrational behaviors (Ferraro et al., 2005; Goldenberg et al., 2002) and religious affiliation (Jonas & Fischer, 2006) under mortality threat. Future studies should also examine the mechanisms through which the neurocognitive modulation of the two subtypes of self-reflection influences defense against terror and negative affect.

Several limitations of the current work should be acknowledged. First, although the sample size of the current fMRI study was similar to those in our previous studies that reported reliable MS priming effects on brain activities underlying empathy for pain (Li et al., 2015; Luo et al., 2014), the sample size of our fMRI study was smaller relative to those in the previous behavioral studies of MS priming. Thus, the findings reported in the current work should be tested in future research with a large sample size. Second, the between-group design employed in our work had to deal with potential between-group variability in traits and brain activities. Our participants were randomly assigned to a priming group and age/gender/traits were matched for the three priming groups (although the mean rating scores

of the dispositional death anxiety appeared different but did not differ significantly between any two priming groups). Moreover, participants' brain activities during the pre-priming session did not differ between the three priming groups. Although these reduced the priming-unrelated group difference to a minimum degree, future research should examine individual difference in the MS priming effects on brain activity underlying self-reflection. Finally, the current work did not measure pain thresholds and individuals from different priming groups might show heterogeneous responses in relation with various pain thresholds. Even though this possibility is low because brain activity during the pre-priming session did not differ between the three priming groups, future research should consider this and control pain thresholds in different priming groups.

In conclusion, our fMRI findings provide brain imaging evidence that reminding mortality decreases the brain activity underlying self-related thoughts. Moreover, we showed evidence that reminding mortality or physical pain weakened the default mode activity in the PCC and the MPFC activity underlying instructed self-reflection, respectively, suggesting that reminders of mortality and physical pain produce distinct effects on the neural substrates of the two subtypes of self-related processing. Our findings complement the previous brain imaging findings of MS priming effects on brain activity underlying perception of or interaction with others. Our fMRI findings suggest potential neural mediators of MS-priming induced avoidance of self-focus or self-reflection.

Acknowledgements

This work was supported by the National Natural Science Foundation of China [Projects 31661143039; 31470986; 31421003] and the Ministry of Education of China [Project 20130001110049]. Zhenhao Shi was supported by the grant from the National Institutes of Health: T32 Translational Addiction Research Postdoctoral Fellowship DA028874.

Disclosure statement

The authors declare no competing financial interests.

Funding

This work was supported by the National Natural Science Foundation of China [Projects 31661143039; 31470986; 31421003] and the Ministry of Education of China [Project 20130001110049]. Zhenhao Shi was supported by the grant from the National Institutes of Health: T32 Translational Addiction Research Postdoctoral Fellowship DA028874.

References

- Arndt, J., Greenberg, J., Simon, L., Pyszczynski, T., & Solomon, S. (1998). Terror management and self-awareness: Evidence that mortality salience provokes avoidance of self-focused state. *Personality and Social Psychology Bulletin*, 24, 1216–1227. doi:10.1177/01461672982411008
- Baumeister, R. F. (1991). Escaping the self: Alcoholism, spirituality, masochism, and other flights from the burden of selfhood. New York: Basic Books.
- Boly, M., Baiteau, E., Schnakers, C., Degueldre, C., Moonen, G., Luxen, A., ... Laureys, S. (2007). Baseline brain activity fluctuations predict somatosensory perception in humans. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 12187–12192. doi:10.1073/pnas.0611404104
- Buckner, R. L., Andrews-Hanna, J. R., & Schacter, D. L. (2008). The brain's default network: Anatomy, function, and relevance to disease. *Annals of the New York Academy of Sciences*, 1124, 1–38. doi:10.1196/annals.1440.011
- Buckner, R. L., & Carroll, D. C. (2007). Self-projection and the brain. *Trends in Cognitive Sciences*, 11, 49–57. doi:10.1016/j.tics.2006.11.004
- Burke, B. L., Martens, A., & Faucher, E. H. (2010). Two decades of terror management theory: A meta-analysis of mortality salience research. *Personality and Social Psychology Review*, 14, 155–195. doi:10.1177/1088868309352321
- Carver, C. S., Blaney, P. H., & Scheier, M. F. (1979). Focus of attention, chronic expectancy, and responses to a feared stimulus. *Journal of Personality and Social Psychology*, 37, 1186–1195. doi:10.1037/0022-3514.37.7.1186
- Craig, A. D. (2009). How do you feel—now? The anterior insula and human awareness. *Nature Reviews Neuroscience*, 10, 59–70. doi:10.1016/j.neuroimage.2007.05.026
- D'Argembeau, A., Stawarczyk, D., Majerus, S., Collette, F., Van Der Linden, M., & Salmon, E. (2010). Modulation of medial prefrontal and inferior parietal cortices when thinking about past, present, and future selves. *Social Neuroscience*, 5, 187–200. doi:10.1080/17470910903233562
- Eysenck, S. B. G., Eysenck, H. J., & Barrett, P. (1985). A revised version of the psychoticism scale. *Personality and Individual Differences*, 6, 21–29. doi:10.1016/0191-8869(85)90026-1
- Ferraro, R., Shiv, B., & Bettman, J. R. (2005). Let us eat and drink, for tomorrow we shall die: Effects of mortality salience and self-esteem on self-regulation in consumer choice. *Journal of Consumer Research*, 32, 65–75. doi:10.1086/jcr.2005.32.issue-1
- Fink, G. R., Markowitsch, H. J., Reinkemeier, M., Bruckbauer, T., Kessler, J., & Heiss, W. D. (1996). Cerebral representation of one's own past: Neural networks involved in autobiographical memory. *Journal of Neuroscience*, 16, 4275–4282.
- Fossati, P., Hevenor, S. J., Graham, S. J., Grady, C., Keightley, M. L., Craik, F., & Mayberg, H. (2003). In search of the emotional self: An fMRI study using positive and negative emotional words. *American Journal of Psychiatry*, 160, 1938–1945. doi:10.1176/appi.ajp.160.11.1938
- Fransson, P., & Marrelec, G. (2008). The precuneus/posterior cingulate cortex plays a pivotal role in the default mode network: Evidence from a partial correlation network analysis. *NeuroImage*, 42, 1178–1184. doi:10.1016/j.neuroimage.2008.05.059
- Goldenberg, J. L., Cox, C., Pyszczynski, T., Greenberg, J., & Solomon, S. (2002). Understanding human ambivalence about sex: The effects of stripping sex of its meaning. *Journal of Sex Research*, 39, 310–320. doi:10.1080/00224490209552155
- Greenberg, J., Pyszczynski, T., Solomon, S., Rosenblatt, A., Veeder, M., Kirkland, S., & Lyon, D. (1990). Evidence for terror management theory II: The effects of mortality salience on reactions to those who threaten or bolster the cultural worldview. *Journal of Personality and Social Psychology*, 58, 308–318. doi:10.1037/0022-3514.58.2.308
- Greicius, M. D., & Menon, V. (2004). Default-mode activity during a passive sensory task: Uncoupled from deactivation but impacting activation. *Journal of Cognitive Neuroscience*, 16, 1484–1492. doi:10.1162/0898929042568532
- Han, S., Gu, X., Mao, L., Ge, J., Wang, G., & Ma, Y. (2010). Neural substrates of self-referential processing in Chinese Buddhists. *Social Cognitive and Affective Neuroscience*, 5, 332–339. doi:10.1093/scan/nsp027
- Han, S., Mao, L., Gu, X., Zhu, Y., Ge, J., & Ma, Y. (2008). Neural consequences of religious belief on self-referential processing. *Social Neuroscience*, 3, 1–15. doi:10.1080/17470910701469681
- Hart, J., Shaver, P. R., & Goldenberg, J. L. (2005). Attachment, self-esteem, worldviews and terror management: Evidence for a tripartite security system. *Journal of Personality and Social Psychology*, 88, 999–1013. doi:10.1037/0022-3514.88.6.999
- Hayes, J., Schimel, J., Arndt, J., & Faucher, E. H. (2010). A theoretical and empirical review of the death-thought accessibility concept in terror management research. *Psychological Bulletin*, 136, 699–739. doi:10.1037/a0020524
- Henry, E. A., Bartholow, B. D., & Arndt, J. (2010). Death on the brain: Effects of mortality salience on the neural correlates of ingroup and outgroup categorization. *Social Cognitive and Affective Neuroscience*, 5, 77–87. doi:10.1093/scan/nsp041
- Jonas, E., & Fischer, P. (2006). Terror management and religion: Evidence that intrinsic religiousness mitigates worldview defense following mortality salience. *Journal of Personality and Social Psychology*, 91, 553–567. doi:10.1037/0022-3514.91.3.553
- Jonas, E., Schimel, J., Greenberg, J., & Pyszczynski, T. (2002). The Scrooge effect: Evidence that mortality salience increases prosocial attitudes and behavior. *Personality and Social Psychology Bulletin*, 28, 1342–1353. doi:10.1177/014616702236834
- Kelley, W. M., Macrae, C. N., Wyland, C. L., Caglar, S., Inati, S., & Heatherton, T. F. (2002). Finding the self? An event-related fMRI study. *Journal of Cognitive Neuroscience*, 14, 785–794. doi:10.1162/08989290260138672
- Kjaer, T. W., Nowak, M., & Lou, H. C. (2002). Reflective self-awareness and conscious states: PET evidence for a common midline parietofrontal core. *NeuroImage*, 17, 1080–1086. doi:10.1006/nimg.2002.1230
- Klackl, J., Jonas, E., & Kronbichler, M. (2013). Existential neuroscience: Neurophysiological correlates of proximal defenses against death-related thoughts. *Social Cognitive and Affective Neuroscience*, 8, 333–340. doi:10.1093/scan/nss003
- Klackl, J., Jonas, E., & Kronbichler, M. (2014). Existential neuroscience: Self-esteem moderates neuronal responses to

- mortality-related stimuli. *Social Cognitive and Affective Neuroscience*, 9, 1754–1761. doi:10.1093/scan/nst167
- Landau, M. J., Greenberg, J., Sullivan, D., Routledge, C., & Arndt, J. (2009). The protective identity: evidence that mortality salience heightens the clarity and coherence of the self-concept. *Journal of Experimental Social Psychology*, 45, 796–807. doi:10.1016/j.jesp.2009.05.013
- Li, X., Liu, Y., Luo, S., Wu, B., Wu, X., & Han, S. (2015). Mortality salience enhances racial in-group bias in empathic neural responses to others' suffering. *NeuroImage*, 118, 376–385. doi:10.1016/j.neuroimage.2015.06.023
- Lieberman, M. D., & Cunningham, W. A. (2009). Type I and Type II error concerns in fMRI research: Re-balancing the scale. *Social Cognitive and Affective Neuroscience*, 4, 423–428. doi:10.1093/scan/nsp052
- Liu, X., Shi, Z., Ma, Y., Qin, J., & Han, S. (2013). Dynamic neural processing of linguistic cues related to death. *Plos One*, 8, e67905.
- Liu, Y. (1990). *Modern Lexicon of Chinese Frequently-used Word Frequency*. Beijing: Space Navigation Press.
- Luo, S., Shi, Z., Yang, X., Wang, X., & Han, S. (2014). Reminders of mortality decrease midcingulate activity in response to others' suffering. *Social Cognitive and Affective Neuroscience*, 9, 477–486. doi:10.1093/scan/nst010
- Ma, Y., Bang, D., Wang, C., Allen, M., Frith, C., Roepstorff, A., & Han, S. (2014). Sociocultural patterning of neural activity during self-reflection. *Social Cognitive and Affective Neuroscience*, 9, 73–80. doi:10.1093/scan/nss103
- Ma, Y., & Han, S. (2010). Why respond faster to the self than others? An implicit positive association theory of self advantage during implicit face recognition. *Journal of Experimental Psychology: Human Perception & Performance*, 36, 619–633.
- Ma, Y., & Han, S. (2011). Neural representation of self-concept in sighted and congenitally blind adults. *Brain*, 134, 235–246. doi:10.1093/brain/awq299
- Ma, Y., Li, B., Wang, C., Shi, Z., Sun, Y., Sheng, F., ... Han, S. (2014). 5-HTTLPR polymorphism modulates neural mechanisms of negative self-reflection. *Cerebral Cortex*, 24, 2421–2429. doi:10.1093/cercor/bht099
- Macrae, C. N., Moran, J. M., Heatherton, T. F., Banfield, J. F., & Kelley, W. M. (2004). Medial prefrontal activity predicts memory for self. *Cerebral Cortex*, 14, 647–654. doi:10.1093/cercor/bhh025
- Mason, M. F., Norton, M. I., Van Horn, J. D., Wegner, D. M., Grafton, S. T., & Macrae, C. N. (2007). Wandering minds: The default network and stimulus-independent thought. *Science*, 315, 393–395. doi:10.1126/science.1131295
- McKiernan, K. A., D'Angelo, B. R., Kaufman, J. N., & Binder, J. R. (2006). Interrupting the stream of consciousness: An fMRI investigation. *NeuroImage*, 29, 1185–1191. doi:10.1016/j.neuroimage.2005.09.030
- Mikulincer, M., & Florian, V. (2000). Exploring individual differences in reactions to mortality salience: Does attachment style regulate terror management mechanisms? *Journal of Personality and Social Psychology*, 79, 260–273. doi:10.1037/0022-3514.79.2.260
- Moberly, N. J., & Watkins, E. R. (2008). Ruminative self-focus and negative affect: An experience sampling study. *Journal of Abnormal Psychology*, 117, 314–323. doi:10.1037/0021-843X.117.2.314
- Mor, N., & Winquist, J. (2002). Self-focused attention and negative affect: A meta-analysis. *Psychological Bulletin*, 128, 638–662. doi:10.1037/0033-2909.128.4.638
- Moran, J. M., Macrae, C. N., Heatherton, T. F., Wyland, C. L., & Kelley, W. M. (2006). Neuroanatomical evidence for distinct cognitive and affective components of self. *Journal of Cognitive Neuroscience*, 18, 1586–1594. doi:10.1162/jocn.2006.18.9.1586
- Northoff, G., & Bermpohl, F. (2004). Cortical midline structures and the self. *Trends in Cognitive Sciences*, 8, 102–107. doi:10.1016/j.tics.2004.01.004
- Northoff, G., Heinzel, A., De Greck, M., Bermpohl, F., Dobrowolny, H., & Panksepp, J. (2006). Self-referential processing in our brain—a meta-analysis of imaging studies on the self. *NeuroImage*, 31, 440–457. doi:10.1016/j.neuroimage.2005.12.002
- Northoff, G., Qin, P., & Nakao, T. (2010). Rest-stimulus interaction in the brain: A review. *Trends in Neurosciences*, 33(6), 277–284. doi:10.1016/j.tins.2010.02.006
- Phan, K. L., Taylor, S. F., Welsh, R. C., Ho, S. H., Britton, J. C., & Liberson, I. (2004). Neural correlates of individual ratings of emotional salience: A trial-related fMRI study. *NeuroImage*, 21, 768–780. doi:10.1016/j.neuroimage.2003.09.072
- Pyszczynski, T., Greenberg, J., & Solomon, S. (1999). A dual-process model of defense against conscious and unconscious death-related thoughts: An extension of terror management theory. *Psychological Review*, 106, 835–845. doi:10.1037/0033-295X.106.4.835
- Pyszczynski, T., Greenberg, J., Solomon, S., Arndt, J., & Schimel, J. (2004). Why do people need self-esteem? A theoretical and empirical review. *Psychological Bulletin*, 130, 435–468. doi:10.1037/0033-2909.130.3.435
- Qin, P., & Northoff, G. (2011). How is our self related to midline regions and the default-mode network? *NeuroImage*, 57, 1221–1233. doi:10.1016/j.neuroimage.2011.05.028
- Quirin, M., Loktyushin, A., Arndt, J., Küstermann, E., Lo, Y., Kuhl, J., & Eggert, L. (2012). Existential neuroscience: A functional magnetic resonance imaging investigation of neural responses to reminders of one's mortality. *Social Cognitive and Affective Neuroscience*, 7, 193–198. doi:10.1093/scan/nsq106
- Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, D. L. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America*, 98, 676–682. doi:10.1073/pnas.98.2.676
- Rosenberg, M. (1965). *Society and the adolescent self-image*. Princeton, NJ: Princeton University Press.
- Rosenblatt, A., Greenberg, J., Solomon, S., Pyszczynski, T., & Lyon, D. (1989). Evidence for terror management theory I: The effects of mortality salience on reactions to those who violate or uphold cultural values. *Journal of Personality and Social Psychology*, 57, 681–690. doi:10.1037/0022-3514.57.4.681
- Shi, Z., & Han, S. (2013). Transient and sustained neural responses to death-related linguistic cues. *Social Cognitive and Affective Neuroscience*, 8, 573–578. doi:10.1093/scan/nss034
- Silvia, P. J. (2001). Nothing or the opposite: Intersecting terror management and objective self-awareness. *European Journal of Personality*, 15, 73–82. doi:10.1002/(ISSN)1099-0984
- Silvia, P. J., & Duval, T. S. (2001). Objective self-awareness theory: Recent progress and enduring problems.

- Personality and Social Psychology Review*, 5, 230–241. doi:[10.1207/S15327957PSPR0503_4](https://doi.org/10.1207/S15327957PSPR0503_4)
- Slotnick, S. D., Moo, L. R., Segal, J. B., & Hart, J. (2003). Distinct prefrontal cortex activity associated with item memory and source memory for visual shapes. *Cognitive Brain Research*, 17, 75–82. doi:[10.1016/S0926-6410\(03\)00082-X](https://doi.org/10.1016/S0926-6410(03)00082-X)
- Smallwood, J., Nind, L., & O'Connor, R. C. (2009). When is your head at? An exploration of the factors associated with the temporal focus of the wandering mind. *Consciousness and Cognition*, 18, 118–125. doi:[10.1016/j.concog.2008.11.004](https://doi.org/10.1016/j.concog.2008.11.004)
- Taubman-Ben-Ari, O., Florian, V., & Mikulincer, M. (1999). The impact of mortality salience on reckless driving: A test of Terror Management mechanisms. *Journal of Personality and Social Psychology*, 76, 35–45. doi:[10.1037/0022-3514.76.1.35](https://doi.org/10.1037/0022-3514.76.1.35)
- Templer, D. I. (1970). The construction and validation of a Death Anxiety Scale. *Journal of General Psychology*, 82, 165–177. doi:[10.1080/00221309.1970.9920634](https://doi.org/10.1080/00221309.1970.9920634)
- Vanhaudenhuyse, A., Demertzi, A., Schabus, M., Noirhomme, Q., Bredart, S., Boly, M., ... Laureys, S. (2011). Two distinct neuronal networks mediate the awareness of environment and of self. *Journal of Cognitive Neuroscience*, 23, 570–578. doi:[10.1162/jocn.2010.21488](https://doi.org/10.1162/jocn.2010.21488)
- Wang, G., Mao, L., Ma, Y., Yang, X., Cao, J., Liu, X., ... Han, S. (2012). Neural representations of close others in collectivistic brains. *Social Cognitive and Affective Neuroscience*, 7, 222–229. doi:[10.1093/scan/nsr002](https://doi.org/10.1093/scan/nsr002)
- Wheeler, H. A., Adams, G. R., & Keating, L. (2001). Binge eating as a means for evading identity issues: The association between an avoidance identity style and bulimic behavior. *Identity*, 1, 161–178. doi:[10.1207/S1532706XID0102_04](https://doi.org/10.1207/S1532706XID0102_04)
- Whitfield-Gabrieli, S., Moran, J. M., Nieto-Castañón, A., Triantafyllou, C., Saxe, R., & Gabrieli, J. D. E. (2011). Associations and dissociations between default and self-reference networks in the human brain. *NeuroImage*, 55, 225–232. doi:[10.1016/j.neuroimage.2010.11.048](https://doi.org/10.1016/j.neuroimage.2010.11.048)
- Wisman, A., & Koole, S. (2003). Hiding in the crowd: Can mortality salience promote affiliation with others who oppose one's worldviews? *Journal of Personality and Social Psychology*, 84, 511–526. doi:[10.1037/0022-3514.84.3.511](https://doi.org/10.1037/0022-3514.84.3.511)
- Yanagisawa, K., Abe, N., Kashima, E. S., & Nomura, M. (2016). Self-esteem modulates amygdala-ventrolateral prefrontal cortex connectivity in response to mortality threats. *Journal of Experimental Psychology: General*, 145, 273. doi:[10.1037/xge0000121](https://doi.org/10.1037/xge0000121)
- Yanagisawa, K., Kashima, E. S., Moriya, H., Masui, K., Furutani, K., Nomura, M., Yoshida, H., & Ura, M. (2013). Non-conscious neural regulation against mortality concerns. *Neuroscience Letters*, 552, 35–39. doi:[10.1016/j.neulet.2013.07.027](https://doi.org/10.1016/j.neulet.2013.07.027)
- Zhu, Y., Zhang, L., Fan, J., & Han, S. (2007). Neural basis of cultural influence on self representation. *NeuroImage*, 34, 1310–1317. doi:[10.1016/j.neuroimage.2006.08.047](https://doi.org/10.1016/j.neuroimage.2006.08.047)