



Mortality threat mitigates interpersonal competition: an EEG-based hyperscanning study

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Abstract

Awareness of death has been shown to influence human cognition and behavior. Yet, how mortality threat (MT) impacts our daily social behavior remains elusive. To address this issue, we developed a dyadic experimental model and recruited 86 adults (43 dyads) to complete two computer-based tasks (i.e. competitive and cooperative button-pressing). We manipulated dyads' awareness of death [MT vs neutral control (NC)] and simultaneously measured their neurophysiological activity using electroencephalography during the task. Several fundamental observations were made. First, the MT group showed significantly attenuated competition and slightly promoted cooperation. Second, compared to NC, MT significantly decreased gamma-band inter-brain synchronization (IBS) in the competitive context, which was associated with increased subjective fear of death within dyads. Notably, those effects were context-specific: we did not observe comparable results in the cooperative context. Finally, a machine-learning approach was successfully used to discriminate between the MT and NC groups based on accumulated IBS. Together, these findings indicate that MT to some extent mitigates interpersonal competition, and such mitigation might be associated with changes in gamma-band IBS.

Key words: mortality threat; competition; cooperation; hyperscanning; EEG

Introduction

In the year 2020, with the global outbreak of the coronavirus disease 2019 (COVID-19) and increasing mortality as a consequence of it, the death-related information is highly accessible to each of us. Terror Management Theory (TMT) posits that awareness of death leads to existential threat and that cultural worldview and self-esteem, which function to buffer the threat, would reshape our behaviors (Rosenblatt *et al.*, 1989; Greenberg *et al.*, 1997). Accordingly, there has been increasing evidence that existential

threat exerts a remarkable influence on cognition, emotion and behavior (Burke *et al.*, 2010; Hayes *et al.*, 2010; Juhl and Routledge, 2016). However, precisely determining its influence on our daily social behaviors has proven more challenging due to the divergent findings unveiled by the bulk of TMT studies (Pyszczynski *et al.*, 2015). In this study, we explored how people reshape their daily social behaviors in response to mortality threat (MT).

There are two conflicting lines of behavioral studies illustrating how MT reshapes social behaviors. First, MT could promote

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benevolence. For instance, when confronted with death-related threats, individuals showed increased forgiveness to violent hockey players (Schimmel et al., 2006) and a more positive attitude toward violators of social norms or dissimilar others (Greenberg et al., 1992; Ma-Kellams and Blascovich, 2011). Moreover, reminders of mortality could result in a more prosocial attitude and engagement in prosocial behaviors (Jonas et al., 2002). Alternatively, MT could, to some extent, cause malicious behaviors, such as more blame on severely injured but innocent victims (Hirschberger, 2006), more aggressive behaviors against the worldview-threatening others (McGregor et al., 1998) and preference for the statements praising suicide attack against the hostile country (Pyszczynski et al., 2006). Although these studies have extensively documented the impact of MT on human behaviors, how morality threat reshapes human behaviors in inconsistent ways remains largely unknown. Animal research has demonstrated that the way to integrate information and interact with others was due in part to the specific context in which the individual was (Chen and Hong, 2018). Given that previous mortality-related studies included only one experimental context, the inconsistent effects of MT may depend on differential explicit contexts. To test this possibility, two classic contexts (i.e. competition and cooperation) as an experimental test bed of human social behaviors were used in the current study while the other factors (e.g. procedure, priming and paradigm) were controlled.

Previous studies were limited to single-brain neuroscience which was static, non-interactive and constrained by conventional brain imaging techniques. However, social behaviors are complex: one unique feature that distinguishes them from non-social behaviors is the dynamic exchange of information with a conspecific involved in the same social interaction (Chen and Hong, 2018). Thus, it might not be safe to conclude that the MT would exert potential influence on our daily life with the effects found in prior single-brain studies. For this reason, it is imperative to adopt the 'second-person neuroscience' approach (also known as 'hyperscanning', Redcay and Schilbach, 2019) to investigate the dynamically reciprocal interaction among individuals in social behaviors. The novel hyperscanning technique requires simultaneous recordings of brain activity from (at least) two individuals during social interaction (Montague et al., 2002; Babiloni et al., 2006). Animal studies have demonstrated that ongoing social interactions would elicit reliable inter-brain synchronization (IBS) in mice (Kingsbury et al., 2019) and bats (Zhang and Yartsev, 2019), beyond that observed in non-social behaviors or chance level (Kingsbury et al., 2019). Similarly, human studies using electroencephalography (EEG)-based hyperscanning also showed IBS in various socially relevant tasks, such as hand imitation (Dumas et al., 2010), decision-making (Hu et al., 2018) and interpersonal touch (Goldstein et al., 2018). In particular, gamma-band IBS was enhanced and mediated the effect of threat on interpersonal coordination under high threat (Mu et al., 2017). Taken as such, gamma-band IBS may play an important role in social behaviors under MT.

This study aimed to provide a neurophysiological test bed for the effect of MT on social behaviors in conflicting contexts. Specifically, we focused on two aspects of social behaviors that showed reliable IBS in previous studies (i.e. competition and cooperation, Cui et al., 2012; Wang et al., 2019) and had persisted throughout evolutionary history (Chen and Hong, 2018). To this end, we recruited two groups of participants [MT vs neutral control (NC)] to perform a modified version of computer-based competitive and cooperative button-pressing tasks (Cui et al., 2012), during which brain activity was simultaneously recorded

by EEG (Babiloni et al., 2006; Dumas et al., 2010; Mu et al., 2017; Hu et al., 2018). Two hypotheses concerning the effects of MT on interpersonal interaction in conflicting contexts (competition and cooperation) were made. First, based on the extent to which MT could promote benevolence, we would expect reduced competition and enhanced cooperation in dyads; alternatively, if MT could cause malicious behaviors, we would anticipate enhanced competition and reduced cooperation in dyads. Furthermore, we tested whether and how such effect(s) would be modulated by synchronous brain activity between individuals. Based on both single-brain (Luo et al., 2007) and dual-brain studies (Mu et al., 2017) in the field of threat, we anticipated that gamma-band IBS possibly underlies the effect of MT on social behaviors. Theta, alpha-mu and beta bands were also included in the brain imaging analyses, considering their roles in social behaviors (Dumas et al., 2010; Kawasaki et al., 2013; Mu et al., 2016). Besides, we also examined the temporal evolution of the effect; this was inspired by a line of studies showing that social behaviors and associated IBS could unfold dynamically over time (e.g. Cui et al., 2012; Wang et al., 2019).

Methods

Participants

Eighty-six volunteers were recruited via advertisement spread within the East China Normal University, resulting in 37 female dyads and 6 male dyads. Forty-four volunteers were randomly assigned to the MT group (mean age \pm SD = 21.5 ± 1.8 years, eight males) and the other forty-two volunteers to the NC group (21.8 ± 1.9 years, four males). The two groups were matched in terms of socioeconomic status [as assessed by subjective childhood socioeconomic status (SES), Griskevicius et al. (2013); MT: 3.60 ± 1.25 , NC: 3.71 ± 1.14 , $t(70) = -0.36$, $P = 0.72$] and empathy level [as assessed by Interpersonal Reactivity Index (IRI), Davis (1980); all P values > 0.05 , Supplementary Table S1]. Same-gender dyads were recruited to control for sex effects on the interactive process (Cheng et al., 2015; Mu et al., 2016; Zhang et al., 2017; Tang et al., 2019). All participants were right-handed, healthy, with normal or corrected-to-normal vision. Data from 7 dyads and 13 dyads were excluded from behavioral and dual-EEG analyses, respectively, due to poor task comprehension or execution or failure in EEG acquisition (see Supplementary Materials for details). The final dataset for behavioral and dual-EEG analyses includes 36 dyads (17 dyads in the MT group and 19 dyads in the NC group) and 30 dyads (15 dyads per group), respectively. All participants signed informed consent before the experiment and were compensated for their participation. The study protocol was approved by the University Committee on Human Research Protection (No. HR 167-2018) at the East China Normal University.

Tasks and procedures

Dyads first went through an experimental manipulation concerning MT. Next, dyads with different manipulations completed a computer-based social interaction game, comprising competition and cooperation tasks. The game was adapted from previous studies (Cui et al., 2012; Cheng et al., 2015; Pan et al., 2017). Within each task, there were three blocks, each consisting of 15 trials. In total, each task included 45 trials. The order of tasks was counterbalanced across dyads. Dyads were allowed for a four-trial practice prior to the formal tasks. Details are described below.

Experimental manipulation. Dyads were asked to read a news article and memorize the main point in the article (Griskevicius et al., 2011a,b). Dyads were randomly assigned to one of the two articles serving as different conditions: the MT (22 dyads) and the NC (21 dyads) conditions. In the MT condition, the article showed a severe threat to public security in dyads' country (in our case, China) due to the sustained increase in violent crimes. With the development of economy, the society had witnessed much more types of crime than ever before. In the NC condition, the article described the well-developed domestic market for electric vehicles as well as the challenge this market faced. The NC condition functioned as a non-threatening baseline. The two articles were matched in the number of words and paragraphs. Our experimental manipulation was checked in a pilot study (see Supplementary Materials) and via subjective ratings (see details in the next section). To estimate valence and general arousal associated with MT and NC, an independent sample was recruited (MT: $n = 20$, 24.8 ± 1.7 years, eight males; NC: $n = 20$, 23.9 ± 2.8 years, nine males) to report subjective feelings evoked by the article on a 7-point Likert scale (general arousal: 1 = not at all, 7 = extremely strong; valence: 1 = extremely negative, 7 = extremely positive). To ensure that dyads had read the article thoroughly, they were asked to recollect the main point of the article and list 3–4 keywords after reading.

Competition. Participants in each dyad sat side-by-side in front of two separate displays (connected to a single host computer) and separated by a board. The whole task consisted of four 30-s rest phases, interspersed by three task blocks (15 trials in each block, see Figure 1A). Within each trial, a hollow gray circle (1 s) appeared first, followed by a 'Go' signal (green circle). Upon seeing the signal, the participants were asked to press the key simultaneously (button '0' on a keyboard for player 1 and button '1' for player 2). They were told that if their actions were faster than their opponent, they would get the winning point(s).

Once both participants had responded, a feedback screen (2 s) was presented. The feedback summarized the following information: (i) win/excellent or lose for each participant, (ii) cumulative point(s) for each participant in the task and (iii) who was faster (a shorter bar on his/her side) or slower (a taller one) (see Figure 1B). To maintain interpersonal competition, we created one threshold for each trial to determine participants' winning or losing points: (i) if the response time (RT) difference was larger than a given threshold $T_{com} = (RT_1 + RT_2) / 3$ (i.e. $|RT_1 - RT_2| > T_{com}$, RT_1 and RT_2 represent the response times of two participants, respectively), the participant with smaller RT won 2 points while the other one lost 2 points; and (ii) if the RT difference was smaller than the threshold (i.e. $|RT_1 - RT_2| < T_{com}$), the participant with smaller RT won 1 point while the other one lost 1 point. Finally, a blank screen (2–4 s), serving as the inter-trial interval, appeared.

Cooperation. The cooperation task was similar to the competition task (see Figure 1C). But unlike the competition task, we created three thresholds for each trial to determine dyads' winning points to maintain dyads' attention and increase cooperative behaviors (Pan et al., 2017): $T_{coo1} = (RT_1 + RT_2) / 18$, $T_{coo2} = (RT_1 + RT_2) / 8$ and $T_{coo3} = (RT_1 + RT_2) / 3$. T_{cooi} denotes the i -th threshold. Those thresholds were adapted from previous studies and recommendations (Cui et al., 2012; Cheng et al., 2015; Baker et al., 2016; Pan et al., 2017), in order to control the difficulty of tasks at a reasonable level. For each dyad, (i) if the difference was smaller than the first threshold (i.e. $|RT_1 - RT_2| < T_{coo1}$), both won 2 points; (ii) if the difference was larger than the first threshold but smaller than the second one (i.e. $T_{coo1} < |RT_1 - RT_2| < T_{coo2}$), both won 1 point; (iii) if the difference was larger than the second threshold but smaller than the third one (i.e. $T_{coo2} < |RT_1 - RT_2| < T_{coo3}$), both lost 1 point; and (iv) if the difference was larger than the third threshold (i.e. $|RT_1 - RT_2| > T_{coo3}$), both lost 2 points. Although the numbers of thresholds

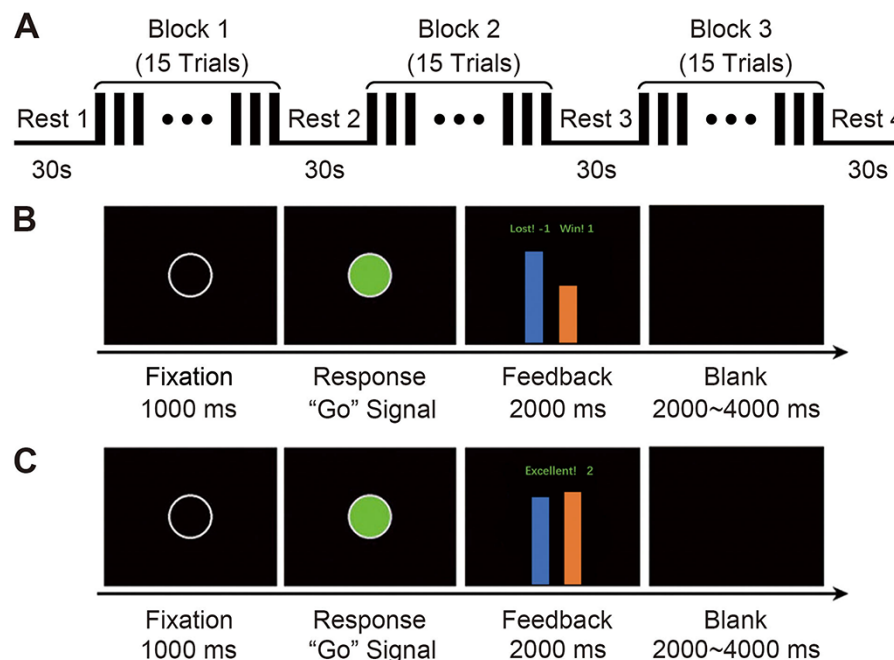


Fig. 1. Experimental design. (A) Task design. In each task, there were three blocks, each consisting of 15 trials. In total, each task included 45 trials. Events and time flow in one trial of the competition task (B) and the cooperation task (C).

differed between the two tasks, the thresholds we used resulted in four possible ways of gaining/losing points for the competition and cooperation tasks, respectively (see Supplementary Table S2 for more details). Thus, the participants were expected to be motivated equally in two tasks. The feedback screen conveyed two kinds of information (i.e. cooperation results and cumulative points) for dyads. Raw data of RTs in both competition and cooperation conditions are summarized in Supplementary Tables S3–4.

Subjective measurements

After experimental manipulation (i.e. article reading), participants completed the perceived childhood SES and IRI questionnaires, which served as a distraction task to ensure the effect of MT on the completion of the ensuing tasks (Routledge and Arndt, 2008; Routledge et al., 2010). We also asked participants to report subjective fear of death to confirm the effect of mortality priming (Lambert et al., 2014). After the whole experiment, participants were asked to complete a word-position task, which measured their Inclination to Avoid Symbolic Mortality Threats (IASMT, Fan and Han, 2018). The word-position task required participants to put target words (e.g. self, famous people and stranger's name) in a circle with a cue word (i.e. death) located at the center of the circle. IASMT was calculated for each participant: $IASMT = (d_1 - d_2) / d_2$, where d_1 was the distance between self's name and cue word, and d_2 was the distance between a stranger's name and cue word. Besides, we collected each participant's subjective attitudes towards the performance: (i) 'How satisfied were you with your performance?' and (ii) 'How satisfied were you with your partner's performance?'. No discussion was allowed while rating.

Behavioral data analyses

Competition. A competition index for each trial was defined by: $Competitionindex_i = |RT_{1,i} - RT_{2,i}| \times (RT_{1,i} + RT_{2,i})$. Extending previous studies (Cui et al., 2012; Wang et al., 2020), this index additionally controls the sum of both participants' RTs. Thus, a smaller competition index indicates more intense competition.

Given the nesting structure, data were analyzed using linear mixed-effects models (Baijella et al., 2000) with lme4 package (Bates et al., 2015) in R 3.6.1 (R Core Team, 2019). Post hoc comparisons were conducted using 'emmeans' package (Lenth, 2019). Competition index values were modeled by GROUP (MT vs NC), BLOCK (1, 2 or 3) and their interaction. The random effect was estimated for DYAD. The P values of fixed-effects factors were assessed by model comparison. Given that the number of pairwise comparisons in post hoc analyses could be large in the current study, Bonferroni correction was more conservative than necessary. Thus, for simple effects, P values were corrected by using the Tukey adjustment.

Cooperation. A cooperation index was calculated for each trial: $Cooperationindex_i = |RT_{1,i} - RT_{2,i}|$ (Cui et al., 2012; Wang et al., 2020). A smaller cooperation index corresponds to better performance. The cooperation index was analyzed using the same mixed-effects modeling described above. Notably, an algorithm controlling for the sum of both participants' RTs [i.e. $Cooperationindex_i = |RT_{1,i} - RT_{2,i}| / (RT_{1,i} + RT_{2,i})$] was also attempted and provided analogous results. However, this algorithm was deemed as less appropriate for the current paradigm, as it might simply reflect the different cooperation strategies

employed by the players (e.g. cooperative button-pressing with or without a delay), rather than cooperation performance *per se*.

Validation analyses. To further verify the differences between blocks under two conditions, we used a bootstrapping method for the contrasts between blocks (Block 3 vs Block 1, Block 3 vs Block 2). This method allowed us to examine the temporal evolution of the MT effect without contamination from individual differences (Mu et al., 2017). The 95% confidence interval and the probability distribution of bootstrapping were estimated with 10 000 times iterations using boot package (Davison and Hinkley, 1997; Canty and Ripley, 2019).

Dual-EEG data acquisition and preprocessing

The brain activity from both participants in each dyad was monitored and recorded simultaneously using two 64-channel EEG systems (Electrical Geodesics, Inc.). The electrodes were placed following the international 10–10 system. Signals were referenced to the electrode at Cz and digitized at a sampling rate of 250 Hz. Impedances were kept below 50 k Ω . Eye movements were recorded using Electro-Oculogram (EOG) channels.

The preprocessing was conducted using the MNE-python software suite (Gramfort et al., 2013). EEG signals were band-pass filtered (1–45 Hz) and re-referenced to an average of the left and right mastoids. Bad channels were excluded from further preprocessing and eye-movement-related artifacts were identified and rejected by independent component analysis (Makeig et al., 1996). Finally, bad channels were interpolated and 21 electrodes (Fp1, Fpz, Fp2, F7, F3, Fz, F4, F8, T7, C3, Cz, C4, T8, P7, P3, Pz, P4, P8, O1, Oz and O2) were selected as electrodes of interest according to previous recommendations (Sänger et al., 2012; Hu et al., 2018).

Dual-EEG data analysis

In line with previous research (Goldstein et al., 2018; Perez et al., 2019) and recommendations (Burgess, 2013), IBS was estimated by circular correlation coefficient (CCorr) using the CircStat toolbox in MATLAB (Berens, 2009). CCorr was calculated by:

$$CCorr = \sum \sin(\phi - \bar{\phi}) \sin(\psi - \bar{\psi}) / \sqrt{\sum \sin^2(\phi - \bar{\phi}) \sin^2(\psi - \bar{\psi})}$$

where ϕ and ψ were the phase for channels from Individuals 1 and 2, respectively. The data were filtered into four frequency bands: theta (4–8 Hz), alpha (9–12 Hz), beta (13–30 Hz) and gamma (30–40 Hz), using Finite Impulse Response filtering. Instantaneous phases were extracted using the Hilbert transform. CCorr was estimated only for the window of response. Then, the values were Fisher's z transformed. Finally, absolute values of transformed CCorr were used for further analyses (Goldstein et al., 2018; Perez et al., 2019).

A major criticism of studies on IBS concerns the lack of a control for spurious synchronization—that is, synchrony caused by random coincidence. To address this issue, we assessed the significant IBS (genuine interactions vs pseudo-interactions) of dyads in the MT and NC groups. It was expected that genuine interactions compared to pseudo-interactions would induce significant higher synchronization. The surrogate dataset for pseudo-interactions was created based on a robust bootstrapped phase-scrambling analysis across all electrode pairs (Regev et al., 2013; Simony et al., 2016), including the following steps. First, randomization of each electrode pair was conducted by

applying a fast Fourier transform to all the epochs, randomizing the instantaneous phase and applying an inverse Fourier transform to epochs. Second, CCorr was calculated on the same electrode pairs selected in the real dataset and averaged across trials, dyads and electrode pairs. Third, the first two steps were repeated 10000 times to create a null distribution for each group. Significance level ($P < 0.05$) was assessed by comparing CCorr from the real dataset with that from the 10000 renditions of the surrogate dataset. For subsequent analyses, only significant electrode pairs were extracted in which CCorr from the genuine dataset was significantly larger than that from the surrogate dataset in at least one condition. By extracting the significant electrode pairs only, we reduced the risk of spurious synchronization findings and hence ensured the robustness of our findings.

To further tease apart the effect of MT-related interaction from general interaction (MT vs NC), electrode pairs that showed significant IBS from surrogate data were entered into mixed-effects models. CCorr of significant pairs was modeled by GROUP (MT vs NC), BLOCK (1, 2 or 3) and their interaction as well as the random intercept of DYAD. When the analysis included a large number of distinct variables in limited individuals, the traditional familywise error rate provided unnecessary stringent control of type I errors. Thus, P values (thresholded at $P < 0.05$) were corrected using the False Discovery Rate (FDR) approach instead of the Tukey adjustment (Benjamini and Hochberg, 1995).

To investigate the temporal evolution of IBS in a more fine-grained way, we conducted a discrimination analysis using a standard logistic regression classifier. The classifier predicted the manipulation dyads had received (i.e. MT vs NC) by using cumulative IBS from significant electrode pairs as classification features. For each dyad, cumulative IBS at trial n was calculated as the average of IBS ranging from the first trial to the n th trial. A time course was generated for the area under the curve of the receiver operating characteristic (AUC). A permutation test was used to statistically compare the difference between AUC from the real and that from data with shuffled labels.

Brain-behavior correlation

To measure the relationship between IBS and subjective fear of death, Spearman correlation analyses were performed for the

MT and NC groups separately. Spearman correlation was used because of its robustness to univariate outliers (Pernet et al., 2013). IBS of each dyad was calculated as the mean of trials trimmed by 10% (Wilcox, 2011).

Results

Behavioral performance

Subjective measurements. After article reading, the subjective fear of death in the MT group was significantly higher than that in the NC group [mean \pm SE, MT: 3.97 ± 0.21 , NC: 1.79 ± 0.20 , $t(70) = 7.46$, $P < 0.001$]. A non-parametric permutation test (because data are not normally distributed) indicated that IASMT in the MT group was significantly higher than that in the NC group (MT: 1.03 ± 0.50 , NC: 0.03 ± 0.30 , $P = 0.044$). These results confirmed that our mortality priming was manipulated successfully.

We also detected significant group differences on rating scores of valence and general arousal [general arousal: MT: 4.20 ± 0.24 , NC: 2.25 ± 0.31 , $t(38) = 5.03$, $P < 0.001$; valence: MT: 2.80 ± 0.22 , NC: 4.15 ± 0.17 , $t(38) = -4.82$, $P < 0.001$]. The ratings on subjective attitudes toward participants' own performance, as well as partners' performance did not show any difference between groups (see Supplementary Table S5).

Competition. We tested the dyads' competitive behavior in two groups over time. There was a main effect of GROUP [$\chi^2(1) = 4.74$, $P = 0.030$] (Figure 2A and Table S6), suggesting alleviated competition in the MT group relative to the NC group. Besides, there was a BLOCK \times GROUP interaction [$\chi^2(2) = 7.70$, $P = 0.021$]. Post hoc analyses showed that dyads in the MT group competed less intensely than dyads in the NC group did only in the third block ($\beta = 0.46$, $P = 0.001$). Specifically, dyads in the MT group showed attenuated competition in the third block relative to the first block ($\beta = 0.24$, $P = 0.027$). To exclude the potential account that these findings resulted from the increased RT rather than attenuated interpersonal competition, we investigated whether there was a significant difference of RTs between groups. The results revealed that there was neither main effect nor interaction (see Supplementary Results for details).

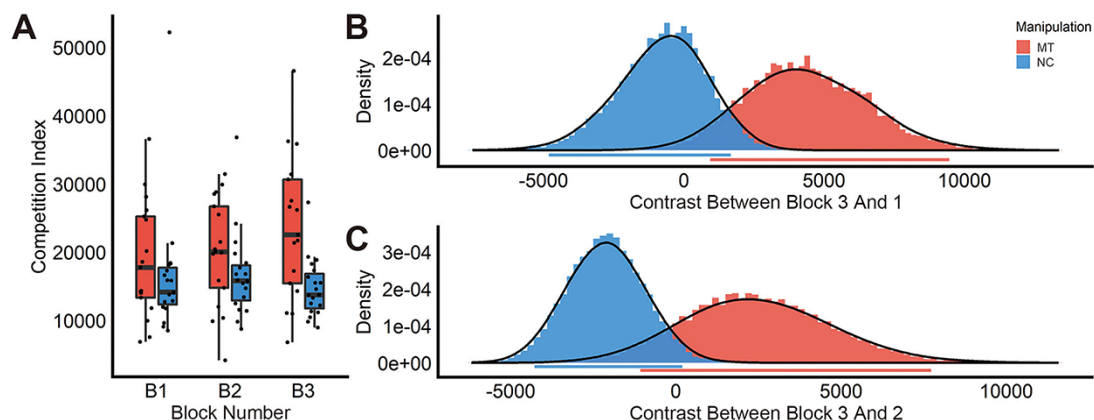


Fig. 2. Behavioral performance in the competitive context. (A) Competition index of two groups in each block. (B) The bootstrap sampling distributions of the difference between Blocks 1 and 3. The histogram illustrates the bootstrap sampling ($N = 10000$) distribution in two groups, showing a more positive shift (i.e. attenuated competition) for the MT group than the NC group. (C) The bootstrap sampling distributions of the difference between Blocks 2 and 3. The histogram illustrates the bootstrap sampling ($N = 10000$) distribution in two groups, showing no difference between these blocks for both groups.

Cooperation. Results from the mixed-effects model revealed that there was no significant main effect of GROUP on cooperation index [MT = 44.64 ± 5.57 , NC = 55.88 ± 7.67 , $\chi^2(1) = 2.10$, $P = 0.148$], and no significant effect of BLOCK nor interaction (P values > 0.05) (see Supplementary Figure S1 and Table S7). Notably, the MT group cooperated slightly better than the NC group, although the difference between the two groups did not reach a significant level. Due to a lack of significant findings, the following validation analyses were only applied to data from competitive behavior.

Validation analyses. With the bootstrapping procedure, we found a robust increase in the contrast between Block 3 and Block 1 in the MT group, but not in the NC group. The 95% confidence intervals of contrast between Block 3 and Block 1 were as follows: [938, 9459] for the MT and [-4814, 1674] for the NC (Figure 2B). The 95% confidence intervals of contrast between block3 and block2 were as follows: [-1073, 7729] for the MT and [-4275, 197] for the CT (Figure 2C). This result further confirmed the simple effect in competition.

Inter-brain synchronization (IBS)

Competition. To first identify electrode pairs in which there was an increased IBS, we compared the dyads' genuine IBS with that from the surrogate data. Our results showed that there were

widespread electrode pairs in each band whose IBS of real data was significantly higher than that of surrogate data (for gamma band, see Figure 3A and B; for other bands, see Supplementary Figure S2).

To directly compare the effect of mortality priming, we performed linear-mixed modeling on electrode pairs with significant IBS in at least one group. In the gamma band, the main effect of GROUP was detected on two electrode pairs (Fp1-P7, Fp1-Oz) after FDR adjustment [$\chi^2(1) > 7.89$, $P < 0.05$, FDR corrected]. Given the GROUP \times BLOCK interaction in behavioral results, we examined the GROUP effect in each block. There were significant group differences in the second (Fp1-P7: $\beta = 0.20$, $P = 0.036$; Fp1-Oz: $\beta = 0.22$, $P = 0.023$) and third blocks (Fp1-P7: $\beta = 0.34$, $P < 0.001$; Fp1-Oz: $\beta = 0.21$, $P = 0.030$, Figure 3C). The linear-mixed models revealed no significant results after FDR correction in other bands.

We further assessed the performance of gamma-band IBS to discriminate between the MT and NC groups overtime using a trial-by-trial logistic regression discriminant analysis. Even though there were sporadic trials during the initial period displaying the effective execution of group discrimination, AUC showed stable discrimination between groups starting at the 25th trial (Figure 4), which resided in the second block. This analysis further confirmed the observed group difference starting in the second block.

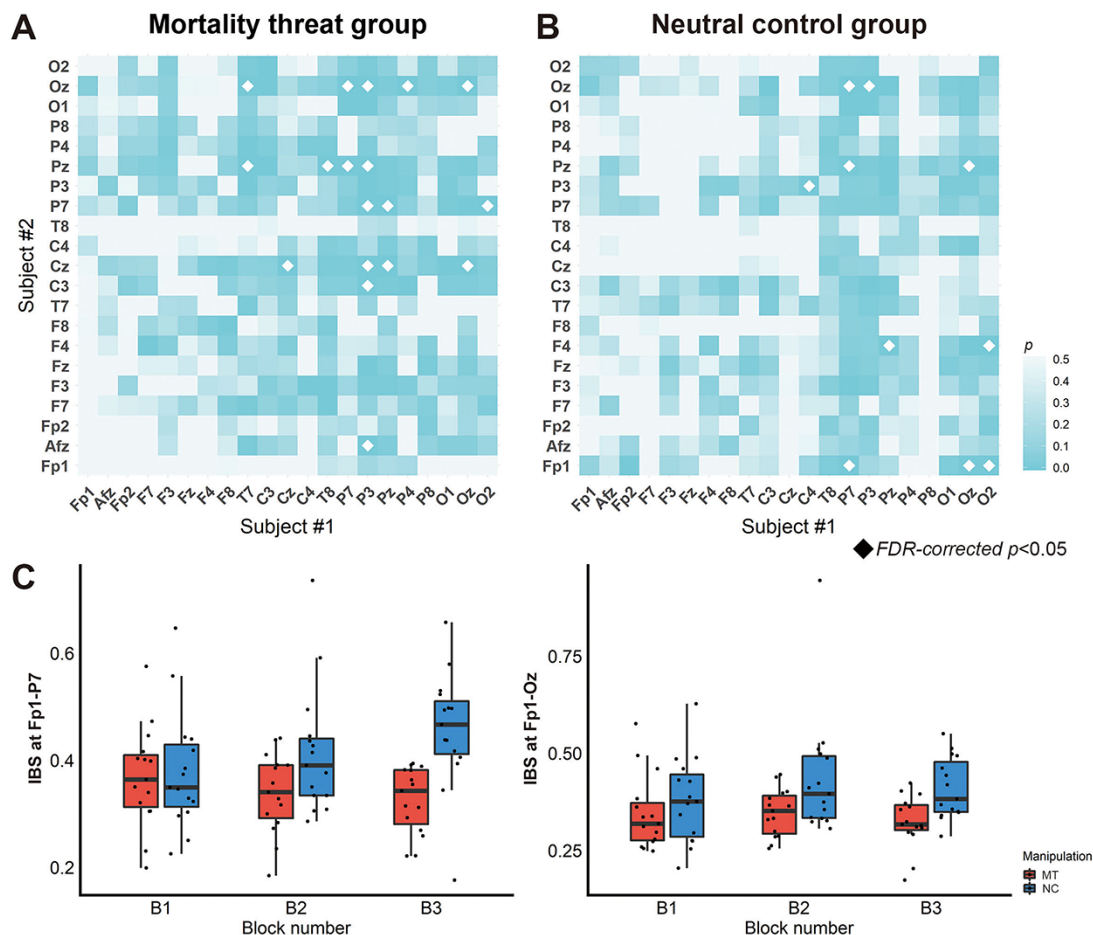


Fig. 3. IBS analysis. Gamma-band IBS matrices between subjects in dyads for MT group (A) and NC group (B). White rhombus indicated significantly coupled electrode pairs, determined by phase-randomization analysis (see Methods) with FDR correction ($P < 0.05$). (C) Significant IBS (at Fp1-P7, Fp1-Oz) as a function of GROUP and BLOCK in the competition task.

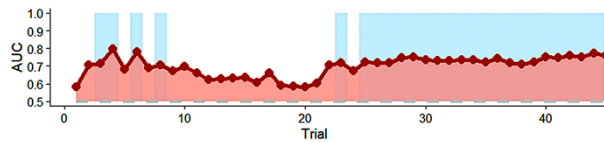


Fig. 4. Discriminant analysis. The AUC was based on the cumulative IBS data. The light blue shading indicates that there is a significant difference between AUC from real data and shuffled data. The dashed line indicates the chance level.

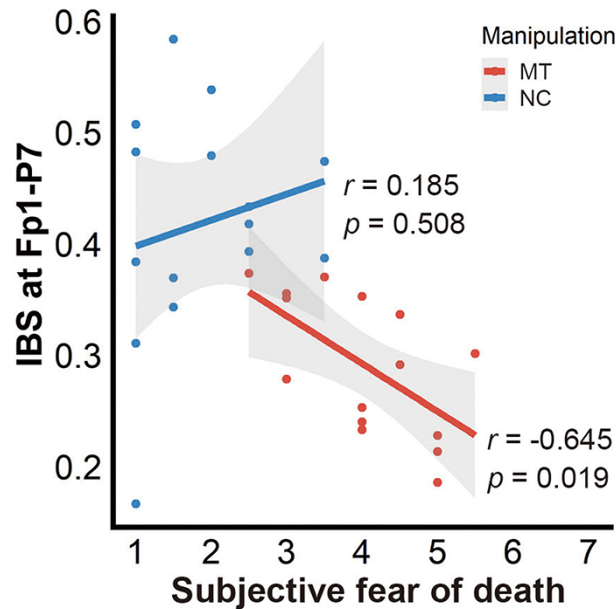


Fig. 5. Brain–behavior correlation. In the MT group, subjective fear of death was associated with decreased IBS in the third block. However, in the NC group, the association was absent.

Cooperation. To validate the increased IBS specific to genuine interactions, the same bootstrapping procedure was applied to the cooperative context. Compared to surrogate data, electrode pairs with stronger IBS were found in each band for both groups (see Supplementary Figure S3). However, neither significant main effects nor interaction on IBS were detected for any electrode pair or any frequency band.

Brain–behavior correlation

Finally, we examined whether the decrease in gamma-band IBS was associated with subjective fear of death. The correlation analyses showed a significant negative association between subjective fear of death and gamma-band IBS at Fp1–P7 electrode pair in the third block only in the MT group [Figure 5, MT: $r(15) = -0.645$, $P = 0.019$, NC: $r(15) = 0.185$, $P = 0.508$, FDR corrected]. To test whether the mortality priming modulated the association between gamma-band IBS and subjective fear of death, we further conducted a bootstrap-based statistical comparison between the two correlation coefficients (i.e. MT vs NC) using boot package (Davison and Hinkley, 1997; Canty and Ripley, 2019). This bias-corrected bootstrap analysis showed that there was a significant difference between two correlations, confirming that the relationship between IBS and subjective fear of death was conditioned by mortality priming, 95% confidence interval: $[-1.45, -0.12]$.

Discussion

The current study investigated the influence of MT on social behaviors in conflicting contexts and the functional role of gamma-band IBS in interpersonal interactions under MT. Our findings provided evidence that MT fostered benevolent behaviors regardless of the explicit context in which they were (i.e. competition and cooperation). The results showed that exposure to MT resulted in attenuated competition across time. Accordingly, gamma-band IBS decreased across time in the MT group rather than in the NC group. Besides, further analyses disclosed a negative association between subjective fear of death and gamma-band IBS in the MT group, while this relationship was absent in the NC group. In contrast, the MT did not significantly, but slightly, promote the cooperation. The IBS in the cooperative context revealed no significant findings between groups in any frequency bands.

The effect of MT on interpersonal interaction differed between cooperative and competitive contexts. There is a potential account for interpreting selectively changed competitive interaction. First, studies indicated that MT increased individuals' adherence to their worldview (Gailliot et al., 2008). With the profound influence of Confucianism on Chinese public life (McMordie and Kumar, 1984; Westman and Canter, 1985; Schumaker et al., 1988; Yen and Cheng, 2010), the increased adherence to the worldview in response to MT would emphasize harmonious relationship (Lau, 2000) and interdependent self (Du et al., 2013) in the current study. Second, previous studies using functional magnetic resonance imaging have shown that death-related priming consistently decreased activity in the anterior midcingulate cortex (Han et al., 2010; Luo et al., 2014, 2017; Feng et al., 2017). A recent study further showed that compared to the control group, participants primed with MT showed reduced anterior midcingulate cortical activity during the period of feedback showing their loss (Luo et al., 2019), suggesting that MT could increase individuals' tolerance to their loss. Thus, MT not only requires a harmonious interpersonal relationship in the Chinese context but also increases loss tolerance. Notably, the participants in the current study were motivated to maximize their interest (e.g. winning as many points as they can) in the tasks. Thus, MT could dampen individuals' willingness to gain points. In sum, MT not only requires a harmonious interpersonal relationship but also dampens willingness to gain points. Thus, the slightly increased cooperation might suggest that, in a cooperative context, a harmonious relationship increased cooperative willingness and behavior, but individuals' dampened willingness to gain points might stop dyads from further cooperation. However, in the competitive context, these two mechanisms worked in parallel, so that both harmonious relationship and dampened willingness to gain points attenuated the competition.

Importantly, in a competitive context, we found significant group differences (MT vs NC) on IBS in the gamma band. It has been suggested that gamma-band brain activity plays a key role in attention and is associated with the emotional process (Keil et al., 2001; Oya et al., 2002; Bichot et al., 2005). For example, gamma-band event-related synchronization has been associated with facial threat processing as revealed by magnetoencephalography (Luo et al., 2007). Recently, using EEG-based hyperscanning, IBS in gamma band has been found to play a crucial role in the social exchange between individuals under threat (Mu et al., 2017). Echoing with these studies, the dyads with higher self-reported fear of death exhibited lower gamma-band IBS only in the MT group, suggesting that the observed

gamma-band IBS might be interpreted in terms of shared emotion between individuals in a dyad under MT. Interestingly, in our study, the significant group difference in IBS started at the second block before the emergence of behavioral divergence (i.e. the third block). The discriminant analysis further confirmed that, shortly after the beginning of the second block, IBS could stably distinguish between the MT and NC groups. These findings demonstrated that gamma-band IBS may lead to earlier, more sensitive identification of MT compared to behavioral patterns.

We note that while our study did not provide any evidence for IBS in response to MT in the cooperative context, a previous hyperscanning study with a similar paradigm showed that IBS was detected in cooperation relative to the control group (Wang et al., 2019). In the cooperative context, we found that IBS in each band also exceeded that of phase-randomized data, which confirmed that the paradigm induced reliable IBS in the current study. The absence of significantly different IBS between groups was in line with our behavioral findings, which only showed slightly promoted cooperative behavior in the MT group. Moreover, whereas the present study used a similar paradigm, the manipulations prior to the paradigm were different (i.e. pain and MT). Such manipulation differences might potentially account for different findings in the cooperative context across studies.

This study has several limitations. First, following previous practice and recommendations (Griskevicius et al., 2011a,b), the manipulations in our study included only MT and NC, without a complementary manipulation of an active control (i.e. mortality-unrelated negative affect, Luo et al., 2014, 2017). Our approach is sufficient to (i) provide a hyperscanning demonstration in the fields of MT and social interactions and (ii) inspire interventions aimed to potentially counteract maladaptive fears in humans (Pan et al., 2020). However, when it comes to the interpretability of our research, we cannot completely exclude the possibility that mortality-unrelated threat could lead to similar results (although this concern might be mitigated by our evidence supporting the association between subjective fear of death and IBS). Thus, for the sake of interpretability and completeness, future studies are strongly recommended to include both MT and mortality-unrelated negative affect. Second, the power of statistical tests might be constrained by our relatively small sample size. In this study, no statistical methods were used to predetermine the current sample size; however, our sample size was similar to those reported in previous mortality-related studies (Shi and Han, 2013; Luo et al., 2014) and to those reported in past research using the similar hyperscanning paradigm (Cui et al., 2012; Wang et al., 2019). A *post hoc* power analysis with *pwr* package in R (Champely et al., 2017) indicated sample size of 15 dyads per group ($\alpha = 0.05$, $r = -0.645$) could achieve statistical power $(1 - \beta) = 0.86$, beyond a recommendation level (i.e. $1 - \beta = 0.80$, Cohen, 1988). Nevertheless, future studies are encouraged to consolidate the current findings by increasing both the sample size and the number of testing blocks. Third, it has been previously illustrated that MT priming induced people in different cultural contexts to respond to the same stimuli differently (Ma-Kellams and Blascovich, 2011). Thus, since only the Chinese cultural context was considered in the current work, our findings are restricted to this cultural context. Given the key role of cultural worldview in TMT and the difference between Eastern and Western culture, it is interesting to investigate the effect of MT on social interactions in a cross-culture context for future research. Fourth, even though the results after controlling gender were analogous to our main results, we could not completely exclude the possibility that the gender imbalance might

impact our results. Future research should explore whether and how gender affects the effects of mortality on social behaviors. Finally, in addition to cultural worldview, self-esteem is also a defensive structure in TMT (Greenberg et al., 1986). Previous studies have shown increased self-esteem striving (Dechesne et al., 2003) and different psychological adjustments between individuals with low and high self-esteem during the period of mortality priming (Routledge et al., 2010). Self-esteem was neither manipulated nor measured in our study. However, due to the random sampling, this character was expected to show no difference between groups, which could have a limited influence on our results.

In summary, the subconscious concerns about the evitable death motivate a mass of our behaviors (Hayes et al., 2010), but little is known about the effect of these concerns on our daily life. With the EEG-based hyperscanning technique and real-time interaction design, the present study revealed that the MT specifically attenuated interpersonal competition along with decreased gamma-band IBS, whereas it did not significantly affect the cooperative behavior among individuals. Accordingly, rather than providing conclusive evidence about the mechanisms underlying the reshaped social behaviors in the face of MT, our findings suggested the possibility that gamma-band coupling contributes to the reshaped behaviors. It is noteworthy that Confucius said, 'sad is the cry of a dying bird, good are the words of a dying man' (Lau, 2000, p. 103). Our findings demonstrated that such benevolent change was observed not only in the social behaviors but also in the downregulation of neural coupling involved in shared emotion. Since the mortality cue is prevalent over the world with the spread of COVID-19 recently, much more interest should be focused on the change of socially behavioral patterns under MT and the way to improve the life of maladaptive individuals in the face of death-related thoughts.

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Conflict of interest

The authors declare that they have no actual or potential conflicts of interest concerning this work.

Data availability

The data that support the findings of this study are available upon request to X.L.

Supplementary data

Supplementary data are available at SCAN online.

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