

Effects of acute psychosocial stress on interpersonal cooperation and competition in young women

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ABSTRACT

Although tend-and-befriend is believed to be the dominant stress response in women, little is known regarding the effects of acute psychosocial stress on different dynamic social interactions. To measure these effects, 80 female participants were recruited, paired into the dyads, and instructed to complete cooperative and competitive key-pressing tasks after experiencing acute stress or a control condition. Each dyad of participants should press the key synchronously when the signal was presented in the cooperative task and as fast as possible in the competitive task. During the tasks, brain activities of prefrontal and right temporo-parietal areas were recorded from each dyad using functional near-infrared spectroscopy (fNIRS). The results showed that acute psychosocial stress evidently promoted competitive behavior, accompanied by increased interpersonal neural synchronization (INS) in the right dorsolateral prefrontal cortex. Despite the lack of a significant difference in the overall cooperation rate, the response time difference between two stressed participants markedly declined over time with more widespread INS in the prefrontal cortex, suggesting that there ensued cooperative improvement among stressed women. These findings behaviorally and neurologically revealed context-dependent response patterns to psychosocial stress in women during dynamic social interactions.

1. Introduction

The world we live in is largely socially constructed, and our daily lives are filled with diverse complicated social interactions. Social behaviors, either cooperative or competitive, are displayed by various species and are indispensable for survival and reproductive success (Chen & Hong, 2018; Ebstein, Israel, Chew, Zhong, & Knafo, 2010; Stanley & Adolphs, 2013). Given the importance of social encounters, it is essential for us to understand how they are affected by environmental influences (Steinbeis, Engert, Linz, & Singer, 2015). Psychosocial stress is ubiquitously present in every aspect of life, stemming from heavy academic burdens, high work intensity, or a substandard living environment. Despite the negative connotations related to everyday stressors, stress is of great value for the adaptive evolution and development of human beings (Ellis & Del Giudice, 2014; Potts, McCuddy, Jayan, & Porcelli, 2019). Considering its vital role in human life,

exploring how stress influences our social behaviors is of great significance and value. In the past decade, the effects of stress on social behaviors have gained marked attention and have been widely explored. However, most studies opted to focus only on men, leading to insufficient investigation in women. Thus, the present study focused on female participants to enrich our understanding of women's stress response in different social interactions.

Based on existing literature, different effects of acute psychosocial stress on female behaviors can be observed in disparate situations. In a study by Buser, Dreber, and Mollerstrom (2017), women were required to perform a simple arithmetic task and to select a payment scheme to receive remuneration for their participation. There were two different payment schemes. According to the piece-rate payment scheme, a correct answer resulted in a \$1 reward. According to the tournament payment scheme, participants had to compete with three other people. The one with the highest score was paid \$4 per correct answer, while the

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others received nothing. In contrast to the control group, more women in the stress group preferred the tournament payment scheme, indicating the positive role of stress in strengthening competition willingness, in line with the “fight-or-flight” response referring to the tendency to either engage in offensive behavior or flee when encountering threats (Cannon, 1932). In addition to aggressive attack or defensive withdrawal (Margittai et al., 2015), women may also present more affiliative and amicable behaviors in a stressful environment, referred to as the “tend-and-befriend” response (Taylor et al., 2000). Combining stress-induction paradigms and economic games, researchers have found that compared to control female participants, stressed female participants offered higher monetary amounts, rejected less unfair offers in the one-shot ultimatum game (Nickels, Kubicki, & Maestriperi, 2017; Prasad et al., 2017; Youssef, Bachew, Bissessar, Crockett, & Faber, 2018), and behaved more cooperatively in the iterated prisoner’s dilemma (Nickels et al., 2017). Moreover, exposure to acute stress can also elevate female prosocial trustworthiness and cooperative reciprocity in the trust game (von Dawans, Ditzen, Trueg, Fischbacher, & Heinrichs, 2019).

In most of these studies, researchers adopted economic games. In these experimental paradigms on cooperation vs. competition, participants’ behaviors were not explicitly specified. They could freely choose to behave cooperatively or competitively. However, it remains unknown how acute stress affects women’s social behaviors in a context with an explicit goal (e.g., cooperation or competition). In addition, the one-shot economic games just include static social decision-making and lack dynamic interpersonal interactions, which restricts the exploration of the effects of acute stress on individual behavioral adjustments in social interactions. Therefore, to clarify these two issues, we set two different human–human interactive tasks, where female participants in a dyad were required to cooperate to realize a double win or contend with each other based on self-interest.

Under the conceptual and methodological framework of two-person neuroscience (Hari & Kujala, 2009; Hari, Henriksson, Malinen, & Parkkonen, 2015), correlated neural activity across the brain was widely found within socially interacting dyads in various settings (Cui, Bryant, & Reiss, 2012; Dumas, Nadel, Soussignan, Martinerie, & Garnero, 2010; Jiang et al., 2012; Piazza, Hasenfratz, Hasson, & Lew-Williams, 2020; Stolk et al., 2014; Tang et al., 2016; Zheng et al., 2018), using an approach termed as “hyperscanning” referring to simultaneous neural recording from individuals during linked social interactions (Montague et al., 2002). Owing to fundamentality in human society, cooperation and competition have gained wide attention in this emerging field. Using the hyperscanning method based on fNIRS and functional magnetic resonance imaging (fMRI), increased interpersonal neural synchronization was detected in the superior frontal cortex (rSFC), frontopolar cortex (FPC), orbitofrontal cortex (OFC), dorsolateral prefrontal cortex (dlPFC) and right temporo-parietal junction (rTPJ) during cooperative key-pressing (Cheng, Li, & Hu, 2015; Miller et al., 2018; Pan, Cheng, Zhang, Li, & Hu, 2017), creativity problem solving (Lu, Xue, Nozawa, & Hao, 2018; Xue, Lu, & Hao, 2018), and joint force-production tasks (Abe et al., 2019), positively correlating with cooperative levels. Similarly, INS has also been detected during turn-based obstructive interactions in the right PFC, inferior parietal lobule (IPL) and posterior superior temporal sulcus (pSTS) (Liu et al., 2015, 2017). In summary, the INS in fronto-temporo-parietal regions is a critical neural mechanism underlying interpersonal cooperation and competition. Taken together, the prefrontal cortex and right temporo-parietal cortex were selected as regions of interest.

As a noninvasive neuroimaging technique, fNIRS holds higher temporal resolution than fMRI and better spatial resolution than electroencephalography. Furthermore, fNIRS has great advantages in terms of cost, tolerance of movement artifacts, and ecological validity (Gvirts & Perlmutter, 2019; Mu, Cerritos, & Khan, 2018; Scholkmann, Holper, Wolf, & Wolf, 2013). In the light of the above advantages, the fNIRS-based hyperscanning technique was adopted in the present study. Before tasks, participants were randomly assigned to a stress condition

or a control condition where they experienced either a stress-induced task or a control one. Afterward, participants completed two interactive tasks, during which, their brain activities were simultaneously recorded with fNIRS. Based on previous literature, it was hypothesized that acute psychosocial stress would increase female prosocial behaviors in the cooperation task and competitiveness in the competition task, accompanied by increased inter-brain coherence.

2. Methods

2.1. Participants

Eighty right-handed female college students (20.9 ± 2.3 years), with normal vision or corrected-to-normal vision, without mental or physical health problems were recruited to participate in this study. Additionally, considering the confounding effects of negative emotions caused by uncomfortable experiences during or near menses, such as dysmenorrhea, women who were in or 2 days before or after menstruation were excluded. Participants, who were not acquainted with each other, were randomly paired into the dyads: 19 dyads for the stress condition, and 21 dyads for the control condition. All participants signed an informed consent form and received the corresponding remuneration according to their performance. The study was approved by the Institutional Review Board of East China Normal University.

2.2. Tasks and procedures

The timeline of the experiment is shown in Fig. 1A. Upon arrival at the laboratory, participants were not allowed to communicate with each other until the end of the experiment. Before the task, they signed the informed consent form, filled in the questionnaire, and received the instructions in the rest room. The questionnaire included a demographic information survey and the Multidimensional Mood Questionnaire (MDMQ) used to measure subjective stress. Afterward, the participants entered the test room and sat across the table (Fig. 1B). Participants underwent a stress condition using the Montreal Imaging Stress Task (MIST) or a comparable control condition at the same time and in the same room. The task included three blocks, 15 trials for each block, separated by 30 s rest. Following the MIST, subjective stress was measured with the MDMQ for the second time. Then, the cooperation and competition tasks were presented in a counterbalanced order. Each interactive task began with 30 s of rest and included 40 trials. Finally, the participants reported their stress levels using the MDMQ again. After the experiment, the participants were fully debriefed and received their remuneration. E-prime 2.0 was used to present the experimental stimuli and collect behavioral data during the interactive tasks.

2.2.1. Montreal Imaging Stress Task

Acute psychosocial stress was induced by adopting the MIST (Dedovic et al., 2005), which has been proven to be an effective method and is widely used in stress studies (Lederbogen et al., 2011; Mizrahi et al., 2012; Pruessner et al., 2008). In the stress condition, participants had to enter answers by selecting numbers presented on the screen with the mouse within a given time constraint, which was dynamically adjusted to be beyond their abilities. As such, the accuracy was controlled within a certain range (20–45%). During the task, two performance indicators were displayed on the screen. The position of the red rectangle reflected the participants’ cumulative accuracy, and the green rectangle showed the artificial average accuracy (70%) of the others (Fig. 1C). Additionally, the investigators, sitting beside the participants, provided further negative feedback, such as head shaking or a slight sigh, when the participants responded erroneously or after the time limit. However, in the control condition, there was no time limit, performance indicators, investigators’ observations, and social evaluative threat during the task.

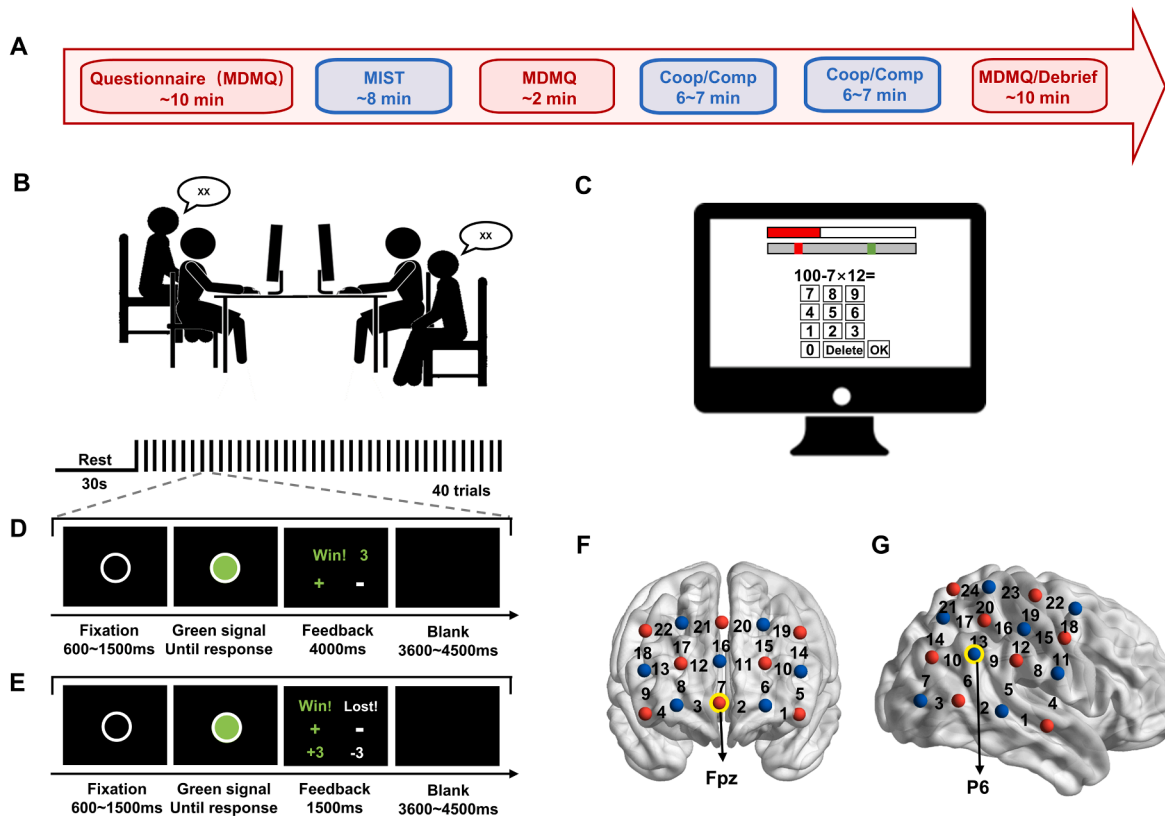


Fig. 1. Experimental design. (A) The timeline of the experiment. MDMQ: Multidimensional Mood Questionnaire; MIST: Montreal Imaging Stress Task; Coop: cooperation task; Comp: competition task. (B) Experimental scene. Participants in a dyad sat across the table, provided with a screen, a keyboard and a mouse, respectively. For the stress dyads, two investigators were seated at their left and gave negative feedbacks on their performance during MIST. (C) The interface of MIST in the stress condition, consisting of four components, a arithmetic problem including addition, subtraction, multiplication or division, a progress bar indicating available time for response, twelve rectangle buttons used to input and submit answers and two performance indicators, one (red) for the participant's cumulative performance and the other (green) for the artificial performance of the "average participant". (D) Schematic of trial events for the cooperation task. (E) Schematic of trial events for the competition task. (F) The placement of the 3×5 patch (8 emitters and 7 detectors forming 22 measurement channels). (G) The placement of the 4×4 patch (8 emitters and 8 detectors forming 24 measurement channels). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.2.2. Cooperation paradigm

Each trial commenced with a gray hollow circle presented on the screen. After a random duration between 600 ms and 1500 ms, a green circle appeared in the hollow graphic, signaling to both participants to press the key simultaneously. Participant A pressed the "1" key, and participant B pressed the "0" key. If the difference in response time between the two participants was smaller than a specific threshold (T), both participants won one point; otherwise, they lost one point. The threshold was defined as follows: $T = (RT_A + RT_B)/8$, where R_A and R_B were the response times for the two participants, respectively (Cui et al., 2012). After the program collected two responses, feedback was displayed for 4 s. It conveyed the following information to the participants: interaction outcome, cumulative points, and response speed, the "+" and "-" sign representing faster and slower responses, respectively. Finally, the trial ended up with a random interval ranging from 3.6 s to 4.5 s (Fig. 1D).

2.2.3. Competition paradigm

The competition task was similar to the cooperation one, but the goal for the participants was to respond faster than their partners to win points. Therefore, when the hollow circle was filled with green color, the participants pressed the key as fast as they could. Likewise, feedback, containing three types of information, was shown on the screen for the two participants: information in white for participant A and in green for participant B (Fig. 1E). The participant who responded faster would win one point, whereas the slower one would lose one point.

2.3. Subjective stress response

The participants' subjective stress was assessed using the 30-item MDMQ (<https://www.metheval.uni-jena.de/mdbf.php>), which originated from the German Mehrdimensionale Befindlichkeitsfragebogen, MDBF (Steyer, Schwenkmezger, Notz, & Eid, 1997). The effectiveness of the MDMQ as a tool for measuring subjective stress has been validated by many researches (Cahlíková & Cingl, 2016; Duesenberg et al., 2019; Li, Weerda, Guenzel, Wolf, & Thiel, 2013; Nedeljkovic, Ausfeld-Hafter, Streitberger, Seiler, & Wirtz, 2012; Nowacki, Duesenberg, Deuter, Otte, & Wingefeld, 2019; Plessow, Kiesel, & Kirschbaum, 2012; Solberger, Bernauer, & Ehlert, 2016). The MDMQ encompasses three dimensions: good-bad mood, calmness-nervousness, and alertness-tiredness, with 10 items for each dimension. The items are rated on a six-point Likert-scale from one ("not at all") to six ("extremely"). Higher scores indicate greater pleasure, calmness, and alertness.

2.4. fNIRS data acquisition

During the interactive tasks, we used an ETG-7100 optical topography system (Hitachi Medical Corporation, Japan) to collect brain signals. Two measurement patches with optode probes separated by 3 cm were used to cover each participant's prefrontal and right temporoparietal cortices. For the 3×5 patch, the center emitter of the bottom row was placed at the Fpz position in accordance with the 10-20

electrode placement system. The probes of the middle column were aligned to the midline, from the nasion to the inion (Fig. 1F). For the 4×4 patch, the left detector of the third row coincided with P6, and the patch was placed horizontally (Fig. 1G). To identify the anatomical location of each probe and measurement channel, coordinates of five reference positions (Nz, Cz, Iz, left, and right preauricular), 31 probes, and 46 channels in real space were acquired from one typical participant by employing the 3D digitizer. Combined with the NFRI fNIRS tools (Singh, Okamoto, Dan, Jurcak, & Dan, 2005) in NIRS-SPM (Ye, Tak, Jang, Jung, & Jang, 2009) and BrainNet Viewer (Xia, Wang, & He, 2013), channel positions in real coordinates were then transformed into the Montreal Neurological Institute space (see Supplementary Tables 1 and 2) and presented on the brain surface template.

Light attenuation was measured at two wavelengths (695 and 830 nm) at a sampling rate of 10 Hz. The concentration changes in oxy-hemoglobin (Hbo) and deoxy-hemoglobin (Hbr) were calculated using the modified Beer–Lambert Law. As a better indicator of changes in the cerebral blood flow compared with Hbr (Hoshi, 2003, 2007), only Hbo signals were analyzed in this study.

2.5. Data analysis

2.5.1. Behavioral data

Two dyads in the control condition were removed because of program malfunctions. The behavioral data of the cooperation task and competition tasks were preprocessed separately, but in the same manner. For each dyad, trials were excluded if they deviated more than ± 3 standard deviations from the average response time difference across 40 trials. Dyads with extreme differences in response time were also excluded from the final analyses (see Supplementary Table 3). Consequently, for the cooperation task, there were 35 valid dyads, 17 in the stress condition and 18 in the control condition. As for the competition task, there were 37 valid dyads, 19 in the stress condition and 18 in the control condition. For both tasks, the number of trials remaining for further analyses did not significantly differ between the conditions, $U_{coop} = 152$, $z_{coop} = -0.02$, $p = 0.99$; $U_{comp} = 155$, $z_{comp} = -0.62$, $p = 0.64$, Mann–Whitney U tests (see Supplementary Table 4).

Parametric tests (e.g., two-sample *t*-test) and nonparametric tests (e.g., Mann–Whitney *U* test) were used in our study employing SPSS 21 (IBM Corp., Armonk, NY, USA), depending on whether the data distributions were normal. To compare the correlation coefficients, a tool on the website (<http://quantpsy.org/calc.htm>) was used to run the required analyses. In addition, given the non-independence of response time data in dyads, we used the linear mixed model via *lme4* (Bates, Mächler, Bolker, & Walker, 2015) and *lmerTest* (Kuznetsova, Brockhoff, & Christensen, 2017) in R 3.6.1 (R Core Team, 2019) to analyze such data. In the model, condition (stress, control) was considered as the fixed effect, while random effect was estimated for nested random intercept (e.g., dyad identity/participant identity).

2.5.2. fNIRS data

The raw Hbo signals were processed based on the platform of Matlab 2018b (Mathworks Inc., Natick, MA, USA). As the first step of data preprocessing, bad channels with poor signal quality were identified by visual inspection and replaced with the mean of neighboring channels (Bauernfeind, Wriessnegger, Haumann, & Lenarz, 2018; Kaiser et al., 2014). Supplementary Table 5 displays the details of the rate of bad channels. To remove motion artifacts, we used the NIRS Analysis Package (Fekete, Rubin, Carlson, & Mujica-Parodi, 2011) to detect and rectify the signal in the contaminated segments.

After preprocessing, the Wavelet Transform Coherence package (Grinsted, Moore, & Jevrejeva, 2004) was applied to quantify the relationships between two NIRS signals (Cui et al., 2012). According to the average durations of the cooperative trials (9.5 s) and competitive trials (7 s), we focused on the frequency band between 6.4 s and 12.8 s (0.08–0.17 Hz), which precluded high-frequency physiological signals,

such as those of cardiac pulsation (~ 1 Hz) and respiration (0.2–0.3 Hz) (Kamran & Hong, 2014; Pierro, Hallacoglu, Sassaroli, Kainerstorfer, & Fantini, 2014). Then, we calculated the average coherence in this band across trials and converted coherence values into z-scores.

To identify the channels with significant INS, we conducted a permutation test on the Hbo data after artifact correction. Phase randomization of each timeseries was performed by taking the discrete Fourier transform, randomizing the phase of each Fourier component and inverting the Fourier transformation. This process can scramble the signal phase while ensuring the intactness of the power spectrum (Honey, Thompson, Lerner, & Hasson, 2012; Lerner et al., 2018; Silbert, Honey, Simony, Poeppel, & Hasson, 2014). Then, INS was calculated again based on surrogate data and averaged across dyads for each channel. This procedure was repeated 1000 times to yield 1000 INS sets, each one containing 46 mean values, corresponding to 46 measurement channels in total. To deal with the multiple-comparison problem, the largest value was selected from each INS set, forming a null distribution of the maximum INS. Then, the family wise error rate was defined as the top 1% of the null distribution of the maximum INS, which exceeded a given threshold (R^*). That is, in the real INS set, only channels with an INS above the threshold (R^*) could be deemed significant after multiple-comparison correction (Nguyen, Vanderwal, & Hasson, 2019; Regev, Honey, Simony, & Hasson, 2013). By calculation, we acquired four thresholds as follows: for the cooperation task, stress condition $R^* = 0.417$, control condition $R^* = 0.409$; for the competition task, stress condition $R^* = 0.391$, control condition $R^* = 0.381$ (Supplementary Fig. 1). For channels with significant synchronization, two-sample *t*-tests were performed with false discovery rate (FDR) correction (Benjamini & Hochberg, 1995) to examine the impact of stress on cooperation and competition at the brain-to-brain level.

3. Results

3.1. Stress response

The efficacy of the stress manipulation was examined by two-way repeated measures ANOVAs with the condition (stress, control) as a between-subject factor and time (pre-MIST, post-MIST, post-task) as a within-subject factor. We found a significant condition-by-time interaction for each MDMQ dimension, $F_{good-bad}(2,148) = 9.20$, $p < 0.001$, $\eta^2 = 0.11$; $F_{calm-nervous}(2,148) = 5.57$, $p < 0.01$, $\eta^2 = 0.07$; $F_{alert-tired}(2,148) = 3.57$, $p = 0.03$, $\eta^2 = 0.05$ (Fig. 2). The simple effect analysis with Bonferroni correction revealed that compared with the control condition, participants in the stress condition experienced bad mood and nervousness to a greater degree only after the MIST ($F_{good-bad}(1,74) = 13.88$, $p < 0.001$, $\eta^2 = 0.16$; $F_{calm-nervous}(1,74) = 11.76$, $p < 0.001$, $\eta^2 = 0.14$). Although alertness after the MIST did not significantly differ between the two conditions, $F(1,74) = 1.78$, $p = 0.19$, $\eta^2 = 0.02$, the stress dyads were wearier after stress induction, $F(2,73) = 4.87$, $p = 0.01$, $\eta^2 = 0.12$. Taken together, the MIST increased the stress dyads' tension and tiredness, while decreasing the sense of pleasure, which confirmed that the experimental manipulation was effective.

3.2. Cooperation task

During the cooperation task, the program recorded the dyad's response time and the number of winning trials. First, we compared the response time between two conditions and found no significant difference, $\beta = -0.28$, $SE = 0.26$, $p = 0.28$ (Fig. 3A). We then analyzed the cooperation level using two indicators: difference in response time (RT difference, $|RT_A - RT_B|$, RT_A , RT_B : response time of participant A or B) and cooperation rate (the percentage of winning trials in the total valid trials). Likewise, there was no significant difference between the two groups for either indicator (RT difference: $U = 134$, $z = -0.63$, $p = 0.55$, Fig. 3B; cooperation rate: $t(33) = 0.09$, $p = 0.93$, Cohen's $d = 0.03$, Fig. 3C). Pearson correlation analyses showed that with the task process

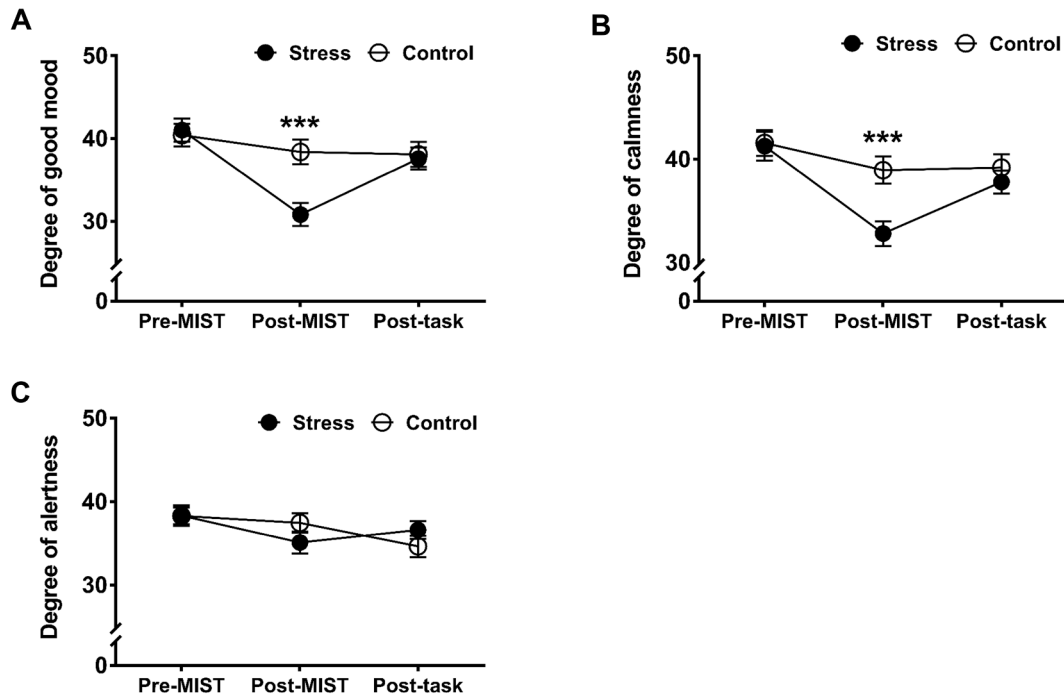


Fig. 2. Subjective stress over the course of the experiment. Subscales of good–bad mood (A), calmness–nervousness (B) and alertness–tiredness (C) of two conditions in different times. Error bars indicate standard errors. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

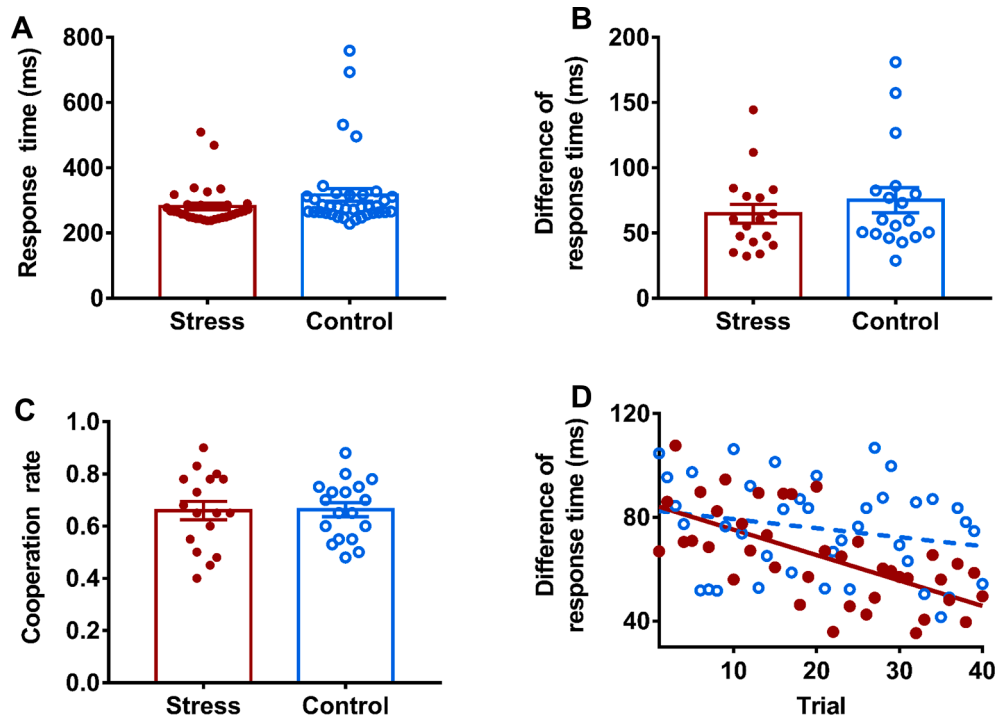


Fig. 3. Cooperation performance. (A) The response time. Stress: 281.64 ± 59.46 ($M \pm SD$) Control: 316.92 ± 117.86 . (B) The RT difference between participants within a dyad. Stress: 64.76 ± 29.85 ($M \pm SD$) Control: 75.25 ± 40.84 . (C) The cooperation rate defined as the ratio of the number of winning trials to the number of valid trials. Stress: 0.66 ± 0.14 ($M \pm SD$) Control: 0.66 ± 0.11 . (D) Pearson correlation analyses for two conditions. Error bars indicate standard errors.

moving forward, the average RT difference of stress dyads underwent a steady decrease, $r = -0.65$, $p < 0.001$, which was not found in control dyads, $r = -0.22$, $p = 0.17$ (Fig. 3D). Moreover, the correlation in the stress group was stronger than that in the control group, $z = -2.28$, $p = 0.02$. This result suggested that acute psychosocial stress affected cooperation in the two-person key-pressing task.

In the stress condition, channels 3, 4, 7, covering the FPC and OFC and 14, located in the left middle PFC, showed a significant INS (Fig. 4A and B), while in the control condition, task-related INS was only seen in channel 3 (Fig. 4C and D). To identify brain areas with increased INS for one condition over the other, we conducted a series of two-sample t -tests on channels with significant INS in at least one condition. No difference

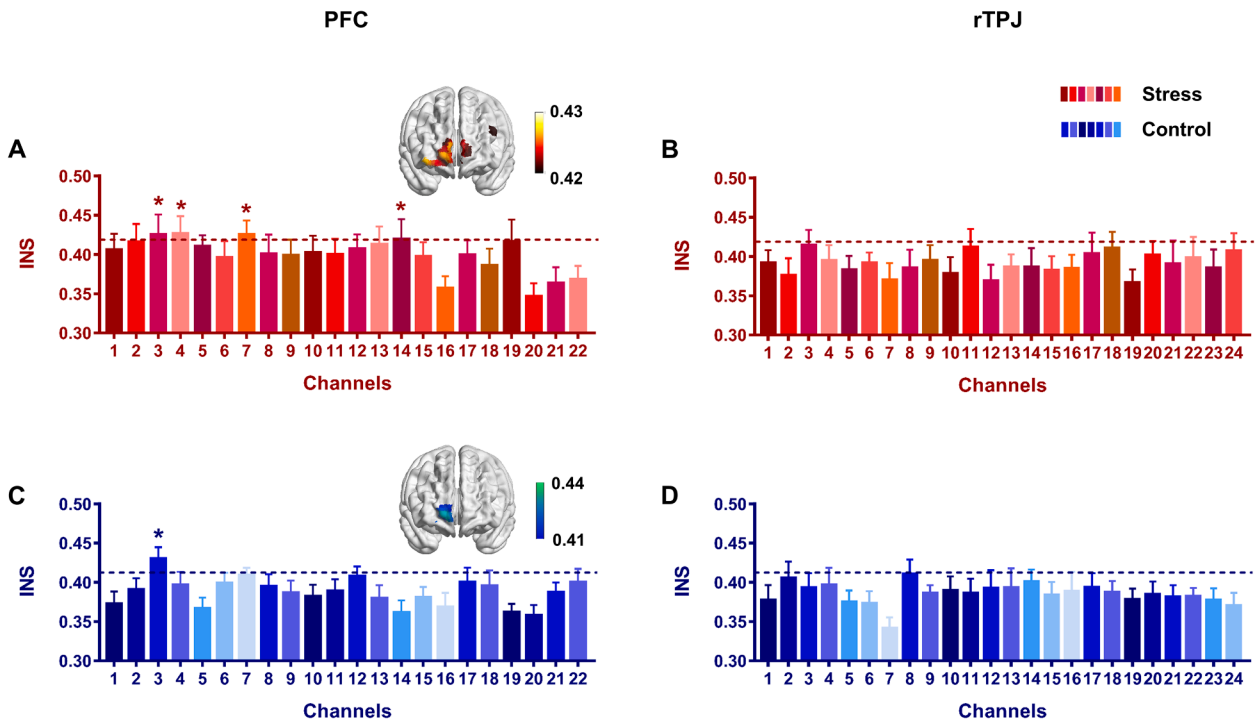


Fig. 4. Interpersonal neural synchronization in cooperation. The INS in prefrontal and right temporo-parietal cortex for stress dyads (A & B) and control dyads (C & D). Error bars indicate standard errors. Dotted lines indicate 99th percentiles of null distributions. * $p < 0.05$.

was observed in any channel, $p_s > 0.05$, FDR corrected.

3.3. Competition task

The analysis based on linear mixed model revealed a marginal significant effect of stress on response time, $\beta = -0.16$, $SE = 0.09$, $p = 0.08$

(Fig. 5A). Mann–Whitney U test showed a significant difference between two groups in RT difference, $U = 107$, $z = -1.95$, $p = 0.05$ (Fig. 5B). To measure the competitive performance more accurately, the competition intensity was quantified using the following formula: competition intensity = $1/[(RT_A + RT_B) * |RT_A - RT_B|]$. The greater the value, the stronger the competition. The result indicated that there was more

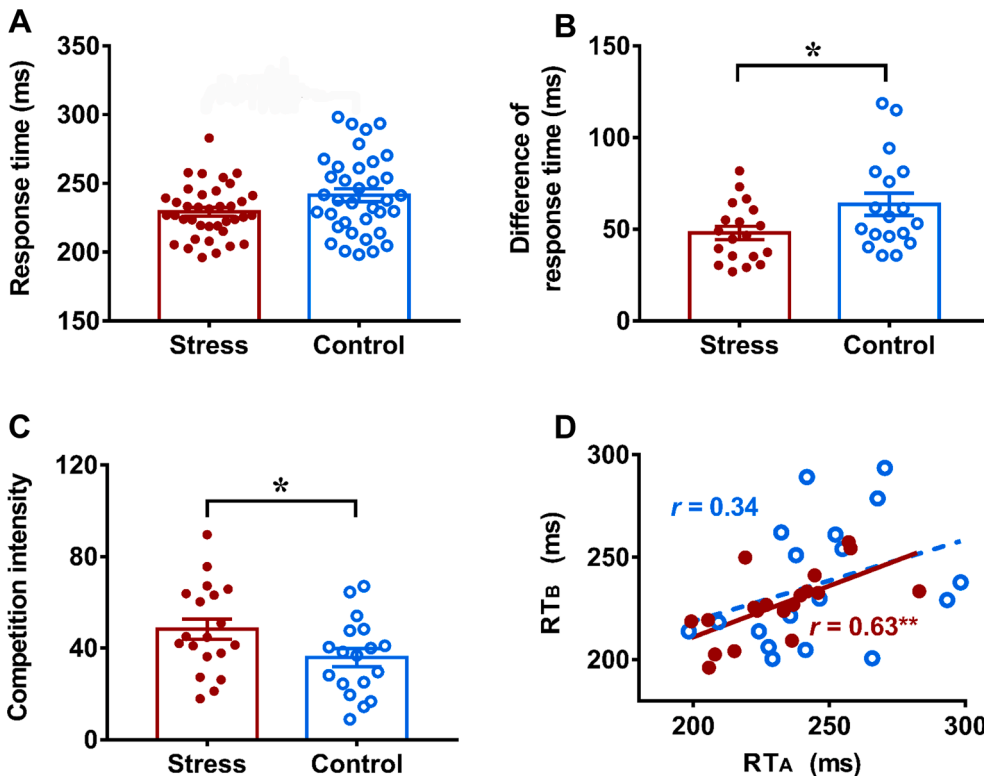


Fig. 5. Competition performance. (A) The response time. Stress: $229.26 \pm 19.03(M \pm SD)$ Control: 241.46 ± 28.37 . (B) The RT difference between participants within a dyad. Stress: $48 \pm 15.96(M \pm SD)$ Control: 63.64 ± 25.57 . (C) The competition intensity defined as the inverse of the product of the absolute of RT difference (in seconds) multiplied by the sum of two participants' response time (in seconds). Stress: $48.31 \pm 19.34 (M \pm SD)$ Control: 35.86 ± 16.54 . (D) The correlation between response times of two participants for different conditions. RT_A : response time of participant A; RT_B : response time of participant B. Error bars indicate standard errors. * $p < 0.05$; ** $p < 0.01$.

intense competition in stress dyads, $t(35) = -2.10, p = 0.04$, Cohen's $d = 0.69$ (Fig. 5C). Furthermore, the positive correlation between two participants' response times revealed the interdependence of competitive behaviors in the stress dyads, $r = 0.63, p < 0.01$, but not in the control dyads, $r = 0.34, p = 0.16$ (Fig. 5D).

For the stress dyads, significant INS was detected in channel 13, located in the right dIPFC (Fig. 6A and B). However, there was no significant coherence in the PFC or in the rTPJ for control dyads (Fig. 6C and D). Compared with the control dyads, the INS in channel 13 was higher in the stress dyads, $t(35) = 4.35, p < 0.001$, Cohen's $d = 1.44$ (Fig. 6E). To clarify the relationship between INS and behavioral performance, Pearson correlation coefficients were calculated. A significant positive correlation between INS and competition intensity was found in the stress condition, $r = 0.47, p = 0.04$, but not in the control condition, $r = 0.08, p = 0.76$ (Fig. 6F).

4. Discussion

In the current study, we manipulated acute psychosocial stress using the MIST and investigated the stress effect on different social interactions in women. The results showed that acute psychosocial stress evidently promoted competition among women and INS in the right dIPFC in the competitive context. Despite the lack of difference in the overall cooperation rate, the response time difference between two participants significantly declined over time in the stress condition, accompanied by more widespread INS in the PFC, suggesting improved cooperation among stressed female participants in the cooperative context.

From an evolutionary perspective, for survival, reproduction and nurturing, women are more inclined to behave in a prosocial manner to create and maintain social networks, which can provide them with support when faced with a threatening situation (Taylor et al., 2000). Thus, tend-and-befriend appears to be an innate and prepotent response to stress for women as a result of natural selection. In studies adopting

social dilemma paradigms, allowing individuals to behave in a cooperative or competitive manner, a greater degree of prosocial behaviors has been observed among stressed female participants (Nickels et al., 2017; Prasad et al., 2017; von Dawans et al., 2019; Youssef et al., 2018), supporting this hypothesis. In the current study, although the stressed and control groups were equally matched in overall cooperation rate and RT difference, it should be noted that stressed participants gradually shortened the RT difference across time. This distinct improvement in cooperation may result from the promotional effect of acute stress on female habitual and prepotent responses in social interactions. In addition, significant INS appeared in the OFC in both groups, and in the right FPC and left middle PFC specific for the stress group in the cooperation task, which provided further support for the established consensus that INS could be a neural marker for interpersonal cooperation (Baker et al., 2016; Cheng et al., 2015; Miller et al., 2018; Reindl, Gerloff, Scharke, & Konrad, 2018; Wang et al., 2019). The more widespread INS in the PFC in the stress condition may provide the evidence for better cooperation among stressed female participants at the neural level.

In the competition task, participants responded more quickly and the RT difference was smaller in the stress condition. To more precisely describe competitiveness, we integrated two indicators into a more accurate and sensitive one, namely competition intensity. The result of competition intensity also corroborated the response pattern of fight-or-flight in stressed female participants. To further clarify the effect of stress on female competitiveness, correlation coefficients between two interacting participants' response times were calculated for both conditions. The results showed that the response time of participants in a dyad was highly correlated in the stress condition, but not in the control one, indicating the interdependence of participants' behaviors within the stressed dyads. If acute stress only accelerated individuals' simple response to the green signals in the task, we could not observe this behavioral interaction and interdependence. Therefore, acute stress indeed enhanced female participants' competitiveness.

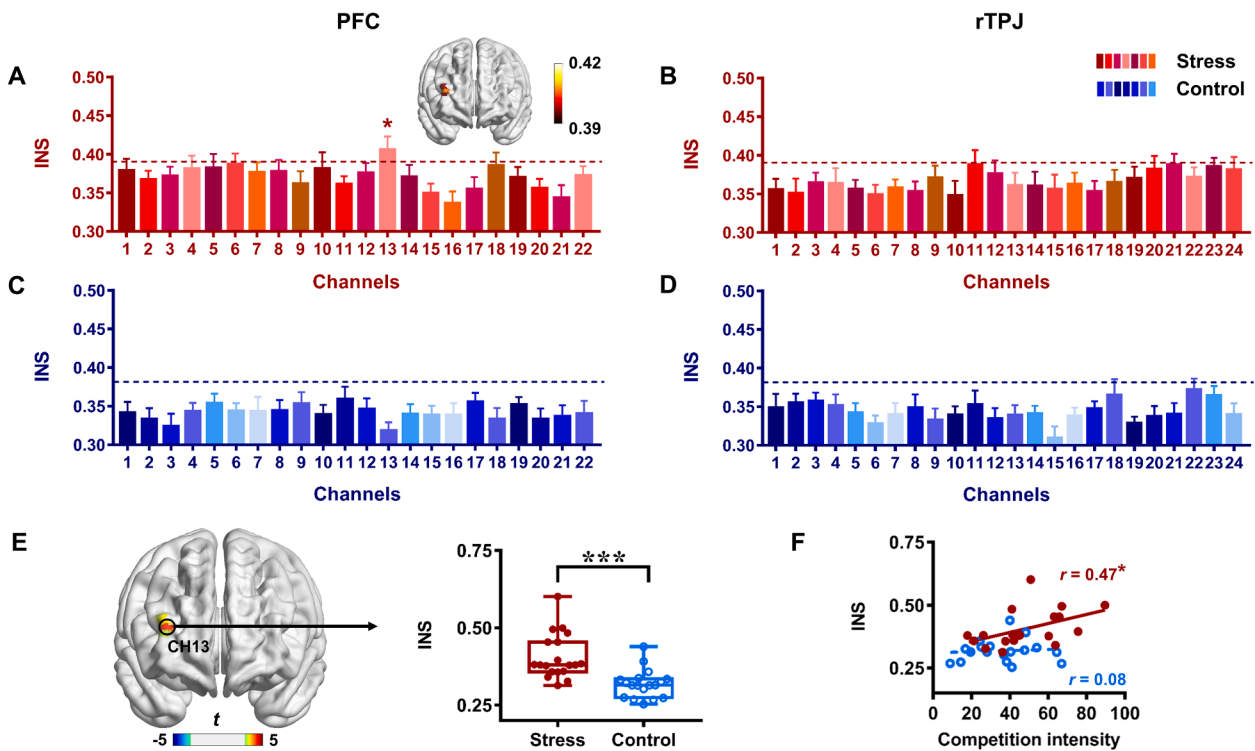


Fig. 6. Interpersonal neural synchronization in competition. The INS in the prefrontal and right temporo-parietal cortex for stress dyads (A & B) and control dyads (C & D). (E) The average INS in channel 13 for two conditions. Stress: $0.41 \pm 0.07(M \pm SD)$ Control: 0.32 ± 0.05 . (F) The correlations between competition intensity and INS in channel 13 for two conditions. Error bars indicate standard errors. Dotted lines indicate 99th percentiles of null distributions. * $p < 0.05$; *** $p < 0.001$.

Our results support the findings of Buser et al. (2017), who also found that acute stress could enhance women's willingness to compete. However, the mechanisms behind this effect remain to be clarified. The study by Buser, Dreber and Mollerstrom showed that for female participants, willingness to compete was sensitive to cortisol changes, which could help individuals prepare for upcoming confrontation or fight. Neuroendocrine hormones are believed to exert certain influence on human fight behaviors; this is especially true for cortisol and testosterone, which are the final output products of two different axes, the hypothalamic–pituitary–adrenal axis, activated in stressful situations, and the hypothalamus–pituitary–gonadal axis, implicated in aggressive behaviors. The dual-hormone hypothesis posits that a high testosterone–cortisol ratio is associated with social aggression (Montoya, Terburg, Bos, & van Honk, 2012; Terburg, Morgan, & van Honk, 2009). In recent years, a series of studies have examined this hormonal pattern in women, but with mixed results (Denson, Mehta, & Ho Tan, 2013; Geniole, Busseri, & McCormick, 2013; Grotzinger et al., 2018). However, in the present study, we did not measure cortisol or testosterone levels. Thus, we could not test this physiological mechanism. More efforts should be made to elucidate the hormonal markers of female aggressive behaviors in stressful situations.

In line with results of previous studies using the same experimental paradigms (Cheng et al., 2015; Cui et al., 2012; Reindl et al., 2018), we did not observe significant INS in the control condition during competition. However, significant INS was detected in the right dlPFC among stressed female participants, whose involvement in executive motor control is well-documented (Cieslik et al., 2010, 2013; Jakobs et al., 2009). In addition, we found that the greater the INS, the fiercer the competition. Taken together, these findings imply that the INS in the right dlPFC, which may reflect similar brain activities involved in action control, can be the neural mechanism of interpersonal competition in the stressful context.

It is noteworthy that for both tasks, no significant INS was found in the rTPJ in our study, a region widely accepted as a crucial neural substrate for theory of mind (Carter & Huettel, 2013; Decety & Lamm, 2007; Koster-Hale & Saxe, 2013). INS enhancement in the rTPJ has become a neural marker for social interaction, not limited to a certain category, but present in diverse social contexts, such as interactive teaching (Zheng et al., 2018), economic exchange (Tang et al., 2016) and group creation (Lu et al., 2018). Nevertheless, in the current study, such INS was not observed. One possible reason for this is that the key-pressing task is a relatively simple social interaction, involving greater reaction coordination, but less interpersonal mentalizing.

In the present study, on one hand, acute psychosocial stress functioned as a cooperation promotor in the cooperative task; on the other hand, it was a competition facilitator in the competitive task. These results seem a little conflicting. However, there is no contradiction between them. One of the possible interpretations is enhanced egoistic motivation. It is believed that acute psychosocial stress might generally activate more self-serving motivations, such as regulating stress-induced negative emotions and maximizing one's own interests (Sollberger et al., 2016; Youssef et al., 2018). Whatever the specific need, greater self-serving motivation can lead to better interpersonal cooperation and more intense competition. In addition to the above interpretation, increased reward sensitivity or loss aversion (Yu, 2016) may also underlie these effects. Further work is needed to clarify the psychological mechanism.

Finally, some inadequacies should be noted, and corresponding directions for improvement should be proposed. First, we did not measure physiological indicators, especially cortisol level, an effective indicator to assess stress. Although the stress manipulation was validated by subjective reports, further verification is needed, also for the potential physiological mechanisms underlying social behavior differences induced by acute psychosocial stress. Second, women's response to acute psychosocial stress can be affected by the menstrual cycle phase (Albert, Pruessner, & Newhouse, 2015; Banis & Lorist, 2017; Duchesne

& Pruessner, 2013; Kirschbaum, Kudielka, Gaab, Schommer, & Hellhammer, 1999). In our study, only women who were in or 2 days before or after menstruation were excluded. The combined effects of acute psychosocial stress and menstrual cycle phase on women's social interactions should be a topic of future research.

5. Conclusions

In the present study, acute psychosocial stress promoted the steady improvement of cooperative behaviors in women, accompanied by inter-brain coherence in the right OFC, FPC and left middle PFC. Conversely, in the competitive context, instead of weakening the willingness to compete with others, acute stress enhanced women's competitiveness, meanwhile increasing neural alignment in the right dlPFC. Taken together, these findings suggested that acute stress strengthened female tend-and-befriend response in interpersonal cooperation and the fight-or-flight response in competition. Thus, our study uncovered evidence for the context dependence of stress responses in women, and further research is needed to shed light on the associated psychological and neurobiological underpinnings.

CRediT authorship contribution statement

Ruqian Zhang: Formal analysis, Validation, Visualization, Writing - original draft, Writing - review & editing. **Xiaoyu Zhou:** Formal analysis, Software, Writing - review & editing. **Danyang Feng:** Conceptualization, Methodology, Investigation. **Di Yuan:** Methodology, Investigation. **Shijia Li:** Conceptualization, Methodology, Writing - review & editing. **Chunming Lu:** Conceptualization, Project administration, Resources, Supervision. **Xianchun Li:** Conceptualization, Resources, Supervision, Writing - review & editing, Funding acquisition, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.bandc.2021.105738>.

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