



The effects of stress and affiliation on social decision-making: Investigating the tend-and-befriend pattern



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ARTICLE INFO

Article history:

Received 18 May 2015

Received in revised form 15 July 2015

Accepted 4 August 2015

Keywords:

Psychosocial stress
Social decision-making
Tend-and-befriend
Fight-or-flight
Trust

ABSTRACT

The prevalence of psychosocial stress in Western societies is constantly on the rise. Its influence on social decision-making, however, remains poorly understood. Whereas, it is known that stress triggers psychological and physiological defense mechanisms, indications of such patterns in social decisions are ambivalent. We sought to elucidate the underlying mechanisms of stress-induced social decisions. We recruited 145 men, who were individually exposed to either a psychosocial stressor or a control condition, while primed with affiliation by interacting either with members of an in- or an out-group. We found that stressed participants were less trusting and engaged in less costly punishment compared to the non-stressed control group. Interacting with out-group members led to less reciprocity and more spiteful punishment. There was no interaction between stress and the affiliation conditions in any of the used social-decision-making paradigms. Lastly, while stress-reactive cortisol levels had no effect on trust behavior, higher baseline cortisol was correlated with greater trust. Our findings suggest that previous ambiguities in data reported on the influence of stress on social decisions, namely tend-and-befriend behavior may have arisen through critical social confounds in the induction of stress. When controlling for potential social confounds, stress may trigger fight-or-flight behavior as indicated by increased social anxiety. These findings highlight the considerable context-dependence of psychosocial stress and its effects on social behavior.

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1. Introduction

Life is fraught with decisions. Particularly for social creatures like humans, many of these decisions are related to direct or indirect social interaction (Fehr and Fischbacher, 2003). Given that social decisions, such as whether to be cooperative or trusting have potentially far-reaching consequences (Axelrod and Hamilton, 1981), it is important to understand how these decisions can be modulated by environmental influences. Here, we isolate one such variable, namely psychosocial stress. Stress is an omnipresent phenomenon in modern western societies. With more than half the world's population living in urban areas (Dye, 2008), an environment particularly conducive to creating stress (Lederbogen et al., 2011), understanding the consequences of stress on social behavior is timely and critical. With the potential to influence both cognitive and emotional processes involved in decision-making (Mather and

Lighthall, 2012), exploring how exactly stress affects our decisions is highly relevant.

Stress refers to a state of threatened homeostasis in an organism due to internal or external adverse effects (Chrousos, 2009). The compensatory physiological response toward such a threat to homeostasis involves the activation of the sympathetic nervous system and the hypothalamic–pituitary–adrenal (HPA) axis. Cortisol as the final output product of the HPA axis is the most frequently assessed biomarker of stress (Hellhammer et al., 2009). Concomitant with the physiological stress response, rises in arousal, vigilance, attention and aggression enable an adaptive behavioral response, such as escaping or opposing the stressor, referred to as the “fight-or-flight” response (Cannon, 1932). It may thus be argued that social decisions made under the influence of stress ought to bear the marks of anxious and aggressive tendencies. While the effects of stress have been shown to be highly variable and subject to specific moderators such as age, gender, personality (Starcke and Brand, 2012), and content of thought (Engert et al., 2014), there is evidence of increased egotism in moral decisions (Starcke et al., 2011) as well as egocentric perspective-taking following stress (at least in men; Tomova et al., 2014). The view of a fight-or-flight response tendency following psychosocial stress is buttressed by

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findings of the involvement of brain regions implicated in detecting environmental threats and instantiating fearful responses such as the amygdala (Lang et al., 1998) when confronted with psychosocial stressors (Dedovic et al., 2009; Rodrigues et al., 2009). In turn the attenuation of amygdala responsivity through the intranasal administration of oxytocin (Meyer-Lindenberg et al., 2011) has been shown to lead to increased approach behavior as well as decreased cortisol concentration (Ditzen et al., 2009). The involvement of the amygdala in social behavior such as trust (Baumgartner et al., 2008) makes a cogent case for social decisions indicative of a fight-or-flight response tendency following psychosocial stress.

An intriguing alternative hypothesis argues that specifically social behavioral stress responses are not necessarily characterized by aggressive and anxious behavior (i.e., a fight-of-flight response), but are rather of an affiliative nature, characterized by a so-called “tend-and-befriend” pattern (Taylor, 2006; Taylor et al., 2000). By befriending and affiliating with social groups, the individual may obtain the necessary resources to overcome stressful conditions and thus maximize the chance of survival. The tend-and-befriend pattern is suggested to be particularly pronounced in women. A recent study reported such a behavioral tendency in men, however, showing that acute social stress can lead to a subsequent increase in prosocial decisions in the context of social-decision-making tasks (von Dawans et al., 2012). Using a group variant of the Trier Social Stress Test (TSST-G; von Dawans et al., 2011), it was shown that trust, reciprocity and sharing measured by game-theoretical paradigms with monetary incentives increased following the induction of acute social stress in a sample of male participants. At the same time, costly punishment and risk-related behaviors were unaffected. Further, behavior was altogether independent of levels of the stress hormone cortisol. Drawing on literature describing stress-buffering effects of social affiliation in times of threat (Baumeister and Leary, 1995; Taylor, 2006), the authors attributed their findings to approach behavior triggered by stress, and designate it as tend-and-befriend behavior.

Thus, theory and current evidence from one laboratory suggest that humans tend to affiliate with others in the context of stress as a suitable coping strategy. However, we contend that the evidence provided so far in support is far from conclusive. For instance, one intriguing aspect of the experimental design by von Dawans et al. (2012) is the fact that stress was induced in a group setting. Given that several lines of research suggest affiliating with others in times of threat is a common mechanism and effective strategy to reduce the perceived threat (Grieve and Hogg, 1999; Hogg, 2000; Hogg et al., 2007), the group experience may have resulted in increased affiliation with the simultaneously stressed individuals. Typically, affiliation has been defined as a need to belong to a social group and wanting to be liked (Baumeister and Leary, 1995). As a result of such feelings, potentially anxious and aggressive effects on subsequent social behavior may be buffered. This hypothesis would predict precisely the same pattern of behavioral results as found by von Dawans et al. (2012) but as a result of the shared stress experience in which affiliative feelings are primed rather than by the affiliative effects of stress per se.

To shed further light on the effect of stress on social decision-making, we designed an experiment where subjects were exposed to a psychosocial stressor or an appropriate control condition individually (i.e., not in a group setting) before performing several game-theoretical social decision-making paradigms. Participants played a series of social decision-making tasks with a member of either their in-group (affiliation condition) or an out-group as determined by a minimal group paradigm. Previous studies have shown that even being part of a group based on arbitrary social categorization (i.e., minimal groups; Tajfel, 1970) can result in biased allocation of resources favoring members of one's own group, and maximizing the difference between in-group and out-group

(Abbink et al., 2012; Yuki et al., 2005). Such in-group favoritism has been shown to be deeply rooted in the positive feelings associated with one's in-group (Van Bavel et al., 2008; Van Vugt and Hart, 2004). Thus, our factors yielded a 2×2 between-subject factorial design with the factors stress (yes/no) and affiliation (in-group/out-group). To comprehensively test for effects of both pro- and antisocial behavior, we employed several established paradigms derived from economic game theory, known to test for trust and trustworthiness (i.e., the trust game), sharing (i.e., the dictator game), and costly and spiteful punishment (i.e., ultimatum and money burning games, respectively).

We predicted that if the effects of stress per se genuinely lead to an affiliative response, then we ought to replicate von Dawans et al. (2012) findings of increased trust, reciprocity and sharing, as well as unaffected punishment and risk behavior after individual stress induction. If however psychosocial stress actually leads to an increase in social anxiety and aggression, but this might have been masked by the previously used group stressor then we ought to detect social decisions indicative of fight-or-flight. Including an affiliation condition where participants interact with in- or out-group members helps to elucidate the potential contradiction, whereby potential affiliation experienced with in-group interaction, increased social anxiety and aggression produced by the stressor ought to be attenuated when playing with in- as opposed to out-group members.

2. Methods

2.1. Participants

A total of 145 men between 19 and 35 years of age (mean age \pm SD: 26.1 ± 3.40 years) were recruited from the Max-Planck-Institute's participant database, and by posting ads on an electronic billboard of the city of Leipzig. The majority of participants (92%) graduated from academic high school with 29% holding a Bachelor's or higher University degree. The remaining 8% graduated from middle school. Women were excluded from participation to avoid the confounding effects of hormonal status on cortisol levels (Kajantie and Phillips, 2006). Given a potential effect on cortisol activity, regular recreational drug users (consumption within the past six months), smokers (>5 cigarettes/week), individuals reporting chronic illness (including psychological disorders) and individuals taking medication targeting the HPA axis were excluded after an initial telephone interview. Also, participants had to be naïve to both the Trier Social Stress Test (TSST; Kirschbaum et al., 1993; Kudielka et al., 2007) and the economic decision-making paradigms. The study was approved by the Research Ethics Board of Leipzig University (ethics numbers: 219-12, 058-12) and performed in agreement with the Declaration of Helsinki. All participants gave their written informed consent, received financial compensation for their time and effort, and could withdraw from the study at any time.

2.2. Experimental design and procedure

The study had a 2×2 between-subject factorial design with the factors stress (stress vs. no-stress) and affiliation (in-group vs. out-group) (stress/in-group: $n = 37$; stress/out-group: $n = 36$; no stress/in-group: $n = 37$; no stress/out-group: $n = 35$). Assignment to the stress and affiliation groups was organized online one week before the experiment. Since cortisol secretion is characterized by a strong circadian rhythm (Dallman et al., 2000; Fries et al., 2009), the 90-min testing session was performed between 12 pm and 5 pm. To simulate a realistic group interaction situation for the decision-making paradigms, participants were tested in groups of 12–18

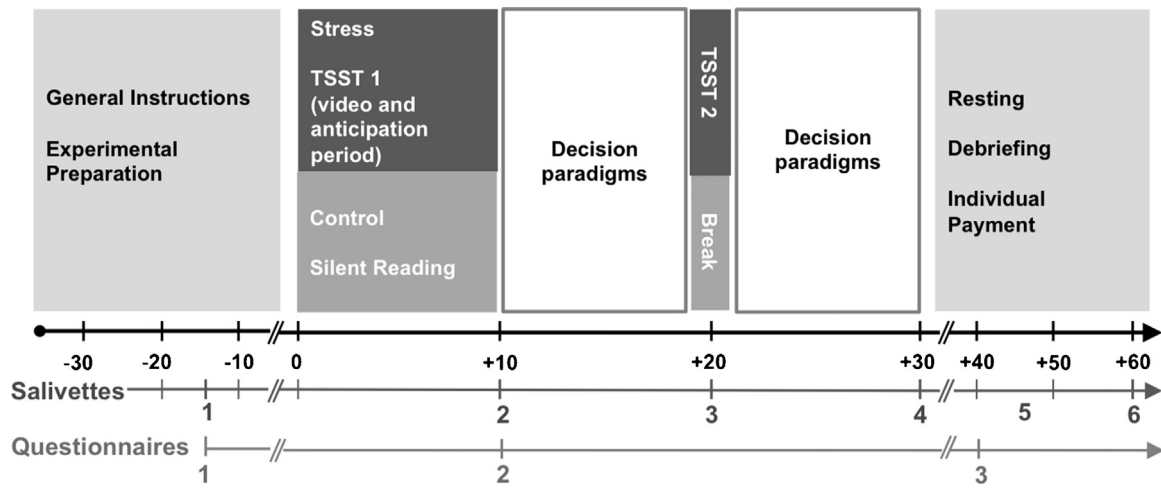


Fig. 1. Overview of the experimental procedure. After the initial instruction phase, the anticipatory stress phase took place in the stress group (duration: 10 min). The no-stress group spent this time silently reading. Following this stress/reading phase, participants immediately proceeded with the 20-min behavioral testing phase. The two 10-min testing blocks were separated by a short (2-min) stress booster in the stress group. Following the behavioral testing, all participants rested for another 30 min to fully capture cortisol recovery in the stress group.

individuals. Upon arrival at the multi-computer laboratory, all participants received instructions on the decision-making paradigms and their understanding of the paradigms was thoroughly tested (duration: 20 min). Participants were then informed about whether they would be playing with in- or out-group members. Subsequently, the anticipatory stress induction and the decision-making paradigms took place. Right before the decision-making phase, participants were once more reminded of whether they were playing with an in- or an out-group member. Following the behavioral testing, all participants rested for another 30 min to fully capture cortisol recovery in the stress group (Fig. 1).

2.3. Decision-making paradigms

To test for our hypothesis of affiliation following group stress, we adhered closely to the design by von Dawans et al. (2012). Since costly punishment has been argued to measure social norm enforcement (Fehr and Fischbacher, 2003) rather than the desire to inflict harm, we added a game known as the money burning game. Overall, a total of five different social decision-making paradigms and one nonsocial paradigm were applied. Blocks of four rounds per social decision-making paradigm were presented in counterbalanced order for each group of participants to measure trust, reciprocity, sharing, costly punishment and spiteful punishment. Eight nonsocial risk scenarios followed the social paradigms. Instructions guaranteed for anonymity and one-shot character of all sets. To further prevent biases, participants received no feedback about their interaction partners' decisions at any given stage of sequential games. Further, individual stations within the laboratory space where the decision-making paradigms took place were each separated by thick wooden panels permitting no visual access to one another while playing the games. Wearing headphones ensured that participants could not hear each other while decisions were being made.

2.3.1. Trust game

Measures of trust and reciprocity were obtained using a slightly modified version of the trust game (Berg et al., 1995). Participants played four one-shot rounds as first mover (player A, trustor) and four one-shot rounds as second mover (player B, trustee). Both movers received an initial endowment of 20 monetary units (MU). Player A could send an amount x ($0 \leq x \leq 20$, $x \in \mathbb{N}$) to player B. Player B received the tripled amount player A had sent and could

choose to return any amount y ($0 \leq y \leq 3x + 20$ MU, $y \in \mathbb{N}$). Thus, trust is measured by means of how much the first mover gives to the second mover and reciprocity by how much the second mover returns to the first mover.

2.3.2. Dictator game

Measures of sharing were obtained using the dictator game (Kahneman et al., 1986). In the current version, participants played four rounds of the game as player A. They received an initial endowment of 20 MU and could decide on how to allocate their endowment by declaring the amount x ($0 \leq x \leq 20$, $x \in \mathbb{N}$) they wanted to share with player B, resulting in final payoff amounts of $20 - x$ MU for player A and x MU for player B.

2.3.3. Ultimatum game

Measures of costly punishment were obtained using the ultimatum game (Güth et al., 1982). In this sequential two-player game, participants played four sets of the game as player B (responder) and could decide whether to accept or reject an offer proposed by player A (proposer). In the event of player B rejecting the offer, neither player received any payoff. If the offer was accepted, final payoffs for each round of this game were $20 - x$ MU for player A and x MU for player B. Offers varied in terms of proportion from the initial endowment (10%, 25%, 40% and 45%). Offers below 25% are generally perceived as unfair (Fehr and Fischbacher, 2003). Costly punishment can be observed in case of the rejection of such an unfair offer, which is costly for the rejector (player B) but punishes the proposer for violating the fairness norm. We limited our analysis of the Ultimatum game to the game set with the most unfair offers of 10%.

2.3.4. Money burning game

Measures of spiteful punishment were obtained using the money burning game (Abbink and Herrmann, 2011). In the current version of the game, both player A and player B played four one-shot rounds, received 20 MU as initial endowment and could simultaneously decide whether or not to reduce (burn) their interaction partner's money. The amount x ($0 \leq x \leq 4$, $x \in \mathbb{N}$) invested by a player reduced the other's endowment by $5x$ MU, while the own income was simply reduced by x . The resulting final payoffs for each round of this game were $20 - xa - 5xb$ MU for player A and $20 - xb - 5xa$ MU for player B with xa reflecting the amount player A chose to invest in burning player B's endowment and xb reflecting

player B's investment. Punishment is costly for each player, but the certainty of multiplied damage to the interaction partner clearly renders this form of punishment a spiteful behavior. Final payoffs could not fall below 0.

2.3.5. Risk game

Measures of participants' risk-taking propensity were obtained using the risk game as implemented by von Dawans et al. (2012). In this nonsocial game, participants played eight sets and could choose between a high-risk alternative A and a low-risk alternative B. The high-risk alternative consisted of one comparably high payoff amount A1 and one comparably low payoff amount A2 (e.g., A1 = 50 MU and A2 = 3 MU). The low-risk alternative had two comparably medium payoffs B1 and B2 (e.g., B1 = 27 MU and B2 = 23 MU). After being presented the possible payoffs, participants chose alternative A or B. In a next step, payoff 1 or 2 was selected at random by the computer.

Importantly, while participants believed they would be interacting with a different in- or an out-group member on each trial depending on which group they had been assigned to they interacted with a computer. This allowed maximal experimenter control, which was particularly important in the context of second-mover games, such as the Trust and the Ultimatum Game. Participants were debriefed accordingly at the end of the experiment.

2.4. Stress induction

Participants in the stress group anticipated the TSST (Kirschbaum et al., 1993; Kudielka et al., 2007). The original TSST consists of an approximately 10-min anticipation phase, an audio- and video-taped mock job talk (5 min) and the performance of difficult mental arithmetic (5 min) while being probed and evaluated by a committee of alleged behavioral analysts. In our anticipatory TSST procedure, participants were individually led to the TSST room and introduced to the fully equipped stress setting. They had to present themselves to the committee members and provide brief information on their current job or career aspirations. Once all participants had undergone the introduction phase and had returned to their individual isles in the computer laboratory (total duration: 5 min), they were simultaneously presented with a 2-min video providing the detailed TSST instructions. The instructions were followed by an 8-min anticipatory preparation phase during which participants geared up for their mock job interview. No-stress control participants spent this time silently reading a neutral text about weather conditions. The preparation phase was followed by two 10-min blocks of decision-making paradigms. The two blocks were interrupted by a 2-min stress booster during which the stress group was presented with a digital image of the TSST room and reminded of the upcoming speech. The no-stress group spent this time at rest. After completion of the behavioral tasks, stress group participants were debriefed and learned that they would not have to undergo the TSST. This anticipatory stress approach allowed us to test several (between 12 and 18) participants simultaneously, which is ideal when studying social decision-making in groups. By this means we could ensure anonymity of participants and individuality in dealing with the stressor, ruling out potential affiliation effects arising from the group stress experience. TSST anticipation has been shown to reliably elicit physiological stress responses (Engert et al., 2013; Juster et al., 2012).

2.5. Affiliation group manipulation

In order to manipulate affiliation, participants were asked to make a preference choice between two paintings (Lichten-

stein/Vermeer) (for details on the validity of such a procedure see also Bornstein et al., 1983). This group selection was organized online one week before the experiment after participants had answered questions related to their level of education and weight. Based on their choice, participants were then randomly assigned to playing with either members from their in- or the out-group. In the main testing session, in-group participants were hence told that they would be interacting solely with members of their own group during the upcoming decision-making tasks (i.e., a participant who preferred Vermeer's painting would only interact with other members of the "Vermeer group"). Out-group participants were told that they would be interacting solely with members of the "opposing" group.

2.6. Measurement of cortisol levels

Cortisol was sampled using Salivette collection devices (Sarstedt, Nuembrecht, Germany) and stored at -30°C . In the stress condition, saliva samples were taken at baseline (10 min prior to the onset of anticipatory stress), after the anticipatory stress period (+10 min) and at +20, +30, +45 and +60 min to fully capture cortisol peak and recovery (Fig. 2A). The sampling timeline was identical in the no-stress group, only that the anticipatory stress phase was replaced by a period of silent reading. As recommended (Rohleder and Nater, 2009), participants placed the saliva collection swabs in their mouths and refrained from chewing for 2 min. Cortisol levels (expressed in nmol/l) were determined using a time-resolved fluorescence immunoassay (Dressendorfer et al., 1992) with intra- and interassay variabilities of less than 10 and 12%.

2.7. Measurement of subjective variables

Anxiety levels were assessed with the 20-item state scale of the State Trait Anxiety Inventory (Spielberger, 1983). The STAI was completed at baseline (10 min prior to the onset of anticipatory stress), after the anticipatory stress period (+10 min) and after the completion of the decision-making paradigms (+40 min) (Fig. 2B). Intergroup bias was assessed using an in-house 18-item questionnaire capturing beliefs about positive (reliable, social, fair, altruistic, trusting, trustworthy, caring, cooperative, friendly, generous) and negative (unreliable, unsocial, unfair, egoistic, aggressive, competitive, malicious, stingy) characteristics of in- and out-group members on 6-point Likert scales.

2.8. Statistical analysis

2.8.1. Data preparation

For the decision-making behavior, answers were averaged over the number of rounds played for each social decision-making paradigm (trust, reciprocity, sharing, costly punishment, spiteful punishment, risk-taking). Cortisol data was log-transformed to account for non-normal distribution. To obtain composite scores of cortisol output over all measurement timepoints, the areas under the curve with respect to the baseline (AUC_B) (Fekedulegn et al., 2007) and with respect to increase (AUC_I) (AUC_I ; Pruessner et al., 2003) were calculated. The AUC_B is solely determined by the baseline value, and therefore independent of reactive cortisol levels. The AUC_I on the other hand, ignores the distance from zero thus emphasizing change over time. For the anxiety data, a change score from the baseline to the anticipatory sample (Δ change) was calculated. To correct for potential multicollinearity, continuous predictors were mean-centered. Analyses were performed with the Statistical Package for the Social Sciences (SPSS) version 22.

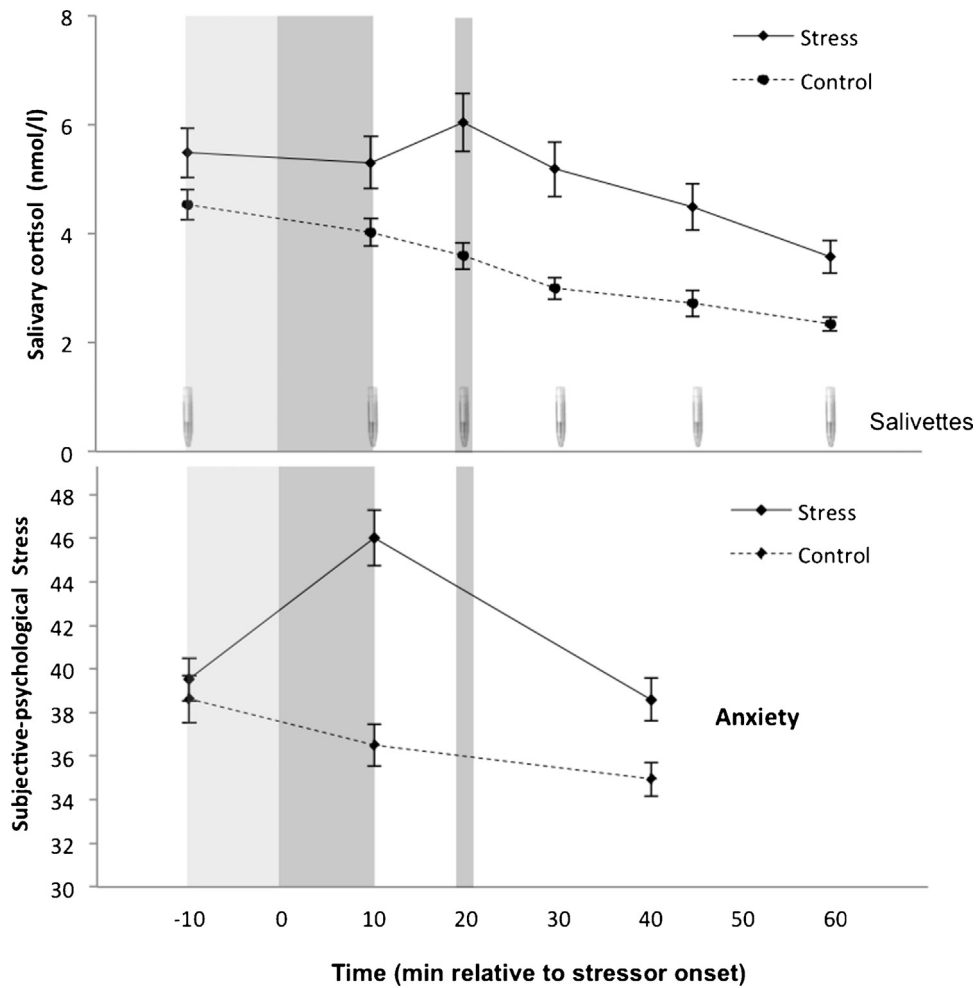


Fig. 2. Effects of social stress on salivary cortisol and anxiety levels. The raw cortisol and subjective-psychological data (mean values and standard errors) are projected onto the experimental timeline showing (A) a physiologically significant cortisol stress response and (B) increased anxiety to the anticipatory TSST.

2.8.2. Preliminary analysis

In an initial reliability check, we verified the efficacy of our anticipatory stress paradigm to elicit significant cortisol and subjective-psychological stress responses. For this purpose, two repeated measures ANOVAs with the outcome variables cortisol (logged) and anxiety over time were calculated. As predictor variable, stress group (stress vs. no-stress) was entered into the model. If applicable, violations of the assumption of sphericity were adjusted using the Greenhouse-Geisser correction. To examine intergroup discrimination, the in- and out-group ratings were averaged to one overall positive and one overall negative characteristics score. Positive and negative scores were then compared between in- and out-group members using independent samples *t*-tests.

2.8.3. Main analysis level 1: effects of group manipulations on decision-making behavior

To assess the effect of the stress and affiliation manipulations on decision-making behavior, a set of four univariate GLMs was constructed. The models tested the associations between group manipulations (predictor variables: stress group, affiliation group, stress by affiliation group interaction) and behavior (outcome variables: trust, reciprocity, sharing, spiteful punishment, risk inclination). To adjust for the participants' general risk-taking propensity, risk inclination was included as a covariate into the analysis of trust behavior. Since costly punishment behavior was coded as a binary variable, it was entered as the outcome into a

logistic regression model. Stress group, affiliation group and the stress by affiliation group interaction were again included as predictors into the model. In detail, the following model was specified for each behavioral component:

Level 1: Decision-making behavior_{*i*} = π_{0i} + e_i ,

Level 2: $\pi_{0i} = \beta_{00} + \beta_{01}(\text{stress group})_i + \beta_{02}(\text{affiliation group})_i + \beta_{03}(\text{stress group})_i \times (\text{affiliation group})_i + r_{0i}$, where β_{00} represents the intercept, β_{01} the stress group, β_{02} the affiliation group and β_{03} the stress by affiliation group interaction of every participant *i*'s estimated behavior. Residuals at the level of individual observations are denoted by r_{0i} .

2.8.4. Main analysis level 2: association of decision-making behavior with cortisol and anxiety levels

Given an effect of stress group on behavior on analysis level 1, cortisol (AUC_B, AUC_I) and anxiety (Δ change) data were included into an additional set of analysis. The resulting multiple linear regression models tested the associations between group manipulations, cortisol and anxiety levels, and all possible interactions of group manipulations and cortisol/anxiety levels. Again, for trust behavior, risk inclination was included as a covariate into the analysis, and for costly punishment behavior, logistic regressions were calculated. The following model was specified:

Level 1: Decision-making behavior_{*i*} = $\pi_{0i} + \pi_{1i}$ (cortisol AUC/ Δ change)_{*i*} + e_i ,

Level 2: $\pi_{0i} = \beta_{00} + \beta_{01}(\text{stress group}) + \beta_{02}(\text{affiliation group}) + \beta_{03}(\text{stress group}) \times (\text{affiliation group}) + r_{0i}$,

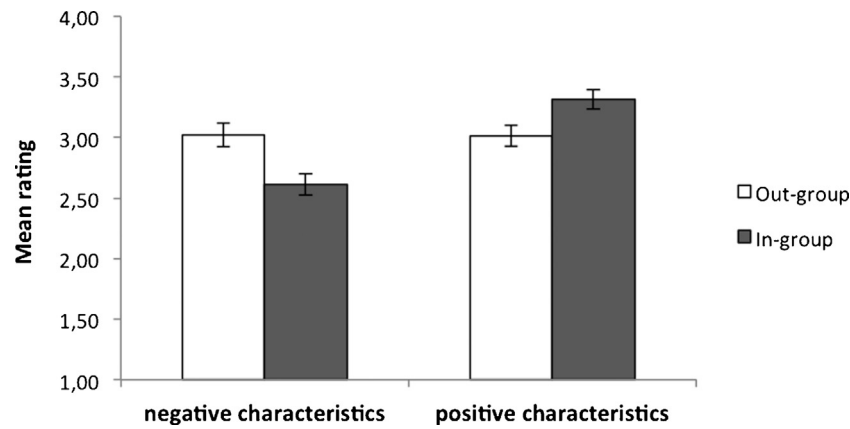


Fig. 3. Ratings given by participants of in-group and out-group members in terms of negative and positive characteristics. In-group members were believed to share more positive characteristics while out-group members were rated as more negative (both significant at $p < 0.05$).

$\pi_{1i} = \beta_{10} + \beta_{11}$ (stress group) + β_{12} (affiliation group) + β_{13} (stress group) \times (affiliation group) + r_{1i} , where π_{0i} represents the intercept and π_{1i} represents the cortisol AUC/ Δ change of estimated decision-making behavior.

3. Results

3.1. Preliminary analysis

Our four experimental groups (stress/in-group, stress/out-group, no stress/in-group, no stress/out-group) did not differ in age ($F_{3,141} = 0.32$, $p > .80$), body mass index ($F_{3,141} = 0.46$, $p > .70$), and educational status (middle school, high school, University degree) ($\chi^2(9, N = 145) = 8.51$, $p > .40$). An initial reliability check confirmed the efficacy of our anticipatory stress paradigm to elicit cortisol and subjective-psychological stress responses. Repeated measures ANOVAs revealed significant main effects of time, stress group and time by stress group interactions for cortisol (time: $F_{5,705} = 79.75$, $p \leq .001$; stress group: $F_{1,141} = 7.69$, $p = .009$; time \times stress group: $F_{5,705} = 8.97$, $p \leq .001$) and anxiety (time: $F_{2,280} = 27.33$, $p \leq .001$; stress group: $F_{1,140} = 13.45$, $p \leq .001$; time \times stress group: $F_{2,280} = 25.90$, $p \leq .001$) (see Fig. 1A and B for a summary of these results). Participants exhibited higher overall cortisol and anxiety levels in the stress than the no-stress group. While the stress group showed a stress-induced increase and subsequent decline in cortisol and anxiety over time, cortisol and anxiety continuously declined in the no-stress group.

A subsistent physiological stress response has been defined by an average cortisol peak of at least 1.5 nmol/l over the baseline (Miller et al., 2013). Within the stress group, 25 out of 73 participants (34%) showed such cortisol increases of at least 1.5 nmol/l. This percentage of responders corresponds to previous investigations into the anticipatory cortisol stress response (Engert et al., 2013).

The exploration of positive and negative characteristics of in- and out-group members revealed that in-group members believed to share more positive characteristics ($t(114) = 2.54$, $p = .012$, $d = 0.33$), while out-group members were rated as more negative ($t(143) = 3.07$, $p = .003$, $d = 0.5$) indicating successful inter-group discrimination (see Fig. 3 and Table 2).

3.2. Main analysis level 1: behavioral effects of group manipulations

The individual stress procedure yielded the following pattern of results: participants exhibited less trust in the stress than the no-stress group. Also, costly punishment was relatively reduced in the

stress group. Affiliation alone had a significant behavioral influence in that participants exhibited more reciprocity toward the in-group and more spiteful punishment toward the out-group. Sharing and risk inclination were uninfluenced by both stress and affiliation. The behavioral stress effects were not modulated by affiliation (see Tables 1 and 3 and Fig. 4 for a summary of these results).

To verify if our measure of costly punishment, namely the rejection of unfair offers in the ultimatum game, correlated with other measures of punishment (spiteful punishment assessed in the money burning game) and social norm-related giving (assessed in the dictator game), we explored Spearman rank correlations of costly punishment with these behaviors. We found no association between costly punishment and the desire to spitefully punish others within the scope of the money burning game ($r_s \leq -.01$, $p > .90$). Instead, the rejection of unfair offers was marginally positively associated with offer sizes in the dictator game (i.e., sharing) ($r_s = .14$, $p = .084$). Therefore, what we observed in the ultimatum game was most likely a decrease in norm enforcement, not in anti-social behavior, under stress.

3.3. Main analysis level 2: associations of decision-making behavior with cortisol and anxiety levels

Trust and costly punishment were influenced by the stress manipulation. For these two behavioral outcomes, cortisol and anxiety levels were consequently included into an additional set of regression analysis. Stress-reactive cortisol levels (AUC_C) had no effect on trust behavior (Table 4; Fig. 5A). Independent of the cortisol stress response, however, interindividual differences in baseline cortisol levels contributed significantly to the prediction of trust behavior in the stress group (stress group by AUC_B interaction): while trust increased with higher levels of baseline cortisol in the stress group, it decreased with higher cortisol output in the no-stress group. This model was trimmed in a post-hoc analysis that excluded the still non-significant affiliation factor. The final model showed a main effect of stress group with less trust behavior in the stress than the no-stress group, and a stress group by AUC_B interaction with reversed associations of trust and baseline cortisol output in stress and no-stress groups (Table 5; Fig. 5B). As revealed by a simple slope analysis, only the positive association of trust and cortisol levels in the stress group was significant (no-stress group: $t = -1.74$, $p = .083$; stress group: $t = 2.74$, $p = .007$). Costly punishment was uninfluenced by either baseline or stress-reactive cortisol output (Table 5). Also, both behavioral outcomes (trust and costly punishment) were uninfluenced by anxiety levels (Table 6).

Table 1
Mean and standard errors (s.e.) of behavioral measures of all economic decision paradigms for stress groups and minimal groups.

	Stress		Control	
	In-group (mean ± s.e.)	Out-group (mean ± s.e.)	In-group (mean ± s.e.)	Out-group (mean ± s.e.)
Given trust (Trust 1st)	11.47 ± 1.09	9.89 ± 1.13	12.93 ± 0.94	12.85 ± 0.94
Returned trust (Trust 2nd)	16.76 ± 1.21	13.28 ± 1.49	16.49 ± 1.37	14.34 ± 1.43
Sharing (Dictator)	6.07 ± 0.61	5.74 ± 0.58	5.72 ± 0.6	6.00 ± 0.61
Costly punishment (Ultimatum)	0.68 ± 0.08	0.53 ± 0.08	0.73 ± 0.07	0.80 ± 0.07
Spiteful punishment (MB)	0.57 ± 0.16	1.31 ± 0.34	0.42 ± 0.15	0.84 ± 0.2
Risk behavior	0.56 ± 0.04	0.49 ± 0.05	0.49 ± 0.05	0.53 ± 0.04

Note. For costly punishment: 1 = reject, 0 = accept; MB = money burning game.

Table 2
Means, standard errors (s.e.) for judgments of in- and out-group members on positive and negative characteristics.

Positive characteristics			Negative characteristics		
Adjective	Ingroup (mean ± s.e.)	Outgroup (mean ± s.e.)	Adjective	Ingroup (mean ± s.e.)	Outgroup (mean ± s.e.)
Reliable	3.17 ± 0.12	2.95 ± 0.1	Unreliable	2.65 ± 0.13	3.07 ± 0.11
Social	3.63 ± 0.12	3.30 ± 0.12	Unsocial	2.55 ± 0.13	2.88 ± 0.11
Fair	3.63 ± 0.13	3.39 ± 0.12	Unfair	2.39 ± 0.13	2.81 ± 0.11
Altruistic	3.00 ± 0.13	2.66 ± 0.13	Egoistic	2.96 ± 0.14	3.51 ± 0.14
Caring	2.87 ± 0.12	2.53 ± 0.1	Aggressive	2.51 ± 0.14	2.81 ± 0.13
Cooperative	3.51 ± 0.13	3.18 ± 0.12	Competitive	2.89 ± 0.13	3.69 ± 0.13
Friendly	3.52 ± 0.12	3.26 ± 0.11	Malicious	1.99 ± 0.13	2.18 ± 0.11
Generous	3.27 ± 0.12	2.88 ± 0.13	Stingy	2.94 ± 0.14	3.34 ± 0.13
Trusting	3.24 ± 0.11	3.07 ± 0.12			
Trustworthy	3.18 ± 0.11	3.00 ± 0.11			

Table 3
Test statistics and significance levels from univariate GLMs (logistic regression for costly punishment) predicting decision-making behavior from the stress group, the affiliation group and the stress by affiliation group interaction^a.

	Trust			Reciprocity			Sharing		
	$F_{(1,140)}$	Sig.	η_p^2	$F_{(1,141)}$	Sig.	η_p^2	$F_{(1,141)}$	Sig.	η_p^2
Intercept	536.73	<.001	.80	487.56	<.001	.78	384.49	<.001	.73
Stress	4.94	.028	.03	0.08	>.70	>.01	0.01	>.90	>.01
Affiliation	0.58	>.40	>.01	4.19	.043	.03	<0.01	>.90	>.01
Stress × affiliation	0.28	>.50	>.01	0.23	>.60	>.01	.26	>.60	>.01
Risk inclination	4.32	.039	.03						

	Costly punishment		Spiteful punishment			Risk inclination		
	B (SE)	Sig.	$F_{(1,141)}$	Sig.	η_p^2	$F_{(1,141)}$	Sig.	η_p^2
Intercept	0.11 (.33)	>.70	48.08	<.001	.25	522.96	<.001	.78
Stress	1.28 (.54)	.018	1.95	>.10	.01	0.10	>.70	>.01
Affiliation	0.62 (.49)	>.10	6.50	.012	.04	0.10	>.70	>.01
Stress × affiliation	−1.02 (.74)	>.10	0.50	>.40	>.01	1.38	>.20	.01

Note. For costly punishment, $R^2 = .04$ (Cox & Snell), .06 (Nagelkerke); $\chi^2(3) = 6.55$, $p = .088$.

^a For the prediction of trust behavior, risk inclination was included as an additional covariate into the model.

Table 4
Test statistics and significance levels from multiple linear regressions predicting trust behavior from baseline (AUC_B) and stress-reactive (AUC_I) cortisol levels, the stress group, the affiliation group, their interactions and risk inclination.

	AUC_B				AUC_I			
	Complete model		Trimmed model		Complete model			
	β	Sig.	β	Sig.	β	Sig.	β	Sig.
Constant		<.001		<.001		<.001		<.001
Stress	−.15	>.10	−.18	.023	−.12	>.30	−.12	>.30
Affiliation	−.06	>.60			.06	>.60	.06	>.60
AUC	−.16	>.40	−.24	.083	−.09	>.70	−.09	>.70
Stress × affiliation	−.04	>.70			−.14	>.30	−.14	>.30
Stress × AUC	.41	.041	.40	.003	.06	>.80	.06	>.80
Affiliation × AUC	−.11	>.50			.43	.092	.43	.092
Stress × affiliation × AUC	−.04	>.90			−.36	>.10	−.36	>.10
Risk inclination	.16	.042	.17	.038	.17	.040	.17	.040

Note. For the AUC_B , $R^2 = .14$; $F_{8,136} = 2.79$, $p = .007$ for the complete model and $R^2 = .13$; $F_{4,140} = 5.14$, $p = .001$ for the trimmed model. For the AUC_I , $R^2 = .10$; $F_{8,136} = 1.83$, $p = .077$.

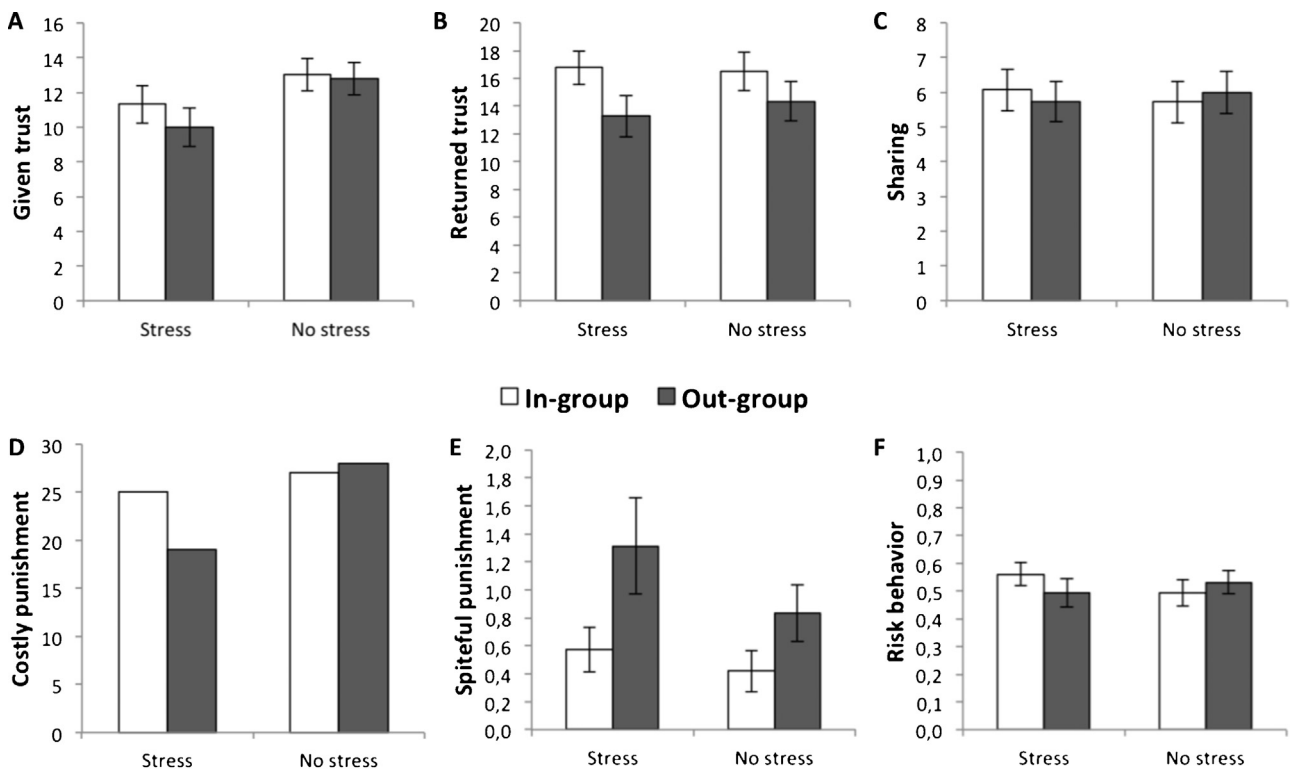


Fig. 4. Decision-making behavior as a function of stress group (yes vs. no) and affiliation group (in-group vs. out-group). Univariate GLMs showed that participants exhibited (A) less trust in the stress than the no-stress group, (B) more reciprocity toward the in- than the out-group, (C) similar levels of sharing in all groups, (D) a decreased number of participants showing costly punishment in the stress than the no-stress group, (E) more spiteful punishment toward the out- than the in-group, and (F) similar levels of risk behavior in all groups.

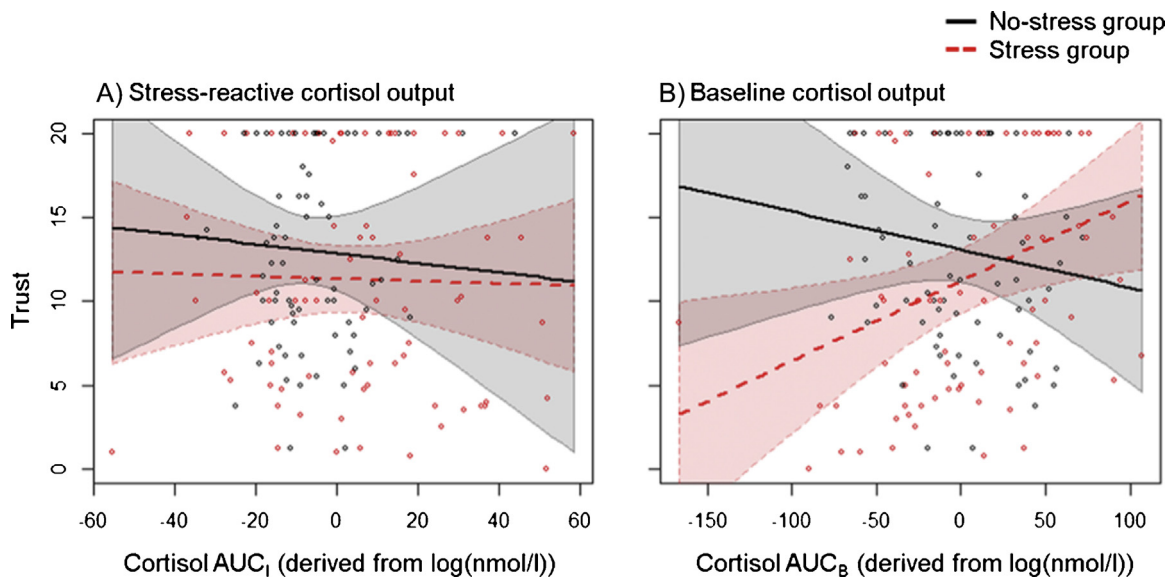


Fig. 5. Associations of trust with (A) stress reactive (AUC₁) and (B) baseline cortisol output (AUC_B). Multiple regression analysis showed that the stress reactive cortisol output (AUC₁) had no effect on trust behavior. Depending on the stress group, baseline cortisol levels (AUC_B) contributed significantly to the prediction of trust behavior ($\beta = 4.00, p = .003$): Trust within the stress group was higher with relatively increased baseline cortisol ($t = 2.74, p = .007$). The association was reversed but non-significant in the no-stress group ($t = -1.74, p = .083$).

4. Discussion

This study set out to elucidate the mechanisms underlying the effects of stress on patterns of social decision-making. Prevalent and opposing views suggest that stress elicits either fight-or-flight behavior, characterized by increased aggression and anxiety (Cannon, 1932), or tend-and-befriend behavior, characterized by

increased affiliation (Taylor, 2006; Taylor et al., 2000). We show that our individual anticipatory stress procedure elicited the expected stress response both at the level of subjective experience and in terms of cortisol activation (observed cortisol responder rate of 34% lies within the range of what can be expected from previous research on anticipatory stress; Engert et al., 2013). Further, we show that participants in the stress group were significantly less

Table 5
Test statistics and significance levels from logistic regression predicting costly punishment behavior from baseline (AUC_B) and stress-reactive (AUC_I) cortisol levels, the stress group, the affiliation group and their interactions.

	AUC_B		AUC_I	
	B (SE)	Sig.	B (SE)	Sig.
Constant	1.10 (.40)	.006	0.73 (.40)	.071
Stress	-0.37 (.53)	>.40	0.06 (.54)	>.90
Affiliation	0.26 (.60)	>.60	0.70 (.61)	>.20
AUC	-0.02 (.01)	>.10	-0.06 (.03)	.081
Stress \times affiliation	-0.91 (.77)	>.20	-1.23 (.80)	>.10
Stress \times AUC	0.01 (.01)	>.20	0.05 (.04)	>.20
Affiliation \times AUC	-0.003 (.02)	>.80	0.07 (.05)	>.10
Stress \times affiliation \times AUC	0.01 (0.02)	>.50	-0.07 (.05)	>.10

Note. For the AUC_B , $R^2 = .08$ (Cox & Snell), .11 (Nagelkerke); $\chi^2(7) = 11.98$, $p = .101$. For the AUC_I , $R^2 = .08$ (Cox & Snell), .11 (Nagelkerke); $\chi^2(7) = 12.31$, $p = .091$.

Table 6
Test statistics and significance levels from multiple linear regressions (logistic regression for costly punishment) predicting trust and costly punishment behavior from anxiety levels, the stress group, the affiliation group and their interactions^a.

	Trust		Costly punishment	
	β	Sig.	B (SE)	Sig.
Constant		<.001	0.72 (.51)	>.10
Stress	-.15	>.30	-0.12 (.66)	>.80
Affiliation	.06	>.60	0.89 (.75)	>.20
AUC	-.11	>.70	-0.06 (.09)	>.40
Stress \times affiliation	-.09	>.60	-1.30 (.93)	>.10
Stress \times AUC	.15	>.50	0.09 (.10)	>.40
Affiliation \times AUC	.23	>.30	0.11 (.11)	>.30
Stress \times affiliation \times AUC	-.28	>.20	-0.16 (.13)	>.20
Risk inclination	.17	.048		

Note. For trust, $R^2 = .08$; $F_{8,135} = 1.44$, $p = .185$. For costly punishment, $R^2 = .06$ (Cox & Snell), .08 (Nagelkerke); $\chi^2(7) = 8.07$, $p > .30$.

^a For the prediction of trust behavior, risk inclination was included as an additional covariate into the model.

trustful and showed less costly punishment than participants in the control group, a pattern, which is indicative of fight-or-flight. Neither sharing nor reciprocity was affected by the individual stress induction. This stands in marked contrast to previous findings indicative of a tend-and-befriend pattern of social decision-making in men (von Dawans et al., 2012) following a psychological group stressor.

Given prior evidence in favor of fight-or-flight responses to psychosocial stress, we aimed at making an additional contribution to the literature by accounting for the potentially anomalous finding of tend-and-befriend behavior in social decisions following psychosocial stress (von Dawans et al., 2012). We hypothesized that such a behavioral pattern might have arisen as a by-product of using a group stressor, which might have inadvertently created greater feelings of affiliation. If this was the case, then we ought to expect a similar finding when participants interact with members of their in-group (i.e., in a state of increased affiliation) compared to members of their out-group. Whereas we show that our minimal group paradigm was effective in creating an intergroup bias (i.e., in-group members were believed to share more positive characteristics, and out-group members were rated as more negative) there was no interaction of stress and affiliation on social decision-making. Thus, our findings do not support the hypothesis that the priming of affiliative tendencies leads to tend-and-befriend behavior under stress. The lack of a stress by affiliation interaction could potentially be due to the fact that our interventions to establish group membership and induce stress were relatively mild. Future studies should expose real life groups to a full-blown stressor to induce the stronger affiliative feelings and stress responses needed for an unequivocal test of the affiliation priming hypothesis. The discrepancy between the present and previous findings (von Dawans et al., 2012) suggests a considerable context-dependence of how stress influences social exchange behavior (see Häusser et al., 2012 for similar findings on cortisol response to psychosocial stress). Importantly however our findings show that when confounds such as

affiliation are explicitly controlled for, behavioral patterns resulting from stress are characteristic of increased anxiety indicative of fight-or-flight response tendencies.

The observed changes in social behavior under stress were not driven by stress-induced changes in either cortisol or anxiety levels. However, stress induction obviously has numerous effects apart from triggering cortisol release and increasing anxiety. Participants in the stress group can be expected to exhibit reduced behavioral control than participants in the baseline control group (Radenbach et al., 2015; Schwabe and Wolf, 2009). Also, they might be feeling more angry (Moons et al., 2010) or even aggressive (Haller and Kruk, 2006; Kruk et al., 2004). Any of these potential stress effects may have driven the observed response pattern. Contrary to the cortisol stress response, baseline cortisol levels in the stress condition were associated with trust behavior. Specifically, individuals that entered the stress situation with a higher cortisol baseline were more likely to show increased trust, irrespective of their hormonal stress response. This finding can be considered as a potential interaction with long-term stress load, for which higher baseline cortisol levels have been taken as proxy (McEwen, 1998). Thus, our findings would suggest that individuals with experience of greater long-term stress may be most in need of affiliation and thereby attempt to maximize their resources the face of an acute challenge to overcome the experienced adversity. Future studies are required to empirically test this hypothesis.

While the observed decrease in trust following psychosocial stress can be interpreted as a decrease in one form of prosocial behavior, the interpretation of a stress-induced decrease in costly punishment is more complex. Although behavior in the ultimatum game is frequently referred to as a form of punishment it can also be seen as a desire for social norm enforcement (Fehr and Fischbacher, 2003). Our data support this alternative interpretation in that we found no association between the rejection of unfair offers (i.e., costly punishment) and the desire to spitefully punish others within the scope of the money burning game. Instead, the

rejection of unfair offers was positively, albeit marginally associated with offer sizes in the dictator game (i.e., sharing). Therefore, what we observe is most likely a decrease in norm enforcement under stress. Since norm enforcement in the ultimatum game has been taken as an indicator of self-control (Knoch et al., 2006; Steinbeis et al., 2012), we conclude that the current stress-induced reduction in norm enforcement can be interpreted as an effect of reduced self-control and increased impulsive behavior. This finding adds to previous work reporting that humans increasingly rely on habitual, quick and automatic processes rather than controlled and flexible cognitive strategies when making decisions under stress (Radenbach et al., 2015; Schwabe and Wolf, 2009). Based on this interpretation of costly punishment, the observed reductions in both trust and norm-reinforcement suggest a stress-related tendency for anxious flight instead of prosocial tend-and-befriend behavior.

In addition to the effects of stress, our affiliation priming influenced decisions. Thus, we found that reciprocity in trust behavior decreased while spiteful behavior increased when interacting with members of the out-group compared to the in-group. The direction of both our findings (i.e., less reciprocal and more spiteful interactions with members of the out-group) is consistent with the literature, which reports partiality toward one's in-group (Bernhard et al., 2006; Halevy et al., 2008; Hewstone et al., 2002). Consistent also with the data on the group impression ratings, these findings show that our induction of group membership was capable of eliciting differences in social behavior indicative of affiliative tendencies and spite. Nevertheless, using a minimal group paradigm may, as discussed earlier, be a relatively weak manipulation compared to using actually existent groups to induce strong feelings of affiliation and associated safety, and this may have masked potential interactions with the stress induction.

One aspect not currently considered is the interaction between effects of stress and individual differences in traits likely to lead to a responsiveness to stress. Thus, it has been shown recently that individual differences in anxiety as well as gender can have profound effects on social behavior (Tomova et al., 2014) as well as decision-making (Goette et al., 2015). Future studies may wish to look at this also in the context of social decisions related to trust by looking at variables like trait anxiety and thus refine their accounts of the effects of stress on social decision-making by including individual differences to account for a greater proportion of the variance.

The present study reports on the effects of stress and its interaction with affiliation on measures of social decision-making. We show that when using a procedure that stresses participants individually, we observe a reduced degree of trust and more impulsive decisions indicative of a pattern of fight-or-flight behavior. At the same time, higher baseline cortisol levels are correlated with greater trust. Affiliative priming has no interactive effect with anticipated stress exposure on behavior. While this could have been due to the relatively moderate induction of both stress and affiliation, at the very least our findings suggest that when removing critical confounds such as affiliation from the stress induction, previously observed patterns of tend-and-befriend switch to behaviors more akin to fight-or-flight. Like the group TSST-G (von Dawans et al., 2011), our anticipatory TSST paradigm offers an effective method of inducing stress simultaneously in a large number of participants. While the anticipatory TSST comes with the disadvantage of a relatively low cortisol responder rate, it has the advantage of deconfounding the modulating influence of the group setting on social behavior. It thus provides an efficient tool to study the unique effects of stress on social behavior. Seeing that the stress induction still retains some basic elements of social interaction (i.e., evaluation by a committee) future studies may wish to directly compare different methods of stress induction, both using psychosocial stressors (e.g., anticipatory TSST, TSST-G) as well as other,

decidedly non-social methods (e.g., cold pressor task; Hines and Brown, 1932).

Conflict of interest

None.

Funding

This study was funded by the Max-Planck Society. The Max-Planck Society had no role in the study design, data collection, analysis or interpretation of the data nor in writing the report or in the decision to submit this manuscript for publication.

Author's contribution

Steinbeis Nikolaus: Design, analysis, discussion and preparation of the manuscript.

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Linz Roman: Design, collection, analysis, discussion and preparation of the manuscript.

Singer Tania: Design, discussion and preparation of the manuscript.

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