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A friend in need: Time-dependent effects of stress on social discounting in men

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ABSTRACT

Stress is often associated with a tend-and-befriend response, a putative coping mechanism where people behave generously towards others in order to invest in social relationships to seek comfort and mutual protection. However, this increase in generosity is expected to be directed only towards a delimited number of socially close, but not distant individuals, because it would be maladaptive to befriend everyone alike. In addition, the endocrinological stress response follows a distinct temporal pattern, and it is believed that tend-and-befriend tendencies can be observed mainly under acute stress. By contrast, the aftermath (>1 h after) of stress is associated with endocrinological regulatory processes that are proposed to cause increased executive control and reduced emotional reactivity, possibly eliminating the need to tend-and-befriend. In the present experiment, we set out to investigate how these changes immediately and >1 h after a stressful experience affect social-distance-dependent generosity levels, a phenomenon called social discounting. We hypothesized that stress has a time-dependent effect on social discounting, with decisions made shortly after (20 min), but not 90 min after stress showing increased generosity particularly to close others. We found that men tested 20 min after stressor onset indeed showed increased generosity towards close but not distant others compared to non-stressed men or men tested 90 min after stressor onset. These findings contribute to our understanding on how stress affects prosocial behavior by highlighting the importance of social closeness and the timing of stress relative to the decision as modulating factors in this type of decision making in men.

Introduction

Stress is a ubiquitous part of modern life, and almost all of us are intuitively aware of the benefits of a supportive social network in difficult times. Although the fight-or-flight response was traditionally seen as the predominant biobehavioral way of responding to acute stress (Cannon, 1932) findings are emerging in favor of an alternative standpoint. According to this new line of evidence and in contrast to the offensive attack or defensive social withdrawal associated with fight-or-flight, in certain situations, the neuroendocrinological stress response can be buffered by the presence of others (Häusser et al., 2012) and acute stress can even promote prosocial behavior (Takahashi et al., 2005; Taylor et al., 2000; Von Dawans et al., 2012).

Taylor et al. (2000) proposed the tend-and-befriend reaction, a putative coping mechanism under which individuals behave generously towards others after stress to seek and provide mutual protection. This was initially thought to be a characteristically female response to stress, however increments in prosocial behavior after acute stress have since also been demonstrated in men (Von Dawans et al., 2012). By contrast, however, Vinkers et al. (2013) found reduced generosity after stress when male subjects were asked about their willingness to donate money to a charity. The key difference between these studies is that, while in that of Von Dawans et al. (2012) participants dealt with anonymous, but real people, in the study by Vinkers et al. (2013), participants were asked about donating to an impersonal charitable organization.

Thus the decision maker's social closeness to the target may be a key factor in determining the way stress affects generosity. This also makes intuitive sense from the perspective of the tend-and-befriend hypothesis, as it is more strategic to focus our costly support efforts on a delimited group of socially close others from whom we may expect support than indiscriminately befriend anyone. This hypothesis blends in with recent findings in social psychology on a phenomenon called social discounting showing that people are generous towards individuals they

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feel close to, such as family or good friends, while generosity decreases hyperbolically with increasing social distance between donor and recipient (Jones & Rachlin, 2006; Strombach et al., 2014, 2015; Takahashi, 2007).

Besides potentially exerting diverging effects on generosity according to social distance, stress may also affect generosity differently with respect to the amount of time that has elapsed between the stressor and the moment of decision making. It has repeatedly been demonstrated that the physiological and endocrinological changes caused by stress affect cognition in two distinct temporal domains (Joels & Baram, 2009). Immediately after stress, short-term actions of corticosteroid hormones in concert with noradrenaline effects synergistically modulate neural activity in brain regions implicated in cognitive and emotional functioning, including amygdala and hippocampus, while suppressing higher cognitive, prefrontal-cortex-dependent functions (Hermans et al., 2014; Joëls et al., 2011). The time-dependent changes in the neuroendocrinological response to stress go along with distinct effects on cognition and behavior: acute stress promotes habitual over goal directed behaviors (Schwabe et al., 2010, 2012), affects memory systems (Schwabe & Wolf, 2013; Zoladz et al., 2011), results in reduced sensitivity to monetary outcomes in the dorsal striatum and orbitofrontal cortex (Porcelli et al., 2012) and reduced strategy-use in economic games (Leder et al., 2013). Altogether, this may result in an increased level of emotional reactivity directly after stress, leading to a heightened tendency to tend-and-befriend as a way of coping. By contrast, in the aftermath of stress, thus >1 h after stressor onset, slower, genomic effects of corticosteroids promote higher cognitive functions and contribute to restoring emotional responses to pre-stress levels (Hermans et al., 2014; Joëls et al., 2011), arguably resulting in less need for tend-and-befriend. In agreement, individuals tested in the aftermath of stress showed decreased levels of altruistic punishment and increased tendency for selfish decisions in the Ultimatum game (Vinkers et al., 2013).

In the current experiment, we formally test the influence of the early and late effects of psychosocial stress in men on generosity across a range of social distances. We expect that individuals tested shortly after being stressed will be more generous towards people at close, but not necessarily towards people at distant social distances, revealing a higher tendency to tend-and-befriend those who are likely to provide comfort and support. Furthermore, we predict to find this social-distance-dependent effect of stress on generosity only shortly after stress, but not in its aftermath. Participants played a variant of the dictator game in which they repeatedly decided how much of an endowment they wanted to share with other people at variable social distances. By fitting a well-established mathematical social-discount function to participants' choice data to approximate their individual social-distance-dependent changes in generosity, we determined a) their generosity at close social distance, and b) the decrease of generosity across social distance.

Materials and methods

Participants

Seventy-eight adult male subjects participated in the experiment, pseudo-randomly allocated to four experimental groups as follows: early control: $N = 20$, early stress: $N = 19$, late control: $N = 19$, late stress: $N = 20$. We used male subjects in order to avoid the differential HPA-Axis reactivity caused by the menstrual cycle and the use of oral contraceptives in women (Kirschbaum et al., 1999). Each subject was screened via a telephone interview prior to the experiment; those who reported current use of psychoactive drugs, steroids, beta blockers, heavy smoking (>5 cigarettes per day), alcohol or drug abuse, current psychological or psychiatric treatment/illness or chronic physical illness were excluded from further participation. These exclusion criteria were chosen to be in line with prior publications investigating the effects of stress on decision making (e.g. Von Dawans et al., 2012). All participants were fluent German speakers and were not enrolled in either Psychology or Economics study programs. None of the participants participated in stress-research before and the subjects were unfamiliar with each other. Sociodemographic characteristics of the participants are listed in Table 1. All participants gave their written, informed consent prior to the experiment. The study was approved by the ethical committee of the Heinrich Heine University Düsseldorf and was performed in line with the Declaration of Helsinki. Participants were financially compensated for their participation and were instructed to refrain from taking alcohol or medicine as well as engaging in sexual activities 24 h before participation, and furthermore to refrain from smoking, exercise, consuming food, caffeine and drinks other than water 2 h before the experiment. The experiment was fully incentive-compatible, did not include deception and met the experimental standards in behavioral economics.

Experimental design

We employed a 2×2 between-subjects design. The two factors were condition (stress/control) and timing of behavioral testing relative to stress induction (early/late). Individuals in the early groups completed the experimental behavioral task 20 min after stress onset, that is, directly after the end of the stress induction procedure (see below), while participants in the late groups carried out their tasks 90 min after stressor onset. These timescales were chosen because they are compatible with the bidirectional time-dependent effects of stress (Joëls et al., 2011) and to facilitate comparisons with other designs using similar temporal profiles, such as Vinkers et al. (2013).

General procedure

After completing a number of online questionnaires (further details below), participants were invited to the laboratory. All experimental sessions took place between 14:00 and 17:00 h to control for diurnal variation in cortisol levels. We tested all participants in groups of 4 subjects. Upon arrival, participants were pseudo-randomly allocated to one of the four experimental conditions (early control, early stress, late control, late stress), so that in each session two participants were allocated to the early and two to the late groups of one of the conditions. The timeline of the experiment is depicted in Fig. 1. After giving informed consent, participants were asked to refrain from communicating with each other for the entire duration of the experiment. After initial baseline saliva and heart rate measurements and questionnaires (details below), participants underwent either a stress protocol, or a control condition.

Participants were subjected to psychosocial stress, using the group version of the Trier Social Stress Test (TSST-G; Von Dawans et al., 2011). Before commencement of the TSST-G, participants received information about the condition they were in. During the 20 min long TSST-G procedure, participants in the stress condition were asked to carry out a fictional job interview and a mental arithmetic task in front of an evaluative panel of experts while being videotaped. The control condition consisted of tasks comparable in terms of cognitive load but without the socio-evaluative aspect: participants were instructed to speak simultaneously, describing a friend and completing the subsequent mental arithmetic task; they were neither videotaped nor directly observed by the panel, who was present in the room but did not watch participants. After completion of the stress induction or control condition participants were asked to carry out the social discounting task immediately (early groups) or 70 min later, that is, 90 min after stress onset (late groups). During the waiting period, participants were provided with individual headphones and laptops showing a neutral, cognitively undemanding documentary film. After the behavioral task participants were asked to complete a demographic questionnaire as well as a manipulation check for the behavioral task, also detailed

Table 1
Baseline parameters and sociodemographic characteristics of all participants. BMI = Body Mass Index, BIS/BAS = behavioral inhibition/approach scale, STAI = State Trait Anxiety Inventory, BIS-15 = Barratt Impulsivity Scale, VAS = visual analogue scale, PANAS = positive and negative affect schedule.

	Early control		Early stress		Late control		Late stress		*F*-value	*P*-value	Effect size (η^2)
	Mean	SD	Mean	SD	Mean	SD	Mean	SD			
BMI	22.36	2.07	23.32	1.86	23.73	2.45	22.42	3.24	1.44	0.24	0.06
Baseline cortisol (nmol/l)	15.32	8.09	14.24	9.50	16.67	9.14	13.71	7.79	0.43	0.73	0.02
Baseline heart rate (bpm)	90.03	21.71	93.94	23.17	89.06	14.84	90.76	20.49	0.20	0.89	0.01
PANAS positive mood	27.90	6.60	26.58	5.62	28.74	6.09	27.85	5.43	0.42	0.74	0.02
Social desirability	8.95	3.43	9.89	2.56	8.68	3.16	8.45	2.72	0.86	0.46	0.03
BIS	15.65	2.91	16.37	3.11	16.58	3.55	15.90	3.01	0.35	0.79	0.01
BAS	23.50	5.38	23.16	4.19	24.00	5.00	22.30	3.77	0.47	0.70	0.02
Empathy	42.65	5.95	39.58	6.30	40.26	3.89	40.80	6.00	1.07	0.36	0.04
STAI	45.20	6.66	40.95	7.07	43.74	3.37	43.75	5.35	1.50	0.22	0.06
BIS-15	34.15	6.11	34.84	6.54	32.00	5.13	34.30	5.28	0.89	0.45	0.04

	Early control	Early stress	Late control	Late stress	X^2	*P*-value	Effect size (η^2)
	Median	Median	Median	Median			
Age	23.00	25.00	24.00	22.00	1.72	0.63	0.01
Baseline alpha amylase (U/ml)	58.39	75.48	73.44	64.29	4.46	0.22	0.02
PANAS negative mood	12.00	12.00	12.00	11.50	2.92	0.40	0.04
VAS baseline	12.50	11.00	20.00	15.00	1.05	0.79	0.02
Morningness	14.00	14.00	13.00	12.00	1.52	0.68	0.06

below. At the end of the experiment, participants were paid for their participation (see below) and fully debriefed.

Elicitation of social environment

As the purpose of the task was to investigate social distance dependent prosocial behavior, participants were asked to describe their social environment before receiving instructions for the experimental behavioral task. We used a method similar to that of Strombach et al. (2014, 2015) to quantify social distances. To introduce the concept of social distance, each participant was shown a scale consisting of 101 icons, with the leftmost icon representing the participant and the others representing his social environment. Participants were told that social distance 1 (the most leftward icon closest to the participant) represents the socially closest person, while distance 100 (the most rightward icon) would be a stranger who they may have randomly met on the street. Social distance 50 stands for a distant acquaintance, whose name they may not know. Once participants were familiar with the concept of social distance, they were asked to write down the names of representatives for the following social distances: 1, 2, 3, 5, 10, 20. Although distances 50 and 100 were also included in the experiment, participants could, but were not required to provide a name, as these distance levels often represent remote individuals. Participants were specifically asked not to include anyone in their list whom they have negative feelings towards.

Social discounting task

We measured generosity using a dictator game where, in each trial, participants were endowed with a fixed amount of money, and asked how much of their endowment they would give up to a person at a

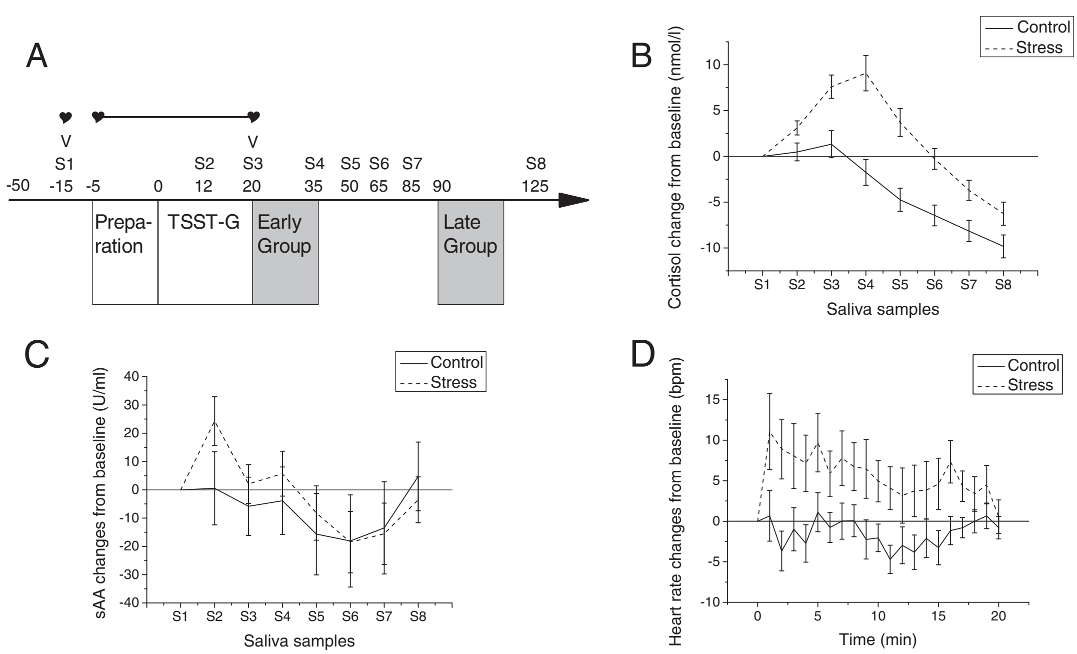

Fig. 1. Task design and physiological measurements. A) Timeline of the experiment: S = saliva samples, ♥ = heart rate measures, V = subjective stress ratings (VAS, PANAS). Numbers indicate time in minutes. B) Salivary cortisol changes from baseline. C) Salivary alpha amylase changes from baseline. D) Heart rate changes from baseline. Error bars indicate +/−1 standard error of the mean, SE.

specific social distance. We used three different endowment levels (EUR13, EUR15 and EUR17), and eight social distance levels (1, 2, 3, 5, 10, 20, 50 and 100; cf. Strombach et al., 2014, 2015). In total, participants completed 24 trials (8 social distances, 3 amounts) presented in a fully randomized order, each lasting 10 s. The main readout of this task was the percentage of money shared with a person at each social distance level. Participants then carried out a further task investigating intertemporal decision making. This task served as a non-publishable pilot study for a different project and is not reported here. Completion of the tasks lasted less than 10 min. Participants were informed that, at the end of the experiment, one of their decisions would be randomly chosen and paid out, therefore they and potentially another person would be able to earn money based on their decisions. The money the participant allocated to themselves was paid out directly after the experiment, in addition to the fixed compensation of EUR20, and for the money shared, subjects were asked to indicate the address of the other person in the randomly chosen trial. In case participants were concerned to disclose the address of a friend for privacy reasons, we asked to only disclose the name of the particular friend to allow us to prepare a cheque that only the recipient could cash and gave this cheque to the participant to forward to the particular person. If the randomly chosen trial was about an anonymous person or stranger, e.g. at higher social distances, a random person on the campus of the University of Düsseldorf, Germany received the reward.

Detailed instructions regarding the behavioral tasks were given before stress induction, followed by a series of multiple-choice questions to ensure participants understood these instructions. In addition, short booster instructions and a test trial were provided on the computer screen directly before the start of the behavioral task. As participants were specifically instructed to think, at each social distance elicitation, of the individuals they indicated prior to the experiment, we performed a stability check at the end of the experiment and asked participants to write down the names of and further information about their relationship to the person (how long and how well they know them) they chose for each social distance prior to the task. The behavioral task was programmed and presented using Presentation Software (Neurobehavioral Systems, Albany, CA).

Saliva sampling

To confirm a hormonal stress response to the TSST-G procedure, saliva samples were collected at 8 different time points throughout the experiment as shown in Fig. 1, using Salivette (Sarstedt, Germany) devices containing a cotton wool swab that participants had to lightly chew on for 60 s to allow the swab to fill with saliva. Saliva samples were analyzed as reported by Rohleder et al. (2004). Samples were frozen and stored at −20 °C until analysis. After thawing, Salivettes were centrifuged at 3000 rpm for 5 min, which resulted in a clear supernatant of low viscosity. Salivary cortisol concentrations were measured using commercially available chemiluminescence immunoassays with high sensitivity (IBL International, Hamburg, Germany). The intra and interassay coefficients for cortisol were below 8%.

Concentrations of alpha amylase in saliva were measured by an enzyme kinetic method: Saliva was processed on a Genesis RSP8/150 liquid handling system (Tecan, Crailsheim, Germany). First, saliva was diluted 1:625 with double-distilled water by the liquid handling system. Twenty microliters of diluted saliva and standard were then transferred into standard transparent 96-well microplates (Roth, Karlsruhe, Germany). Standard was prepared from "Calibrator f.a.s." solution (Roche Diagnostics, Mannheim, Germany) with concentrations of 326, 163, 81.5, 40.75, 20.38, 10.19, and 5.01 U/l alpha amylase, respectively, and double distilled water as zero standard. After that, 80 ml of substrate reagent (α-amylase EPS Sys; Roche Diagnostics, Mannheim, Germany) were pipetted into each well using a multichannel pipette. The microplate containing sample and substrate was then warmed to 37 °C by incubation in a waterbath for 90 s. Immediately afterwards, a first interference measurement was obtained at a wavelength of 405 nm using a standard ELISA reader (Anthos Labtech HT2, Anthos, Krefeld, Germany). The plate was then incubated for another 5 min at 37 °C in the waterbath, before a second measurement at 405 nm was taken. Increases in absorbance were calculated for unknowns and standards. Increases of absorbance of diluted samples were transformed to alpha amylase concentrations using a linear regression calculated for each microplate (Graphpad Prism 4.0c for MacOSX, Graphpad Software, San Diego, CA).

Heart rate measurement

Heart rate was monitored using POLAR RCX3M training computers. Measurements were taken at baseline in an upright standing position to match the position maintained during the stress induction procedure. Heart rate was monitored throughout the stress induction until the end of the TSST-G.

Subjective stress ratings

In order to check whether subjective perception of stress and mood changed in response to the TSST-G procedure, participants completed the Visual Analogue Scale (VAS, 100 mm scale) and the Positive and Negative Affect Schedule PANAS (Watson et al., 1988) before and after the stress induction procedure.

Trait questionnaires

Although trait measures were not the primary focus of our study, we included several questionnaires in our design to ensure that the groups did not differ on characteristics that could modulate generosity. Participants completed the behavioral approach/inhibition scale (BIS/BAS), a widely used measure of reward and punishment sensitivity (Carver & White, 1994) prior to the experimental tasks and stress induction. To control for potential preexisting anxiety that may influence subjects' reaction to the TSST-G procedure, each subject completed the trait scale of the State Trait Anxiety Inventory (Spielberger et al., 1983). As empathy is known to influence prosocial behavior, each participant completed the German version of the Interpersonal Reactivity Index (Davis, 1980). Furthermore, impulsivity was measured using the short German version of the Barratt Impulsiveness Scale (BIS-15; Meule et al., 2011). As the TSST-G procedure involves social evaluation, it is possible that the participants' responses reflected social desirability effects in addition to their true preferences. To control for social desirability, each participant completed the Social Desirability Scale 17 (SDS-17; Ströber, 2001). As chronotype may have an effect on cardiovascular responses to stress, participants also filled out the short version of the Morningness–Eveningness Questionnaire (Randler, 2013).

Data analysis

Baseline parameters

To ascertain that our experimental groups did not differ in baseline parameters, we carried out one-way analyses of variance (ANOVAs) or Kruskal–Wallis H tests (in case of non-normally distributed measures).

Stress induction

We tested whether the psychosocial stress induction resulted in a change in stress-hormone levels as follows: We calculated the area under the curve increase across all eight saliva sample measures (S1-S8; AUCi) for each participant and each hormone, as well as heart rate measures for the 20 min duration of the TSST in line with the procedure described by Pruessner et al. (2003). We additionally calculated the maximum percent change from baseline for sAA during the stress induction procedure. This was done because stress-induced changes in sAA can fade quickly, therefore measures over a longer period of time such as the AUCi involving all 8 sampling time points may not reveal the differences between the two treatment conditions effectively. To assess subjective stress and mood ratings, change scores (post TSST-G minus baseline) were calculated for the VAS as well as the PANAS scales. The AUCi of cortisol as well as the VAS and PANAS positive mood change scores were analyzed using two-way ANOVAs with condition (stress/control) and timing (early/late) as the between subject factors. The AUCi of heart rates and sAA, the maximum percent change in sAA during the TSST-G as well as change in negative affect were analyzed using non-parametric tests, as the data were not normally distributed.

Social discounting

We used a psychometric approach to address the effects of stress on social discounting. The decline of generosity across social distance is best described by the following standard hyperbolic function (Jones & Rachlin, 2006; Strombach et al., 2014, 2015; Takahashi, 2007):

$$v = \frac{V}{(1 + kD)} \tag{1}$$

where v is the discounted other-regarding value of the reward (here: percentage of money shared), V describes the height of the function independent of its steepness and can be interpreted as the generosity level at close social distance, D is a measure of social distance, and k describes the degree of discounting. We fitted this hyperbolic social-discount function to the percentage of money shared at each social distance level, both on an averaged group level (separately for the four experimental groups) and individually for each participant to approximate their individual social-distance-dependent changes in generosity. We used the best-fitting social discount parameters V and k as estimates of a) participants' generosity at close social distance (parameter V), and b) the decrease in generosity across social distance (parameter k), respectively. The time-dependent effects of stress on V (generosity at close social distance) and k (decline in generosity across social distance, log-transformed to obtain non-skewed distributions) parameters were analyzed using two way ANOVAs with condition (stress/control) and timing (early/late) as the between subject factors. In case of significant interaction, t-tests were carried out as post-hoc tests to determine which of the four experimental groups differed from each other. We applied Bonferroni-correction to control for multiple comparisons.

Overall measure of generosity

As an overall measure of generosity independent of social distance, we calculated the area under the curve of the amount shared by each participant (AUCSD) using the same approach that had been used by Strombach et al. (2014). In accordance with the procedure described by Pruessner et al. (2003) we used the ‘area under the curve with respect to ground’ (AUCg) formula for this analysis, as this measure is better suited to assess the overall strength of generosity, rather than focus on changes across social distance (Pruessner et al., 2003).

Neuroendocrinological correlates of generosity

To determine whether there is a relationship between hormone levels and social discounting we carried out a Spearman rank order correlation analysis between the discounting parameters V and k, the overall measure of generosity (AUCSD), changes in hormone levels as well as baseline levels of sAA and cortisol. As we expected diverging relationships between stress and social discounting depending on the time point of testing, we carried out separate tests for the early and late groups.

Effect sizes

The effect sizes reported are eta-squared (η^2) for ANOVAs and Kruskal–Wallis tests, Cohen's d for pairwise comparisons and r for Mann–Whitney U tests.

Results

Baseline parameters

There was no significant difference in any of the trait personality measures (empathy, reward and punishment sensitivity, trait anxiety, social desirability, chronotype and impulsivity), physiological measures (baseline measures of heart rate, cortisol, sAA), personal measures (Body Mass Index, age) and baseline subjective ratings of mood and stress between the experimental groups (Table 1). Age, baseline sAA, PANAS Negative Mood, VAS baseline and Morningness were not normally distributed and hence subjected to non-parametric testing. These parameters are shown separately at the bottom of the table.

Stress induction

Cortisol

One participant had to be excluded from the analysis due to insufficient saliva in the samples. The AUCi of the cortisol response was significantly larger in the stress than in the control condition indicating that our stress manipulation resulted in pronounced increases in cortisol level (main effect of condition: $F_{1,73} = 15.19$, $P < 0.001$, $\eta^2 = 0.17$), while changes in the control group followed circadian rhythms. As expected, there was no significant effect of timing of behavioral testing (early vs. late) or an interaction between timing and condition (timing x condition: $F_{1,73} = 0.69$, $P = 0.41$, $\eta^2 = 0.01$; timing: $F_{1,73} = 0.59$, $P = 0.44$, $\eta^2 = 0.01$; Fig. 1B).

Alpha amylase (sAA)

One participant had to be excluded from the analysis due to insufficient saliva in the samples and a further participant who only provided usable samples at 4 of the 8 measuring time points was also excluded. The AUCi computed over all sample time points (S1–S8) did not differ between the stress ($Mdn = -0.01$) and control ($Mdn = -0.01$) groups (Mann–Whitney U test, $U = 633.50$, $Z = -0.92$, $P = 0.36$, $r = 0.11$). However, we found that the maximum percent increase from baseline in sAA during the stress induction protocol was significantly higher in the stress ($Mdn = 0.37$) than in the control group ($Mdn = 0.11$; Mann Whitney U test, $U = 503.5$, $Z = -2.27$, $P = 0.02$, $r = 0.26$), suggesting that sAA levels significantly rose in response to stress, but that the response was relatively short-lived (Fig. 1C).

Heart rate

Heart rate measures were not recorded for one participant due to technical difficulties with the measuring device. A Mann Whitney U test with the AUCi of heart rates revealed that the stress group had a much larger increase in heart rates than the control group during the stress induction procedure ($Mdn_{Control} = -0.04$, $Mdn_{Stress} = 0.14$, $U = 387$, $Z = -3.61$, $P < 0.001$, $r = 0.41$) (Fig. 1D).

Subjective stress ratings

The 2×2 ANOVA showed that the increase in subjective feelings of stress, measured by changes in VAS scores, did not significantly differ between the control and stress conditions in either the early (early stress: M = 12.21, SD = 15.86, early control: M = 6.13, SD = 15.35) or the late groups, although there was a descriptive difference, with larger increases in the stress groups than in the control goups (late stress: M = 10.15, SD = 8.46, late control: M = 5.58, SD = 19.03; main effect of condition: $F_{1,74} = 2.43$, $P = 0.12$, $\eta^2 = 0.03$; main effect of timing: $F_{1,74} = 0.15$, $P = 0.70$, $\eta^2 = 0.002$).

Changes in negative affect did not differ between the stress and control conditions ($Mdn_{Control} = 0$, $Mdn_{Stress} = 1$; Mann–Whitney U test: $U = 624.50$, $Z = -1{,}37$, $P = 0.17$, $r = -0.16$).

Positive affect increased in the stress group (early stress: M = 1.68, SD = 7.77, late stress: M = 1.65, SD = 4.94) after the TSST-G, while it decreased in the control group (early control: M = −1.55, SD = 3.87, late control: M = −2.26, SD = 4.56), resulting in significant differences between the two conditions, with no difference between the early and the late groups (main effect of condition: $F_{1,74} = 8.33$, $P = 0.005$, $\eta^2 = 0.10$, main effect of timing: $F_{1,74} = 0.09$, $P = 0.77$, $\eta^2 = 0.001$, timing × condition: $F_{1,74} = 0.08$, $P = 0.79$, $\eta^2 = 0.000$).

Stress modulates generosity to close others in a time-dependent manner

We examined whether stress had an effect on the shape of the social discounting function in our male sample, reflecting changes in generosity to close others as well as changes in the decline of generosity with increasing social distance. To this end, we fitted, for each participant individually, a standard hyperbolic model (Eq. 1) to the individual percentages of money shared with recipients at variable social distance levels, similar to the procedures reported in previous publications (Jones & Rachlin, 2006, Strombach et al., 2014, 2015). The hyperbolic model provided a good fit to the data (averaged adjusted R^2 early control: 0.99, early stress: 0.98, late control: 0.95, late stress: 0.98). Fig. 2 shows the mean amounts shared and the best-fitting hyperbolic function to the mean amounts shared for each experimental group.

As described above, the hyperbolic equation contains two free parameters. V describes the height of the function independent of its steepness (Jones & Rachlin, 2006) and could be interpreted as an indicator of generosity at close social distances, with larger values indicating higher generosity to close others. The parameter k describes the degree of social discounting, that is, the general degree of decline in generosity with increasing social distance, with higher values indicating a steeper decline.

First, to test for stress- and time-effects on generosity towards close others, we calculated a two-way ANOVA with condition (stress/control) and timing (early/late) as between-subject factors and V as the dependent variable. This analysis revealed a significant main effect of timing ($F_{1,74} = 11.31$, $P = 0.001$, $\eta^2 = 0.14$) and a non-significant main effect of condition ($F_{1,74} = 1.22$, $P = 0.27$, $\eta^2 = 0.01$). Most importantly, as predicted, a significant interaction effect between condition and timing on V ($F_{1,74} = 9.01$, $P = 0.004$, $\eta^2 = 0.09$) was found. In line with our hypothesis, Bonferroni corrected post hoc tests revealed that the early stress group had significantly higher V parameters than the late stress group ($t(37) = 4.60$, $P < 0.001$, $d = 1.47$) confirming that generosity to socially close persons was affected by stress in a time-dependent manner. The early stress group also had significantly higher V parameters than the early control group ($t(37) = -2.51$, $P = 0.02$, $d = 1.07$), indicating that generosity towards socially close individuals was increased directly after stress. The late stress group had on average lower V parameters than the late control group, but this difference was not significant ($t(37) = 1.66$, $P = 0.11$, $d = 0.53$; Fig. 3). Overall, our analyses revealed that stress had a time-dependent effect on generosity towards socially close individuals in men, with increased generosity right after stress, but not in its aftermath. The non-significant difference between the V parameters of the late control and late stress groups leaves open the possibility that the stress effects on generosity were only transient.

We next tested whether stress or time-point of testing had an effect on the log-transformed k-values, i.e. on the general decline in generosity as a function of social distance. We found no significant difference in log-k between any of the conditions (main effect of condition: $F_{1,74} = 0.01$, $P = 0.92$, $\eta^2 = 0.000$; main effect of timing: $F_{1,74} = 0.13$, $P = 0.73$, $\eta^2 = 0.002$, condition × timing interaction: $F_{1,74} = 3.24$, $P = 0.08$, $\eta^2 = 0.042$; Fig. 3).

Effect of stress on overall generosity

Our analyses showed that stress had no effect on overall generosity, i.e., average generosity independent of social distance, measured as the area under the curve of the shared fractions of the endowments (AUCSD; main effect of condition: $F_{1,74} = 0.09$, $P = 0.77$, $\eta^2 = 0.001$; main effect of timing: $F_{1,\ 74} = 0.37$, $P = 0.55$, $\eta^2 = 0.01$ condition x timing: $F_{1,74} = 0.12$, $P = 0.73$, $\eta^2 = 0.002$).

Neuroendocrinological correlates of generosity

We found no significant correlation between any of the hormonal measures and the discount parameter V, neither in the early, nor the late groups (all $P > 0.36$), suggesting that the stress-effects on V may have been mediated by stress-related factors other than noradrenaline or cortisol action. There was a significant negative correlation between k and the changes in sAA levels ($r_s = -0.32$, $P = 0.05$) in the late stress group, while correlations between k and hormonal measures remained non-significant in the early stress group (all $P > 0.13$). Overall generosity (AUCSD) showed a negative relationship with baseline cortisol levels in the early ($r_s = -0.34$, $P = 0.04$) group, but correlation between hormonal measures and overall generosity remained non-significant in the late group (all $P > 0.12$).

Discussion

In the present study, we demonstrated that psychosocial stress altered social discounting in male decision-makers. Critically, the way stress affected the social discount function was dependent on the time

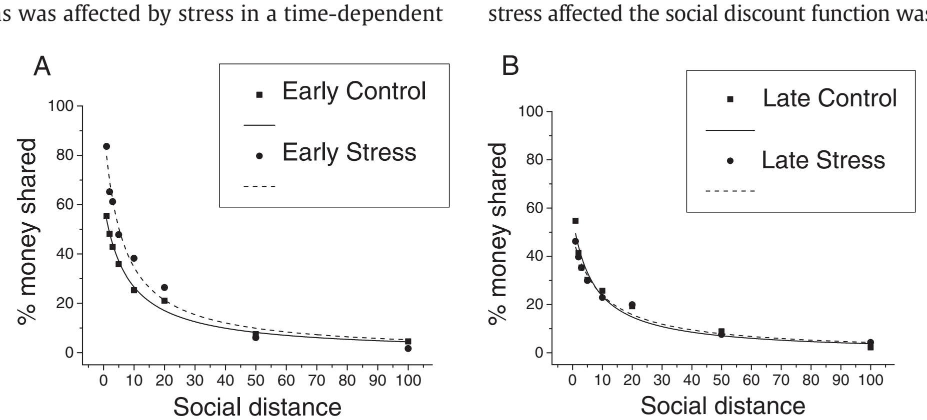

Fig. 2. Mean percentage of money shared with recipients at variable social distance levels: The lines represent the best-fitting hyperbolic model to the mean values in the early (A) and late (B) groups.

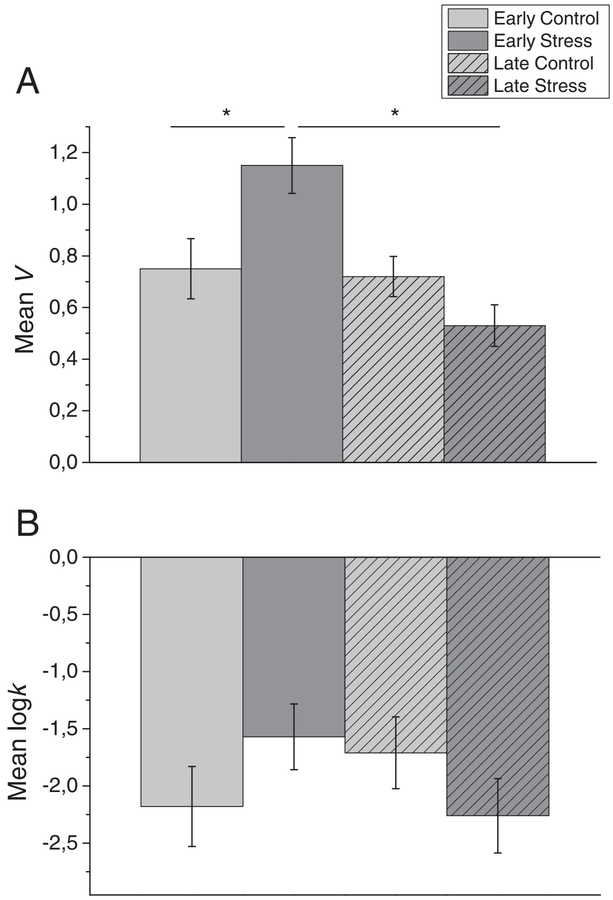

Fig. 3. The effects of stress and time point of testing on social discounting parameters A) V parameter of the four experimental groups. B) log-transformed k parameters. Error bars indicate +/− 1 standard error of the mean, SE. Significant differences are indicated by an asterisk.

that elapsed between the stressor and the task. To elicit social discounting, we used an adapted version of the dictator game in which participants had to indicate how much money of an initial endowment they were willing to share with recipients at variable social distances. During decisions made shortly after stress induction, stressed participants, relative to non-stressed control subjects, showed elevated levels of generosity specifically towards socially close individuals, as reflected by differences in the V parameter of the social discount function. However, the steepness by which generosity levels decayed across social distance was less affected by stress, as reflected by the non-significant effects of stress on the k parameter of the social discount function. Taken together, our results confirm and extend the tend-and-befriend hypothesis by the observation that directly after stress higher generosity levels are restricted to socially close others from whom support in stressful times could be expected.

Our study reconciles findings from two earlier studies in male samples that found opposing effects of stress on generosity. Using the dictator game, Von Dawans et al. (2012) showed that exposure to acute stress increased sharing, while Vinkers et al. (2013) presented evidence to the contrary. The fundamental difference between the two studies was that in the former, participants made decisions to share money with real human individuals, while Vinkers et al. (2013) asked participants about donating to an impersonal charitable organization. We show here that social distance is an essential factor that modulates the way stress affects prosocial behavior.

Evidence has recently emerged showing that the physiological stress response follows a particular temporal pattern (Joels & Baram, 2009) with specific time-dependent neuroendocrinological changes that have differential effects on memory retrieval (Schönfeld et al., 2014; Schwabe & Wolf, 2014) as well as economic (Takahashi et al., 2005) and social decision making (Vinkers et al., 2013). It has already been demonstrated that decision making >1 h after stress was associated with decreased levels of altruistic punishment and increased tendency for material self-interest compared to decisions made directly after stress (Vinkers et al., 2013). Accordingly, we hypothesized and confirmed that stress may also have a time-dependent effect on the stress-related increase in generosity towards close others, reflected in the V parameter of the social discount function. These results fit well with neurobiological findings about time dependent effects of cortisol on prefrontal functioning. Henckens et al. (2010) showed that slow, genomic effects of corticosteroids increased connectivity between the amygdala and the mPFC, facilitating prefrontal control over hypervigilance and anxiety associated with increased amygdala activation. This heightened prefrontal functioning increases executive control and reduces emotional reactivity which may have resulted in the observed patterns of normalized generosity to close others, suggesting a reduced need for a tend-and-befriend reaction >1 h after stress.

We found a negative relationship between the changes in sAA levels and the parameter k in the late stress group, indicating that altered levels of sympathetic activation did indeed modulate prosocial behavior by making the decline in generosity as a function of social distance less steep. Similarly, we found that in the early group, overall generosity showed a negative relationship with changes in sAA levels, thus indicating that a heightened sympathetic drive response is associated with heightened generosity in the early group as well. However, these effects were rather weak and we found no relationship between stress-induced hormonal changes and V, i.e. generosity to close others. Thus, the exact physiological or psychological mechanisms by which stress modulates generosity seem to be complex, and not merely the linear consequence of altered cortisol and/or noradrenergic action. In order to establish the precise role of the hormones cortisol and noradrenaline in modulating prosocial behavior, a direct, causal, pharmacological manipulation is necessary and should be the topic of future research.

A minor point that remains to be addressed is the unexpected results we found in subjective ratings of mood and stress, such as no significant difference between the stress and control conditions in subjective feeling of stress, and increase in positive mood in the stress group as well as decrease in positive mood in the control group. We believe this was due to the fact that we only took subjective measures at baseline and *after* the TSST-G, at which point feelings of relief could have overshadowed feelings of stress. In hindsight, it would have been better to take these measures during the stress protocol as well. Overall we find it unlikely that these subjective reports in mood interfere with our results, as hormonal stress responses confirmed a successful stress manipulation and control condition.

A limitation of our study is that we only used male participants. Therefore we cannot generalize our findings to women. A direct comparison of men and women should be a topic of future research. Nonetheless our findings add further support to the presence of a tend-and-befriend reaction in men, which was, until recently thought to be a characteristically female response to stress (Taylor, 2006).

Conclusion

In conclusion, our study demonstrated that the modulation of prosocial behavior by stress in men is time- and social-distance-dependent. We showed that generosity increases after direct exposure to psychosocial stress, but only towards socially close individuals and only directly after stress. These results support and extend the tend-and-befriend hypothesis and reconcile findings from previous studies that found divergent effects of stress on prosocial behavior. Furthermore, our study has important real life implications by highlighting that not only does our social closeness to individuals in our social environment influence the way we make prosocial decisions, but that exposure to stress can shift the balance in those decisions favoring socially close others, perhaps sharpening distinctions between those others perceived as ingroup and outgroup. Our study thus opens up new avenues to understand and tackle tensions arising whenever individuals make decisions within a stressful social network, in the contexts of cultural and ethnic conflicts, parochialism, and racism.

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