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PNEC-2331; No. of Pages 9
ARTICLE IN PRESS

Psychoneuroendocrinology (2013) xxx, xxx—xxx

Available online at www.sciencedirect.com

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Time-dependent changes in altruistic punishment following stress

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Received 7 October 2012; received in revised form 22 November 2012; accepted 19 December 2012

KEYWORDS
Stress;
Cortisol;
Alpha-amylase;
Trier Social Stress Test;
Non-genomic;
Genomic;
Social decision making;
Dictator Game;
Ultimatum Game;
Temporal

Summary Decisions are rarely made in social isolation. One phenomenon often observed in social interactions is altruistic punishment, i.e. the punishment of unfair behavior by others at a personal cost. The tendency for altruistic punishment is altered by affective states including those induced by stress exposure. Stress is thought to exert bi-directional effects on behavior: immediately after stress, reflex-like and habitual behavior is promoted while later on more far-sighted, flexible and goal-directed behavior is enhanced. We hypothesized that such time-dependent effects of stress would also be present in the context of altruistic punishment behavior. Healthy male participants ($N = 80$) were exposed to either a grouped stress test or a control condition. Participants were tested in prosocial decision making tasks either directly after stress or 75 min later. Altruistic punishment was assessed using the Ultimatum Game. General altruism was assessed with a one-shot version of the Dictator Game in which an anonymous donation could be offered to a charitable organization. We found that stress caused a bi-directional effect on altruistic punishment, with decreased rejection rates in the late aftermath of stress in response to ambiguous 30% offers. In the Dictator Game, stressed participants were less generous than controls, but no time-dependent effect was observed, indicating that the general reward sensitivity remained unchanged at various time-points after stress. Overall, during the late aftermath after acute stress exposure (i.e. 75 min later), participants acted more consistent with their own material self-interest, and had a lower propensity for altruistic

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0306-4530/$ — see front matter
http://dx.doi.org/10.1016/j.psyneuen.2012.12.012

Please cite this article in press as: Vinkers, C.H., et al., Time-dependent changes in altruistic punishment following stress. Psychoneuroendocrinology (2013), http://dx.doi.org/10.1016/j.psyneuen.2012.12.012

punishment, possibly through upregulation of cognitive self-control mechanisms. Thus, our findings underscore the importance of time as a factor in simple, real-life economic decisions in a stressful social context.

1. Introduction

Human decisions are often made in the context of social interactions (Fehr and Fischbacher, 2003). Balancing self-interest and altruistic preferences, people sometimes voluntarily decide to forego monetary benefits in order to punish violations of social norms (altruistic punishment) (Fowler, 2005). This enforcement of social norms by punishing non-reciprocity may even occur at a personal cost and generally does not yield any obvious material benefits. One approach to examine such responses to fairness is the Ultimatum Game (UG) (Güth et al., 1982). In the UG, two players must divide a sum of money, with one subject proposing the specific division. The other subject then decides to accept or reject this offer. If the offer is accepted, the sum is split as proposed. If it is rejected, neither player receives anything. The UG thus measures strategic social decisions about resource allocation and can be used to assess altruistic punishment behavior by determining how rejection rates depend on the absolute offered amount or on the offered percentage of the stake.

Several studies have suggested that altruistic punishment strategies and social decision making induce an emotional response. Thus, unfair offers in the UG elicited higher emotional arousal as measured by skin conductance responses (van't Wout et al., 2006), and also elicited activity in the anterior insula (Sanfey et al., 2003), a brain area involved in negative emotions (Phillips et al., 1997). Also, rejection of unfair offers in the UG was accompanied with an increase in alpha-amylase (Takagishi et al., 2009). Conversely, stress and emotion are known to alter altruistic punishment strategies and social decision making (Takahashi, 2005). For instance, sadness induced by a movie clip resulted in increased rejection rates of unfair (but not fair) offers in the UG (Harle and Sanfey, 2007), a finding that was later replicated and accompanied by increased activation of the anterior insula (Harle et al., 2012). Also, cortisol levels in response to stress were found to correlate positively with egoistic decision-making in emotional moral dilemmas (Starcke et al., 2011).

Studies have already shown that stress affects various cognitive domains including memory, attention, decision making, and social reward systems (Henckens et al., 2009; van den Bos et al., 2009; Wolf, 2009; Merz et al., 2010; Starcke and Brand, 2012) including social approach behavior (von Dawans et al., 2012). It has increasingly become evident that stress-induced changes in behavior may follow a distinct temporal pattern (de Kloet et al., 2005). Thus, immediately after stress, individuals rapidly adjust behavior to promote instrumental and habitual short-term behavior (Schwabe et al., 2010). This process most likely involves catecholamines and the fast (non-genomic) effects of corticosteroids (Joels and Baram, 2009). In contrast, later on — in the late aftermath of stress — behavior is assumed to aim at restoring higher cortical functions, with more flexible behavior to meet long-term goals (Diamond et al., 2007; Williams and Gordon, 2007). Using hydrocortisone administration, these late restorative effects of stress have been ascribed to genomic corticosteroid actions (Henckens et al., 2010). We hypothesized that changes in altruistic punishment strategies under stressful conditions may also follow a time dependent course. Specifically, we expect that acute stress may result in more habitual and less goal-directed behavior, which could be expressed as stronger emotional reactions to unfairness and consequently higher impulsive rejection rates in the UG. By contrast, later on, an increase in deliberative and goal-directed behavior is expected to lead to enhanced cognitive control and therefore reduced rejection rates of perceived unfair offers. Alternatively, altruistic punishment could be considered as an act of self-control rather than an impulsive response to unfair treatment (Nowak et al., 2000; Knoch et al., 2006, 2008). According to this idea, a responder may reject unfair offers in the UG to prevent a reputation of being easily exploitable and to enforce social norm compliance at the cost of failing to maximize economic self-interest. Thus, rejecting unfair offers would require an inhibition of the impulse to maximize economic interests (Knoch et al., 2006; Yamagishi et al., 2009).

To our knowledge, no published studies have directly investigated the time-dependent effects of acute social stress on altruistic punishment. Therefore, eighty healthy male participants were exposed to either a grouped stress test (Grouped Trier Social Stress Test, TSST-G) or a control condition (von Dawans et al., 2011). Social decision making was assessed either directly after stress (incompatible with genomic actions of corticosteroids) or 75 min later (sufficiently long to allow the development of gene-mediated events) using a 2 (stress/control) $\times$ 2 (early/late) between-subjects design. It is possible that stress-induced changes in altruistic motivations may result in a non-specific inclination to reward others (von Dawans et al., 2012), and social evaluation has been found to increase money allocation (Takagishi et al., 2009). Such altruistic rewarding (as opposed to altruistic punishment) could confound the interpretation of the UG results. As a control test, we therefore measured the altruistic inclination using a one-shot version of the Dictator Game (DG). In this simplified version of the DG, a second party is the passive recipient of the proposer's offer and therefore cannot reject it. The magnitude of allocated amount in the DG is considered a proportional measure of altruism because there is no direct personal gain for the proposer (Kahneman et al., 1986; Rilling and Sanfey, 2011). To measure altruism beyond the interpersonal and economic domain, we chose a variant of the DG in which an anonymous donation could be offered to a charitable organization (Moll et al., 2006).

2. Methods

2.1. Participants

Male adult healthy participants were recruited (N = 80, Table 1). The study was approved by the Utrecht Medical Center

Table 1 Baseline sociodemographic characteristics of all groups. Data are presented as mean (standard deviation). BMI: body-mass index. BIS/BAS: behavioral inhibition/avoidance system. STAI: Spielberger State and Trait Anxiety Inventory.

	Control Early	Control Late	Stress Early	Stress Late	F value	P value
Age	23.2 (2.6)	22.6 (1.7)	22.7 (3.0)	22.9 (2.5)	0.27	0.85
BMI	23.3 (3.6)	23.7 (3.9)	21.4 (2.5)	22.7 (2.4)	1.96	0.13
BIS	18.2 (4.1)	19.5 (3.8)	20.3 (3.8)	18.2 (2.7)	1.63	0.19
BAS Drive	11.3 (2.2)	11.3 (1.9)	11.5 (2.0)	11.1 (1.9)	0.10	0.96
BAS Reward Responsiveness	17.3 (2.2)	17.3 (1.6)	17.8 (1.5)	17.4 (1.4)	0.44	0.73
BAS Fun Seeking	11.6 (2.4)	11.6 (1.8)	11.7 (2.2)	12.0 (1.9)	0.18	0.91
STAI Trait	32.3 (7.9)	35.5 (9.3)	31.1 (7.2)	32.1 (7.4)	1.14	0.34
Testosterone (pmol/l)	188.5 (47.9)	193.2 (51.5)	163.7 (44.5)	201.4 (63.1)	1.85	0.15
Baseline cortisol (nmol/l)	9.9 (3.9)	9.3 (2.5)	8.9 (3.1)	9.4 (2.6)	0.35	0.79
Baseline alpha-amylase (100,000 U/ml)	2.7 (2.4)	2.1 (1.2)	2.5 (1.7)	2.8 (1.2)	0.58	0.63

ethical review board and performed according to the ICH guidelines for Good Clinical Practice and the Declaration of Helsinki and its latest amendments. All participants gave their written informed consent prior to their inclusion in the study. Participants were not eligible to participate in case of current drug use, use of self-reported psychoactive medication, physical or mental illness, smoking, or not being fluent in Dutch. Current use of psychoactive substances (amphetamines, MDMA, barbiturates, cannabinoids, benzodiazepines, cocaine, and opiates) was determined with a urine multi-drug screening device (InstantView) and participants that scored positive were excluded from participation. Participants were financially compensated (see below) and were instructed to refrain from eating, drinking and heavy exercise at least 2 h before the experimental session, as well as to refrain from caffeine use at least 4 h before the experimental session. All participants reported that they adhered to these instructions. Participants had not previously been enrolled in stress-related research and were unfamiliar with each other.

2.2. General procedure

All experiments occurred between 1200 h and 1700 h to control for diurnal variations of cortisol secretion. Participants were instructed not to communicate with each other. After inclusion, participants were randomized to either the stress condition (group-wise Trier Social Stress Test; TSST-G) or a validated non-stressful control condition (Fig. 1A). The UG and DG were completed either directly after the stress/control condition (early groups) or 75 min later (late groups, 90 min after the onset of the TSST-G) (Fig. 1A). Thus, a 2 (stress/control) × 2 (early/late) between-subjects design was employed. The stress condition was carried out in accordance with previously published methods (von Dawans et al., 2011). Five minutes before the stress or control intervention, all participants received written instructions for the appropriate test condition. In the stress condition, up to four participants sequentially delivered a public speech and performed mental arithmetic in front of an evaluative panel while being videotaped and recorded. The control condition consisted of a speech and arithmetic performance carried out simultaneously by all participants, ensuring a comparable cognitive load but without the social evaluative aspects.

2.3. Behavioral tasks

2.3.1. General

All behavioral tasks were programmed and presented using Presentation software (Neurobehavorial Systems, Albany, CA, USA). After inclusion on the experimental day, participants received written instructions on the aim and methodology of the behavioral tasks. These instructions were accompanied by test exercises to ensure that all participants had understood the instructions. Also, participants were informed that financial compensation would be partially determined by randomly averaging several trials at the end of procedure and paying out whatever choice the subject made in that trial. In addition to written instructions prior to the tasks, an instruction screen preceded both the UG and DG during the actual test, briefly explaining the specific task again. The UG was presented first, immediately followed by the DG.

2.3.2. Ultimatum Game

The UG was used to examine altruistic punishment behavior. Each participant was offered a proposed division of a sum of money by different anonymous players via the computer. The participant then had the option of accepting or rejecting this offer. In order to make participants believe they were facing real opponents, instructions stated that participants were part of a larger study and that offers were actual offers by previous participants. To further increase credibility, participants first received 10, 15, 20 and 25 € in a random order and were asked to share a certain amount for future participants (i.e. to act as proposer). Thereafter, participants acted as responder and received a total of 20 trials in random order during which they could either accept or reject a proposed division. Every proposal offered 10, 20, 30, 40 or 50% of 10, 15, 20 and 25 € in a way that all percentages were proposed for each amount. This design ensured that not only the percentage but also the absolute amount of money functioned as a variable, enabling to control for the order of magnitude of offers. In each trial, an offer was made by a different proposer whose putative identity was revealed by showing a first name accompanied by the first letter of their last name. All identities were hypothetical and equally balanced for gender. The design of each trial consisted out of the presentation of the proposers name (2 s), the total offered stake (5 s) and the proposed division of the offer that

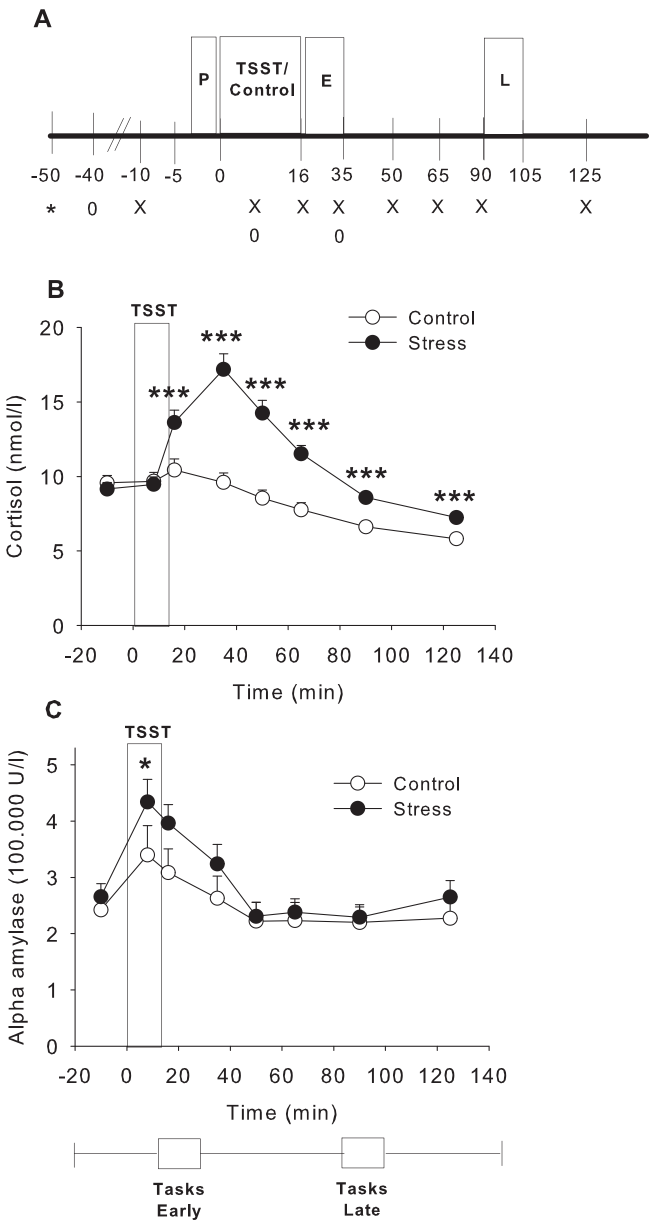

Figure 1 Timeline of the experimental session **(A)**. P: preparation period; TSST: Trier Social Stress Test; E: early tasks (immediately after the TSST/control condition); L: late tasks (75 min after the TSST/control condition); x: saliva sample; 0: subjective stress assessment; *: general questionnaires). Saliva cortisol **(B)** and alpha-amylase **(C)** levels were measured throughout the experiment. Error bars indicate S.E.M.*$P < 0.05$;***$P < 0.001$.

they could accept or reject (5 s). The main outcome parameter was the relative fraction of rejected offers per offered percentage, or the absolute offers, respectively.

2.3.3. Dictator Game

To measure altruism, we chose a one-shot variant of the DG in which a participant could choose to anonymously donate an amount (0—10 €) to a charitable organization. On a computer screen, participants were offered 10 € with the possibility to donate any amount to Unicef and keep the remaining amount to themselves. Participants were asked to enter the amount which they would like to donate ranging from 0 to 10 €.

2.4. Questionnaires

2.4.1. Subjective mood

At baseline ($t = -40$ min), during the stress/control condition ($t = +8$ min) and after the experimental condition ($t = +35$ min), perceived and subjective levels of stress, anxiety and insecurity, feelings of warmth and sweating were assessed using visual analog scales (VAS, 118 mm scale) ranging from 0 (not at all) to 100 (maximum) (Fig. 1A).

2.4.2. Reward- and punishment sensitivity

Differences of punishment and reward sensitivity have been shown to influence decision making in the UG and the DG (Scheres and Sanfey, 2006). Therefore, participants completed the BIS/BAS (behavioral inhibition/activation system) questionnaire at baseline ($t = -40$ min). This questionnaire contains a BIS scale that measures punishment sensitivity and three BAS scales measuring different elements of reward sensitivity (drive, reward responsiveness, and fun seeking) (Carver and White, 1994).

2.4.3. Trait anxiety

To rule out bias due to pre-existing anxiety we assessed participants' trait anxiety at baseline ($t = -40$ min) using the Spielberger State Trait Anxiety Inventory (STAI) (Spielberger, 1989).

2.5. Saliva sampling

To ascertain a hormonal stress response, saliva samples were collected (Salivette, Sarstedt, Nümbrecht, Germany). In total, eight saliva samples were collected at baseline ($t = -10$ min relative to the initiation of the stress/control condition), during the stress/control condition ($t = +8$ min), and at various time points afterwards ($t = +16, +35, +50, +65, +90$, and $+125$) (Fig. 1A). Samples were stored at -20 °C until analysis. Cortisol in saliva was measured without extraction using an in house competitive radio-immunoassay employing a polyclonal anticortisol-antibody (K7348). [1,2-^{3}H(N)]-Hydrocortisone (PerkinElmer NET396250UC) was used as a tracer. The lower limit of detection was 1.0 nmol/l and inter-assay variation was <6% at 4—29 nmol/l ($n = 33$). Intra-assay variation was <4% ($n = 10$). Samples with levels > 100 nmol/L were diluted 10x with assay buffer. Concentrations of salivary alpha-amylase (sAA) were determined as an index for adrenergic activity in response to stress (Nater and Rohleder, 2009). Amylase was measured on a Beckman-Coulter AU5811 chemistry analyzer (Beckman-Coulter Inc, Brea, CA). Saliva samples were diluted 1000x with 0.2% BSA in 0.01 M phosphate buffer pH 7.0. Inter assay variation was 3,6% at 200.000 U/L ($n = 10$). Additionally, one baseline saliva sample was used to determine testosterone levels because testosterone has been reported to influence decision making in the UG (Burnham, 2007). Testosterone in saliva was measured using an in house competitive radio-immunoassay employing a polyclonal anti-testosteron-antibody (Dr. Pratt AZG 3290). [1,2,6,7-3H]-Testosterone (NET370250UC, PerkinElmer) was used as a tracer following chromatografic verification of its purity. The lower limit of detection was 20 pmol/L. Inter-assay variation was 15,5–6,8% at 36–160 pmol/L respectively ($n = 20$).

2.6. Data Analysis

All statistics were carried out using SPSS version 20 (SPSS Inc., Chicago, IL, USA). One way ANOVAs were used to check for differences in baseline parameters between groups. Changes in VAS scales (% change during experimental condition compared to baseline) were analyzed using a one way ANOVA with condition (stress or control) as between-subject factor. Changes in salivary cortisol and alpha-amylase concentrations were analyzed using a repeated measures ANOVA with condition (stress or control) as between-subject factor with post hoc simple contrasts. Results were corrected by the Greenhouse-Geisser procedure where appropriate (indicated by an ε value). Also, the area under the curve increase (AUC_i) of cortisol and alpha-amylase were calculated for each participant as previously described (Pruessner et al., 2003). Moreover, the percentage increase was calculated for cortisol (4th sample – 1st sample) and alpha-amylase (2nd sample – 1st sample) as a measure for the temporal changes in both parameters. Both the increase and the AUC_i were analyzed using a one way ANOVA. For the UG, mean rejection rates were calculated for offers in the 10, 20, 30, 40, and 50% category. A repeated measures two-way ANOVA was used with the five different percentages as within-subject factors, and condition (stress/control) and time (early/late) as between-subject factors. Planned post hoc analysis was carried out where appropriate for separate percentages. For the DG, the donated amount was analyzed using a two-way ANOVA with condition (stress/control) and time (early/late) as between-subject factors. Mean rejection rates (UG) and donated amount (DG) were correlated with the AUC_i and the percentual change in cortisol and alpha-amylase using Spearman's correlation coefficients. The significance level was set at $P < 0.05$.

3. Results

3.1. Baseline parameters

The experimental groups did not differ in any of the measured baseline parameters regarding personal variables (age, body mass index), baseline hormonal values (cortisol, alpha-amylase, and testosterone) and personality characteristics (BIS, BAS drive, BAS reward responsiveness, BAS fun seeking and STAI trait) (all P values > 0.12, Table 1).

3.2. Subjective self-reported parameters

As expected, compared to the control condition, stress exposure significantly increased levels of self-reported perceived levels of stress during the experimental condition compared to baseline stress levels (VAS increase, $P < 0.001$) (Table 2). Also, exposure to stress acutely increased levels of self-reported insecurity (VAS increase, $P < 0.001$), warmth (VAS increase, $P < 0.05$) and sweatiness (VAS increase, $P < 0.001$) compared to the control condition (Table 2). No significant effect or interaction of timing (early and late groups) was present. After the experimental condition (t = +35 min), self-report levels of stress ($P = 0.62$), anxiety ($P = 0.64$), insecurity ($P = 0.63$), warmth ($P = 0.99$), and sweatiness ($P = 0.22$) were not statistically significant from baseline levels ($t = -40$ min).

Table 2 Changes in visual analog scale (% change during experimental condition compared to baseline) in parameters of subjective stress. Data are presented as mean (standard deviation). VAS: visual analog scale.

	Control	Stress	F value	P value
VAS stress	4.3 (12.6)	32.2 (23.4)	43.2	<0.001
VAS anxiety	2.1 (8.2)	7.2 (11.0)	5.3	<0.05
VAS insecurity	0.9 (12.6)	25.1 (17.7)	48.7	<0.001
VAS warmth	-4.3 (11.8)	4.3 (20.1)	5.4	<0.05
VAS sweatiness	2.0 (12.8)	23.5 (21.9)	28.1	<0.001

3.3. Saliva samples

In total, 628 saliva samples of 79 participants were included in the analyses (4 samples contained insufficient saliva) all saliva samples of one participant (control early) could not be analyzed due to insufficient saliva and were therefore excluded from the analysis. Stress resulted in increased cortisol levels compared to the control condition (condition × time interaction, $F_{7,525} = 35.6$, $P < 0.001$, $\varepsilon = 0.35$). Planned simple contrasts showed that compared to baseline, this effect was significant from t = +16 min onwards (all P values < 0.001, Fig. 1B). In support, the AUCi ($P < 0.001$) and the percentual increase in cortisol relative to baseline ($P < 0.001$) were larger in the stress group compared to the control condition, supporting that the stress procedure was effective. Stress significantly increased alpha-amylase levels (condition × time interaction, $F_{7,525} = 2.98$, $P < 0.05$, $\varepsilon = 0.55$). Planned simple contrast revealed a significant stress effect at t = +8 min ($P < 0.05$). The AUC_i of alpha-amylase did not significantly differ between the stress and control condition ($P = 0.51$), but the increase in alpha-amylase due to the condition was larger in the stress group ($P < 0.05$). These data indicate a transient but rather short-lived increase in salivary alpha-amylase level due to stress (Fig. 1C). Separate post hoc analysis of the control condition revealed a time-dependent effect on salivary alpha-amylase levels (time effect, $F_{7,266} = 8.01$, $P < 0.01$, $\varepsilon = 0.39$), indicating that alpha-amylase levels significantly increased in the control condition.

3.4. Behavioral tasks

3.4.1. Ultimatum Game

Data of one participant (UG, stress-late group) was not available due to technical problems. In total, data from 10 out of 1580 trials (79 participants with each 20 trials) were missing due to an absent or late response (0.6%). Missing trials did not influence any of the outcomes.

Participants were more likely to reject lower offers and accept higher offers as indicated by a significant percentage

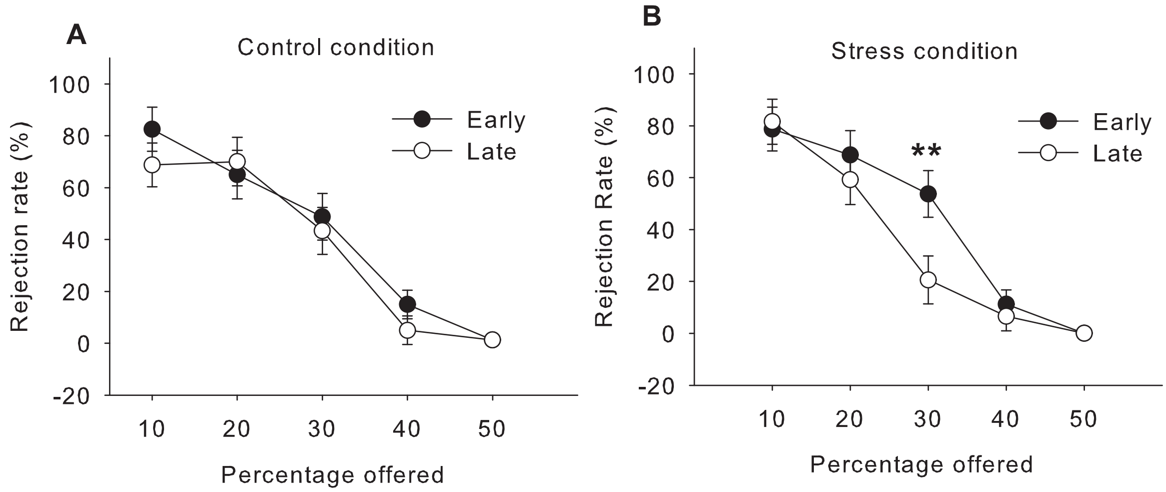

Figure 2 Time-dependent effect of stress on percentage accepted in the Ultimatum Game. In the control condition, the accepted percentage did not differ between the early and late completion of the Ultimatum Game (A). In contrast, after stress exposure, the late group displayed decreased rejection rates of 30% offers compared to the early group (B). Error bars indicate the S.E.M. $^{**}P = 0.01$.

effect ($F_{4,72} = 79.76$, $P < 0.001$) (Fig. 2). Indeed, a majority of offers was rejected at the 10% level, with decreased rejection rates at subsequent higher percentages with an almost 0% rejection rate at the 50% level. However, the amount of rejected offers not only depended on the offered percentage (10—50% of the total stake), but also on the condition (stress/control) in interaction with the timing (early/late) (percentage × stress × time interaction, $F_{4,72} = 2.90$, $P < 0.05$). This three-way interaction suggests that the stress late group rejected less 30% offers compared to the other conditions (Fig. 2B). In contrast, two-way interactions did not reach significance: stress itself did not significantly affect the percentage-dependent rejection rates (percentage × condition interaction: $F_{4,72} = 0.84$, $P = 0.51$) nor did the timing of the UG significantly affect the percentage-dependent rejection rates in the UG (percentage × time effect: $F_{4,72} = 1.66$, $P = 0.13$). Post hoc analysis of the control condition revealed that the early and late groups displayed similar rejection rates ($P = 0.53$) (Fig. 2A). By contrast, separate analysis of the stress condition showed a timing effect on rejection rates with the late stress group having lower rejection rates than the early group ($F_{4,34} = 2.9$, $P < 0.05$) (Fig. 2B). Further comparisons of the separate percentages in the stress groups showed that this overall decreased rejection rate in the stress-late group was due to decreased rejection rates of the 30% offers ($P = 0.011$), whereas other percentages did not significantly differ between the stress-early and stress-late groups ($P > 0.05$). Participants in the late stress group tended to reject offers in the 30% range less often than participants in the late control group, but this trend did not reach statistical significance ($P = 0.078$). No significant stress or timing effects nor any interaction were found when the rejection rates were regressed against the absolute amounts offered (10, 15, 20, 25 €, with 10—50% offers of each absolute amount) instead of percentages of the total stake. This indicates that the absolute offer did not significantly influence rejection behavior across the different groups, i.e. participants responded to the relative unfairness of the offer independent of the actual offer magnitude.

3.4.2. Dictator Game

Data for three participants (DG, stress-early group) were not available due to technical problems. The mean donated monetary amount was compared between groups. Stress overall reduced the allocated amount to Unicef ($F_{1,76} = 4.67$, $P < 0.05$), with the stress groups donating an average of 2.8 € compared to 4.3 € for the control condition (Fig. 3). This stress effect was independent of the timing of the DG (condition × time interaction, $P = 0.73$) (Fig. 3). In support, no overall significant difference in donated amount was found in the early and late groups (time effect, $P = 0.40$).

3.4.3. Correlations between behavioral tasks and hormones

For the UG, no significant correlations were found between overall and 30% rejection rates in the UG and the AUC_i of

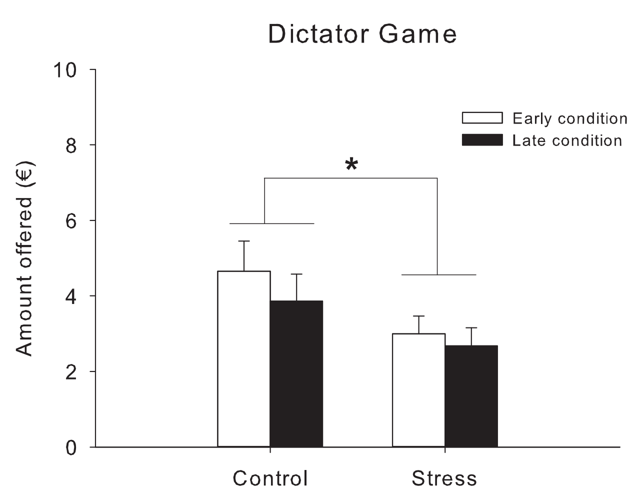

Figure 3 Effect of stress on altruism in the Dictator Game. Stress exposure resulted in reduced altruistic offers in the early and late stress group compared to the control condition. Error bars indicate S.E.M. $^{*}P < 0.05$.

cortisol (overall: $P = 0.68$; 30% offers: $P = 0.67$) and alpha-amylase (overall: $P = 0.27$; 30% offers: $P = 0.42$), or relative increase in cortisol (overall: $P = 0.33$; 30% offers: $P = 0.38$) and alpha-amylase (overall: $P = 0.41$; 30% offers: $P = 0.43$). Also, no overall significant correlations were found for the donated amount in the DG and the AUC_i for cortisol ($P = 0.80$) and alpha-amylase ($P = 0.39$), nor the relative increase in cortisol ($P = 0.72$) and alpha-amylase ($P = 0.64$). Significant correlations were also absent when the separate experimental groups were analyzed separately (control early, control late, stress early and stress late group; $P > 0.05$).

4. Discussion

In the present study we examined whether stress modulates altruistic punishment as measured in the UG. In the UG, a proposed offer of a certain monetary division can be either accepted (split as proposed) or rejected (neither player receives anything). Overall, rejection rates in the UG depended on the offered percentage of the total stake with decreasing rejections with increasing relative offers. This is in line with previous studies which reported decreased rejections for offers greater than 30% and increasing rejection rates for offers less than 30% (Crockett et al., 2010a). These data suggest that the 30% offer is the most ambiguous offer in terms of conflict between acceptance and rejection. The main finding of our study is that — in line with our hypothesis — stress causes a time-dependent effect on altruistic punishment in the UG, depending on the interval after stress. More specifically, stress differentially affected rejection rates of 30% offers of the total stake, with decreased rejection rates when the UG was played 90 min after onset of stress exposure compared to UG-testing directly after stress. Thus, rejection rates in response to ambiguous offers change depending on the time interval after stress. In a simplified one-shot version of the DG, we found that stress decreased the amount of money allocated to a charitable donation independent of time. Because the donations in the DG cannot be rejected by the recipient, behavior in the DG is thought to reflect pure other-regarding preferences devoid of any proximate strategic motifs.

One hypothesis regarding altruistic punishment states that it is an impulsive act, driven by the emotional response to perceived unfairness (Harle and Sanfey, 2007; Crockett et al., 2010b). In support, social evaluation was found to alter generosity (Takahashi et al., 2007b), and cortisol and alpha-amylase levels influenced temporal discounting (Takahashi, 2004; Takahashi et al., 2007a, 2008, 2010). This means that meeting the long-term goal of maximizing economic self-interest by accepting unfair offers requires self-control, in the sense that the impulse to sanction acts of unfairness needs to be suppressed. In support of this view, one study reported that altruistic punishment behavior was correlated with the propensity to make impulsive, non-social decisions over time (Crockett et al., 2010b). In contrast, another theory states that altruistic punishment is not an impulsive response, but an act of self-control (Knoch et al., 2006). According to this view, the default 'impulse' is selfishly maximizing economic self-interest. However, because selfishly accepting any monetary gain, including gains resulting from perceived unfair treatments, could lead to a reputation of being easily exploitable, it is strategically advisable to enforce fairness norms by punishing unfair behavior, even if this implies personal costs (Nowak et al., 2000). According to this view, behavioral inhibition would be required to nullify the selfish urge to accept any offer, however unfair. Because in the late aftermath of stress behavior is thought to aim at restoring behavioral performance through enhanced cognitive control (Diamond et al., 2007; Williams and Gordon, 2007), it is tempting to speculate that the decreased rejection rates in the UG reflect an upregulation of cognitive mechanisms related to self-control. According to this notion, stress crucially alters the temporal course of the balance between negative emotional reactions to unfairness and the 'cool' promotion of long-term material self-interest (Crockett et al., 2010b).

The fact that stress reactivity affects altruistic punishment in a time-dependent way has implications on the way we look at how people make decisions in social contexts. A previous study has shown that emotional states do not influence the reaction to unfair offers when individuals are tested directly after stress (von Dawans et al., 2012), which was replicated in the current study when participants were tested directly after stress exposure. By contrast, our effects of stress-induced changes in altruistic punishment strategies were more pronounced in the late aftermath of stress, i.e. 75 min later; it should be emphasized that differences only reached significance when tested against the early-stress group and were only borderline significant from the corresponding control group. Therefore, we cannot exclude the possibility that the difference between the early-stress and late-stress groups is the result of a return to baseline. Nevertheless, our findings suggest that when choices were made more than one hour after stress exposure, stress resulted in a beneficial long-term strategy with material gain in the UG. The novel element of our study is therefore that stress exposure is not by default detrimental, but should be interpreted with regard to temporal aspects.

Our time-dependent stress effects on UG performance could be explained by assuming that participants may care more about their own payoff in the late aftermath of a psychosocial stressor compared to directly after stress exposure. However, due to the absence of a time effect in the DG, our data do not support such a hypothesis. A recent study by von Dawans and colleagues reported an increase in sharing in response to stress (von Dawans et al., 2012). Although this seems to conflict with our data, an important difference is the fact that in our experimental setup, the donated amount goes to an anonymous recipient rather than an actual person. Von Dawans et al. interpreted their findings in the framework of the interpersonal tend-and-befriend hypothesis, according to which stressed participants show an increased tendency for prosocial behavior in order to seek and provide comfort and support by peers. However, because our version of the DG involved donating to anonymous charity, which does not qualify as a potential peer who could provide comfort in stressful times, behavior was most likely not driven by tend-and-befriend motives. Thus, the modulation of generosity by stress probably depends on the identity, or anonymity, respectively, of the partner with whom resources are being shared.

One limitation of the study is that we have not directly investigated the neurobiological mechanisms underlying the time-dependent effects of stress on social decision making. It may be speculated that the difference between the two stress groups is explained by the mechanism of action by which stress mediators (e.g. cortisol) change neuronal function, i.e. in a rapid time domain involving non-genomic actions and in a later time-domain, when gene-mediated signaling cascades have been activated (Joels et al., 2012). At this stage, we can only speculate about a role of the glucocorticoid and mineralocorticoid receptors and hormonal balance in this phase. Secondly, even though exposure to the control condition did not result in significant increases in salivary cortisol and subjective stress levels, salivary alpha-amylase levels also significantly increased (Fig. 1C). Therefore, the control condition itself, with up to four persons delivering a speech simultaneously, may still have caused a (limited) amount of stress. A third limitation is that no significant correlation between behavior in the UG and the cortisol stress response was observed, which may argue against an exclusive role of corticosteroid hormones in the mediation of the effects. A more direct manipulation of cortisol and/or noradrenaline by psychopharmacological means should yield better insights into the specific neuroendocrine mechanisms underlying the time-dependent effects of stress on altruistic punishment. A final limitation of this study is that only male participants were recruited, preventing the generalization of our results to female participants. Important differences exist between genders in HPA axis responses after stress as well as in stress-induced decision making (van den Bos et al., 2009). A complicating factor is that the menstrual cycle and use of hormonal contraceptives play a role in the female hormonal stress response. Future studies need to address the gender effects of stress-induced changes in altruistic punishment.

In conclusion, our findings suggest that altruistic punishment behavior is susceptible to environmental factors and provide evidence for the existence of time-dependent stress effects on altruistic punishment. Importantly, in the late aftermath of stress, behavior is not guided by selfish motives but implements restrain, which maximizes long-term economic advantages. Overall, this underscores the importance of time as a factor in simple, real-life economic decisions in a stressful social context.

Funding body agreements and policies

None.

Conflicts of interest

The authors declare no conflict of interest.

Contributors

Authors CHV, JVZ, SC, LCH, JCV, BO, TK and MJ designed the study and wrote the protocol. Authors CHV, JVZ, SK and LCH carried out the study. Authors CHV, RSK, MPM, TK and MJ discussed and managed the literature searches and analyses. Authors CHV, JVZ, SC, TK and MJ undertook the statistical analysis, and author CHV wrote the first draft of the manuscript. All authors contributed to and have approved the final manuscript.

Acknowledgements

The authors would like to thank Loes Mehlkopf, Laura Peeters, Suzanne Kamps, Renske Penning, André Sollie, Lotte Lütgerhorst, and Lieske Hems for their help with the stress protocol, and Inge Maitimu for the analysis of the saliva samples.

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Please cite this article in press as: Vinkers, C.H., et al., Time-dependent changes in altruistic punishment following stress. Psychoneuroendocrinology (2013), http://dx.doi.org/10.1016/j.psyneuen.2012.12.012