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Acute stress alters neural patterns of value representation for others

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ABSTRACT

Acute stress is often evoked during social interactions, by feelings of threat or negative evaluation by other people. We also constantly interact with others while under stress – in the workplace or in private alike. However, it is not clear how stress affects social interactions. For one, individuals could become more selfish and focused on their own goals. On the other hand, individuals might also become more focused on affiliating with potential social partners, in order to secure their support. There is, indeed, accumulating behavioral evidence that prosocial behaviors increase rather than decrease under stress. Here, we tested the underlying brain processes of such findings, by assessing the effects of stress on the neural representations of (monetary) value for self and other. Participants (N = 30; male, 18–40 years) played a gambling task for themselves and for another participant while undergoing functional magnetic resonance imaging (fMRI). Each participant played the gambling task twice: once immediately following acute stress induction, and once in a control session. We compared neural patterns of value representation in the dorsomedial prefrontal cortex (dmPFC), ventromedial prefrontal cortex (vmPFC) and striatum using representational similarity analysis (RSA). We found that under stress, dmPFC and striatum showed higher dissimilarity between neural patterns underlying high and low value for the other. Dissimilarity of neural patterns underlying high and low value for the self was unaffected by stress. These findings suggest that participants track the magnitude of possible rewards for others more under stress, suggesting increased prosocial orientation.

1. Introduction

Our lives are filled with various stressors and many social interactions occur when individuals are under stress. While intuitively many people assume that stress increases selfishness and egocentric behavior, converging evidence from behavioral research indicates that stress can also increase prosocial behavior (Takahashi et al., 2007; von Dawans et al., 2012; Margittai et al., 2015; Buchanan and Preston, 2014; Singer et al., 2017; von Dawans et al., 2019). This has been interpreted in light of the "tend-and-befriend" hypothesis stating that individuals become more prosocial under stress in order to secure help from others (Taylor et al., 2000). While originally the hypothesis proposed that such a "tend-and-befriend" behavior represents an alternative stress response of women (as opposed to the classic "fight-or-flight" response, which was suggested to represent a male stress response), empirical evidence so far suggests that also men engage in "tend-and-befriend" behavior when under stress (Takahashi et al., 2007; von Dawans et al., 2012; Margittai et al., 2015; Singer et al., 2017). For example, in a functional magnetic resonance imaging (fMRI) study, acutely stressed men showed increased activity in the "empathy for pain network" (i.e., anterior insula and anterior midcingulate cortex;Lamm et al., 2019) when seeing someone else in pain, and this correlated with later prosocial behavior (Tomova et al., 2017). Thus, "tend-and-befriend" might represent a more general stress response engaged by both men and women.

What are the cognitive mechanisms underlying stress-induced prosociality? One possibility is that under stress, the distinction between one's own and others' emotions becomes more porous, leading to more emotion sharing. Self-other distinction is an essential ingredient in many interpersonal phenomena (Lamm et al., 2016), and weak self-other distinction can have both positive and negative consequences for social interaction and understanding (see e.g. (Milward and Sebanz, 2016), for review (Riva et al., 2016; Riecansky et al., 2015, 2019)). There is some

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evidence that self-other distinction is weakened under stress (Tomova et al., 2014; although this effect was only found in men, while women showed increased self-other distinction). Thus, people may become more prosocial under stress when others' emotions become conflated with and less distinguishable from their own.

An alternative, though not mutually exclusive possibility, is that under stress people more clearly represent the needs and values of others, as a means to affiliate with them and attain their support (as proposed by the "tend-and-befriend" hypothesis (Taylor et al., 2000)). By contrast to a weakened self-other distinction, this hypothesis predicts a more precise and potentially distinctive representation of others' needs and values under stress.

In order to illuminate the brain processes underlying increased prosociality under stress, we here investigated how acute stress modulates the representation of value for self and others. Importantly, the domain of valuation and reward is of particular interest due to its powerful effects on behavior (Berridge and Robinson, 2003). Indeed, there have been persistent efforts to identify the neural signals associated with the representation of subjective value of choice alternatives (for review and meta analysis, see Bartra et al., 2013; Clithero and Rangel, 2014). Subjective value is thought to serve as a common currency, allowing complex and qualitatively different alternatives to be compared on a common scale. Activity in the medial prefrontal cortex, especially its ventral part, and the ventral striatum has been shown to correlate positively with increasing stimulus value across different reward modalities (Bartra et al., 2013; Clithero and Rangel, 2014). While the dissociation between value computation and computation of reward prediction errors is difficult, those studies that have directly looked at separating these computations have found that ventromedial prefrontal cortex (vmPFC) rather reflects value computation whereas ventral striatum reflects prediction errors (Hare et al., 2008; Rohe et al., 2012). Importantly, the mPFC has been also shown to reflect value computations if the recipient is another person and not the self (Sul et al., 2015; Zaki et al., 2014), particularly in the dorsomedial prefrontal cortex (dmPFC), and such value computations for others were shown to reflect individual differences in prosocial behavior (Sul et al., 2015).

In the present study, we therefore aimed to specifically investigate how acute stress affects neural signals of value for self and others in vmPFC, dmPFC and the ventral striatum. More specifically, we aimed to assess two main questions: (1) How does acute stress affect the similarity of neural representations of high vs. low value? (2) How does acute stress affect the similarity of neural representation of value for self and for others?

In order to address these questions, we analyzed fMRI data recorded during valuation of potential rewards benefitting either the self or another person, using representational similarity analysis (RSA; Kriegeskorte et al., 2008). The basic approach of RSA is that information is encoded in patterns of brain activity, and that this can be decoded in analyses of multivariate fMRI patterns associated with different stimuli or cognitive states (Haxby et al., 2014). Thus, investigating the similarity of multivariate neural patterns allows to study the similarity of cognitive states – and, in the present study, how stress affects those cognitive states.

Prior studies document that stress increases reward sensitivity (Kumar et al., 2014; Maier et al., 2015; Ironside et al., 2018) when measures are taken under acute stress (i.e., when the stress-to-task latency is low; for a review, see Porcelli and Delgado, 2017), and when cortisol levels are reliably increased (Oei et al., 2014) which is possibly related to stress triggering increased dopamine release (Inglis and Moghaddam, 1999; Piazza and Le Moal, 1997; Pruessner et al., 2004). Assuming, thus, that stress increases sensitivity to rewards, high value stimuli should become more salient compared to low value stimuli. Consequently, we hypothesized that the neural patterns underlying high value and low value representation should become *more dissimilar* under stress. For neural patterns associated with value for the *self*, increased dissimilarity would mean that participants become more sensitive to rewards for the self under stress. Similarly, for the *other*, increased dissimilarity of neural patterns underlying high and low value would mean that participants become more sensitive to rewards for the other, which might indicate increased concern for the welfare of another person under acute stress.

In addition, we aimed to directly test how acute stress affects similarity of neural representation of value for self and others. We hypothesized that if stress indeed decreases self-other distinction, the representation of value should become less specific of the recipient (i.e., self or others), and therefore neural patterns underlying self and other (for both, high and low value representation) should become more *similar* under stress.

To test these hypotheses, we measured the effects of acute stress on the neural representation of one's and others' expected rewards. We designed a novel gambling task to evoke consideration of predicted rewards for self and other. Each trial offered a high or low value gamble (implemented in a "wheel of fortune game"), and the participant acting as a player could choose to play the wheel or to skip to the next trial. Male adult participants alternatingly played for reward accruing to themselves, or for another person. To ensure the validity of this manipulation, participants (who were previously unknown to each other) were scanned in pairs, met repeatedly during the experimental protocol, and actually received the rewards from their partner's choices.

This design allowed us to test whether stress directly affects the representation of predicted rewards, either for the self or for the other.

2. Methods

2.1. Materials and methods

Participants. Thirty male participants between 18 and 40 years were included in a within-subjects design. We included only male participants due to previous findings of gender differences in the effects of stress on social cognition (Tomova et al., 2014; Smeets et al., 2009) and because of the higher variability in the psychoendocrinological stress response in women (Kirschbaum et al., 1999). All participants were recruited via online advertisements. Individuals who expressed interest in participating in the study were asked to fill out a screening questionnaire before the experiment to assess exclusion criteria for the experiment and trait socio-cognitive abilities (see below for a description of the screening questionnaires). The study was approved by the ethics committee of the Medical University of Vienna. After a description of the study, written informed consent was obtained. All participants received between 30 and 40 € for participation, depending on their winnings during the lottery task. We excluded two participants: One whose second session was interrupted by a technical problem of the scanner, and one because of an incidental finding in the anatomical scan. Thus, our final sample consisted of 28 participants. For cortisol analyses, one additional participant was excluded because two samples (T2 and T3 of the control run) did not contain a sufficient volume of saliva for testing. However, the participant showed an increase in cortisol levels in the stress condition (T3 – T1 = 5.28 nmol/L) that was comparable to the mean increase in the stress condition of the rest of the sample (mean T3 – T1 = 7.133 nmol/L) indicating that the stress manipulation worked also in this participant.

2.1.1. Screening questionnaires

We used an online screening questionnaire to exclude participants who reported acute or chronic psychiatric illness, taking prescription medication, abuse of psychoactive drugs or alcohol, or smoked daily. Socio-cognitive abilities were determined using the perspective taking (PT) scale (analyzed also with subscales as recommended by Koller and Lamm, 2015) and the empathic concern (EmC) scale from the Interpersonal Reactivity Index (IRI; Davis, 1983), the Emotion Contagion Scale (EC; Doherty, 1997), and the Reading the Mind in the Eyes Test (Baron-Cohen et al., 2001). We included an additional exclusion criterion into our recruitment, which was that participants who scored more than two standard deviations below or above the group mean in any of those

measures would not be invited to the experiment. This was included to make sure all participants displayed average social-cognitive traits. However, no individual who completed the screening scored outside of this range.

2.1.2. Experimental procedures

Participants completed the lottery task twice during the same visit; once following stress induction and once as a control session, in counterbalanced order. Each participant also underwent a functional localizer scan at the end of their experimental session (see Fig. 1 for a graphical depiction of the timeline of the experimental procedures). Participants were instructed to abstain from drinking alcohol, smoking, and taking medication 24 h prior to the experiment, and to abstain from consuming caffeine on the day of the experiment. All experimental sessions took place at the same time (6:00 p.m. - 9:00 p.m.) to control for diurnal cortisol variation. Participants were selected from a pool of forty-five participants who completed the screening on a first-come basis and were invited to the experiment in pairs of two. We started with measures of baseline cortisol levels and subsequently the first participant received instructions about the general experimental procedures. All participants were instructed that their task was to gain as much money as possible for themselves and their partner in the lottery task. The second participant was asked to come in 30 min after the first participant so that they would start instructions while the first participant started their first session. We made sure that participants briefly met before starting each session of the experiment. This setup increased face validity of the social dimension of the task: Participants met and interacted with the target of their social decisions and subsequently acted as the target of the social decisions of the second participant (see section 2.1.4 *Lottery task* for more details). Stress levels were assessed via cortisol measures six times during the experiment using *Sarstedt Salivette* saliva collection devices (Sarstedt, Wr. Neudorf, Austria), along with subjective stress measures using visual analogue scales (see *Stress measures* for detailed description). Each participant underwent two sessions inside the MRI scanner (i.e., stress and control session) separated by a 30-min break. The order of stress and control session was counterbalanced across participants with approximately half of the participants (n = 16) starting with the stress condition in the first session and the control condition in the second session, while the other half of the participants (n = 14) started with the control condition in the first session and the stress condition in the second session. After the preparation phase, the first participant was positioned in the scanner and the first session of scanning commenced with the stress paradigm (either stress or control version of an adapted version (Tomova et al., 2017) of the Montreal Imaging Stress Task (MIST; Dedovic et al., 2005a, see below). Immediately afterwards, we implemented the first run of the lottery task. Subsequently participants underwent an anatomical scan and were then taken out of the scanner for a 30-min break. We took another two saliva samples at the beginning and at the end of this break. Note that overall, the offset of the first run of the MIST (i.e., either stress or control) and the beginning of the second run of the MIST (again, either stress or control) were separated by 60 min, allowing the cortisol levels to return to baseline (Dickerson and Kemeny, 2004). During the break, participants were given an adapted version of a risk aversion questionnaire (Holt and Laury, 2002) and were then instructed to relax until the beginning of the next session. The second session started again with the stress paradigm (stress or control condition) and was followed by the second run of the lottery task. Finally, participants underwent the functional localizer task in order to identify the mPFC functionally in each subject individually (Saxe et al., 2006) which served as our method of feature selection for the subsequent representational similarity analysis (see 2.2.4 *Defining regions of interest* for details). After the first participant was finished with the experiment, he stayed in the laboratory until the last saliva sample was taken (45 min after onset of the MIST in the second session) and was debriefed. The same procedure was implemented for the second participant after he finished his second session.

2.1.3. Stress paradigm

Stress was induced by an adapted version (Tomova et al., 2017) of the Montreal Imaging Stress Task (MIST; Dedovic et al., 2005b). In the stress condition, participants attempt to solve mental arithmetic problems under time pressure, together with social evaluative threat. The social evaluative threat was induced by giving participants the information that the display would show the average performance of an individual in their

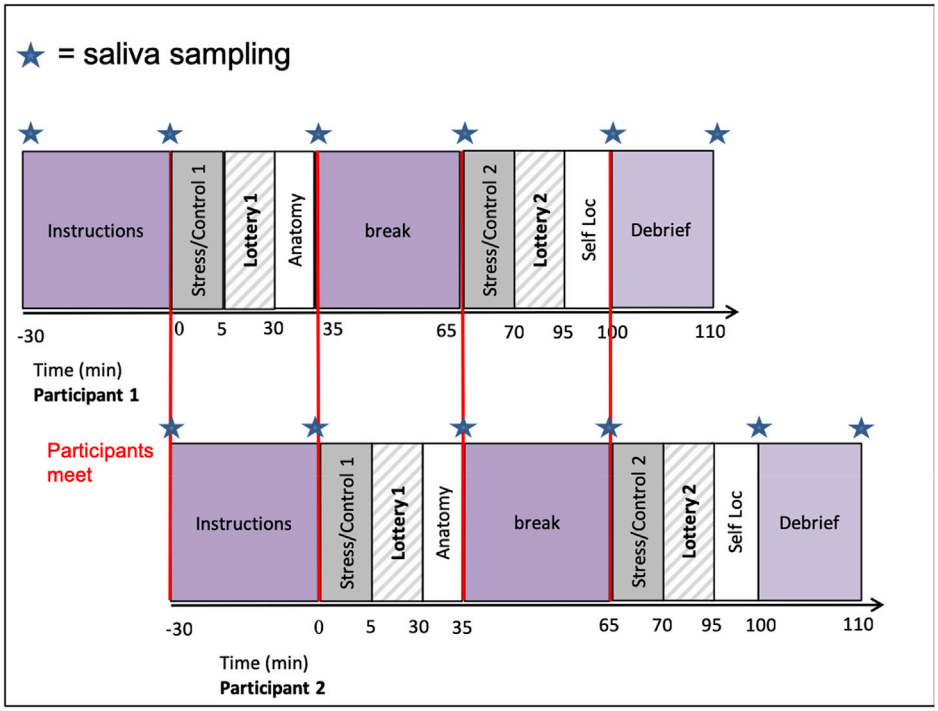

Fig. 1. Sequence of experimental procedures. Time point zero indicates begin of scanning. Time epochs in purple represent procedures outside the scanner. Stress/Control 1/2 = MIST run 1 and run 2, which was either the stress or the control condition (order of conditions was counterbalanced across participants); Lottery 1/2 = Lottery task run 1 and run 2; Anatomy = structural anatomical scan; Selfloc = functional localizer task; Debrief = debriefing of participants. Red lines indicate time points during which participants met each other while being transitioned in and out of the scanner. Importantly, participants briefly encountered the other participant before each run, to emphasize that they were making choices for another individual.

age range together with their own current performance, which was updated after each arithmetic problem. Unknown to the participants, the program is set to a time limit that is 10% below the participant's average response time, which induces a high failure rate (see Dedovic et al., 2005b for a detailed description of the task). Thus, participant's performance will gradually decline in comparison to the average performance they are instructed to reach, inducing a threat of negative social evaluation, which has been shown to result in a stress response (Dickerson and Kemeny, 2004). We furthermore increased the social evaluative threat in the task by adding an observer during the stress condition (see Tomova et al., 2017 for details). In the control condition of the MIST, the mental arithmetic problems are presented without time pressure and without social evaluative threat to match the stress condition in all elements, except the stress inducing features.

2.1.4. Lottery task

We adapted a lottery task (Lockwood et al., 2015), previously used to assess reward anticipation for self and others. While in the original paradigm participants passively viewed lotteries for self and others, our version asked participants to make an active decision whether or not to play a specific lottery gamble for each trial as we were specifically interested in targeting neural processing that is relevant to subsequent decision making for others.

In the present task, each trial presented a lottery gamble, with high or low winning probabilities (high winning probability wheels (= high value condition) had winning probabilities of 85%–70% and low winning probability wheels (= low value condition) had winning probabilities of 15–30% represented as colored wheels, presented for 3 s), and one of two targets for the reward (self or other). Participants actively decided whether to play the specific trial or not. Each trial included a small incentive to play the lottery, as every trial played earned € 0.10 (for either the participant or the other player, depending on trial type). In addition, at the end of the experiment 10 trials were randomly selected and earned € 1 for each win (i.e., up to € 10, for either the participant or the other player, depending on trial type). These payoffs were designed to encourage participants to play many trials (in order to accumulate small certain rewards) but also to prefer playing trials with high probability of winning (i.e., high value trials) to enrich the pool of wins, from which 10 trials are chosen for larger payoffs. Our goal was to create an experienced trade-off between trying to play many trials while also trying to play many high value trials in order to engage participants in active value-based decision making during each trial. We had piloted this task (N = 12) and found that pilot participants indeed reported that they were trading off playing many trials and playing many high value trials on each trial. Winning probabilities on each trial were presented explicitly, so the task did not involve any reward learning component. Fig. 2 shows an example trial of the lottery task.

Importantly, our task was specifically designed to focus on reward related processing and not on risk aversion, which is why participants were not able to lose any money on a given trial (i.e., even on the non-win trials participants earned € 0.10 for playing that trial). We chose to design the task in this way because of well documented findings of stress effects on risk aversion (Starcke and Brand, 2012; for review), which was not the objective of this study. In addition, we added a risk aversion questionnaire (see 2.1.6 *Risk Aversion Questionnaire*) after each condition in order to assess whether risk aversion was affected by stress as a potential confounding variable.

If participants decided to play the trial, they saw the wheel spinning for a jittered period of 3–6 s (with mean duration of 4.5 s; uniform distribution) and then stopping at either a win or no-win field, with probabilities corresponding to number of win and non-win fields on the wheel. The outcome of the gamble (i.e., the stopping of the wheel on either a win or a non-win field) was presented for 3 s. If participants decided to not play a trial, the rest of the trial was skipped. We assessed effects of target (self vs. other) and value (high vs. low), on neural responses time-locked to the cues indicating the probability of winning as we were specifically interested in neural patterns underlying value representation for self and others. Participants played 100 trials in total, including 25 trials for each condition (i.e., self - high value, self – low value, other – high value, other – low value) and the overall duration of

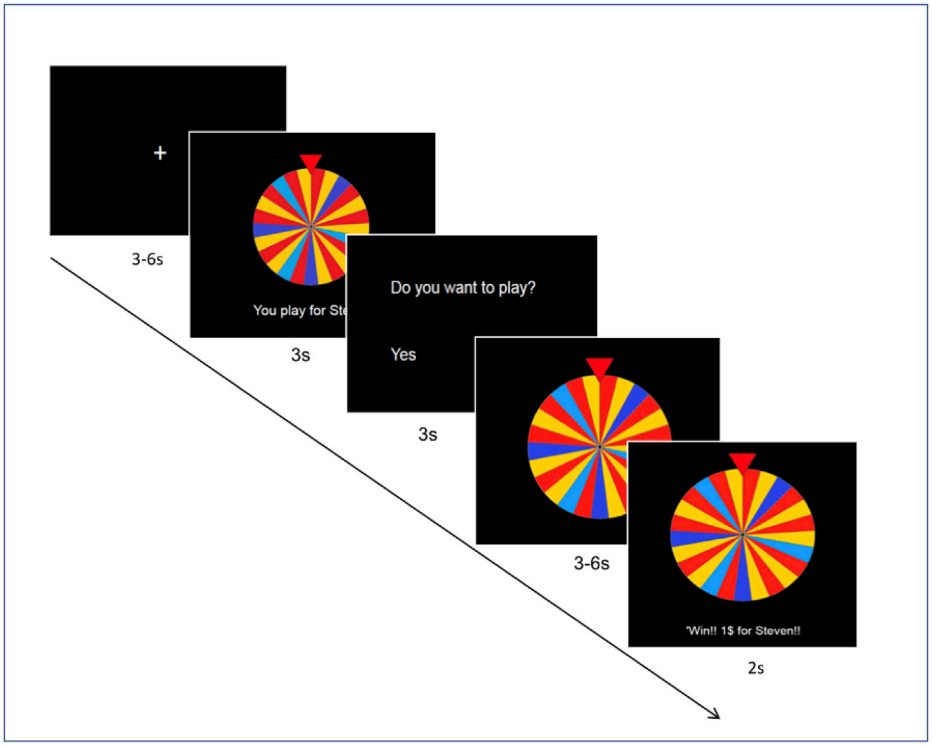

Fig. 2. Example of one trial of the lottery task. After a fixation cross, participants saw the probability of winnings (as indicators of high vs low value) in the upcoming trial, and the target of the trial ("self" or "other", indicated by a written statement below the wheel: "You play for yourself" or "You play for [Name of other participant]"; note that the original instructions for the task were in German, the native language of all participants). The winning colors were counterbalanced between participants and winning fields were either red/yellow (while blue/turquois resulted in no win) or blue/turquois (while red/yellow resulted in no win). Participants were then able to decide whether they wanted to play a trial, or not. If they decided to play the trial, they saw the wheel spinning for a jittered period of 3–6 s (mean = 4.5 s), after which the final outcome was presented for 2 s. The subsequent trial started with a fixation cross with a jittered duration of 3–6 s (mean = 4.5 s).

the task was approx. 25 min.

2.1.5. Functional localizer task

The functional localizer task was designed to activate the medial prefrontal cortex associated with self-related and reward-related processing in order to localize it functionally and individually in each participant. This allowed us to independently select the voxels for our representational similarity analysis in each participant (see Saxe et al., 2006 for more details on the logic and implementation of functional localization). Participants were presented with two written adjectives on the screen and were asked to decide either which one is more true of themselves (*Self* condition) or which has more syllables (*Syllables* condition). This task was an adaptation of a previous verbal attribution task (Kelley et al., 2002). As in the original task, positive adjectives were selected from a pool of normalized personality trait adjectives (Anderson, 1968) and then translated into German. All adjectives depicted positive qualities and were similar in their length and complexity. The adjectives were presented in six blocks (i.e., three blocks for each condition in randomized order). Each block consisted of six trials of the same condition (i.e., either Self or Syllables) depicting randomized combinations of adjectives. One trial lasted 5 s during which participants gave their response. A fixation cross was presented for 2 s between each trial in a block. Between each block, a fixation cross was presented with jittered duration between 9 s and 15 s (mean = 12 s; uniform distribution).

2.1.6. Risk aversion questionnaire

We collected measures of risk aversion (Holt and Laury, 2002) after each experimental session (i.e., stress and control) in order to assess whether stress affected risk aversion as a potential confounding variable. We used a shortened version of a risk aversion task (Holt and Laury, 2002) in which participants were presented with six lottery choices and required to choose between riskier and safer options. The maximum amount to be gambled increased in each of the six choices; the switch point between choosing the gamble and safe option served as an indicator of risk aversion.

2.2. Data analysis

2.2.1. Analyses of behavioral data

Behavioral data (i.e., number of trials played) from the lottery task were analyzed in a repeated-measures ANOVA with the within-subjects factors *value* (high, low), *target* (self, other), and *stress* (stress, control). We also ran a separate ANOVA for response times on high value trials on which participants decided to play (we did not use response times on low value trials as participants only played very few of those trials). This ANOVA was implemented with the within-subjects factors *target* (self vs. other) and *stress* (stress, control).

Bonferroni-corrected post-hoc pairwise comparisons were computed to examine interactions and omnibus main effects. Responses in the two runs of the risk questionnaire were processed by assessing the switch point between gambles and save options for each participant for the stress and control condition separately. *A* Wilcoxon Signed-Ranks Test was used to assess whether the switch point differed between the stress and the control condition. All data were analyzed using SPSS (v. 20) and the significance threshold was set to $\alpha = 0.05$. Effect sizes of the ANOVA terms are reported as η_p^2.

2.2.2. Stress measures

Time points for saliva sampling were for each session session: baseline (T1; 30 min before onset of stressor), directly before onset of the stress task (T2), 35 min after onset of the stress task (T3). After the first session (either stress or control condition), participants had a break of 30 min and then we repeated the procedure for the second session (either stress or control). After each experiment, collected samples were stored at −20 °C. Salivary cortisol concentrations were determined by a commercially available chemiluminescence-immunoassay kit with high sensitivity (IBL, Hamburg, Germany). Inter- and intra-assay coefficients of variation were below 10%. All biochemical analyses were conducted at the biopsychology laboratory of Technical University of Dresden (head: C. Kirschbaum, http://biopsychologie.tu-dresden.de). Subjective stress levels were measured by means of visual analogue rating scales ranging from 0 (not stressed at all) to 100 (very stressed). Participants indicated their respective responses by placing a mark on a continuous line. Time points at which the subjective rating scales were used were the same as the time points for saliva sampling (participants filled out the scales while providing the saliva samples). For cortisol levels and subjective stress measures, the areas under the individual response curves with respect to ground (labelled AUC_G) and with respect to increase (labelled AUC_I) were calculated with the trapezoid formula (Pruessner et al., 2003). By this, an aggregated measure of physiological changes over time is provided. We calculated AUC_G and AUC_I for each condition (stress/control) separately and subsequently computed paired-sample t-tests to compare stress levels between stress and control condition. We adjusted the p-value for calculating two statistical analyses per stress measure (i.e., AUC_I and AUC_G) and report results as significant for $p < 0.025$ (i.e., 0.05/2).

2.2.3. Acquisition and preprocessing of fMRI data

MRI data were acquired using a 3 T PRISMA scanner (Siemens, Erlangen Germany) at the High Field MR Centre of the Medical University of Vienna using a 64-channel head coil for signal reception. Structural images were acquired using a magnetization-prepared rapid gradient-echo (MPRAGE) sequence (repetition/echo time (TR/TE) = 2000/2.88 ms, 176 sagittal slices, voxel size = 1.0 × 1.0 × 1.0 mm, field of view (FOV) = 256 mm, flip angle = 9°). Using an echo-planar imaging (EPI) sequence, blood oxygen level dependent (BOLD) signal was acquired in 32 axial slices using 3 × 3 × 3-mm voxels at TR/TE = 2000/30 ms, FOV = 192 mm, flip angle = 75°. Data processing and analyses were performed using Statistical Parametric Mapping 8 (http://www.fil.ion.ucl.ac.uk/spm/software/spm8) and in-house code. The data were motion corrected via rigid rotation and translation about the three respective orthogonal axes of motion, normalized onto a common brain space (MNI), spatially smoothed using a Gaussian filter (full-width half-maximum 5-mm kernel). Difference in movement between the stress and control run was assessed using paired-sample t-tests for mean translation per run (averaged across axes) and mean rotation per run (averaged across axes). Mean translation did not differ between the stress run (mean = 0.0281; SD = 0.0094) and the control run (mean = 0.0283; SD = 0.0101; $t(27) = -0.163$, $p = 0.872$). We also detected no difference in mean rotation between the stress run (mean = 0.01647; SD = 0.0063) and the control run (mean = 0.0162; SD = 0.0052; $t(27) = 0.448$, $p = 0.658$).

2.2.4. Defining regions of interest

To define subject-specific ROIs, we used individual activations of each participant in the localizer task. Blocks were modeled as a 42 s boxcar (6 trials of 5 s duration in addition to a fixation cross of fixed duration of 2 s presented after each trial in a block) convolved with a standard hemodynamic response function (HRF). A general linear model (GLM) was implemented in SPM8 to estimate β values for *Self* blocks and *Syllables* blocks. We conducted high-pass filtering at 128 s and residual head movement effects were accounted for by including the six rigid-body motion parameters (translation and rotation) as nuisance regressors. For each participant, we calculated the target contrast Self > Syllables and entered it into a second-level random-effects model using a one-sample *t*-test implemented in SPM8. From the resulting activation map we identified the peak *t* value within our a priori region of interest, mPFC. We identified two clusters within the mPFC ($p < 0.05$ FWE corrected on voxel-level) one dorsal and one ventral). We drew a 9 mm sphere around the peak voxel for each cluster, which represented the search space for the selection of individual ROIs.

To select individual ROIs, we selected the peak voxel within each

search space in each subject and drew a 9-mm sphere around that peak voxel. Within these individual ROIs, we selected the 80 most active voxels based on the *t* values from the Self > Syllables contrast for each subject, for dorsal and ventral mPFC. These voxels defined the features entering the subsequent representational similarity analysis.

We performed additional exploratory analyses using ROIs from the literature to complement our functional localizer ROI analysis. We selected coordinates from a meta-analysis on subjective value representation (Bartra et al., 2013) (SELF-VALUE ROIs) resulting in 3 ROIs (left striatum, right striatum and vmPFC) and coordinates from a study on reward anticipation for others (Carter et al., 2009) (OTHER-VALUE ROIs) resulting in 4 ROIs (left striatum, right striatum, insula and thalamus). We found that while both studies used for ROI determination report coordinates in the striatum, the resulting ROIs were mostly non-overlapping (see below for details on overlap). We selected those two sources in order to investigate effects of stress on value representation in regions previously associated with subjective value and regions previously associated with other-related value representation. For the OTHER-VALUE ROIs, we chose the Carter et al., 2009 coordinates because in this study participants were gambling for others but there was no trade-off between their own winnings and winnings for others - i.e., winnings to the charity did not take away winnings from the self as in many other studies on prosocial decision making, such as Hutcherson et al., 2015 (Hutcherson et al., 2015)) and because it also did not involve any learning about probability outcomes (such as in Sul et al., 2015) or an observation of gambles for self and other without an active response component (such as in Lockwood et al., 2015) . Thus, the gambling task used in this study was targeting the most similar processes to our present study. However, it should be noted that due to slice coverage being optimized to collect data from midbrain and striatum, Carter et al. did not collect fMRI data from superior frontal and parietal cortex. We created ROIs using the peak coordinates reported in those studies (table 3 in Carter et al., 2009; and table 3 (decision stage) in Bartra et al., 2013), drew 9 mm spheres around them and selected all voxels within each sphere (281–389 voxels in each ROI). We masked each ROI by its overlap to the adjacent ROIs (defined to be mutually exclusive) such that there was no overlap in the voxels contained in each ROI.

For the Carter et al., 2009 coordinates, we did not create ROIs for the midbrain peak as this part of the brain was not covered in the present study. In addition, we excluded the dorsal striatum peak because of its very close proximity to the ventral striatum peak, which would have resulted in two almost completely overlapping ROIs.

2.2.5. Statistical analyses of fMRI data in lottery task

The fMRI time series were analyzed using an event-related design approach implemented in the context of the GLM. The model contained four regressors separately modeling the presentation of lottery wheels period (i.e., when the wheel and target were presented, 3 s) in four conditions (self - high value (sh), self - low value (sl), other - high value (oh), and other - low value (ol)). We also included one regressor for the time period of outcome when participants were presented with the outcome of the spinning wheel (i.e., win or non-win). Because participants played almost all high value trials and almost no low value trials, most outcomes were wins with only a small fraction of outcomes presenting non-wins (corresponding to the winning probability of 70–85% on high value trials; for more details on playing behavior, see results section 3.3 *Behavioral data lottery task*). We therefore did not model outcome separately for wins and non-wins, but only included one outcome regressor (but see Supplemental Material for results from an analysis modeling wins and losses separately). Each effect was modeled as a boxcar function, and then convolved with the canonical hemodynamic response function as implemented in SPM8. Residual head movement effects were accounted for by including the six rigid-body motion parameters (translation and rotation) as nuisance regressors. Beta values associated with each condition (sh, sl, oh, ol; during presentation of lottery wheels) for each voxel in an ROI were extracted for stress and control run separately.

2.2.6. Univariate group analysis

First, we aimed to validate that our paradigm elicits the expected modulations in univariate brain signals in the control condition for the self - i.e., stronger activity in brain reward regions such as vmPFC and ventral striatum to stimuli signaling high value compared to stimuli signaling low value (Bartra et al., 2013; Clithero and Rangel, 2014). We also included the other conditions for exploratory analyses. Thus, we set up a flexible factorial model with the factors *subject, target* (self, other) and *stress* (stress, control). We entered the first-level contrasts sh > sl (for condition self) and oh > ol (for condition other) into a group-level analysis to assess univariate group activity during value representation. We performed family wise error (FWE, voxel-level) correction within a predefined and independently determined mask of brain valuation regions. More specifically, we used a mask combining the voxels identified in two meta-analyses investigating brain regions which positively correlate with the value of reward across reward types and decision contexts (Bartra et al., 2013; Clithero and Rangel, 2014) available at http://www.rnl.caltech.edu/resources/index.html.

Furthermore, we implemented exploratory analyses to assess differences in univariate activity for *stress* and *target* within the same flexible factorial model design using the first-level contrasts sh > sl (for condition self) and oh > ol (for condition other). This allowed us to test two crucial questions: a) whether there is any difference, on average, between the h > l contrast for self vs. other (contrasts: sh – sl > oh – ol and oh - ol > sh – sl); b) whether there is a *target* × *stress* interaction (contrasts: sh – sl_stress > sh – sl_control; sh – sl_control > sh - sl_stress; oh – ol_stress > oh – ol_control and oh – ol_control > oh – ol_stress).

2.2.7. Representational similarity analysis

A neural representational dissimilarity matrix (RDM; Kriegeskorte et al., 2008) was computed for the two mPFC ROIs (ventral and dorsal mPFC) and the exploratory ROIs in each subject. In the following, we describe each step of the analysis which follow the methods described in (Kriegeskorte et al., 2008). For an in-depth description and discussion of the methodological steps, see (Kriegeskorte et al., 2008). Here, we averaged voxel response vectors for each condition (sh, sl, oh, ol) across volumes and then computed dissimilarity (correlational distance; i.e., 1 - correlation) between the average voxel patterns for each condition, yielding two neural RDMs for each participant (i.e., one for stress and one for control) for each ROI. Subsequently, we averaged the RDMs for each condition (i.e., stress and control) across subjects for each ROI. As a first analysis, the overall difference between the dissimilarity matrices between stress and control was assessed by calculating the Spearman correlation between the upper triangular region of each RDM (as dissimilarity matrices are symmetrical about a diagonal of zero (Kriegeskorte et al., 2008)) under the null hypothesis that the two RDMs are identical. We were particularly interested in stress effects on similarity of neural patterns between high and low value, and between self and others. In order to assess this, we calculated the similarity between neural patterns between the four pairs of conditions: sh – sl, oh – ol, sh – oh, and sl - ol by calculating Pearson correlations between the voxel responses of the respective conditions. Note, that we use two different methods for computing correlations (Spearman vs. Pearson) at different steps in this analysis. For a description and discussion of the reasoning behind this, see (Kriegeskorte et al., 2008). In order to statistically test whether the similarity between those patterns changes under stress, we calculated paired t-tests between stress and control condition. Since t-tests assume that variables are normally distributed, which is not the case in correlations (as correlations are bounded between −1 and +1), we applied Fisher z-transformation to the correlations before calculating the t-tests.

For each ROI, we also calculated the mean within and across condition similarity (i.e., correlation) in the control RDMs to assess whether the mean within condition similarity was higher than the mean across condition similarity (using a paired *t*-test).

3. Results

3.1. Questionnaire data

Risk aversion did not differ between stress and control run (Z = −0.378, p = 0.705).

3.2. Stress manipulation

Participants showed larger cortisol AUC_I in the stress condition compared to the control condition (t(26) = 3.412; p = 0.002), documenting higher increase in cortisol responses in the stress condition compared to the control condition. Cortisol AUC_G did not differ between stress and control condition (t(26) = 1.171; p = 0.252). Thus, the overall magnitude of cortisol levels did not differ between the two conditions. For self-reported stress, we found larger AUC_G in the stress condition compared to the control condition (t(26) = 2.575; p = 0.016) indicating that the overall magnitude of self-reported stress was larger in the stress condition. AUC_I for self-reported stress did not differ between the conditions (t(26) = 1.214; p = 0.236) indicating that the increase in self-reported stress did not differ significantly between stress and control condition. Fig. 3 shows the stress levels during the experiment as indicated by free salivary cortisol levels (top) and subjective stress ratings (bottom).

3.3. Behavioral data lottery task

A 2 × 2 × 2 repeated measures ANOVA with factors *value* (high vs. low); *target* (self vs other); *stress* (stress vs control)) with number of trials played as the dependent variable revealed a significant main effect of value ($F(1,27) = 1115.775$, $p < 0.001$, $\eta_p^2 = 0.98$). All other main effects and interactions were non-significant (all p-values ≥ 0.110). Participants played more trials in the high value condition (mean number of trials played = 23.6; SD = 0.37) compared to the low value condition (mean number of trials played = 2.23; SD = 0.51). A 2 × 2 repeated measures ANOVA with factors *target* (self vs other); *stress* (stress vs control)) with response time on high value trials (on played trials) as the dependent variable revealed no significant effects or interactions but a trend significant main effect of stress ($F(1,27) = 3.339$, $p = 0.079$, $\eta_p^2 = 0.11$). Participants responded faster in the control condition (mean RT = 925 ms; SD = 29 ms) compared to the stress condition (mean RT = 1023 ms; SD = 53 ms).

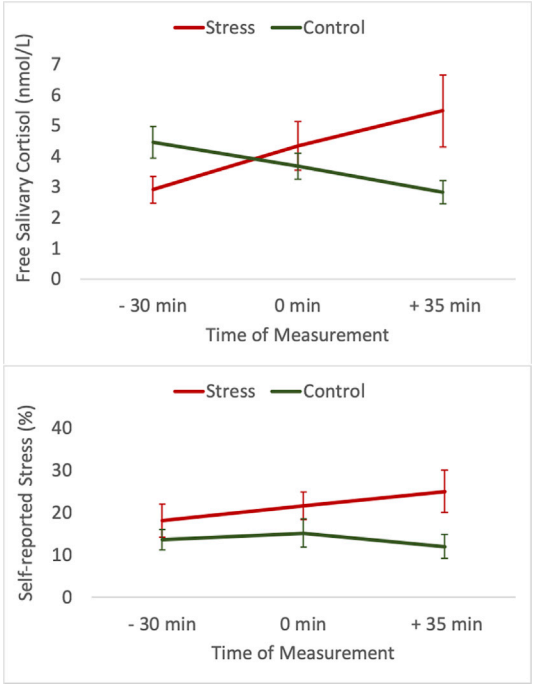

Fig. 3. Stress levels during stress and control condition assessed by (top) free salivary cortisol and (bottom) subjective stress ratings on a visual analogue scale (ranging from 0 to 100). Error bars indicate standard errors of the means. Time point zero indicates onset of stress task (stress or control version depending on condition).

3.4. Correlations stress measures and behavioral data

We calculated correlations between AUC_I and AUC_G stress measures (for cortisol and self-reported stress) and response times for each condition (sh, sl, oh, ol) in the lottery task. We did not find significant correlations between stress measures and behavioral data (all p-values ≥ 0.118).

3.5. fMRI results: functional localizer

A random effects group analysis on the contrast Self > Syllables of the functional localizer task yielded two ROIs in the mPFC – a ventral ROI (MNI coordinates vmPFC peak: 8 48–2) and a dorsal ROI (MNI coordinates dmPFC peak: 10 58 20) at p < 0.05 (whole brain voxel-wise FWE corrected). The subsequent analyses are conducted using individually defined ROIs within these group-level ROIs (see section 2.2.4 for details).

3.6. fMRI results: univariate group analysis of lottery task

In order to check whether our paradigm elicits activation in line with previous research on value representation (Bartra et al., 2013; Clithero and Rangel, 2014), we calculated univariate contrasts between high and low value in the control condition. The contrast sh > sl showed activity in the right vmPFC (peak voxel at MNI coordinates x = 10, y = 44, z = 8; T = 4.26; significance level set to p < 0.05 small volume FWE corrected using a binary mask representing the conjunction of the voxels shown in two meta-analyses on valuation during decision-making (Bartra et al., 2013; Clithero and Rangel, 2014)), see Fig. 4. The contrast oh > ol for the control condition did not show any activation that survived correction for multiple comparisons. We also performed exploratory whole brain analyses (p < 0.05 whole brain voxel-level FWE corrected) on the effects of stress on univariate signals of value for self and other. For the contrast oh > ol: control > stress we found increased activation in the right temporal lobe (x = 54, y = −2, z = 4; T = 5.42). All other contrasts did not show any activation that survived correction for multiple comparisons. For the sake of completeness, we also explored the data using a cluster-level correction approach and report the results in the supplemental material.

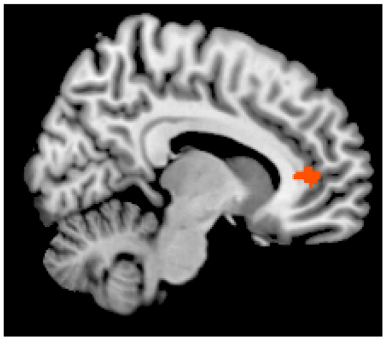

Fig. 4. Activation (MNI peak coordinates: 10, 44, 8) for the contrast sh > sl for the control condition (p < 0.05 small volume FWE voxel-level corrected).

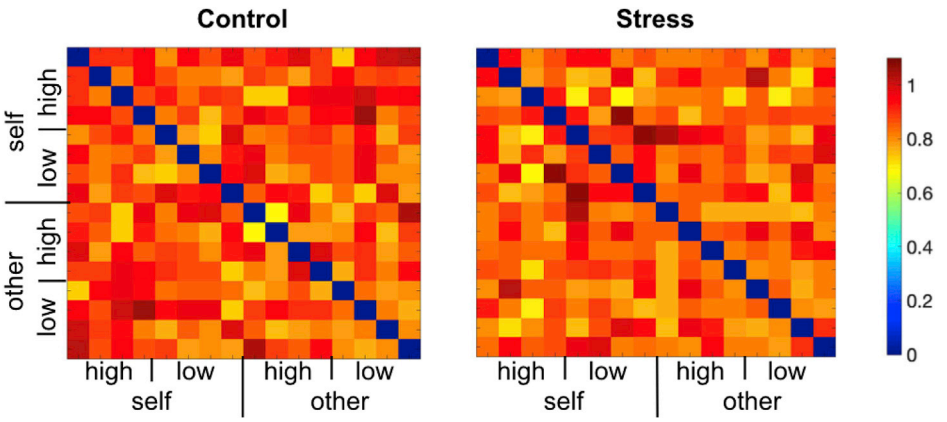

Fig. 5. Representational dissimilarity matrix in vmPFC ROI for control (left) and stress (right) condition depicting dissimilarities of neural patterns between each condition of the lottery task (i.e., self – high value, self – low value, other – high value and other – low value), time-locked to the cues presenting the winning probabilities of the specific trial (i.e., the lottery wheels). The cells represent the different stimuli within each condition: self – high value includes lottery wheels with winning probabilities of 85%, 80%, 75% and 70% and self – low value includes lottery wheels with winning probabilities of 30%, 25%, 20% and 15% (and the same for the other condition).

3.7. fMRI results: representational similarity analysis

3.7.1. vmPFC ROI

The target analysis of assessing change in similarity of neural patterns for sh-sl, oh-ol, sh-oh, sl-ol showed no significant difference in neural patterns between stress and control (all p-values > 0.41). Exploratory analyses of the overall dissimilarity of the stress and control RDMs showed that the two RDMs were not correlated: Spearman correlation rs $= -0.055$, p $= 0.553$. However, exploratory analyses assessing change in similarity of mean neural patterns for conditions outside of our target analysis (i.e., sh-ol and oh-sl) showed no significant differences in neural patterns between stress and control (all p-values > 0.55). Mean within-across condition similarity in the control RDM was not significantly different (t(27) $= 1.065$, p $= 0.296$). Fig. 5 displays RDMs for the stress and control condition.

3.7.2. dmPFC ROI

The target analysis of assessing change in dissimilarity of neural patterns for the conditions sh-sl, oh-ol, sh-oh, sl-ol showed that the dissimilarity between neural patterns for other-high value (oh) and other-low value (ol) was significantly different between stress and control condition (df(27), t $= 2.936$, p $= 0.007$), with higher dissimilarity during stress than control. No other dissimilarity differed significantly between stress and control (all p-values > 0.16). Comparison of mean RDMs for stress and control condition across subjects showed that the two RDMs were correlated: Spearman correlation rs $= 0.251$, p $= 0.006$. Mean within-across condition similarity in the control RDM was not significantly different (t(27) $= 0.276$, p $= 0.785$).

Fig. 6 displays RDMs for stress and control condition.

3.8. Exploratory analyses in group ROIs

The additional exploratory analyses using ROIs from the literature to complement our target functional localizer ROI analysis revealed the results as follows.

3.8.1. Right striatum

We calculated two RSA analyses in the right striatum, one using the SELF-VALUE ROI and one using the OTHER-VALUE ROI and report significant results at p < 0.025 (i.e., 0.05/2).

SELF-VALUE ROI. Mean within-across similarity was different (t(27) $= 2.413$, p $= 0.024$) with higher within-condition similarity. The target analysis of assessing change in dissimilarity of neural patterns for the conditions sh-sl, oh-ol, sh-oh, sl-ol showed a trend significant difference in the dissimilarity between neural patterns for other-high value (oh) and other-low value (ol) between stress and control condition (df(27), t $= 2.317$, p $= 0.051$), with higher dissimilarity during stress than control (all other p-values > 0.15). Comparison of mean RDMs for stress and control condition across subjects showed that the two RDMs were correlated: Spearman correlation rs $= 0.462$, p < 0.001.

OTHER-VALUE ROI. Mean within-across similarity was not different (t(27) $= 1.693$, p $= 0.102$). The target analysis of assessing change in dissimilarity of neural patterns for the conditions sh-sl, oh-ol, sh-oh, sl-ol showed that the dissimilarity between neural patterns for other-high value (oh) and other-low value (ol) was significantly different between stress and control condition (df(27), t $= 2.323$, p $= 0.019$), with higher dissimilarity during stress than control (all other p-values > 0.43). Comparison of mean RDMs for stress and control condition across subjects showed that the two RDMs were correlated: Spearman correlation rs $= 0.5420$, p < 0.001.

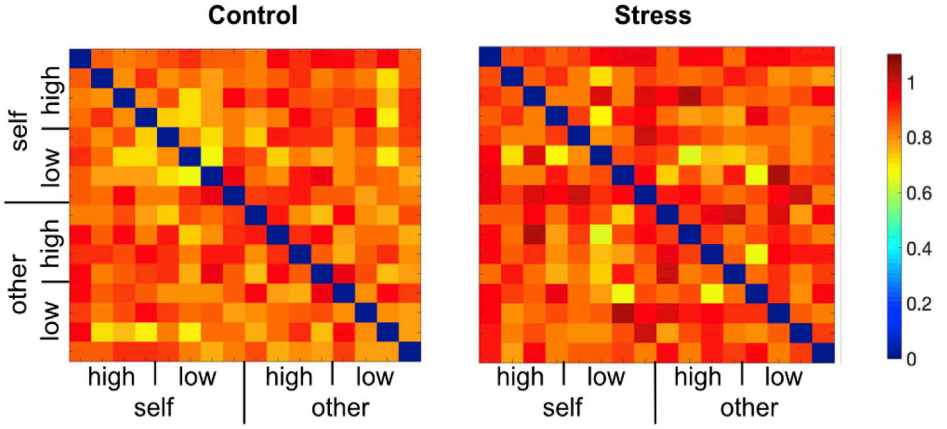

Fig. 6. Representational dissimilarity matrix in dmPFC ROI for (left) control and (right) stress condition depicting dissimilarities of neural patterns between each condition of the lottery task (i.e., self – high value, self – low value, other – high value and other – low value) time-locked to the cues presenting the winning probabilities of the specific trial (i.e., the lottery wheels). The cells represent the different stimuli within each condition: self – high value includes lottery wheels with winning probabilities of 85%, 80%, 75% and 70% and self – low value includes lottery wheels with winning probabilities of 30%, 25%, 20% and 15% (and the same for the other condition).

3.8.2. Left striatum

Again, we calculated two RSA analyses in the left striatum, one using the SELF-VALUE ROI and one using the OTHER-VALUE ROI and report significant results at $p < 0.025$ (i.e., 0.05/2).

SELF-VALUE ROI. Mean within-across similarity was different ($t(27) = 2.399$, $p = 0.016$) with higher within-condition similarity. The target analysis of assessing change in dissimilarity of neural patterns for the conditions sh-sl, oh-ol, sh-oh, sl-ol showed a difference in dissimilarity between neural patterns for other-high value (oh) and other-low value (ol) between stress and control condition which did not survive correction for multiple comparisons ($df(27)$, $t = 2.317$, $p = 0.031$), with higher dissimilarity during stress than control (all other p-values > 0.18). Comparison of mean RDMs for stress and control condition across subjects showed that the two RDMs were correlated: Spearman correlation $rs = 0.50$, $p < 0.001$.

OTHER-VALUE ROI. Mean within-across similarity was not different ($t(27) = 1.151$, $p = 0.260$). The target analysis of assessing change in dissimilarity of neural patterns for the conditions sh-sl, oh-ol, sh-oh, sl-ol showed a marginal difference in dissimilarity between neural patterns for self-high value (oh) and self-low value (ol) between stress and control condition ($df(27)$, $t = 2.317$, $p = 0.061$), with lower dissimilarity during stress than control (all other p-values > 0.34). Comparison of mean RDMs for stress and control condition across subjects showed that the two RDMs were correlated: Spearman correlation $rs = 0.585$, $p < 0.001$.

3.8.3. SELF-VALUE vmPFC ROI

Mean within-across similarity was different ($t(27) = 2.222$, $p = 0.035$) with higher within-condition similarity. The target analysis of assessing change in dissimilarity of neural patterns for the conditions sh-sl, oh-ol, sh-oh, sl-ol showed no difference between stress and control (all p-values > 0.18). Comparison of mean RDMs for stress and control condition across subjects showed that the two RDMs were correlated: Spearman correlation $rs = 0.327$, $p < 0.001$.

3.8.4. Additional OTHER-VALUE ROIs

Insula. Mean within-across similarity was not different ($t(27) = 1.130$, $p = 0.269$). The target analysis of assessing change in dissimilarity of neural patterns for the conditions sh-sl, oh-ol, sh-oh, sl-ol showed no difference between stress and control (all p-values > 0.14). Comparison of mean RDMs for stress and control condition across subjects showed that the two RDMs were correlated: Spearman correlation $rs = 0.621$, $p < 0.001$.

3.8.5. Thalamus

Mean within-across similarity was not different ($t(27) = 1.410$, $p = 0.170$). The target analysis of assessing change in dissimilarity of neural patterns for the conditions sh-sl, oh-ol, sh-oh, sl-ol showed no difference between stress and control (all p-values > 0.23). Comparison of mean RDMs for stress and control condition across subjects showed that the two RDMs were correlated: Spearman correlation $rs = 0.3154$, $p < 0.001$.

3.9. Correlations brain and behavior

We were interested whether dissimilarity of neural patterns between high and low value for other (oh-ol) under stress correlated with behavior during the task. We used number of trials played as our behavioral measure for the correlations as response times were only analyzed for high value trials (see methods section 2.2.1 *Analyses of behavioral data* for details). We calculated these correlations using the Fisher transformed similarity data of the dmPFC ROI and the OTHER OTHER-VALUE right ventral striatum ROI for the stress condition and number of trials played for oh and ol during the stress condition. Thus, we calculated two Spearman correlations (oh-ol x trials_played_oh and oh-ol x trials_played_ol per ROI; and report results as significant for $p < 0.025$ (0.05/2)). We found a significant negative correlation between similarity oh-ol in the ventral striatum ROI and trials_played_oh ($r = -0.439$, $p = 0.019$). Thus, participants who showed more dissimilarity in their neural patterns between oh and ol, played more high value trials for the other.

In addition, we aimed to explore whether the dissimilarity between stress and control RDMs in vmPFC (self-localizer ROI) was associated with behavior in the lottery task. We calculated a dissimilarity (1-correlation) measure between the stress RDM and the control RDM in ventral mPFC for each participant and correlated this measure (using Pearson correlation) with response times on sh, sl, oh and ol trials (we report results as significant for $p < 0.0125$ (0.05/4)). We found that dissimilarity between stress and control RDMs correlated significantly with response times on oh trials ($r = 0.473$, $p = 0.011$) and we found a trend-significant positive correlation for sh trials ($r = 0.421$, $p = 0.026$). We calculated the same correlation with the dissimilarity (1-correlation) measure between the stress RDM and the control RDM in dorsal mPFC and did not find any significant correlations (all p-values > 0.20).

4. Discussion

The present study investigated the effects of acute stress on the similarity of neural representations of value for self and others. Our central finding is that stress increased dissimilarity of neural patterns between high and low value for others in dorsal mPFC and in the right striatum. We also find that more dissimilarity in neural patterns between high and low value for others in the striatum correlated with playing more high value trials for the other.

Thus, the neural representation of high and low value for another person becomes more distinct under stress. This suggests that individuals are more sensitive to the rewards for another person when they are stressed than when not stressed. Our initial hypothesis that value representation between self and others becomes more *similar* under stress – possibly due to a decreased capacity to differentiate between own rewards and rewards for others - was not confirmed. Instead, our findings rather suggest that stress specifically alters the neural representation of value for others, which is in line with the arguments set forth in the "tend and befriend" hypothesis (Taylor et al., 2000).

A number of control measures speak for the validity of our findings. First, the behavioral measures show that participants played more trials in the high value condition than the low value condition. This implies that participants were actively engaged in the task and attempted to maximize their and the other player's benefits. Second, the number of trials played was not overall different between self and other trials indicating that participants complied with the instructions to gain as much money as possible for themselves and their partner in the experiment. Third, we validated the success of our stress induction using both cortisol levels and subjective stress ratings. Both measures show higher stress in the stress compared to the control condition. Fourth, the fact that the risk aversion control measures were not affected by stress indicates that our effects of interest were not confounded by differences in risk aversion between the stress conditions.

Interestingly, while stress did not affect the number of trials played in each condition during the lottery task, participants did respond faster in the control condition than in the stress condition. However, participants did not seem to have experienced a speed-accuracy tradeoff as the actual decisions did not differ between conditions. Note however, that we did not find a significant interaction between stress (stress, control) and target (self, other) in these effects. Thus, it might be that decision-making was easier or entailed less extensive cognitive processing in the control condition.

We did not find an effect of stress in our target comparisons of neural patterns in the vmPFC (neither in the functional ROI nor in the SELF-VALUE ROI). However, our finding that stress only affected value representation for others in the dorsal but not ventral mPFC is in line with prior research showing a spatial gradient in value representation along the mPFC with other-regarding values being represented predominantly in the dorsal parts of mPFC while the ventral parts were predominantly

representing self-regarding values (Sul et al., 2015).

Even though previous research has suggested that reward sensitivity increases under stress (Kumar et al., 2014; Maier et al., 2015; Ironside et al., 2018) we did not find any significant effects of stress on neural similarity between high and low value for the self (sh-sl) – in neither of our ROIs. We speculate that the highly social nature of our gambling task might have abolished stress effects on own value processing. More specifically, because participants were playing the lottery task with a real other person, whom they met in-between each scanning run, the salience of the other might have been very high throughout the task. As stress has been shown to shift cognitive processing to a salience-focused mode (Hermans et al., 2014), the fact that we introduced a salient other person in the task might have led participants to focus more on the other under stress, which might have abolished the increased reward sensitivity for the self, found in previous studies. If this interpretation holds true, this might mean that the presence of a relevant other person might shift stress-induced increased reward sensitivity to the other instead of the self, which would be in line with previous findings showing that participants give away more of their own money in a dictator game when stressed (von Dawans et al., 2012; Tomova et al., 2017). However, because in our experiment participants did not have to prioritize the self or the other in their behavior (i.e., they were instructed to play equally for self and other and playing more for the other did not take away resources from the self), we do not have any behavioral measures on trade-offs between gains for self versus other. Furthermore, it is important to note that this conclusion is based on a null finding (i.e., no effects of stress on neural dissimilarity between high and low value for the self (sh-sl)). There are many reasons for observing a null finding including, for example, ceiling effects in the dissimilarity level in the control condition. Future studies experimentally manipulating the presence of self and other, and their salience, are thus needed to follow up this conceptually and practically highly relevant research avenue.

Our assessment of within-across condition correlations in the RDMs in all ROIs (only performed for the control condition) showed that the mean within-condition correlations (mean across all conditions) were higher than the mean across-condition correlations in all three SELF-VALUE ROIs. This finding indicates that neural patterns in these ROIs showed more similar responses to stimuli within one condition than to stimuli across conditions thus indicating that they were more reliably similar. We did not find a significant within-across difference in any of the other ROIs indicating that signals in these ROIs might be less reliable. However, we find the same general pattern of results in the SELF-VALUE ROIs as in our other ROIs: differentiation between high and low rewards for others increases under stress. Thus, our results did not differ based on differences in the within-across condition similarities.

The present findings connect to prior research showing that stress increased the magnitude of responding in "empathy for pain" brain regions in response to seeing someone else in pain (Tomova et al., 2017). A potential common mechanism that could relate our present findings to these prior results might be that under stress, individuals become more other-oriented, which increases empathy for others and also valuation of others' rewards. Importantly, though, it needs to be noted that these effects might be specific for social stress. I.e., in our experiment we used social evaluative threat in combination with time pressure to induce stress. Thus, it might be that different effects would be observed when using a non-social stressor. In addition, the present study only included male participants, so it is important to investigate in future studies whether the observed effects can be replicated in a female sample.

In the present study, we implemented a within-subjects design in which each participant underwent an acute stress induction and a control condition. While overall, we find that our cortisol and subjective stress measures indicate that participants were more stressed during the stress compared to the control condition, a potential limitation of our study is that our baseline measures of cortisol show a difference between conditions, which might be attributed to carry-over effects from one condition to the other. We note, however, that in the stress condition, participants show a clear increase in cortisol levels, while cortisol levels decrease in the control condition, which also corresponds to the effects on subjective stress levels, indicating that the stress manipulation worked successfully. Another potential limitation of our study is that cortisol measures and subjective stress levels were not correlated. Indeed, stress studies often find a mismatch between physiological and endocrinological measures and self-reported stress measures. I.e., the subjective experience of stress is, at least acutely, not directly related to adrenaline release or cortisol release allowing for discrepancies in these measures (see Ali et al., 2017 for an experimental study on this topic).

Another possible limitation of the study is that our value manipulation (high and low value) is confounded with choosing to play. Because participants played most high value trials and decided to not play most low value trials, it is possible that the observed effect reflects a cognitive process related to anticipating the gamble (e.g. task engagement or arousal) instead of a representation for high vs. low value. In that case, our results could imply that participants under stress showed higher task engagement or arousal in response to high rewards compared to low rewards for others. Future studies illuminating the exact cognitive process that is responsible for stress induced increases in differentiation between high and low value for others are thus needed to illuminate the findings in more detail. .

5. Conclusions

In conclusion, the initial hypothesis that stress decreases differentiation between self and others was not supported by our data. However, our findings show that under stress neural patterns in response to high and low value for others become more dissimilar. Furthermore, participants who showed more neural differentiation between high and low value for others played more favorably for the other. Thus, our results imply that stress appears to increase reward sensitivity for another person. This would be in line with converging evidence from behavioral research indicating that stress increases prosocial behavior (Takahashi et al., 2007; von Dawans et al., 2012; Margittai et al., 2015; Buchanan and Preston, 2014; Singer et al., 2017; von Dawans et al., 2019), which has been interpreted in light of the "tend-and-befriend" hypothesis stating that individuals become more prosocial under stress in order to secure help from others (Taylor et al., 2000). Furthermore, previous research has shown that stress increases the magnitude of brain activity in "empathy for pain areas" when viewing others in pain, and this predicted later prosocial behavior (Tomova et al., 2017). The results of the present study extend this research by showing that in the domain of value computation, stress leads to an increased differentiation between high and low value for others suggesting that stressed individuals track the potential reward for others more closely which is also associated with playing more favorably for the other.

These findings might be particularly relevant for highly stressful environments that require close cooperation — such as in medicine, science, education, police or military. Indeed, more prosocial stress coping strategies have been shown to be associated with better leadership skills in the military environment (Nakkas et al., 2016). Thus, the behavioral implications of a prosocial stress coping response, in addition to the classical fight and flight response, should be investigated in more detail in order to advance our understanding of how humans respond to and cope with stress.

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Author contributions

L.T., R.S. and C.L. designed the study; L.T. wrote the code for the paradigm with input from R.S. and C.L.; L.T. implemented the experiments with support from M.K. and R.L.; L.T. performed all data analyses with input from C.L., R.S. and M.K.; L.T. wrote the manuscript and all authors performed review and editing.

Declaration of competing interest

All authors declare no competing financial interests or potential conflicts of interest in relation to the work described. RL received conference speaker honorarium within the last three years from Shire, support from Siemens Healthcare regarding clinical research using PET/MR, and he is shareholder of BM Health GmbH since 2019.

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Appendix A. Supplementary data

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References

Ali, N., Nitschke, J.P., Cooperman, C., Pruessner, J.C., 2017. Suppressing the endocrine and autonomic stress systems does not impact the emotional stress experience after psychosocial stress. Psychoneuroendocrinology 78, 125–130.
Anderson, N.H., 1968. Likableness ratings of 555 personality-trait words. J. Personal. Soc. Psychol. 9, 272–279.
Baron-Cohen, S., Wheelwright, S., Hill, J., Raste, Y., Plumb, I., 2001. The "Reading the Mind in the Eyes" Test revised version: a study with normal adults, and adults with Asperger syndrome or high-functioning autism. JCPP (J. Child Psychol. Psychiatry) 42, 241–251.
Bartra, O., McGuire, J.T., Kable, J.W., 2013. The valuation system: a coordinate-based meta-analysis of BOLD fMRI experiments examining neural correlates of subjective value. Neuroimage 76, 412–427.
Berridge, K.C., Robinson, T.E., 2003. Parsing reward. Trends Neurosci. 26, 507–513.
Buchanan, T.W., Preston, S.D., 2014. Stress leads to prosocial action in immediate need situations. Front. Behav. Neurosci. 8, 5.
Carter, R.M., Macinnes, J.J., Huettel, S.A., Adcock, R.A., 2009. Activation in the VTA and nucleus accumbens increases in anticipation of both gains and losses. Front. Behav. Neurosci. 3, 21-21.
Clithero, J.A., Rangel, A., 2014. Informatic parcellation of the network involved in the computation of subjective value. Soc. Cogn. Affect. Neurosci. 9, 1289–1302.
Davis, M.H., 1983. Measuring individual differences in empathy: evidence for a multidimensional approach. J. Personal. Soc. Psychol. 44, 113–126.
Dedovic, K., Renwick, R., Mahani, N.K., Engert, V., Lupien, S.J., Pruessner, J.C., 2005. The Montreal Imaging Stress Task: using functional imaging to investigate the effects of perceiving and processing psychosocial stress in the human brain. J. Psychiatry Neurosci. 30, 319–325.
Dedovic, K., Renwick, R., Mahani, N.K., Engert, V., Lupien, S.J., Pruessner, J.C., 2005. The Montreal Imaging Stress Task: using functional imaging to investigate the effects of perceiving and processing psychosocial stress in the human brain. J. Psychiatry Neurosci. 30, 319–325.
Dickerson, S.S., Kemeny, M.E., 2004. Acute stressors and cortisol responses: a theoretical integration and synthesis of laboratory research. Psychol. Bull. 130, 355–391.
Doherty, R.W., 1997. The emotional contagion scale: a measure of individual differences. J. Nonverbal Behav. 21, 131–154.
Hare, T.A., O'Doherty, J., Camerer, C.F., Schultz, W., Rangel, A., 2008. Dissociating the role of the orbitofrontal cortex and the striatum in the computation of goal values and prediction errors. J. Neurosci. 28, 5623–5630.
Haxby, J.V., Connolly, A.C., Guntupalli, J.S., 2014. Decoding neural representational spaces using multivariate pattern analysis. Annu. Rev. Neurosci. 37, 435–456.
Hermans, E.J., Henckens, M.J., Joels, M., Fernandez, G., 2014. Dynamic adaptation of large-scale brain networks in response to acute stressors. Trends Neurosci. 37, 304–314.
Holt, C.A., Laury, S.K., 2002. Risk aversion and incentive effects. Am. Econ. Rev. 92, 1644–1655.
Hutcherson, Cendri A., Bushong, B., Rangel, A., 2015. A neurocomputational model of altruistic choice and its implications. Neuron 87, 451–462.
Inglis, F.M., Moghaddam, B., 1999. Dopaminergic innervation of the amygdala is highly responsive to stress. J. Neurochem. 72, 1088–1094.
Ironside, M., Kumar, P., Kang, M.-S., Pizzagalli, D.A., 2018. Brain mechanisms mediating effects of stress on reward sensitivity. Curr. Opin. Behav. Sci. 22, 106–113.
Kelley, W.M., Macrae, C.N., Wyland, C.L., Caglar, S., Inati, S., Heatherton, T.F., 2002. Finding the self? An event-related fMRI study. J. Cogn. Neurosci. 14, 785–794.
Kirschbaum, C., Kudielka, B.M., Gaab, J., Schommer, N.C., Hellhammer, D.H., 1999. Impact of gender, menstrual cycle phase, and oral contraceptives on the activity of the hypothalamus-pituitary-adrenal axis. Psychosom. Med. 61, 154–162.
Koller, I., Lamm, C., 2015. Item response model investigation of the (German) interpersonal reactivity Index empathy questionnaire. Eur. J. Psychol. Assess. 31 (3), 211–221. https://doi.org/10.1027/1015-5759/a000227.
Kriegeskorte, N., Mur, M., Bandettini, P., 2008. Representational similarity analysis – connecting the branches of systems neuroscience. Front. Syst. Neurosci. 2, 4.
Kumar, S., Zigman, M., Patel, T.R., Trageser, B., Gross, J.C., Rahm, K., Boutros, M., Gradl, D., Steinbeisser, H., Holstein, T., Stetefeld, J., Ozbek, S., 2014. Molecular dissection of Wnt3a-Frizzled 8 interaction reveals essential and modulatory determinants of Wnt signaling activity. BMC Biol. 12, 44.
Lamm, C., Bukowski, H., Silani, G., 2016. From shared to distinct self-other representations in empathy: evidence from neurotypical function and socio-cognitive disorders. Philos. Trans. R. Soc. Lond. B Biol. Sci. 371.
Lamm, C., Rutgen, M., Wagner, I.C., 2019. Imaging empathy and prosocial emotions. Neurosci. Lett. 693, 49–53.
Lockwood, P.L., Apps, M.A.J., Roiser, J.P., Viding, E., 2015. Encoding of vicarious reward prediction in anterior cingulate cortex and relationship with trait empathy. J. Neurosci. 35, 13720–13727.
Maier, S.U., Makwana, A.B., Hare, T.A., 2015. Acute stress impairs self-control in goal-directed choice by altering multiple functional connections within the brain's decision circuits. Neuron 87, 621–631.
Margittai, Z., Strombach, T., van Wingerden, M., Joels, M., Schwabe, L., Kalenscher, T., 2015. A friend in need: time-dependent effects of stress on social discounting in men. Horm. Behav. 73, 75–82.
Milward, S.J., Sebanz, N., 2016. Mechanisms and development of self-other distinction in dyads and groups. Philos. Trans. R. Soc. Lond. B Biol. Sci. 371, 20150076.
Nakkas, C., Annen, H., Brand, S., 2016. Psychological distress and coping in military cadre candidates. Neuropsychiatric Dis. Treat. 12, 2237–2243.
Oei, N.Y.L., Both, S., van Heemst, D., van der Grond, J., 2014. Acute stress-induced cortisol elevations mediate reward system activity during subconscious processing of sexual stimuli. Psychoneuroendocrinology 39, 111–120.
Piazza, P.V., Le Moal, M., 1997. Glucocorticoids as a biological substrate of reward: physiological and pathophysiological implications. Brain Res. Rev. 25, 359–372.
Porcelli, A.J., Delgado, M.R., 2017. Stress and decision making: effects on valuation, learning, and risk-taking. Curr. Opin. Behav. Sci. 14, 33–39.
Pruessner, J.C., Kirschbaum, C., Meinlschmid, G., Hellhammer, D.H., 2003. Two formulas for computation of the area under the curve represent measures of total hormone concentration versus time-dependent change. Psychoneuroendocrinology 28, 916–931.
Pruessner, J.C., Champagne, F., Meaney, M.J., Dagher, A., 2004. Dopamine release in response to a psychological stress in humans and its relationship to early life maternal care: a positron emission tomography study using [11C]raclopride. J. Neurosci. 24, 2825–2831.
Riecansky, I., Paul, N., Kolble, S., Stieger, S., Lamm, C., 2015. Beta oscillations reveal ethnicity ingroup bias in sensorimotor resonance to pain of others. Soc. Cogn. Affect. Neurosci. 10, 893–901.
Riecansky, I., Lengersdorff, L.L., Pfabigan, D.M., Lamm, C., 2019. Increasing self-other bodily overlap increases sensorimotor resonance to others' pain. Cognit. Affect Behav. Neurosci. https://doi.org/10.3758/s13415-019-00724-0.
Riva, F., Triscoli, C., Lamm, C., Carnaghi, A., Silani, G., 2016. Emotional egocentricity bias across the life-span. Front. Aging Neurosci. 8, 74.
Rohe, T., Weber, B., Fliessbach, K., 2012. Dissociation of BOLD responses to reward prediction errors and reward receipt by a model comparison. Eur. J. Neurosci. 36, 2376–2382.
Saxe, R., Brett, M., Kanwisher, N., 2006. Divide and conquer: a defense of functional localizers. Neuroimage 30, 1088–1096 discussion 1097-1089.
Singer, N., Sommer, M., Döhnel, K., Zänkert, S., Wüst, S., Kudielka, B.M., 2017. Acute psychosocial stress and everyday moral decision-making in young healthy men: the impact of cortisol. Horm. Behav. 93, 72–81.
Smeets, T., Dziobek, I., Wolf, O.T., 2009. Social cognition under stress: differential effects of stress-induced cortisol elevations in healthy young men and women. Horm. Behav. 55, 507–513.
Starcke, K., Brand, M., 2012. Decision making under stress: a selective review. Neurosci. Biobehav. Rev. 36, 1228–1248.
Sul, S., Tobler, P.N., Hein, G., Leiberg, S., Jung, D., Fehr, E., Kim, H., 2015. Spatial gradient in value representation along the medial prefrontal cortex reflects individual differences in prosociality. Proc. Natl. Acad. Sci. U.S.A. 112, 7851–7856.
Takahashi, T., Ikeda, K., Hasegawa, T., 2007. Social evaluation-induced amylase elevation and economic decision-making in the dictator game in humans. Neuroendocrinol. Lett. 28, 662–665.
Taylor, S.E., Klein, L.C., Lewis, B.P., Gruenewald, T.L., Gurung, R.A., Updegraff, J.A., 2000. Biobehavioral responses to stress in females: tend-and-befriend, not fight-or-flight. Psychol. Rev. 107, 411–429.

Tomova, L., von Dawans, B., Heinrichs, M., Silani, G., Lamm, C., 2014. Is stress affecting our ability to tune into others? Evidence for gender differences in the effects of stress on self-other distinction. Psychoneuroendocrinology 43, 95–104.
Tomova, L., Majdandžić, J., Hummer, A., Windischberger, C., Heinrichs, M., Lamm, C., 2017. Increased neural responses to empathy for pain might explain how acute stress increases prosociality. Soc. Cogn. Affect. Neurosci. 12, 401–408.
von Dawans, B., Fischbacher, U., Kirschbaum, C., Fehr, E., Heinrichs, M., 2012. The social dimension of stress reactivity: acute stress increases prosocial behavior in humans. Psychol. Sci. 23, 651–660.
von Dawans, B., Ditzen, B., Trueg, A., Fischbacher, U., Heinrichs, M., 2019. Effects of acute stress on social behavior in women. Psychoneuroendocrinology 99, 137–144.
Zaki, J., Lopez, G., Mitchell, J.P., 2014. Activity in ventromedial prefrontal cortex co-varies with revealed social preferences: evidence for person-invariant value. Soc. Cogn. Affect. Neurosci. 9, 464–469.