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The interaction of acute and chronic stress impairs model-based behavioral control

Christoph Radenbach[a,*,1], Andrea M.F. Reiter[a,b,*,1], Veronika Engert[c], Zsuzsika Sjoerds[a], Arno Villringer[d,e,f,g], Hans-Jochen Heinze[h,i], Lorenz Deserno[a,i,j], Florian Schlagenhauf[a,j]

[a] *Max Planck Fellow Group 'Cognitive and Affective Control of Behavioral Adaptation', Max Planck Institute for Human Cognitive and Brain Sciences, 04103 Leipzig, Germany*
[b] *International Max Planck Research School on Neuroscience of Communication (IMPRS NeuroCom), 04103 Leipzig, Germany*
[c] *Department of Social Neuroscience, Max Planck Institute for Human Cognitive and Brain Sciences, 04103 Leipzig, Germany*
[d] *Department of Neurology, Max Planck Institute for Human Cognitive and Brain Sciences, 04103 Leipzig, Germany*
[e] *Day Clinic of Cognitive Neurology, University Hospital Leipzig, 04103 Leipzig, Germany*
[f] *IFB Adiposity Diseases, University of Leipzig, 04103 Leipzig, Germany*
[g] *Berlin School of Mind & Brain Institute, Humboldt-University, 10099 Berlin, Germany*
[h] *Department of Behavioral Neurology, Leibniz Institute for Neurobiology, 39118 Magdeburg, Germany*
[i] *Department of Neurology, Otto-von-Guericke University, 39120 Magdeburg, Germany*
[j] *Department of Psychiatry and Psychotherapy, Campus Charité Mitte, Charité — Universitätsmedizin Berlin, 10115 Berlin, Germany*

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Summary It is suggested that acute stress shifts behavioral control from goal-directed, model-based toward habitual, model-free strategies. Recent findings indicate that interindividual differences in the cortisol stress response influence model-based decision-making. Although not yet investigated in humans, animal studies show that chronic stress also shifts decision-making toward more habitual behavior. Here, we ask whether acute stress and individual vulnerability factors, such as stress reactivity and previous exposure to stressful life events, impact the balance between model-free and model-based control systems. To test this, 39 male participants (21—30 years old) were exposed to a potent psychosocial stressor (Trier Social Stress

* Corresponding authors at: Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstrasse 1a, 04103 Leipzig, Germany. Tel.: +49 341 9940 109; fax: +49 341 9940 2221.
E-mail addresses: radenbach@cbs.mpg.de (C. Radenbach), reiter@cbs.mpg.de (A.M.F. Reiter).
[1] Both these authors contributed equally to this work.

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Test) and a control condition in a within-subjects design before they performed a sequential decision-making task which evaluates the balance between the two systems. Physiological and subjective stress reactivity was assessed before, during, and after acute stress exposure. By means of computational modeling, we demonstrate that interindividual variability in stress reactivity predicts impairments in model-based decision-making. Whereas acute psychosocial stress did not alter model-based behavioral control, we found chronic and acute stress to interact in their detrimental effect on decision-making: subjects with high but not low chronic stress levels as indicated by stressful life events exhibited reduced model-based control in response to acute psychosocial stress. These findings emphasize that stress reactivity and chronic stress play an important role in mediating the relationship between stress and decision-making. Our results might stimulate new insights into the interplay between chronic and acute stress, attenuated model-based control, and the pathogenesis of various psychiatric diseases.

1. Introduction

Making effective decisions is particularly relevant in stressful situations and may depend on individual responsiveness during acute stress as well as on the long-term stress load. Dual-system theories of decision-making postulate a goal-directed system and a habitual system to compete for behavioral control (Balleine and Dickinson, 1998; Balleine and O'Doherty, 2010). Recently, computational modeling accounts of reinforcement learning have amended these theories (Daw et al., 2005): here, goal-directed, model-based behavior is seen as a flexible, albeit computationally complex strategy, which builds an internal mental model of the environment. Thereby, future actions and their potential outcomes are planned in a forward manner. In contrast, habitual, model-free control is seen as a retrospective and therefore more rigid strategy driven by past rewards which neglects environmental structure for the advantage of computational efficiency. Crucially, human decision-making involves both control systems with considerable interindividual variability (Daw et al., 2011). However, it remains an intriguing question how control over actions is allocated between the two systems depending on the particular situation and on interindividual trait differences (Dolan and Dayan, 2013).

Among situational factors that influence this allocation of control, stress is a key candidate for biasing the balance of the two systems toward habitual decision-making (Schwabe and Wolf, 2009, 2011, 2013). At the neurobiological level, cortisol, the endproduct of the hypothalamus-pituitary-adrenal (HPA-) axis, might affect prefrontal executive capacities, which may thus limit the degree of control exerted by the more sophisticated, model-based system. On the behavioral level, stress has been shown to influence decision-making, e.g. in terms of dysfunctional strategy use, automatic responding, goal implementation, response conflicts, risk taking, feedback processing per se and reward vs. punishment sensitivity (Petzold et al., 2010; Plessow et al., 2011, 2012; Starcke and Brand, 2012). In a recent study, Otto et al. (2013b) compared acutely stressed and non-stressed participants and did not observe between-group differences in the balance of behavioral control. However, interindividual differences in physiological stress response, as measured by cortisol increase, were negatively correlated with the degree of model-based control across both groups. Importantly, this points to the direction that interindividual differences in stress reactivity, rather than a stress-eliciting condition per se, might impact decision-making.

Beyond acute stress, animal studies suggest that chronic stress shifts decision-making toward more habitual strategies: Dias-Ferreira et al. (2009) observed that chronically stressed rats became insensitive to outcome devaluation, a key characteristic of habitual behavior. In humans, the effect of chronic stress and the interplay between previous stress experience and acute stress on model-based decision-making has not yet been investigated.

Here, we utilized a within-subjects design to assess the influence of a potent acute psychosocial stressor on the balance between model-based and model-free control as assessed via sequential decision-making (Daw et al., 2011). By means of computational modeling, we first asked if acute psychosocial stress diminishes the degree of model-based control within individuals. Second, we tested if interindividual variations in physiological and subjective stress reactivity predict the balance of behavioral control per se. Finally, we examined the interaction of chronic and acute stress levels in human decision-making.

2. Materials and methods

2.1. Participants

Thirty-nine healthy male subjects recruited by Internet advertisements completed the study (mean age: 25.2, $SD = 2.73$, range: 21—30 years). All participants except for one had obtained university entrance qualification, one held the general certificate of secondary education. The average years of education (including school, university etc.) was 16.32 ($SD = 3.21$), the average duration of unemployment counted 0.19 years ($SD = 0.44$). Exclusion criteria comprised presence or history of any neurological or psychiatric disorder and smoking, as nicotine impacts the neuroendocrine stress response (Mendelson et al., 2005). Exclusion criteria were assessed prior to study participation during a semi-structured telephone-screening. The study was approved by the ethics committee of the University of Leipzig. Written informed consent was obtained from all participants prior to the study.

2.2. Procedure

In two separate sessions (interval between testing sessions: $M = 7.03$ days, $SD = 0.28$), participants performed a Markov two-step sequential decision task (Daw et al., 2011). One of the sessions involved the standardized protocol Trier Social Stress Test (TSST) (Kirschbaum et al., 1993) to induce psychosocial stress before task performance (stress condition). In the control session, individuals were asked to read a neutral text before they executed the decision task (control condition). The order of the two sessions (stress vs. control) was counterbalanced across all participants (Fig. 1). On the first test day, participants were introduced to the study procedures, provided with instructions, and underwent training of the decision task. Before the stress or control protocol was applied, participants rested for 16 min in order to adapt to the testing situation. Importantly, both experimental sessions were scheduled at exactly the same time of day and always between 12:00 pm and 6:00 pm to control for circadian effects on task performance and cortisol levels (Kudielka et al., 2004). In a third testing session, trait questionnaires and working-memory were assessed (interval between the second and the third session: $M = 15.69$ days, $SD = 17.50$).

2.3. Stress protocol

The TSST is a well-established experimental protocol to reliably induce acute psychosocial stress in the laboratory and to prompt an increase in saliva cortisol levels as described in detail elsewhere (Kirschbaum et al., 1993; Kudielka et al., 2007). After a 10 min anticipation period participants were asked to assume the role of a job applicant and to present themselves in front of an evaluation committee while they thought they were being audio- and video-recorded (5 min). The job talk was followed by a challenging 5 min mental arithmetic task under evaluation by the committee. In the control condition, participants were undisturbed and requested to read a neutral, non-arousing, non-fiction text on the Mesozoic era for 20 min.

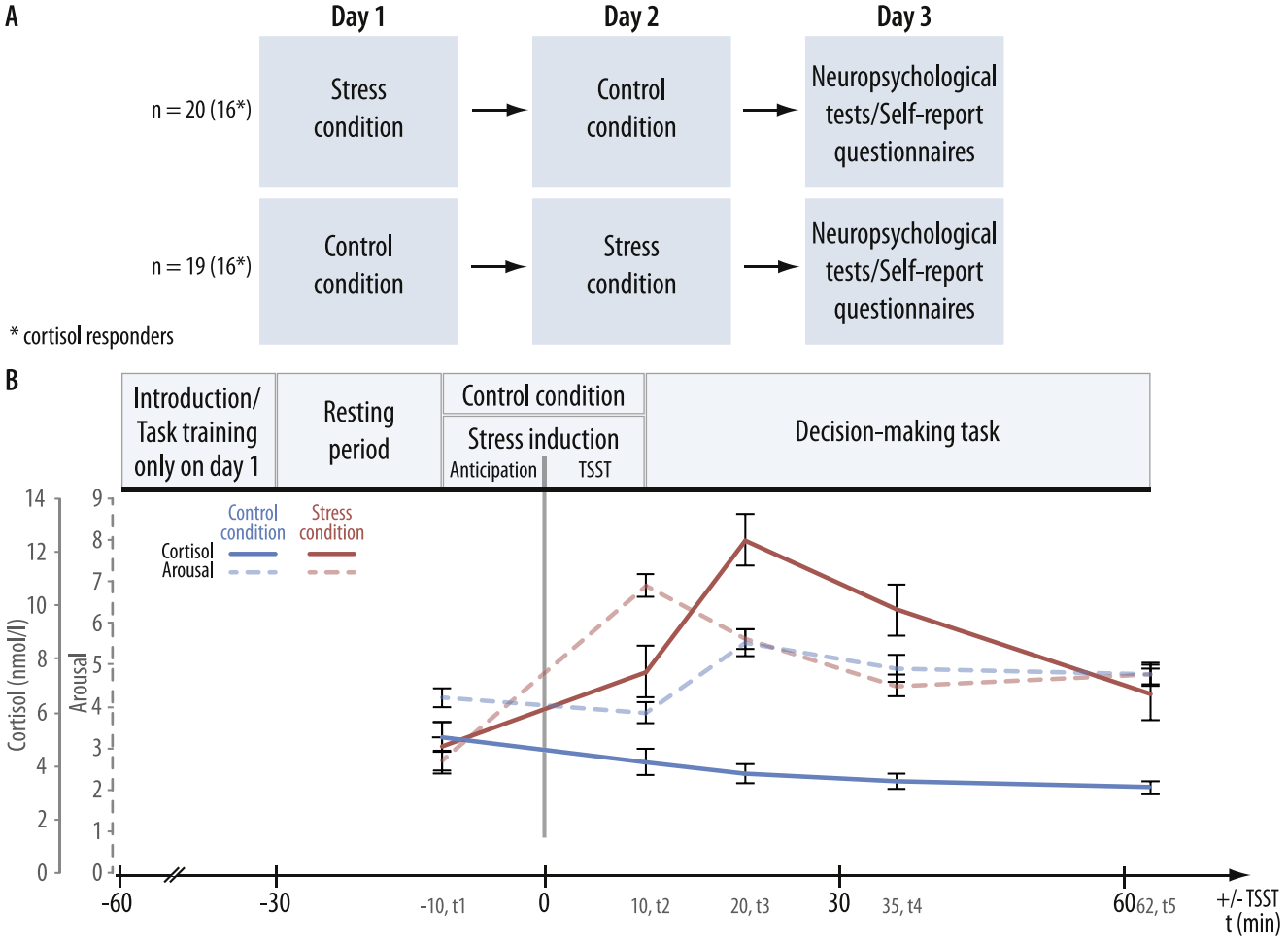

Figure 1 Within-subjects study design and time line of stress intervention. (A) All participants underwent the stress and the control condition. Order of conditions was counterbalanced across all participants. Trait measurements and working-memory capacity were assessed during a third testing session. (B) Course of one experimental session with salivary cortisol responses (in nmol/l, bold lines) and arousal response (Affect Grid Rating, dashed lines) to the stress (red lines) and the control condition (blue lines). Time scaling is relative to the onset of the 'Trier Social Stress Test' (TSST). Note that the decision-making task was performed during the peak cortisol period in the stress condition.

2.4. Assessment of cortisol response

To assess the physiological stress response of the hypothalamic pituitary adrenal axis, salivary cortisol was acquired five times throughout the experiment (Fig. 1). Samples were collected using a Salivette device (SalivetteCortisol®, Sarstedt, Nuembrecht, Germany) at the following time points: after 16 min of rest (baseline, $t1$), directly after the termination of the TSST or control condition, respectively ($t2$), ∼20 min ($t3$) and ∼35 min ($t4$) after the onset of the stressor or control condition (during short breaks in the experimental task) and after completion of the task (∼62 min after the onset, $t5$). Saliva samples were frozen at −20 °C and analyzed using a time-resolved fluorescence immunoassay. The intra-assay coefficient of variation was between 4.0% and 6.7%, and the corresponding inter-assay coefficients of variation were between 7.1% and 9.0%. Different cut-offs for relevant cortisol surges have been discussed in the literature; here, using a strict cut-off, a physiologically relevant cortisol surge was defined as an increase of at least 2.5 nmol/l above the individual baseline (Schommer et al., 2003; Van Cauter and Refetoff, 1985).

Cortisol values were log-transformed to approximate normal distribution and then subjected to a repeated-measures ANOVA with the within-subjects factors time ($t1$−$t5$) and acute stress (stress vs. control). In case of violation of sphericity as indicated by Mauchly's test we report p-values based on Greenhouse Geisser estimates of sphericity (p_{gg}). To compute peak cortisol increases, log-transformed cortisol levels in the stress condition were first normalized for those in the control condition by subtraction of the corresponding time points (stress − control). Subsequently, individual cortisol increases were computed by subtracting normalized baseline levels ($t1$) from normalized peak levels ($t3$) (Starcke et al., 2011).

2.5. Heart rate

As a marker of sympathetic stress response, heart rate data were collected using a POLAR RS800sd heart rate monitor (POLAR, Buettelborn, Germany). Due to a technical failure data were available in $n = 29$ subjects.

Individual heart rate increases were computed for stress and control condition separately by subtracting the mean of a 5 min interval in the middle of the resting period from the mean of a 5 min interval in the middle of the job interview or control condition, respectively. A paired t-test was performed comparing increases of the stress and control condition.

2.6. Subjective stress response

At the predefined points of time ($t1$−5, see Fig. 1), participants completed the following questionnaires (five times throughout the experimental session, respectively, Fig. 1): the Affect Grid (Russell et al., 1989), the state scale of State-Trait Anxiety Inventory (STAI) (Laux et al., 1981) and the Aktuelle Stimmungsskala (ASTS), which is a German version of the Profile of Mood States scale (Dalbert, 1992; McNair et al., 1971). *Arousal* and *valence* (measured by the Affect Grid), *negative mood* (measured by the ASTS), and *state anxiety* (measured by the STAI) were assessed to verify the subjective effects of the stress induction by comparing the scores with the control condition. Peak increases in these scales were computed in a similar way to cortisol peak increases. For all correlations with arousal we use Spearman's correlation coefficient.

2.7. Sequential decision task

A two-stage decision task (Daw et al., 2011; Eppinger et al., 2013; Otto et al., 2013b; Smittenaar et al., 2013; Wunderlich et al., 2012) was used to assess the degree of model-based and model-free behavioral control.

The task was programmed in MATLAB (The MathWorks, Inc., Natick, MA, United States) with Psychophysics Toolbox extensions. It consisted of 201 trials with two stages each with a total length of approximately 35 min (Fig. 2A). At the first stage, participants chose between two gray boxes randomly displayed on the left and right side of the screen each with different Chinese characters by pressing either a left or right button. The chosen stimulus was surrounded with a red frame and moved to the top of the screen after the 2 sec decision time and remained there for 1.5 sec. At the second stage, one of the two differently colored pairs of boxes, again with distinctive Chinese symbols, appeared on the screen and participants had to choose again between one of the two boxes. Similar to the first step, the chosen stimulus was framed in red and moved to the top of the screen. This second-stage choice could either be rewarded with 20 euro cents or not.

Each of the first choices was predominantly associated with one of the two second-stage stimulus pairs (70% → common) and consequently less with the other (30% → rare) (Fig. 2B). These fixed transition frequencies remained constant during the task. Reward probabilities at the second stage changed slowly according to Gaussian random walks in order to induce ongoing learning (Fig. 2C). In line with Daw et al. (2011), participants were explicitly introduced to the task structure (including the stable transition frequencies and the independent slow changes of the reward probabilities) and informed that the amount of money they would get after the testing session was completed would depend on the reward they received in the task. The instruction included a training period of 55 trials with different stimuli and reward probabilities and a post-training teach-back. In the main experiment, the task was paused after 41 and 121 trials for the collection of saliva samples ($t3$ and $t4$, see Fig. 1).

In order to account for potential retest effects, two versions of the task differing in Gaussian random walks and Chinese characters were implemented. These two versions were counterbalanced between experimental days and participants (compare Wunderlich et al. (2012) and Smittenaar et al. (2013) for other within-subjects designs of this task).

2.8. Analysis of first-stage stay-switch behavior

Stay-switch behavior at the first stage was analyzed as a function of reward (reward vs. non reward) and state (common vs. rare) in the previous trial. These individual stay probabilities were subjected to a repeated-measures ANOVA

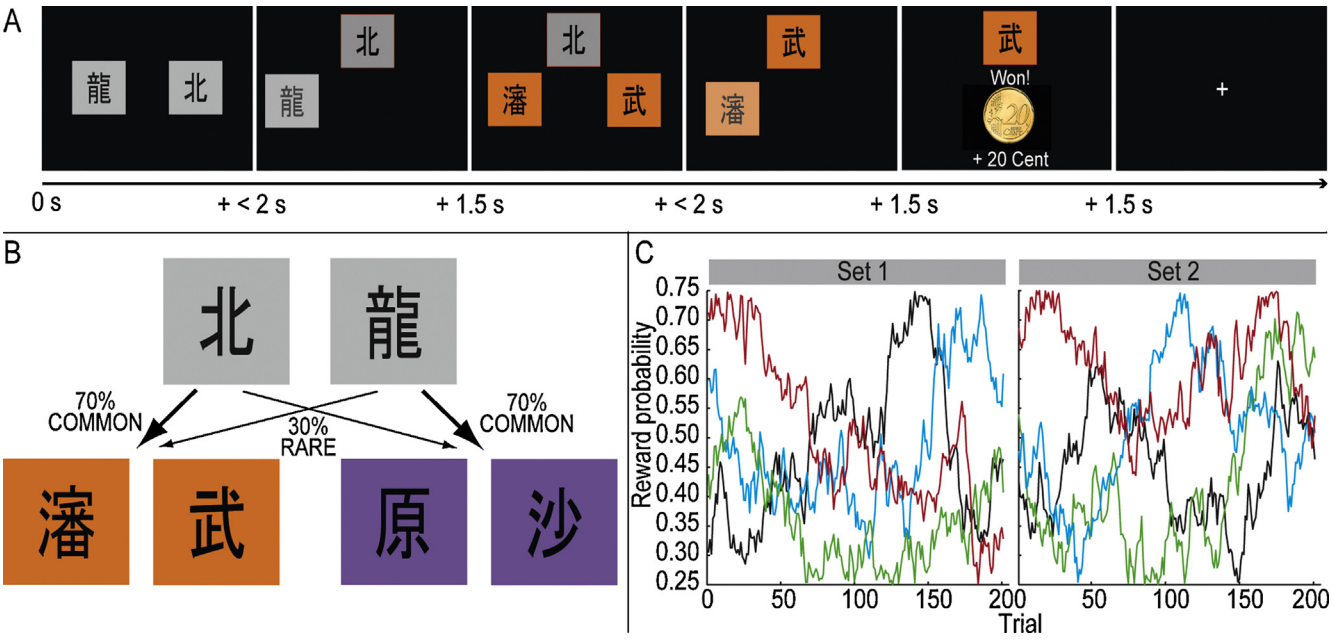

Figure 2 Sequential decision-making task. (A) Trail sequence. Subjects are instructed to find the box with money inside and have to open first one of the two gray boxes before the selected box moves up and a second pair of boxes appears. After one of those second step boxes is selected monetary reward is received depending on reward probability. (B) State transition structure in the sequential decision-making task. Each first-step choice (gray box) is predominantly associated with one of the second-step states (orange and purple boxes) and leads there 70% of the time. These second-stage choices are probabilistically reinforced with money. (C) Reward probabilities of the second step options change slowly over the course of the experiment according to Gaussian random walks. Random walks differed between the two experimental sessions to rule out retest effects.

with reward, state, and acute stress (stress vs. control) as within-subjects factors.

2.9. Computational modeling

Trial-by-trial computational modeling of the observed behavioral responses is a powerful analysis technique that has recently been suggested to enrich the mechanistic understanding of stress effects on learning (Schwabe and Wolf, 2013). Here, the aim of model-free (MF) and model-based (MB) algorithms is to learn values for each of the stimuli, which appear in the task as three pairs (S_A, S_B, S_C). S_A refers to the first-stage stimuli and S_B and S_C to the two pairs of second-stage stimuli. In the following, a refers to the chosen stimuli and the indices i and t denote the stage ($i = 1$ for S_A at the first stage and $i = 2$ for S_B or S_C at the second stage) and the trial, respectively.

First, the model-free algorithm was SARSA(λ):

$$Q_{MF}(s_{i,t+1}, a_{i,t+1}) = Q_{MF}(s_{i,t,}, a_{i,t}) + \alpha_i \delta_{i,t} \quad (1)$$

$$\delta_{i,t} = r_{i,t} + Q_{MF}(s_{i+1,t}, a_{i+1,t}) - Q_{MF}(s_{i,t}, a_{i,t}) \quad (2)$$

Notably, $r_{1,t} = 0$ because no reward is delivered after a first-stage choice and $Q_{MF}(s_{3,t}, a_{3,t}) = 0$ because the task has only two states. We allowed different learning rates α_i for each stage i. Further, we allowed for an additional stage-skipping update of first-stage values by introducing another parameter λ, which connects the two stages and allows the reward prediction error at the second stage to influence first-stage values:

$$Q_{MF}(s_{1,t+1}, a_{1,t+1}) = Q_{MF}(s_{1,t+1}, a_{1,t}) + \alpha_1 \lambda \delta_{2,t} \quad (3)$$

The parameter λ additionally accounts for the main effect of reward as observed in the analysis of first-stage stay-switch behavior but not an interaction of reward and state.

Second, the model-based algorithm learns values in a forward-planning way and computes first-stage values by simply multiplying the better option at the second stage with the transition probabilities P:

$$Q_{MB}(S_A, a_j) = P(S_B|S_A, a_j) \max Q_{MF}(S_B, a) + P(S_C|S_A, a_j) \max Q_{MF}(S_c, a) \quad (4)$$

Third, the hybrid algorithm connects Q_{MF} and Q_{MB}:

$$Q(S_A, a_j) = \omega Q_{MB}(S_A, a_j) + (1 - \omega) Q_{MF}(S_A, a_j) \quad (5)$$

$$Q(s_{2,t}) = Q_{MB}(s_{2,t}) = Q_{MF}(s_{2,t}) \quad (6)$$

Importantly, ω gives a weighting of the relative influence of model-free and model-based values and is therefore the model's parameter of most interest.

Finally, we transformed values into action probabilities using a softmax for Q:

$$p(a_{i,t} = a|S_{i,t}) = \frac{\exp(\beta_i[Q(s_{i,t}, a) + \rho^* \text{rep}(a)])}{\sum_{a'} \exp(\beta_i[Q(s_{i,t}, a') + \rho^* \text{rep}(a')])} \quad (7)$$

Table 1 Model comparison.

	−LL	BIC	BIC_{int}	XP
Control				
Full hybrid model	7,324	14,715	15,298	0.9999
	Δ−LL hybrid	**ΔBIC hybrid**	**ΔBIC_{int} hybrid**	
$\lambda = 0$	−136	263	213	0
$\omega = 1$	−188	346	206	0
$\omega = 0$	−258	506	424	0.0001
$\omega = 0$, $\lambda = 0$	−484	948	804	0
Stress				
Full hybrid model	7,643	15,354	15,908	0.9997
	Δ−LL hybrid	**ΔBIC hybrid**	**ΔBIC_{int} hybrid**	
$\lambda = 0$	−63	117	70	0.0002
$\omega = 1$	−121	212	108	0.0001
$\omega = 0$	−226	441	393	0
$\omega = 0$, $\lambda = 0$	−345	671	554	0.0001

Here, β controls the stochasticity of the choices and we assume this to be different between the two stages. The additional parameter ρ captures first-stage choice perseveration and rep is an indicator function that equals 1 if the previous first-stage choice was the same. In summary, the algorithm has a total of 7 parameters and can be reduced to its special cases $\omega = 1$ and $\omega = 0$. We fit bounded parameters by transforming them to a logistic (α, λ, ω) or exponential (β) distribution to render normally distributed parameter estimates. To infer the maximum-a-posteriori estimate of each parameter for each subject, we set the prior distribution to the maximum-likelihood given the data of all participants and then used Expectation-Maximization. For an in-depth description please compare Huys et al. (2011) and Huys et al. (2012). To compare models for their relative goodness of fit, we report the Bayesian Information Criterion (BIC) based on the log-likelihood (Table 1). Second, we computed the model evidence by integrating out the free parameters. This integral was approximated by sampling from the empirical prior distribution and we therefore added the subscript 'int' to the BIC (Table 1; Huys et al., 2011, 2012.). Third, we subject the integrated likelihood to the spm_BMS function, a random-effects model selection procedure, contained in SPM8 (http://www.fil.ion.ucl.ac.uk/spm/software/spm8/) to compute so-called exceedance probabilities (Stephan et al., 2009).

Testing the hypothesis that acute psychosocial stress shifts the balance of the two decision-making systems toward model-free control, the weighting parameter ω is of most interest here because it gives a measure of this balance. To analyze stress effects on model parameters, all 7 parameters were entered into a repeated-measures MANOVA with the within-subjects factor condition. To test for an effect of physiological and subjective stress responses, assessed by cortisol increase and rating scales respectively, ω from the stress and control condition were entered into a repeated-measures ANOVA with the within-subjects factor condition and the following stress response measures as covariates: cortisol increase, arousal increase, valence decrease, anxiety increase, and increase of negative mood.

2.10. Influence of individual trait characteristics on stress-induced changes of the balance of the two systems

One aim of the study was to elucidate the impact of chronic stress levels and their interaction with acute stress on decision-making processes. During a third, independent testing session, we therefore assessed questionnaires of chronic stress levels. Using the PSS-10 we measured perceived stress during the month before the second testing session (Cohen et al., 1983). Applying the Life stress scale we ask for stressful life events both within the last 24 months and within the whole life (Holmes and Rahe, 1967).

To characterize interaction effects of acute and chronic stress on the change in the balance between model-based vs. model-free control, while accounting for possible influences of working-memory capacity, we entered scores of Life Stress (24 months and whole life, respectively), PSS-10, and the Digit Span Number-Backwards-Test (Von Aster et al., 2006; Wechsler, 1945) as independent variables into a multiple regression analysis. The dependent variable was $\Delta\omega$ (ω_stress − ω_control) which reflects the changes in the relative degree of model-based behavior under stress compared with the control condition. Individual's working-memory capacity was assessed during the third test session with the Digit Span. It was entered due to evidence that interindividual differences in basic neurocognitive functioning, in particular working-memory, may play an important role in the degree of model-based control and might mediate the influence of acute stress on model-based vs. model-free decision-making strategies (Otto et al., 2013a, 2013b).

3. Results

3.1. Physiological and subjective stress response

3.1.1. Cortisol and heart rate response

Seven participants did not display a cortisol increase of at least 2.5 nmol/l and thus were considered as non-responders

(Schommer et al., 2003; Van Cauter and Refetoff, 1985). The responder rate (~82%) was in line with other studies using the TSST (Kudielka et al., 2007; Petzold et al., 2010). Cortisol response in $n = 32$ responders was analyzed using a repeated-measures ANOVA with the within-subjects factors time ($t1-t5$) and acute stress (stress vs. control). A significant main effect of acute stress ($F(1, 31) = 92.51$, $p < 0.001$, $\eta^2 = 0.749$), a significant main effect of time ($F(2.25, 69.66) = 39.48$, $p_{gg} < 0.001$, $\eta^2 = 0.560$) and a significant time and acute stress interaction ($F(2.07, 64.07) = 107.41$, $p_{gg} < 0.001$, $\eta^2 = 0.776$) was found. A comparison between the peak cortisol response in the stress condition with the corresponding response in the control condition (both $t3$) showed a significant difference ($t = 14.36$, $p < 0.001$, Cohen's $d = 3.001$). Baseline cortisol showed no significant difference between the conditions ($t = 0.35$, $p = 0.732$, Cohen's $d = 0.062$) (Fig. 1B). The average peak was at $t3$. The cortisol level of the last sample which was determined after task performance was still significantly higher as compared with baseline cortisol levels ($t = 6.75$, $p < 0.001$), indicating that the whole task was performed in a state of elevated cortisol levels.

Comparing heart rate increase using a paired t-test, we found a significantly higher increase in the stress condition than in the control condition ($t = 2.39$, $p = 0.042$, Cohen's $d = 0.983$), indicating a significant increase in sympathetic nervous activity during the stress intervention.

3.1.2. Subjective ratings

Subjective arousal ratings over the course of the experiment were analyzed using a repeated-measures ANOVA with the factors time ($t1-t5$) and acute stress (stress vs. control). We found a significant main effect of acute stress (acute stress, $F(1, 31) = 7.75$, $p = 0.009$, $\eta^2 = 0.200$), a significant main effect of time ($F(4, 124) = 8.51$, $p < 0.001$, $\eta^2 = 0.215$) and a significant time and acute stress interaction ($F(4, 124) = 17.75$, $p = 0.007$, $\eta^2 = 0.364$). A paired sample t-test showed that participants scored significantly higher directly after the TSST than after silent reading during the control condition ($t = 7.4$, $p < 0.001$, Cohen's $d = 2.118$). The average peak of arousal was found at $t2$. Ratings of unpleasantness, anxiety, and negative mood revealed similar results. Thus, subjective experience was significantly affected by the stress condition (Fig. 1B).

3.2. Effects of acute social stress on model-based vs. model-free behavioral control

3.2.1. Analysis of stay-switch-behavior

In line with previous studies (Daw et al., 2011), a three factors repeated-measures ANOVA (acute stress × reward × state) revealed a main effect of reward ($F(1, 31) = 29.09$, $p < 0.001$, $\eta^2 = 0.484$) and an interaction effect of reward × state ($F(1, 31) = 65.44$, $p < 0.001$, $\eta^2 = 0.679$) on the first-stage stay probabilities in cortisol responders ($n = 32$). This confirms that first-stage decisions are influenced by both rewards and states from the previous trials (Fig. 3A).

With respect to the acute psychosocial stress intervention, we found a main effect of acute stress on first-stage choices ($F(1, 31) = 5.69$, $p = 0.023$, $\eta^2 = 0.155$). This was due to higher switching in the stress compared with the control condition regardless of the previous trial's reward or state (Fig. 3B). However, the hypothesized interaction effect of acute stress × reward × state was not significant ($F(1, 31) = 0.23$, $p = 0.634$, $\eta^2 = 0.007$, all other interactions with acute stress $ps > 0.2$), indicating that the stress intervention did not influence the interaction of state and reward in the task. Thus, the analysis of stay-switch behavior does not indicate a direct impact of acute social stress on the balance between model-free and model-based control (Fig. 3A). Including order (stress on day 1 or day 2) as a between-subjects factor in the ANOVA did not change the observed results.

3.2.2. Computational modeling

Across all participants and for both conditions, the hybrid model explained the observed data best (XP control condition = 0.99; XP stress condition = 0.99, see Table 1). This replicates previous studies in non-stressed participants (Daw et al., 2011). Furthermore it indicates that the stress intervention did not change the learning mechanism, as a hybrid model which engages both systems gave the best account of the observed data in both conditions. There was no effect of acute stress on the weighting parameter ω, which represents the balance of the two decision systems ($t = 0.01$, $p = 0.990$, Cohen's $d = 0.011$). This is in line with the absence of such an effect on stay-switch raw data reported above.

A comparison of all model parameters between stress and control condition using a repeated-measures MANOVA revealed a main effect of acute stress ($F(7, 25) = 2.92$, $p = 0.022$, $\eta^2 = 0.450$). Post hoc paired t-tests showed significantly higher stochasticity of the participants' choices at the first stage during stress compared with the control condition ($\beta 1$: $t = 2.60$, $p = 0.014$, Cohen's $d = 0.427$), which resembles the main effect of acute stress on stay-switch raw data. Further, the stage-skipping update λ, which connects reward prediction errors at the end of each trial to first-stage Q-values, was significantly lower in the stress compared with the control condition (λ: $t = 2.08$, $p = 0.046$, Cohen's $d = 0.424$). There were no differences for the remaining model parameters (β_1, α_1, α_2, ρ all $ps > 0.2$) (Table 2). Including order (stress on day 1 or day 2) as a between-subjects factor in the MANOVA did not change the observed results.

3.2.3. Power analysis

For the purpose of a power analysis, we used effect sizes from two published within-subjects studies using a similar sequential decision-making task. We assume that an effect of the psychosocial stress intervention used here lies in a similar range as compared to the interventions used in these studies (a pharmacological challenge with L-DOPA (Wunderlich et al., 2012), Cohen's $d = 0.67$ and a transcranial magnetic stimulation intervention (Smittenaar et al., 2013), Cohen's $d = 0.49$). Given a two-tailed alpha of 0.05 and a sample size of 32 (cortisol non-responders excluded), power analysis revealed a power of 0.96 and 0.77, respectively. Thus, even when assuming a medium effect size (Cohen, 1988), the present study was well-powered to detect an effect of psychosocial stress on model-based behavior.

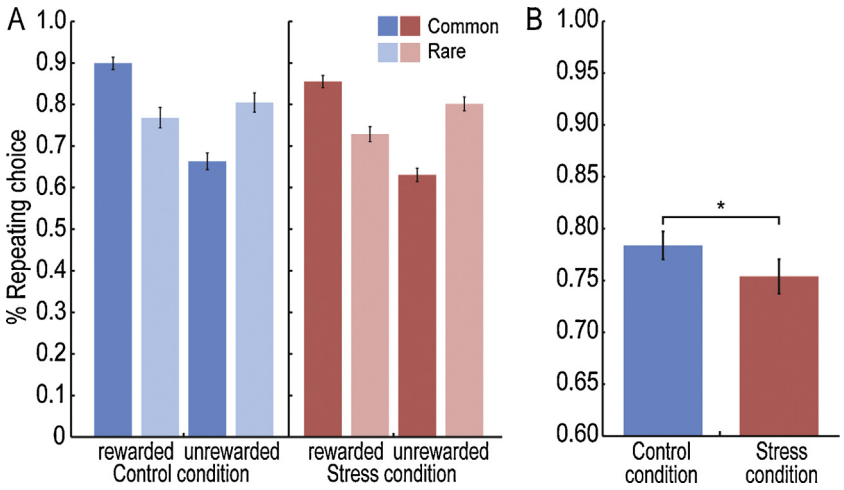

Figure 3 Stay probabilities of first-stage choices depending on second-stage states and rewards in the control condition (blue bars) as well as in the stress condition (red bars). (A) In both conditions, participants' choices showed a main effect of reward and a reward × state interaction, indicating a mixture of model-based and model-free strategy to solve the task. (B) Participants switched more in the stress compared with the control condition, irrespective of reward and state, indicated by overall reduced stay probabilities.

3.3. Association of subjective and physiological stress responses with model-based control

In a next step, we tested for an effect of physiological and subjective stress responses on the balance of model-free and model-based control as quantified by the parameter ω in all participants that completed the study ($n = 39$). Note that the effect of individual stress reactivity, including a potentially dampened cortisol response, was of central interest in this analysis. Thus, we explicitly included the cortisol non-responders into this analysis because we consider a non-significantly elevated cortisol level after stress induction as one important possible manifestation of individual cortisol reactivity. The model parameter ω during the stress and control conditions (=within-subjects factor 'acute stress') was subjected to a repeated-measures ANOVA with cortisol increase, arousal increase, valence decrease, anxiety increase, and increase of negative mood as covariates: this revealed a main effect of the two covariates cortisol increase and arousal increase, respectively (cortisol increase: $F(1, 33) = 6.81$, $p = 0.014$, $\eta^2 = 0.171$, arousal increase: $F(1, 33) = 9.82$, $p = 0.004$, $\eta^2 = 0.229$) but no interactions with acute stress (all $ps > 0.2$). With respect to cortisol, post hoc correlations showed that this effect was driven by a significant negative correlation of ω during acute stress with cortisol increase (i.e. the change from baseline to peak calculated from the normalized cortisol stress data) ($r = -0.46$, $p = 0.004$, Fig. 4A) and a negative relationship between cortisol increase and ω during the control condition that did not reach significance ($r = -0.24$, $p = 0.149$,

Table 2 Descriptive values of subjective stress related measurements, distribution of best fitting parameters and the negative log-likelihood (hybrid model) in $n = 32$ participants.

		Mean (± SD)
Life stress score (whole life)		508.97 (±171.81)
Life stress score (24 months)		271.94 (±185.88)
Perceived stress scale (within the last month)		14.12 (±6.10)
Digit Span		7.50 (±1.93)
Normalized arousal increase		2.62 (±2.15)
Normalized cortisol increase		9.43 (±4.13)
	Control	**Stress**
β_1	7.89 (±3.07)	6.70 (±2.50)
β_2	3.80 (±1.26)	3.86 (±1.17)
α_1	0.52 (±0.18)	0.47 (±0.17)
α_2	0.49 (±0.18)	0.49 (±0.24)
λ	0.55 (±0.13)	0.50 (±0.11)
ω	0.66 (±0.09)	0.66 (±0.09)
ρ	0.13 (±0.04)	0.13 (±0.04)
−LL	−182.13 (±39.29)	−188.83 (±43.48)

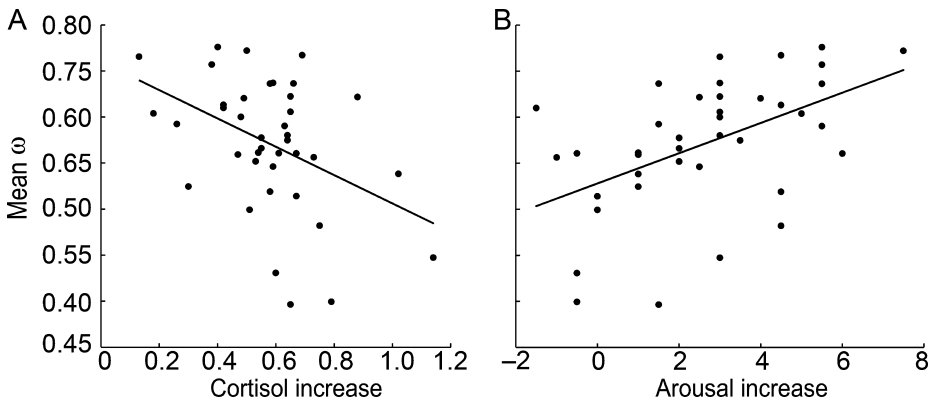

Figure 4 Correlation of stress reactivity with ω (averaged over the two sessions). (A) Cortisol reactivity showed a significantly negative correlation with the model-parameter ω ($r = -0.46$). (B) Arousal reactivity showed a significantly positive correlation with ω ($r = 0.41$).

Fig. 4A). Regarding arousal, post hoc correlations showed that this effect resulted from significant positive correlations between arousal increase with ω during the acute stress condition ($r = 0.406$, $p = 0.010$, Fig. 4B) and during the control condition ($r = 0.409$, $p = 0.010$, Fig. 4B). All reported correlations remained significant when excluding cortisol non-responders and when using a different normalization procedure (peak during stress induction minus resting phase measure on the same day, i.e. without normalization on the control day data).

3.4. Lifetime stress influences the change in model-based vs. model-free control during acute social stress

In order to investigate the influence of previous stressful life events on a change in the balance of the control systems induced by acute social stress, we calculated the difference of ω from the control and from the stress condition ($\Delta\omega$). We used a linear regression analysis for the cortisol responders ($n = 32$) with $\Delta\omega$ as the dependent variable and Life Stress Scale (24 months and whole life), PSS-10, and the Digit Span (due to the finding of Otto et al., 2013b) as independent variables (Table 2). Only chronic life stress in the past 24 months was significantly negatively associated with $\Delta\omega$ ($Beta = -0.622$, $t = -2.93$; $p = 0.007$) (Fig. 5). This indicates that in individuals with high levels of chronic stress (24 months) the degree of model-based behavioral control is impaired after stress induction compared with the control condition. Since we detected one outlier who scored more than three standard deviations above the mean of the chronic life stress scale for the past 24 months ($z = 3.029$), we repeated the linear regression analysis without this participant and found similar results ($Beta = -0.648$, $t = 2.39$; $p = 0.036$).

In an exploratory analysis, in order to test for possible neuroendocrine correlates of the chronic stress measure, a correlation of the Life Stress Score (24 months) with cortisol increase was tested, which did not indicate a significant association ($r = 0.009$, $p = 0.957$).

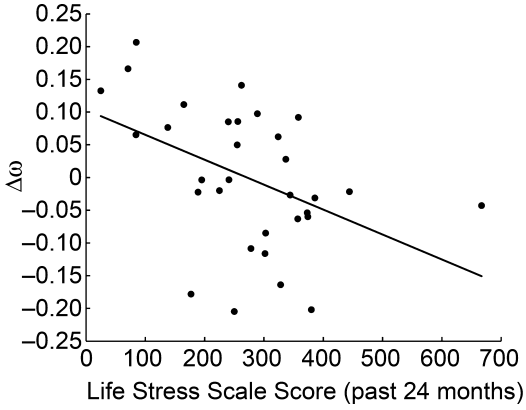

Figure 5 Association between chronic stress and shift in behavioral control due to acute social stress. Negative correlation between the Life Stress Scale Score and the difference score of ω ($\Delta\omega$ = stress minus control condition) as determined by the computational model ($Beta = -0.622$, $t = 2.93$). The higher the score on the Life Stress Scale (24 months), the lower the values of the model parameter ω in the stress condition. Higher levels of chronic stress as measured by the Life Stress Scale correlated with a decrease in model-based behavior.

4. Discussion

This study investigated the influence of stress on the balance of model-based and model-free behavioral control during a two-step decision task in a within-subjects design. First, after inducing acute psychosocial stress, we did not observe a shift toward model-free behavioral control across the entire sample. Second, we showed that variability in physiological and psychological stress reactivity is associated with interindividual differences in the balance between model-free and model-based control. Third, we revealed that subjects with higher chronic stress as indicated by stressful life events displayed a shift toward reduced model-based control under acute social stress. Crucially, this finding demonstrates an interaction between acute and chronic

stress and for the first time elucidates their joint consequences on behavioral control in humans.

4.1. Effects of acute psychosocial stress on sequential decision-making

First-stage decisions were affected by acute stress in terms of more frequent switching between options. In the computational modeling analysis, this effect was mirrored in the parameter β at the first stage, which was found to be significantly lower in the stress than in the control condition. Lower values of β indicate a higher degree of stochastic choices unrelated to the current choice value with respect to first-stage choices. Thus, our findings might be interpreted as pronounced although unsystematic exploration behavior triggered by acute stress. Moreover, the parameter λ, linking prediction errors at the end of each trial with first-stage choice values of the next trial, was reduced in the stress condition. As λ represents a parameter of the model-free system, hypothesized to be predominant during stress, this finding seems counterintuitive at first glance. However, in line with the observations of enhanced stochasticity of first-stage choices under stress, it appears conceivable that in a state where decisions are marked by unspecific switching behavior at the first-stage, the use of prediction errors to update exactly these first-stage decision-values becomes attenuated.

Notably, apart from these general effects, our results do not suggest an acute stress-induced shift from model-based toward model-free strategies. In line with this, model-selection revealed no evidence for differences in model-fit between the stress and control condition, supporting the conclusion that the task-solving strategy was not affected by acute stress. Further, the study was well-powered to detect such an effect. By using a different study design and stress induction protocol, these results replicate Otto et al. (2013b): The authors used a similar sequential decision-making task and did not find an acute effect of stress induction on behavioral control, as indicated by the reported non-significant 3-way-interaction of stress $\times$ reward $\times$ state in the decision-making task. In contrast to our findings, pioneering studies (Schwabe and Wolf, 2009, 2011) reported more habitual behavior after acute stress. However, these studies differ from our current study and Otto et al. (2013b) in terms of the paradigm used to examine behavioral control: there, a selective outcome devaluation protocol was applied (e.g. Valentin et al., 2007). Importantly, similar to our findings, but without dissecting model-free versus model-based contributions to learning via computational modeling, Schwabe and Wolf (2009) did not observe differences in instrumental learning following acute stress. However, they provide evidence that acute stress promotes responding for the devalued outcome during a test in extinction as a measure of habitual behavior. These discrepant findings may reflect a stress-induced persistence of acquired behaviors rather than an effect of acute stress on different modes of instrumental acquisition. Accordingly, a recent validation study comparing both paradigms (selective devaluation and sequential decision making) suggests relatedness of both measurements in terms of goal-directed/model-based behavior, but points to the direction that both experiments might offer different insight into the habitual system (Friedel et al., 2014).

4.2. Effects of physiological and subjective stress reactivity on the balance of model-based vs. model-free control

Our findings suggest that physiological and subjective stress reactivity are associated with model-based control rather as trait factors in general, irrespectively of the acute exposure to psychosocial stress. Interestingly, both stress measures relate to behavioral control in opposite directions: stronger cortisol-reactivity was related to a lower degree of model-based control, whereas reactivity in terms of subjective arousal was associated with a higher frequency of model-based choices. These opposite effects are in line with the dissociation of subjective and physiological stress responses frequently described in the literature (Campbell and Ehlert, 2012).

Regarding physiological stress reactivity, we replicate the inverse relationship of cortisol increase and the degree of model-based behavior described by Otto et al. (2013b). However, we go beyond Otto et al.'s interpretation by arguing that the negative correlation across a stressed and non-stressed group reported in their between-group study likely captured a similar effect to the one observed in our within-subjects design: the importance of the persistent trait factor stress reactivity rather than an effect of acute neuromodulatory cortisol on model-based decision-making. Crucially, such an effect cannot be detected in a between-subjects design, whereas both factors are dissociable by the within-subjects design used here.

The relationship between subjective arousal reactivity and decision-making has, to our knowledge, not been directly addressed by previous studies. However, there is a substantial body of work on the interplay between arousal per se and decision-making: The somatic marker hypothesis (SMH) suggests bodily arousal feedback as a guiding influence on decision-making (Bechara et al., 1996, 1997; Critchley, 2005; Damasio, 1999). A tendency to react to challenging environmental conditions by a higher arousal increase may therefore foster the integration of arousal feedback in the decision-making process. This might enable the individual to evaluate future outcomes of actions more precisely, boost mental mapping of environmental features and consequently promote the use of model-based strategies.

4.3. The interaction of chronic and acute stress attenuates model-based decision-making

It is widely accepted that stress influences cognition differently depending on the timing and duration of exposure, e.g. with varying influences of acute and chronic stress (Lupien et al., 2009). So far, the interaction of chronic and acute stress has not been addressed in the decision-making literature which has hitherto primarily focused on acute stress effects in between-subjects designs (Otto et al., 2013b; Schwabe and Wolf, 2009). Evidence from animal studies indeed indicates that chronically stressed rats turn toward habit behavior (Dias-Ferreira et al., 2009). The authors showed that chronic stress was associated with structural

changes in fronto-striatal networks known to be critically involved in decision-making. One study investigating subacute stress exposure in humans suggests that this shift can be translated to human behavioral control (Soares et al., 2012). Interaction effects of chronic and acute stress are widely discussed with respect to volume reduction in hippocampus and prefrontal regions and volume increase in amygdala as a result of chronic stress exposure, rendering the individual more susceptible for acute stress effects (Lupien et al., 2009; Tse et al., 2014). However, empirical evidence of interaction effects between acute and chronic stress on cognition is scant in humans as well as in rodents. Here, we extend these findings by providing first evidence for an interaction effect of chronic and acute stress on model-based control in human decision-making. It appears plausible that repeated exposure to stressful life events renders the individual more susceptible to detrimental changes in behavioral control brought about by an acute stressor. Further investigations are warranted to elucidate the underlying neural mechanisms of this suggested vulnerability-stress interaction.

Interestingly, stressful life events within the last 24 months, but neither whole-life stress nor perceived stress within the preceding month predicted acute stress-induced changes in model-based behavior. Given that reversibility of stress-induced effects on cognitive processes has been postulated (Liston et al., 2009; Luine et al., 1994; Soares et al., 2012), it is conceivable that participants with more chronic stress over the whole course of their life might yet have had the chance to recover from the deteriorating effects of their stress experiences. In contrast, perceived stress within the last month might be too recent to significantly affect behavioral control in response to acute stress.

4.4. Limitations

It is to be noted that the sample selection criteria of this study might limit the generalizability of our results: only males within an age range of 21—30 years were included. Our findings emphasize the notion that interindividual differences are crucial in the relationship between stress and model-based decision-making, and it is plausible that factors like age and gender are important covariates here (Eppinger et al., 2013). We acknowledge that further studies are needed to replicate our findings in a broader range of the population.

5. Conclusion

We show that interindividual differences in acute subjective and physiological stress response impact the degree of model-based behavioral control. Furthermore, a reduction in model-based control in response to acute stress was only observed in subjects with higher levels of chronic stress as indicated by a higher score in the Life Stress scale for the last 24 months.

By defining interindividual differences in acute stress response and in chronic stress experience as crucial factors in behavioral control, our findings contribute to the intriguing question why some individuals shift toward attenuated model-based behavior whereas others do not (Dolan and Dayan, 2013; Schwabe and Wolf, 2013). This might be relevant for psychiatric conditions characterized by impaired model-based behavior like addiction, binge eating or obsessive compulsive disorder (Sebold et al., 2014; Voon et al., 2014) for which, notably, chronic as well as acute stress is postulated to be a pivotal factor in pathogenesis, maintenance, and relapse (Gluck, 2006; Gluck et al., 2004; Koob, 2008; McEwen, 2004). Longitudinal designs are required to tackle the exact interplay of different dimensions of stress reactivity (subjective versus physiological), chronic versus acute stress and impaired model-based decision-making.

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Conflict of interest

None declared.

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