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Stress-induced impairment in goal-directed instrumental behaviour is moderated by baseline working memory

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ABSTRACT

Acute stress has been found to impair goal-directed instrumental behaviour, a cognitively flexible behaviour that requires cognitive control. The current study aimed to investigate the role of individual differences in baseline and stress-induced changes in working memory (WM) on the shift to less goal-directed responding under stress. To this end, 112 healthy participants performed an instrumental learning task. In phase 1, participants learned instrumental actions that were associated with two different food rewards. In phase 2, one of these food rewards was devalued by eating until satiety. Before the extinction test in phase 3, participants were subjected to the Maastricht Acute Stress Test or a no-stress control procedure. Results showed that the effect of stress on instrumental behaviour is modulated by baseline, but not stress-induced changes in WM capacity. Specifically, only at low baseline WM capacity did stress induce a shift to less goal-directed behaviour. These findings highlight that our cognitive resources are limited and for those who already have limited resources at baseline taking into account motivational value is impaired under stress.

1. Introduction

We all learn that specific behaviours are followed by specific consequences. This is referred to as instrumental learning. Instrumental learning can be controlled by two distinct processes: goal-directed behaviour is based on learning action-outcome associations considering the motivational value of the outcome associated with an action, whereas habitual behaviour is based on more direct stimulus-response associations in which outcome value is not considered (Balleine & O'Doherty, 2010; Dickinson, 1985). Accordingly, goal-directed and habitual behaviour differ in their sensitivity to changes in outcome value. Reducing the outcome value of an action reduces the frequency of that behaviour if it is goal-directed (for review see O'Doherty, Cockburn, & Pauli, 2017). Human and rodent studies suggest that stress changes the competition between outcome- and stimulus-controlled behaviour by impairing the outcome-based prefrontal cortex system (chronic stress: Dias-Ferreira et al., 2009; acute stress: Fournier, d'Arripe-Longueville, & Radel, 2017; Guenzel, Wolf, & Schwabe, 2014; Schwabe & Wolf, 2009, 2010, 2011; Schwabe, Tegenthoff, Hoffken, & Wolf, 2012; Smeets, van Ruitenbeek, Hartogsveld, & Quaedflieg, 2018; for review see Quaedflieg & Schwabe, 2017; Wirz, Bogdanov, & Schwabe, 2017). Stress exposure counts as a prominent risk factor for addictive behaviour (Schwabe, Dickinson, & Wolf, 2012) and an impairment in goal-directed behaviour control is thought to play a key role in the development of and relapse to addictive behaviour (Everitt & Robbins, 2016; Everitt, Dickinson, & Robbins, 2001; Vandaele & Janak, 2018). Understanding how individual differences in working memory contribute to less goal-directed behaviour during periods of stress may shed light on the mechanisms by which stress shapes the development of addictive behaviour.

Stressful events provoke an orchestrated physiological response including the release of catecholamines and glucocorticoids (Joels & Baram, 2009). Within seconds following stressor onset, the release of catecholamines, including noradrenaline and dopamine, is triggered in the brain. With a delay of several minutes, the activity of the hypothalamic-pituitaryadrenal (HPA) axis results in an increased secretion of glucocorticoids. The effect of stress on instrumental learning is thought to depend on concurrent glucocorticoid and noradrenergic activation, as post-stress blockade of the beta-adrenergic receptors by propranolol prevents the stress-induced bias towards habits (Schwabe,

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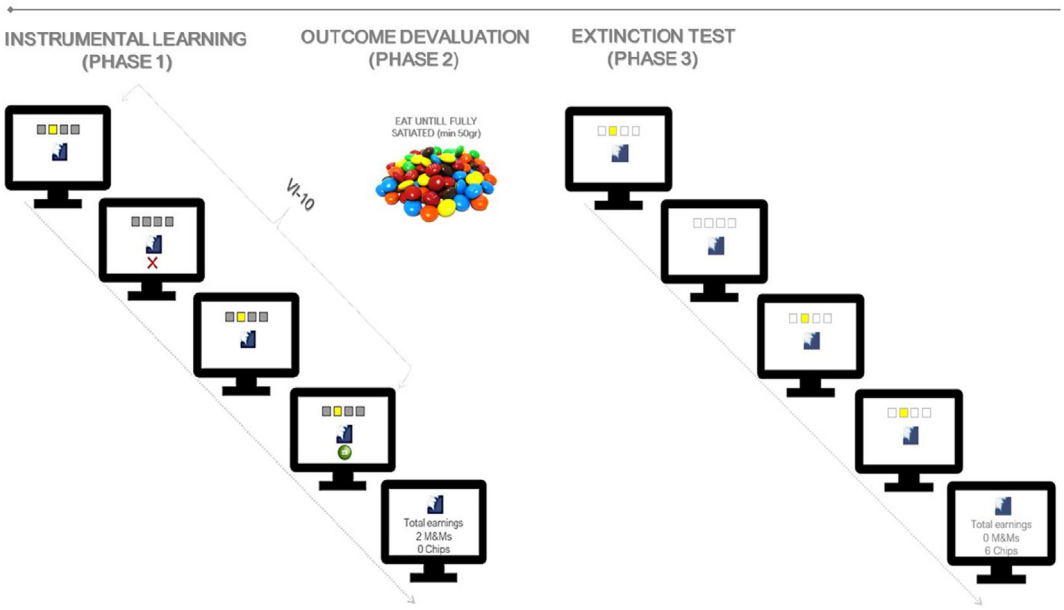

Fig. 1. Overview of the Instrumental task. Phase 1 instrumental learning. One of two fractal cues was associated with a keyboard button (depicted in the yellow squares) and a food outcome (savoury or sweet). In phase 1 and 3, participants were instructed to obtain as much food reward as possible. During phase 3, extinction test, reward feedback was provided at the end of the 2 blocks. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Hoffken, Tegenthoff, & Wolf, 2011). Furthermore, it was found that the combined enhancement of glucocorticoids (via hydrocortisone administration) and noradrenaline (via blocking of the α2-adrenoceptor with yohimbine) shifted instrumental learning to less goal-directed behaviour control whereas either enhancing glucocorticoids or noradrenergic activity alone did not (Schwabe, Tegenthoff, Hoffken, & Wolf, 2010). This, together with findings indicating that stress initially reallocates neuronal resources to the salience network at the expense of deliberate executive control processes during the acute stress phase (Hermans et al., 2011; Hermans, Henckens, Joels, & Fernandez, 2014) argues in favour of the idea that impaired prefrontal cortex (PFC) functioning accounts for the stress-induced shift to less outcome-controlled behaviour.

Goal-directed processes are the default determinant of behaviour (Moors, Boddez, & De Houwer, 2017) and the process of comparing a stimulus with a goal requires cognitive control, which is strongly (but not exclusively) mediated by the PFC. Working memory (WM) is a form of cognitive control sub-served by the PFC (Arnsten, 1998; Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004; Veltman, Rombouts, & Dolan, 2003). Interestingly, using computational modelling, it has been found that baseline WM capacity modulates the stress-induced reduction of goal-directed (e.g., model-based) trial-by-trial value learning (Otto, Raio, Chiang, Phelps, & Daw, 2013). Specifically, only in individuals with low baseline WM, stress decreased goal-directed learning. It is known that stress affects PFC functioning (McEwen & Morrison, 2013) and often has been found to impair WM (Elzinga & Roelofs, 2005; Oei, Everaerd, Elzinga, van Well, & Bermond, 2006; Qin, Hermans, van Marle, Luo, & Fernandez, 2009; Schoofs, Preuss, & Wolf, 2008; Schoofs, Wolf, & Smeets, 2009; Wolf et al., 2001; for review see Wolf, 2003). Based on the finding that acute stress induction reduces working memory, the aim of the current study was two-folded: first, we wanted to replicate the finding that baseline working memory moderates the stress-induced shift to less goal-directed behaviour in a large sample using a free-response instrumental learning task. Secondly, we wanted to extend previous findings by investigating the influence of stress-induced changes in working memory on the shift to less goal-directed behaviour under stress. Acute stress was elicited using the Maastricht Acute Stress Test (MAST), a potent and reliable procedure to elicit subjective, autonomic and glucocorticoid stress responses (Quaedflieg, Meyer, van Ruitenbeek, & Smeets, 2017; Shilton, Laycock, & Crewther, 2017; Smeets et al., 2012), and which is capable of impairing instrumental learning in cortisol responders (Smeets et al., 2018).

2. Methods

2.1. Participants

One-hundred-and-twelve healthy male ($n = 56$) and female ($n = 56$) undergraduates (mean age = 22.38 years; *SEM* = 0.25; range: 18–34) participated in the experiment. Participants were screened for eligibility (i.e., Body Mass Index (BMI) within 18–30 kg/m^2, age 18–35, no current or lifetime psychiatric disorders, no current or history of drug abuse). Participants with food allergies were excluded to avoid allergic reactions to foods used in the instrumental learning task (ILT). For women, an extra inclusion criterion was the use of oral contraceptives, to reduce variability in cortisol responses related to hormonal alterations throughout the menstrual cycle (Kudielka, Hellhammer, & Wust, 2009). All participants provided written informed consent and were given minor incentives in form of course credits or vouchers for participation. Test protocols were approved by the standing ethics committee of the Faculty of Psychology and Neuroscience, Maastricht University.

2.2. Instrumental learning task

A three-phase instrumental learning task (ILT; Alvares, Balleine, & Guastella, 2014; Tricomi, Balleine, & O'Doherty, 2009), consisting of instrumental learning (phase 1), outcome devaluation using rewarding food outcomes (phase 2), and an extinction test (phase 3) was used (see Fig. 1).

During *instrumental learning* (phase 1), participants could earn outcome rewards based on their responses. One of two fractal cues signalling reward availability was associated with a keyboard key (depicted as yellow squares on the screen) and a food outcome that was either savoury or sweet. Participants were instructed to obtain as "much

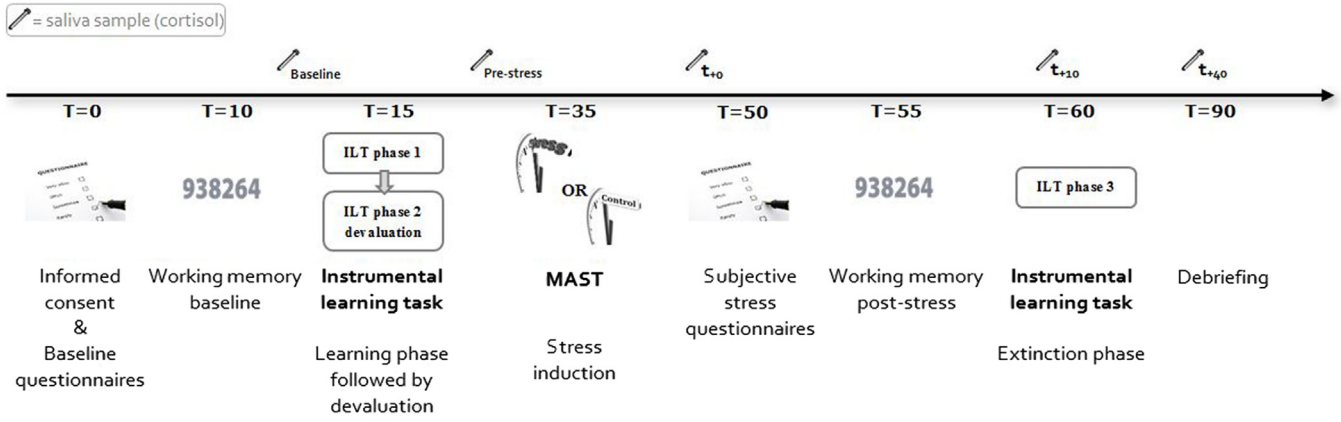

Fig. 2. Overview of the procedure.

food reward as possible" by pressing on the highlighted key associated with the fractal cue. Food outcomes were available on a variable interval schedule with an average of one outcome per ten seconds (VI-10). Participants received one practice block and two six-minute blocks of training (twelve sets of trials per block, with rest trials in which no reward was available randomly presented in-between trials). After each block, the cumulative earnings of each food outcome were shown on the screen, although no actual food was presented during phase 1. Following the learning phase, participants' acquisition of action-outcome associations was assessed using 10-point Likert scale contingency awareness questionnaires.

The second phase, *outcome devaluation*, involved the actual eating of one of the food outcomes (i.e., savoury or sweet) until satiety.

During the *extinction test* (phase 3), participants responded to the same fractal stimuli as in phase 1, but pictures of outcomes were no longer available after responding. Participants were again instructed to earn as "many food rewards as possible" and were told that after completing the task, they would have to eat the earned food.

A *devaluation ratio was* calculated by dividing the response rate for the valued action, that is, the action that would lead to the food outcome that was not devalued in stage 2, by overall responding on both actions. Hence, higher values indicate more goal-directed actions (i.e., a preference for actions that continue to be valued), and lower ratios signify more habitual responding towards the devalued action.

2.3. Working memory

The Digit Span Task (DST), from the Wechsler Adult Intelligence Scale-Revised (Wechsler, 1981) was used to measure WM capacity. Participants were presented with a series of digits read out loud at a steady pace of one digit per second. After the last digit was presented, participants had to repeat the numbers in the same (forward condition) or reverse (backward condition) order. On each successful attempt, the number of digits per list increased. When a participant failed to accurately reproduce a list of numbers on two successive trials, the task was ended. Raw scores reflect the maximum number of digits correctly recalled.

2.4. Stress Induction: MAST

The Maastricht Acute Stress Test is a combined psychological and physical stress test (Smeets et al., 2012). The protocol consists of a five-minute preparation phase, in which instructions are given about the upcoming task. This is followed by a ten-minute acute stress phase comprising repeated exposures to ice-cold water (2 °C) alternated with mental arithmetic tasks, in which participants have to count backwards in steps of 17 starting at 2043 as fast and accurately as possible. To induce social evaluation stress, negative feedback was provided on performance and participants were presented with self-depicting online video recordings. Four women quitted the MAST because they perceived it to be exceedingly stressful. In these cases, participants were fully debriefed, the test day was discontinued and their data were excluded from the analysis.

Participants in the control condition were exposed to a validated no-stress control condition that was equal in length to the MAST and comprised hand immersion into lukewarm water (35 °C) and a simple counting task (see Smeets et al., 2012, Exp. 3).

2.5. Stress Response: Salivary cortisol and subjective stress

To determine individuals' reactivity to the stressor, salivary cortisol samples were obtained with synthetic Salivette (Sarstedt®, Etten-Leur, The Netherlands) prior to and in response to the MAST (i.e., five samples in total; see 2.6 Procedure). Subjective stress was assessed using three 100 mm visual analogue scales (VAS) on which participants rated how stressful, painful, and unpleasant they had perceived the MAST (anchors: 0 = "*not at all*"; 100 = "*extremely*"). A sum score of the three VAS scales was computed to yield a single total subjective stress response.

2.6. Procedure

Participants were randomly assigned to one of the two conditions (stress: $n = 56$ or control: $n = 56$). All testing took place between 12:30 and 6:00 pm to avoid morning fluctuations in the circadian rhythm of cortisol. Participants were instructed via email to refrain from eating, exercising extensively or drinking anything but non-sparkling water for 2 h prior to the experimental session. A timeline of the experimental session is displayed in Fig. 2.

Upon arrival, participants received information on the experimental procedure and gave written consent. Next, a bogus saliva sample was taken to enhance truth-telling about the adherence to the instructions not to eat, drink, and exercise (see Quaedflieg, Schwabe, Meyer, & Smeets, 2013; Quaedflieg et al., 2016). Participants were then asked to complete some questionnaires including demographic information, the eating attitude test (EAT; Garner, Olmsted, Bohr, & Garfinkel, 1982) to detect problematic eating behaviours, and a food preference questionnaire. The food preference questionnaire consisted of a 10-point Likert scale for six different foods (savoury: chips, tucs, party mix; sweet: M&M's, wine gums, liquorices) to identify each participant's preferred sweet and savoury foods. These two food items were then used in the instrumental learning task to ensure the use of individually-tailored, highly rewarding outcomes.[1] After the questionnaires,

[1] The food used for the devaluation was not individually-tailored but

participants rated their baseline hunger and the subjective degree of "pleasantness" of the two food items using a 10-point Likert scale to assess pre-satiation. The digit span task was administered as a measure of baseline WM capacity and a baseline saliva sample ($t_{baseline}$) was obtained. Hereafter, the ILT learning phase was performed in which participants could earn outcome rewards. Directly after learning, participants were instructed to eat the most earned food item until they "felt really full" to induce satiety (*outcome devaluation*). To assess post-satiation, participants rated their hunger and ranked the two food items on their degree of "pleasantness" using a 10-point Likert scale. A pre-stress saliva sample ($t_{pre\text{-}stress}$) was then taken and subsequently, the Maastricht Acute Stress Test (MAST) or a no-stress control task was administered. After the MAST/no-stress control task, a third saliva sample (t_{+0}) was obtained. Participants were then asked to fill in a subjective stress questionnaire, which was followed by a post-stress assessment of WM using the digit span task. Participants rated their hunger and the two food types on their degree of "pleasantness" using 10-point Likert scales to assess satiation directly before extinction (i.e., pre-extinction) and a fourth saliva sample was taken ten minutes after the MAST (t_{+10}). Hereafter, participants performed the extinction phase on the computer, followed by a post-extinction satiation rating of hunger and of the degree of "pleasantness" of the two food items using a 10-point Likert scale (i.e., post-satiation). A fifth saliva sample (t_{+40}) was taken 40 min after the MAST. Lastly, participants were debriefed, thanked and compensated for their participation.

2.7. Data analysis

Thirteen participants did not learn the action-outcome associations according to the contingency awareness questionnaire, and four participants prematurely stopped the MAST. The final sample included in the analysis thus consisted of 96 participants (stress: $n = 47$; control: $n = 48$). The data were first examined for accuracy of data entry and missing values. Shapiro-Wilk tests of normality and Q-Q plots were used to test for normal distributions. Cortisol data were log-transformed due to a typical skewness of the data. Data were analysed by means of ANOVAs and multiple regression. *P*-values were Greenhouse–Geisser corrected when appropriate. *P*-values smaller than .05 (two-tailed) were considered statistically significant. When analyses yielded significant findings, ANOVAs were supplemented with Partial Eta Squared (η_p^2) values as a measure of effect size (η_p^2 of 0.01 indicate small effects, η_p^2 of 0.06 medium effects, and η_p^2 of 0.14 large effects; Fritz, Morris, & Richler, 2012).

3. Results

3.1. Hunger and pleasantness ratings

To ensure that the devaluation (eating until satiety) was effective, hunger ratings for pre- and post-devaluation and pre- and post-extinction were examined with repeated measures ANOVA with time (4) as within-subject variable and condition as between-subjects variable. There was a significant main effect of time ($F_{(2.52,231.74)} = 101.10$, $p < .001$, $\eta_p^2 = 0.52$), but no significant time × condition interaction ($F_{(2.51,231.74)} = 1.72$, $p = .17$). Pairwise comparisons with Bonferroni adjustment revealed significant decreases in hunger between pre-satiation and post-satiation ($p < .001$) and pre-satiation and pre-extinction ($p < .001$) but not between pre-extinction and post-extinction ($p > .99$; see Table 1).

Pleasantness ratings of food outcomes were analysed using a repeated measures ANOVA with value (2 levels: devalued and non-devalued) and time (4) as within-subject variables and condition as

Table 1
Means (± SE) of the subjective stress, working memory, hunger and pleasantness ratings for the stress and control condition, separately.

	Subjective stress				Working memory							
					$Baseline_{forward}$		$Baseline_{backward}$		$MAST_{forward}$		$MAST_{backward}$	
Control	16.86 (± 2.36)				5.40 (± 0.14)		5.02 (± 0.14)		5.94 (± 0.16)		5.21 (± 0.17)	
Stress	71.24 (± 2.33)				5.47 (± 0.15)		4.81 (± 0.15)		5.51 (± 0.17)		5.19 (± 0.18)	
	Hunger				Pleasantness							
					Devalued				Non-devalued			
	Pre-satiation	Post-satiation	Pre-extinction	Post-extinction	Pre-satiation	Post-satiation	Pre- extinction	Post-extinction	Pre-satiation	Post-satiation	Pre-extinction	Post-extinction
Control	6.71 (± 0.30)	2.96 (± 0.30)	3.85 (± 0.33)	3.54 (± 0.34)	7.32 (± 0.27)	5.17 (± 0.32)	4.60 (± 0.29)	4.45(± 0.33)	7.13(± 0.28)	7.04 (± 0.22)	6.81 (± 0.29)	6.64 (± 0.28)
Stress	6.94 (± 0.30)	3.04 (± 0.31)	4.11 (± 0.34)	4.59 (. ± 35)	7.04 (± 0.27)	5.83 (± 0.32)	5.07 (± 0.29)	5.11 (± 0.33)	6.79 (± 0.28)	6.98 (± 0.23)	6.77 (± 0.29)	6.64 (± 0.27)

(*footnote continued*)
randomly chosen for the first 15 particpants.

between-subjects variable. There was a significant interaction between time and value ($F_{(2.62,241.72)} = 28.52$, $p < .001$, $\eta_p^2 = 0.24$), but no other significant interactions (*all ps* > .08). Simple effect analysis per value revealed a significant main effect of time for the pleasantness of devalued food ($F_{(2.41,223.78)} = 51.10$, $p < .001$, $\eta_p^2 = 0.36$), but no significant time × condition interaction ($F_{(2.41,223.78)} = 2.63$, $p = .07$). Pairwise comparisons with Bonferroni adjustment revealed significant decreases between pre-satiation and post-satiation pleasantness ($p < .001$) and between pre-satiation and pre-extinction pleasantness ($p < .001$) but not between pre-extinction and post-extinction pleasantness ($p > .99$; see Table 1). The analysis of pleasantness ratings of non-devalued food revealed no significant interactions or main effects (*all ps* > 0.13), indicating that there was no change in the rewarding value of non-devalued food (see Table 1).

3.2. Neuroendocrine and subjective stress responses

Changes in subjective stress were evaluated using a one-way ANOVA with condition (stress, control) as between-subjects variable on the total subjective stress response (i.e., sum score of the three VAS scales). As shown in Table 1, participants in the stress condition perceived the MAST as distressing, indicated by their ratings of subjective stress and the resulting significant main effect of condition ($F_{(1,93)} = 268.49$, $p < .001$, $\eta_p^2 = 0.74$).

The effectiveness of the stress induction procedure on salivary cortisol levels were assessed using repeated measures ANOVA with time (5 levels: $t_{baseline}$, $t_{pre\text{-}stress}$, t_{+0}, t_{+10}, t_{+40}) as the within-subject variable and condition (2 levels: stress and control) as the between-subjects variable. There was a significant two-way interaction ($F_{(2.37,213.48)} = 32.09$, $p < .001$; $\eta_p^2 = 0.26$). Follow up Bonferroni corrected simple effect analysis at baseline revealed that cortisol was not different between the stress and control condition at baseline ($t_{baseline}$: $F_{(1,92)} = 2.67$, $p = .11$) and immediately before the stress manipulation ($t_{pre\text{-}stress}$: $F_{(1,91)} = 3.70$, $p = .06$). Hereafter, increases in cortisol were observed until 40 min after the stress induction, causing significant differences between conditions (t_{+0min}: $F_{(1,93)} = 22.15$, $p < .001$, $\eta_p^2 = 0.19$; t_{10min}: $F_{(1,92)} = 62.71$, $p < .001$, $\eta_p^2 = 0.41$; t_{40min}: $F_{(1,93)} = 44.59$, $p < .001$, $\eta_p^2 = 0.32$), with higher cortisol levels in the stress group (see Fig. 3).

Previous work by Smeets et al. (2018) showed that a stress-induced shift to less goal-directed behaviour was found only in cortisol responders (i.e., participants with a cortisol increase equal to or larger than 1.5 nmol/l; see Miller, Plessow, Kirschbaum, & Stalder, 2013) within the stress group, we determined the number of cortisol non-responders within the current sample. As there were only 4 cortisol non-responders in the stress group, we excluded them from the analysis of the WM and ILT data.[2]

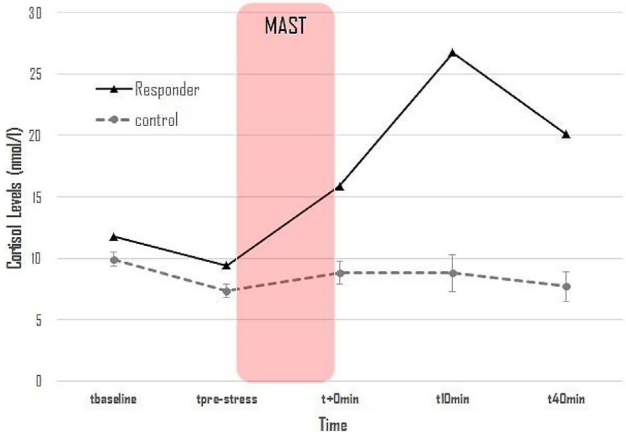

Fig. 3. Mean raw cortisol levels (± SE) for the stress and control condition. In total four non-responders were identified in the stress condition.

3.3. Stress-induced changes in working memory

WM scores are shown in Table 1. We first assessed whether there were differences in baseline working memory between conditions. Two univariate ANOVAs with condition (stress, control) as between-subjects factor revealed that there were no differences between conditions on baseline $WM_{forward}$ ($F_{(1,89)} = 0.11$, $p = .74$) and $WM_{backward}$ ($F_{(1,89)} = 0.32$, $p = .38$).

To investigate the stress-induced changes in working memory, we calculated the change score by subtracting baseline WM from WM after the MAST i.e., $WM_{(MAST\text{-}BASE)}$. The univariate ANOVA for $WM_{forward(MAST\text{-}BASE)}$ revealed a significant main effect of condition ($F_{(1,89)} = 7.09$, $p = .009$, $\eta_p^2 = 0.07$), indicating that stress abolished the improvement in working memory seen on the second assessment in the control condition (see Table 1). For $WM_{backward(MAST\text{-}BASE)}$, the main effect of condition was non-significant ($F_{(1,89)} = 0.94$, $p = .34$).

3.4. Moderation of working memory on the effect of stress on goal-directed behaviour

A multiple regression analysis was conducted using the PROCESS tool for SPSS. Model 1 with 1000 bootstrapping was used to assess whether baseline WM and stress-induced changes in WM moderate the effect of condition on goal-directed behaviour. A simple slopes analysis was used to further explore significant moderator effects.

For baseline WM, two separate multiple regressions revealed that the overall model for both $WM_{forward}$ and $WM_{backward}$ including condition was significant ($WM_{forward}$: $F_{(3,87)} = 7.20$, $p < .001$; $WM_{backward}$: $F_{(3,87)} = 3.66$, $p = .02$) and accounted for a significant amount of variance in goal-directed scores ($R^2 = 0.20$ and $R^2 = 0.11$ respectively). In line with previous findings, condition significantly predicted the change in goal-directed behaviour ($WM_{forward}$:$b = -0.86$, $t(87) = -4.56$, $p < .001$, 95% CI [−1.23, −0.48]; $WM_{backward}$:$b = -0.56$, $t(87) = -3.05$, $p = .01$, 95% CI [−0.93, −0.20]). Interestingly, the interaction between baseline WM and condition was significant ($WM_{forward}$: $b = 0.15$, $t(87) = 4.33$, $p < .001$, 95% CI [0.08, 0.22]; $WM_{backward}$: $b = 0.10$, $t(87) = 2.82$, $p = .01$, 95% CI [0.03, 0.18]) Using simple slope analysis, the interaction was probed by testing the conditional effects of condition at three levels of baseline WM, low (one standard deviation below the mean), average (at the mean), and high (one standard deviation above the mean). When looking at the simple slope analysis for baseline WM capacity, only for low values a significant negative relationship ($WM_{forward}$: $b = -0.20$, SE = 0.05; $p < .001$, 95% CI [−0.29, −0.11]; $WM_{backward}$: $b = -0.15$, SE = 0.05; $p < .001$, 95% CI [−0.25, −0.05]) between condition and goal-directed behaviour was obtained indicating no reduced responding to the devalued action after stress (see Fig. 4 for a visualization of the moderation).

To investigate the influence of stress-induced changes in working memory on the shift to less goal-directed behaviour under stress we conducted regression analyses with $WM_{forward(MAST\text{-}BASE)}$ change score. $WM_{forward(MAST\text{-}BASE)}$ was only assessed as stress had no effect on $WM_{backward}$. For $WM_{forward(MAST\text{-}BASE)}$ the overall model was non-significant ($F_{(3,87)} = 1.34$, $p = .27$).[3]

[2] The repeated measures ANOVA with condition (3 levels: responders, non-responders and control) as the between-subjects variable yielded similar results (two-way interaction $F_{(5,220.007)} = 22.12$, $p < .001$; $\eta_p^2 = 0.34$) and showed that responders and non-responders significantly differed from t_{+0min} until 40 min (Bonferroni corrected simple effect analysis per time point: $t_{baseline}$ $p = .15$; $t_{pre\text{-}stress}$ $p = .99$; t_{+0min}:$p = .007$, t_{10min}: $p < .001$, t_{40min}: $p < .001$).

[3] The multiple regression including the 4 non-responders revealed similar albeit weaker results. Baseline WM: overall model significant ($WM_{forward}$: $F_{(3,91)} = 5.96$, $p < .001$, $R^2 = 0.16$; $WM_{backward}$: $F_{(3,91)} = 4.11$, $p = .01$,

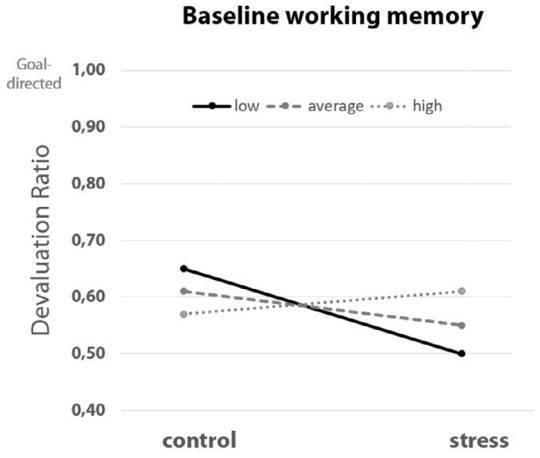

Fig. 4. Visualisation of the effect of stress on goal-directed behaviour as a function of individual baseline working memory capacity. Examination of the simple slopes interaction plot shows that only at low baseline WM capacity, stress induced a shift to less goal-directed control of behaviour. Dashed lines indicate non-significant moderation. Values for baseline $WM_{BACkWARD}$ are shown.

4. Discussion

The aim of the current study was two-folded: to replicate the finding that baseline working memory moderates the stress-induced shift to less goal-directed behaviour, and to extend previous findings by assessing the influence of stress-induced changes in working memory on this shift. Based on the idea that goal-directed behaviour is sensitive to changes in the value of the outcome, we employed an outcome devaluation paradigm. The current results indicate that the outcome devaluation was effective as subjective hunger and pleasantness ratings for the devalued food decreased, whereas no such decrease was found for the valued food. We found that less goal-directed responding was modulated by baseline, but not stress-induced changes in WM capacity. Specifically, only at low baseline WM capacity did stress result in less goal-directed behaviour. The current results replicate those of Otto et al. (2013): the effect of stress on probabilistic decision making was moderated by baseline WM capacity. Recent computational modelling findings demonstrate that the influence of the motivational value of the outcome on behaviour is dependent on the relative engagement of WM (Collins, Albrecht, Waltz, Gold, & Frank, 2017). The current results suggest that for those who already have limited cognitive resources at baseline taking into account motivational value under stress is impaired.

Instrumental action remained unaffected by the change in $WM_{forward}$ after stress. This could be related to the absence of a stress-induced impairment in working memory. Specifically, we found that stress abolished the improvement in working memory seen for the second assessment in the control condition. This latter finding is in line with the study of Elzinga and Roelofs (2005), which also reported testing effects with repeated administration of the DST. Future studies could profit from including two different assessments of WM pre and post-stress induction to further investigate the role of stress-induced changes in WM in the shift to less goal-direct behaviour under stress. Previous studies that investigated the effects of stress on WM capacity using the DST have observed mixed results. Some studies report no effect of stress on both $WM_{forward}$ and $WM_{backward}$ (Grossman et al., 2006; Hoffman & Al'Absi, 2004; Smeets, Jelicic, & Merckelbach, 2006), whereas others only found a stress effect on $WM_{backward}$ (Lewis, Nikolova, Chang, & Weekes, 2008; Schoofs et al., 2009) and still others only on $WM_{forward}$ in cortisol responders (Elzinga & Roelofs, 2005). In accordance with Elzinga and Roelofs (2005), we only found a group difference for $WM_{forward}$, indicating that rather passive maintenance of information was more sensitive to stress than the manipulation of information.

Goal-directed processes are the default determinant of behaviour (Moors et al., 2017). This is supported by the values obtained in the current study in both conditions (i.e., > 0.50) implicating goal-directed behaviour control. Previous studies have shown that stress decreased reward-related responses in the PFC (Ossewaarde et al., 2011) and that the stress-induced decrease in goal-directed behaviour was not associated with changes in brain regions implicated in habit learning like the striatum (Schwabe et al., 2012), supporting the idea that stress changes the competition between the two behavioural control systems by impairing the goal-directed PFC system.

One limitation of the current study is particularly worth mentioning. We included only women using hormonal contraceptives to reduce variability in cortisol responses related to hormonal alterations throughout the menstrual cycle phase. Psychophysiological studies suggest a role for hormonal activity during stress that is specifically related to the menstrual cycle, reward-related behaviour, and underlying brain areas. For example, hormonal alterations throughout the menstrual cycle have been related to the variability in cortisol responses after acute stress in women (Kudielka et al., 2009). Moreover, it has been found that high estradiol levels attenuate the subjective stress response and activity in brain areas involved in the stress response and its regulation, as for example the hippocampus, amygdala, anterior cingulate cortex (ACC), and orbitofrontal cortex (OFC; Albert, Pruessner, & Newhouse, 2015; Goldstein, Jerram, Abbs, Whitfield-Gabrieli, & Makris, 2010; for review see Montoya & Bos, 2017). Furthermore, it has been found that dependent on the menstrual phase, estradiol influences reward sensitivity via regulation of dopamine (Montoya & Bos, 2017). Thus, it is conceivable that ovarian hormone levels, which are low in OC users, alter the impact of stress on goal-directed behaviour in women. Future studies may opt to include females during the various phases of the menstrual cycle, which would provide a unique opportunity to investigate the impact of sex-specific hormones.

In addition to cortisol, there are several other neurotransmitters and hormones that are released in response to stress and may have affected instrumental action, including corticotrophin-releasing hormone and catecholamines like noradrenaline and dopamine. It has been demonstrated that trait-like stress-induced neuroendocrine responses relate to catecholamine-dependent activity in frontoparietal regions associated with working memory functionality (Hernaus, Quaedflieg, Offerman, Casales Santa, & van Amelsvoort, submitted for publication). Moreover, enhanced dopaminergic activity during learning accelerated the transition from goal-directed to habitual performance in rats (Wickens, Horvitz, Costa, & Killcross, 2007). Thus, it is conceivable that an interaction between dopamine and glucocorticoids underlie the stress-induced shift in behavioural control in individuals with low WM. Like most paradigms used in the field of instrumental learning, the ILT and devaluation task from the current study only probe the expression of response-outcome associations. As habits are defined as stimulus-response associations, these types of paradigms cannot demonstrate the reliance on a habit per se but rather tap the degree of goal-directedness of the instrumental actions. These findings question whether previous studies in humans truly tested habitual behaviour (De Houwer, Tanaka, Moors, & Tibboel, 2017; Foerde, 2018; Watson & de Wit, 2018). The current results together with the studies using computational modelling suggest that individual differences in working memory influence the

(*footnote continued*)
R^2 = 0.12), *interaction baseline WM × condition significant* ($WM_{forward}$: *b = 0.15, t(91) = 4.13, p < .001, 95% CI [0.08, 0.22] with at low* $WM_{forward}$: *b = −0.17, SE = 0.05; p < .001, 95% CI [−0.27, −0.08];* $WM_{backward}$: *b = 0.11, t (91) = 3.11, p < .01, 95% CI [0.04, 0.19] with at low* $WM_{backward}$: *b = −0.14, SE = 0.05; p = .01, 95% CI [−0.24, −0.04]).Stress-induced change in WM: overall model* $WM_{forward(MAST-BASE)}$ *non-significant* ($F_{(3,91)}$ = 0.27, *p = .85).*

effect of stress on taking into account motivational value, indicating that instrumental learning does not rely exclusively on one cognitive system but probably involve a wider array of higher-level executive functions.

Conflict of interest

None.

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