

BRIEF COMMUNICATIONS

Stress Impairs Retrieval of Socially Relevant Information

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Several studies have reported that stress impairs memory retrieval, even though findings are not unequivocal. Moreover, memory for socially relevant information was not previously investigated. The present study aimed to test the effects of stress on the retrieval of social memory (e.g., memory concerning names, birthdays, or biographies). In a randomized cross-over experiment, the cognitive performance of 29 subjects (15 women) was tested twice. Social memory was tested in a stress session, in which participants were exposed to a brief standardized psychosocial laboratory stressor between encoding and retrieval. Performance was compared with a stress-free control session. Stress exposure caused an increase in cortisol concentrations and changes in several mood measures. Social memory retrieval was reduced in the stress compared with the control session. An association between the cortisol stress response and poorer retrieval was significant in responders, that is, those participants displaying a cortisol rise after stress onset. Thus, similar to other forms of declarative memory, the retrieval of declarative memory for socially relevant information learned from biographical notes is impaired after acute stress exposure. This effect is linked to the stress-induced cortisol increase.

Keywords: cortisol, mood, responder, retrieval, social memory

Imagine a short interesting conversation with a new colleague about her or his background. After a while, you meet the colleague again, but in this situation, you are stressed because of a recent conflict with your boss. Irritatingly, you fail to retrieve several aspects of your last talk. What could have happened?

It is well established that stress can influence long-term memory by activating the autonomous nervous system (ANS) and the hypothalamus–pituitary–adrenal (HPA) axis. The resulting (nor)adrenaline and glucocorticoid (GC; cortisol in humans, corticosterone in rodents) releases are involved in memory modulation, with the underlying occupation of central nuclear and membrane-bound mineralocorticoid receptors (MRs) and glucocorticoid receptors (GRs; de Kloet, Joëls, & Holsboer, 2005; Joëls, Karst, DeRijk, & de Kloet, 2008; Lupien, Maheu, Tu, Fiocco, & Schramek, 2007).

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For the example mentioned above, the effects of stress on memory retrieval are most relevant. There are several stages of memory, which are differently modulated (Roosendaal, 2002; Wolf, 2009). Stress exposure before memory consolidation can enhance memory (Beckner, Tucker, Delville, & Mohr, 2006; Cahill, Gorski, & Le, 2003; Preuss & Wolf, 2009; Smeets, Otgaar, Candel, & Wolf, 2008); a similar stressor or cortisol administration impairs it when administered before retrieval (Buchanan & Tranel, 2008; Buchanan, Tranel, & Adolphs, 2006; de Quervain, Roosendaal, & McGaugh, 1998; de Quervain, Roosendaal, Nitsch, McGaugh, & Hock, 2000; Kuhlmann, Piel, & Wolf, 2005; Smeets et al., 2008; Tollenaar, Elzinga, Spinhoven, & Everaerd, 2008; Wolf et al., 2001). The emotionality of the material can further potentiate these effects (Roosendaal, McEwen, & Chattarji, 2009; van Stegeren, 2008; Wolf, 2008). When discussing effects of stress on memory retrieval, it has to be acknowledged that some studies have failed to find impairing effects on retrieval (e.g., Beckner et al., 2006; Schoofs & Wolf, 2009; Schwabe et al., 2009).

Thus, previous experimental studies would suggest that GCs were partly responsible for the retrieval deficit of the conversation with the new colleague. However, the form of memory involved here has a more social component, which has been neglected in stress research so far. Most of the studies cited above have used stimuli (long word lists or series of slides) without a social contextual component. In a first attempt, Takahashi and colleagues (2004) could demonstrate that deficits in a social memory task, consisting of a simple face–name association, were related to stress-induced cortisol levels. However, social memory incorpo-

rates more aspects than simple recognizing the name of a person when seeing the related picture. It refers to the remembrance of facts and processes with a more contextual or interrelated content, that is, names of persons, their living conditions and life stories, phone numbers, birthdays, pictures, related towns, and so forth (cf. Insel & Fernald, 2004; Olick & Robbins, 1998). This social impact is also, at least partially, emotionally relevant. Although it might be assumed that stress influences this kind of memory in the same way as typically used paradigms (retrieval of simple nouns or pictures), this has not been shown as of today.

In the present study, we tested the impact of stress on several aspects of declarative memory for socially relevant information learned from biographical notes (in this article, we refer to this as *social memory*). Participants were tested twice; they had to learn details from two biographical notes, and were afterward exposed to stress or a control situation. Retrieval took place at a time during the stress session when cortisol levels were expected to be elevated.

We hypothesized that social memory retrieval would be impaired after stress. Furthermore, we expected an association between cortisol concentrations and the stress-induced social memory decline. Given that sex is a modulator of the stress response (Kudielka & Kirschbaum, 2005) as well as a modulator of learning and memory (Dalla & Shors, 2009; Wolf, 2006), we further tested possible sex differences in an explorative manner.

Method

Subjects

In the present study, 15 women with a mean age of 23.6 ± 0.5 (standard error of the mean; *SEM*) years and a body mass index (BMI) of 22.3 ± 0.6 kg/m² and 14 men with a mean age of 22.7 ± 0.5 years and a BMI of 23.5 ± 1.0 kg/m² volunteered to participate. There were no significant differences between women and men with respect to age or BMI. Participants were all healthy and mostly students of psychology recruited via personal address and paid for participation in two experimental sessions. None of them was taking regular medication (except for oral contraceptives; see below) or had a history of any psychiatric treatment. Exclusion criteria were somatic and in particular endocrine diseases known to influence endogenous hormone levels (e.g., acute asthma, hyper- or hypothyroidism).

During both testing sessions, all women took their monophasic oral contraceptives, which guaranteed a constant level of estrogens and gestagens in the first 3 weeks of pill intake. Therefore, sex steroid fluctuations, which might influence the HPA response to stress (see Kirschbaum, Kudielka, Gaab, Schommer, & Hellhammer, 1999), could be ruled out for the experimental days. The sessions were scheduled for the afternoon at 3 or 5 p.m. to control the circadian fluctuations of cortisol (Lupien et al., 2002, 2007). Participants were not allowed to smoke, eat, or drink anything but water for the 2 hr before the experiment. Moreover, subjects were instructed to refrain from alcohol consumption the day before testing. At their arrival, participants were informed that their cognitive performance would be tested, and that they would have to deliver a public speech on 1 day of the two sessions. All subjects gave written informed consent to both sessions. The study protocol

was approved by the ethics committee of the German Psychological Association.

Study Design

A randomized balanced cross-over design was chosen with 2 days of testing (stress vs. control session in counterbalanced order) starting both at the same time of the day with a 1-week interval between both sessions. At the beginning of the stress session, which was a modified version of the Trier Social Stress Test (cf. Kirschbaum, Pirke, & Hellhammer, 1993), participants had to encode two biographical notes (Memory subtask from the WILDE-Intelligence-Test [WIT]; Jäger & Althoff, 1994; see below). They were then asked to provide saliva samples for the assessment of cortisol prestress levels (first measurement: 0 min¹). Subsequently, participants were instructed that they would have to deliver a public speech 10 min later without prior knowledge of the topic. After this anticipation period, the second sample (15 min) was taken. Afterward, they performed a simulated job interview in front of a camera for 5 min. Immediately after the speech (third sample: 25 min) and another 25 min later (fourth sample: 50 min) additional samples were collected. Between the third and fourth saliva samples, participants performed filler memory tasks (short-term memory: Memorize Numbers subtest from the WIT and Memory subtest from the Intelligence-Structure-Test; Amthauer, Brocke, Liepmann, & Beauducel, 2001). Finally, they were asked to recall the previously encoded biographical notes from the WIT (for details see below). A last (fifth: 75 min) saliva sample concluded the stress session (see Figure 1 for the timing of stressor and memory testing).

In the control session, no stress was induced and no saliva samples were taken. Cognitive testing took place within the same time span between encoding and retrieval as in the stress condition. After encoding the biographical notes, participants were asked to fill in the same short-term memory tasks as in the stress session as well as a personality questionnaire to ensure that sessions were comparable. These data were used to distract the participants from remembering the biographical notes between encoding and retrieval but were not further analyzed.

Assessment of Cognitive Performance

The Memory subtask of the WIT (Jäger & Althoff, 1994) was used to assess social memory. Parallel versions in counterbalanced order were presented to the participants according to the session (stress vs. control). This subtask consists of two biographical notes (from a woman and a man) including photos, telephone numbers, birth dates, hometowns, and parts of their life stories. This material aims at the specific interrelation of facts in the context of the respective biography to represent social memory. Participants had to carefully learn both notes (3 min encoding time for each note). The delayed recall was carried out 50 min after having learned the details by use of standardized answering sheets, yielding information on three aspects of memory: (a) recognition (participants had to select the correct item from five alternatives; score range: 0 to 13); (b) correction (participants had to mark the incorrect item

¹ Saliva sampling time did not exceed 5 min.

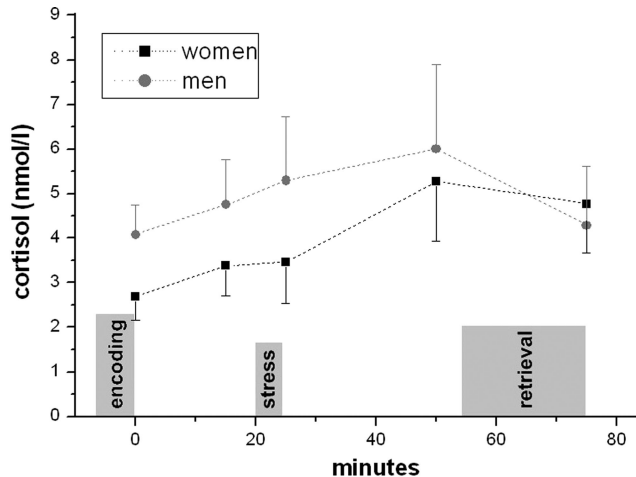


Figure 1. Mean (SEM) cortisol concentrations in response to the public speaking paradigm, separated for women and men. Included is the timing of the memory testing with description of minutes starting after the end of encoding.

from five alternatives; score range: 0 to 11); and (c) reproduction (participants had to write the correct answer in a semiopen answering format; score range: 0 to 16). An average of the three subtasks resulted in a global memory score.

Stress Paradigm

A standardized laboratory stressor was used consisting of a free public speech for 5 min (cf. Hennig, Netter, & Voigt, 2001; Alexander et al., 2009). Participants were told to imagine being in a job interview where they had to illustrate why they were the most adequate candidate for this particular job. A video camera was placed in front of the participant with the information that the interview would be projected to an audience that would evaluate the speech simultaneously in an adjacent room. Instead of a real audience, however, a videotape of a recorded audience was presented via TV. This procedure was used to guarantee a comparable situation for all of the participants by eliminating differences in behavior of the audience.

Furthermore, participants were informed that their videotape would be evaluated afterward by a linguist and two psychologists for the formal and verbal content as well as their social interaction skills. Prior to the talk, the experimenter turned to the camera and asked the audience whether the talk could begin. The timing of this question was based exactly on the counter of the video recorder, resulting in nodding by the audience. This protocol has previously been shown to cause robust activations of the HPA axis and the ANS (e.g., Alexander et al., 2009; Hennig et al., 2001).

Saliva Sampling, Cortisol Analysis, and Mood Questionnaire

On the day of the public speech, full saliva samples for the analysis of free cortisol were collected from the participants by use of glass tubes. Immediately after sampling, saliva was stored at -30°C until assayed. Saliva cortisol was determined by use of a commercial chemoluminescence immunoassay (IBL, Hamburg,

Germany). All samples were analyzed within one lot and in duplicates. Intraassay coefficient of variation (CV) was below 6%, with an interassay CV below 10%. On the control day, no saliva samples were taken because no cortisol response to the control condition was expected (see Payne et al., 2007; Het, Rohleder, Schoofs, Kirschbaum, & Wolf, 2009; Tollenaar et al., 2008).

During saliva sampling, participants had to complete a questionnaire on emotional states for a manipulation check of the stress protocol. This questionnaire was adapted from the mood adjective list introduced by Janke and Debus (1978) and consisted of 25 items that were measured via a visual analogue scale. A factor analysis was computed to reduce these data because several items were correlated. Five separate factors were extracted from factor analysis, explaining 80% of the total variance: Alertness, Vegetative Symptoms, Psychological Disturbance, and Negative and Positive Mood.

Statistical Analysis

Data were analyzed using SPSS 17.0 software (SPSS Inc., Chicago). Cortisol responses as well as changes in mood were analyzed with a repeated measures analysis of variance (ANOVA; within-subjects factor: time; between-subjects factor: sex). Analyses of covariance were performed for the four social memory measures to compare retrieval after stress with the control session (within-subjects factor: stress) and to detect possible sex differences (between-subjects factor). Order of session (stress vs. control session first) was treated as covariate to control for practice effects. To correct for violations of sphericity, we corrected all results by the Greenhouse–Geisser degrees of freedom adjustment where appropriate.

Pearson product–moment correlations between cortisol responses and the memory test scores in the stress condition were computed to test for associations between hormonal responses and the social memory performance. Subtraction of the prestress cortisol levels from the mean of the fourth and fifth times of measurement ($[\text{concentration } 4 + \text{concentration } 5]/2 - \text{concentration } 1$) was used to reflect more realistically the cortisol elevation at the time of memory retrieval during the stress session.

Results

Endocrine Responses and Subjective Mood

The repeated measures ANOVA for cortisol revealed a significant main effect of time, $F(1.645, 44.427) = 4.155, p < .05$ (see Figure 1). No further main effect or interaction with the factor sex was observed. Thus, the stressor led to elevated cortisol concentrations, independent of sex. Post hoc *t* tests revealed increases at the second ($p = .012$), third ($p = .109$), fourth ($p = .012$), and fifth ($p = .057$) measurements, compared with the first measurement.

Concerning the mood ratings, the repeated measures ANOVA detected a main effect of time for psychological disturbance, $F(2.635, 71.157) = 9.308, p < .001$, vegetative symptoms, $F(2.837, 76.603) = 19.604, p < .001$, and negative mood, $F(3, 80.994) = 4.283, p < .01$. In the course of the stress induction, participants were more disturbed, reported more vegetative symptoms, and had a higher negative mood. Subjective ratings for alertness and positive mood as well as the

between-subjects factor sex did not result in any significant main or interaction effects.

Stress Effects on Social Memory

As depicted in Figure 2, participants made significantly more mistakes in the stress compared with the control session in the recognition task, $F(1, 26) = 4.223$, $p = .050$, the reproduction task, $F(1, 26) = 19.508$, $p < .001$, and the global memory score, $F(1, 26) = 4.738$, $p < .05$, as indicated by a main effect of stress. The main effect of stress for the correction task was not significant, $F(1, 26) = 1.864$, $p > .10$. No significant interaction effects with sex could be detected ($ps > .10$).

Correlation analyses with all participants revealed a significant association between the cortisol response during memory retrieval and the recognition subtask ($r = -.371$, $p < .05$). Performance in the other retrieval tasks was not significantly related to cortisol. Previous work has suggested that associations between cortisol and memory retrieval can sometimes only be detected in those participants showing a stress-induced cortisol increase (cortisol responder; see Buchanan et al., 2006). Therefore, on a post hoc basis, participants were grouped into responders if their change in cortisol from the first to the fourth time of measurement (25 min after ceasing of the stressor to reflect the peak of cortisol response; cf. Dickerson & Kemeny, 2004) exceeded 0 nmol/l; otherwise, they were grouped as nonresponders (cf. Buchanan et al., 2006).² In nonresponders, no significant correlation was observed. However, the mean cortisol response during memory retrieval of responders ($n = 19$) was significantly related to the recognition task ($r = -.574$, $p = .01$) and the global memory score ($r = -.527$, $p < .05$). The association between cortisol and the reproduction task depicted a nonsignificant trend ($r = -.401$, $p = .089$).

Discussion

The present study investigated the retrieval of socially relevant information under normal and stress conditions paying attention to

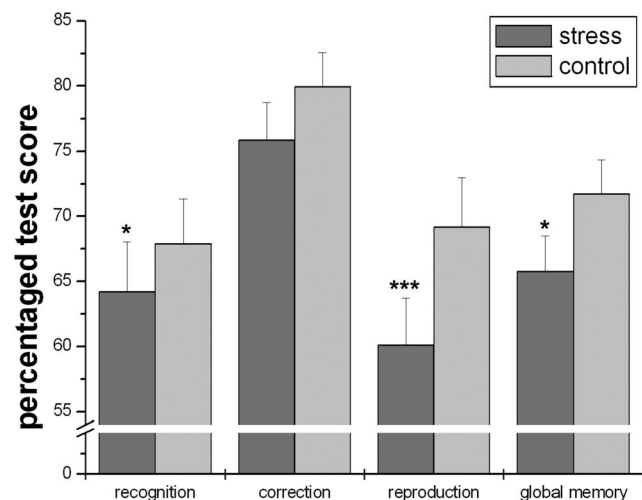


Figure 2. Percentage of means (*SEM*) of the memory performance in the recognition, correction, and reproduction task as well as the global memory score of the WILDE-Intelligence-Test; separated for the control and stress sessions. * $p \leq .05$; *** $p < .001$, in comparison with the respective control condition.

possible sex differences. As indicated by significant changes in cortisol secretion and mood, the stress induction was successful. Social memory retrieval was significantly reduced after stress, and this could be related to the cortisol response.

Previous studies investigating stress effects on memory retrieval repeatedly have observed an impairing effect of stress (Buchanan et al., 2006; Kuhlmann et al., 2005; Smeets et al., 2008; Tollenaar et al., 2008; Wolf, 2009). Those previous studies used word lists containing neutral and emotional words as stimuli. The present study extended these findings to declarative memory for socially relevant information by demonstrating impaired social memory retrieval after a stressful public speaking task. The findings are in line with those from Takahashi et al. (2004). Those authors reported that stress impaired memory for face–name associations. However, in this study, stress was administered before learning, so that no conclusion about the specific memory phase influenced by stress could be obtained. Our current findings suggest that primarily retrieval was influenced. A strength of our study is that we used a standardized method to examine social memory (WIT). Biographical notes had to be remembered, a task with high ecological validity. In addition, we tested recognition, correction, and reproduction of previously encoded material, thereby providing a broader assessment of social declarative memory.

Stress effects were stronger in the reproduction than in the recognition task. This is in line with the dual process theory suggesting the hippocampus, with its stress-sensitive MRs and GRs, to be more relevant for recollection than for recognition memory (Aggleton & Brown, 1999; Eichenbaum, Yonelinas, & Ranganath, 2007). Cortisol was associated with social memory performance in responders only, as has previously been observed with a word recognition task (Buchanan et al., 2006).

In the present experiment, the effects of stress on social memory retrieval were not modulated by sex. This is in line with a previous study (Smeets et al., 2008) that tested a large group of women, most of whom probably took oral contraceptives. Similar to our present findings, stress impaired memory retrieval. In contrast, a recent study exploring the effects of stress on memory retrieval in women during the luteal phase reported no impairing effect of the stressor (Schoofs & Wolf, 2009). The current results indicate that women using monophasic contraceptives show a memory retrieval impairment after stress. This suggests that the cognitive response to stress might be reduced only at times of high endogenous sex steroid concentrations (e.g., during the luteal phase of the menstrual cycle; Schoofs & Wolf, 2009).

Studies in rodents have revealed that social memory is linked to the pituitary hormones oxytocin and vasopressin (Bielsky & Young, 2004; Neumann, 2008). Hints for an effect of at least oxytocin in humans pinpoint a crucial role of the amygdala on

² This is in contrast to the approach of the correlational analyses, which used the mean of the fourth and fifth times of measurement relative to the prestress levels. Responders were classified on basis of the peak cortisol response, whereas correlations with memory were computed with the cortisol level during retrieval testing, which is more appropriately reflected in the mean concentration of the fourth and fifth samples.

social cognition (Domes et al., 2007; Kirsch et al., 2005). Further research on social cognition in humans concerning the interaction among oxytocin, vasopressin, and stress is clearly warranted (for stress and social cognition, see Smeets, Dziobek, & Wolf, 2009).

The current study has some limitations that need to be acknowledged. First, the stressor was administered between memory encoding and memory retrieval. Because of the relatively short delay between these two processes (a little less than 1 hr), we cannot clearly distinguish between a stress effect on consolidation or retrieval. The existing literature reports enhancing effects of stress on consolidation and impairing effects on retrieval, when stress or GC application took place before the respective memory stage (consolidation: Beckner et al., 2006; Cahill et al., 2003; Preuss & Wolf, 2009; retrieval: Buchanan et al., 2006; Roozendaal, 2000; both consolidation and retrieval: Smeets et al., 2008). Recent reviews on this topic are provided by van Stegeren (2009) and Wolf (2009). Given that impairing effects of stress were observed in the present study, we can conclude that stress had most likely affected retrieval. Consolidation studies would rather suppose an enhancement of declarative memory if stress were induced after encoding (cf. Beckner et al., 2006; Cahill et al., 2003; Preuss & Wolf, 2009). Second, we did not measure markers of (nor)adrenergic activation as heart rate or alpha-amylase. The ANS has been shown to modulate memory processes based on (nor)adrenergic effects on the amygdala (Roozendaal, Okuda, de Quervain, & McGaugh, 2006); therefore, the concomitant assessment of ANS markers would have provided a further insight into the underlying neuroendocrine mechanism. Third, no saliva samples were taken in the control session as no cortisol response was suggested given previous reports (Het et al., 2009; Payne et al., 2007; Tollenaar et al., 2008). Nevertheless, we cannot exclude the possibility of elevated cortisol levels in some participants during the control condition. Fourth, the sample size of the present study was rather small, even though this is not uncommon in this line of research (e.g., Buchanan & Tranel, 2008; Buchanan et al., 2006). We cannot exclude the possibility that additional effects might have been obtained with a larger sample size. Lastly, we cannot contribute to the question of whether the sort of social memory tested in our study is a separate memory domain or rather a subcategory of declarative memory characterized by the use of social stimuli. A better understanding of the neural correlates involved in this task and its modulation by stress hormones might come from future studies using a pharmacological approach in combination with functional MRI.

In sum, the present experiment demonstrates that acute stress impairs the retrieval of socially relevant information. Moreover, the stress-induced retrieval impairments were associated with the cortisol response to the stressor. The relevance of impaired social memory retrieval after stress is obvious in daily experiences such as partnership conflicts or concerning the example of the new colleague mentioned at the beginning of this article. These effects become even more important during courtroom testimony or similarly important stressful retrieval conditions. Future studies might explore pharmacological (de Quervain, Aerni, & Roozendaal, 2007) or behavioral (Scholz et al., 2009; Schwabe & Wolf, 2009) approaches aimed at preventing the stress-induced memory retrieval impairment in these situations.

References

- Aggleton, J. P., & Brown, M. W. (1999). Episodic memory, amnesia and the hippocampal–anterior thalamic axis. *Behavioral and Brain Sciences*, *22*, 425–489.
- Alexander, N., Küpper, Y., Schmitz, A., Osinsky, R., Kozyra, E., & Hennig, J. (2009). Gene–environment interactions predict cortisol responses after acute stress: Implications for the etiology of depression. *Psychoneuroendocrinology*, *34*, 1294–1303.
- Amthauer, R., Brocke, B., Liepmann, D., & Beauducel, A. (2001). *Intelligenz-Struktur-Test 2000 R (2. erweiterte und revidierte Auflage)* [Intelligence-Structure-Test (2nd extended and rev. ed.)]. Göttingen: Hogrefe.
- Beckner, V. E., Tucker, D. M., Delville, Y., & Mohr, D. C. (2006). Stress facilitates consolidation of verbal memory for a film but does not affect retrieval. *Behavioral Neuroscience*, *120*, 518–527.
- Bielsky, I. F., & Young, L. J. (2004). Oxytocin, vasopressin, and social recognition in mammals. *Peptides*, *25*, 1565–1574.
- Buchanan, T. W., & Tranel, D. (2008). Stress and emotional memory retrieval: Effects of sex and cortisol response. *Neurobiology of Learning and Memory*, *89*, 134–141.
- Buchanan, T. W., Tranel, D., & Adolphs, R. (2006). Impaired memory retrieval correlates with individual differences in cortisol response but not autonomic response. *Learning & Memory*, *13*, 382–387.
- Cahill, L., Gorski, L., & Le, K. (2003). Enhanced human memory consolidation with post-learning stress: Interaction with the degree of arousal at encoding. *Learning & Memory*, *10*, 270–274.
- Dalla, C., & Shors, T. J. (2009). Sex differences in learning processes of classical and operant conditioning. *Physiology & Behavior*, *97*, 229–238.
- de Kloet, E. R., Joëls, M., & Holsboer, F. (2005). Stress and the brain: From adaptation to disease. *Nature Reviews Neuroscience*, *6*, 463–475.
- de Quervain, D. J.-F., Aerni, A., & Roozendaal, B. (2007). Preventive effect of beta-adrenoceptor blockade on glucocorticoid-induced memory retrieval deficits. *American Journal of Psychiatry*, *164*, 967–969.
- de Quervain, D. J.-F., Roozendaal, B., & McGaugh, J. L. (1998, August 20). Stress and glucocorticoids impair retrieval of long-term spatial memory. *Nature*, *394*, 787–790.
- de Quervain, D. J.-F., Roozendaal, B., Nitsch, R. M., McGaugh, J. L., & Hock, C. (2000). Acute cortisone administration impairs retrieval of long-term declarative memory in humans. *Nature Neuroscience*, *3*, 313–314.
- Dickerson, S. S., & Kemeny, M. E. (2004). Acute stressors and cortisol responses: A theoretical integration and synthesis of laboratory research. *Psychological Bulletin*, *130*, 355–391.
- Domes, G., Heinrichs, M., Glaescher, J., Büchel, C., Braus, D. F., & Herpertz, S. C. (2007). Oxytocin attenuates amygdala responses to emotional faces regardless of valence. *Biological Psychiatry*, *62*, 1187–1190.
- Eichenbaum, H., Yonelinas, A. P., & Ranganath, C. (2007). The medial temporal lobe and recognition memory. *Annual Review of Neuroscience*, *30*, 123–152.
- Hennig, J., Netter, P., & Voigt, K. H. (2001). Cortisol mediates redistribution of CD8+ but not of CD56+ cells after the psychological stress of public speaking. *Psychoneuroendocrinology*, *26*, 673–687.
- Het, S., Rohleder, N., Schoofs, D., Kirschbaum, C., & Wolf, O. T. (2009). Neuroendocrine and psychometric evaluation of a placebo version of the “Trier Social Stress Test.” *Psychoneuroendocrinology*, *34*, 1075–1086.
- Insel, T. R., & Fernald, R. D. (2004). How the brain processes social information: Searching for the social brain. *Annual Review of Neuroscience*, *27*, 697–722.
- Jäger, A. O., & Althoff, K. (1994). *Der WILDE-Intelligenz-Test* [The WILDE-Intelligence-Test (2nd rev. ed.)]. Göttingen: Hogrefe.
- Janke, W., & Debus, G. (1978). *Die Eigenschaftswörterliste (EWL)* [The Adjective Checklist]. Göttingen: Hogrefe.

- Joëls, M., Karst, H., DeRijk, R., & de Kloet, E. R. (2008). The coming out of the brain mineralocorticoid receptor. *Trends in Neurosciences*, *31*, 1–7.
- Kirsch, P., Esslinger, C., Chen, Q., Mier, D., Lis, S., Siddhanti, S., . . . Meyer-Lindenberg, A. (2005). Oxytocin modulates neural circuitry for social cognition and fear in humans. *Journal of Neuroscience*, *25*, 11489–11493.
- 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. *Psychosomatic Medicine*, *61*, 154–162.
- Kirschbaum, C., Pirke, K.-M., & Hellhammer, D. H. (1993). The “Trier Social Stress Test”—A tool for investigating psychobiological stress responses in a laboratory setting. *Neuropsychobiology*, *28*, 76–81.
- Kudielka, B. M., & Kirschbaum, C. (2005). Sex differences in HPA axis responses to stress: A review. *Biological Psychology*, *69*, 113–132.
- Kuhlmann, S., Piel, M., & Wolf, O. T. (2005). Impaired memory retrieval after psychosocial stress in healthy young men. *Journal of Neuroscience*, *25*, 2977–2982.
- Lupien, S. J., Maheu, F., Tu, M., Fiocco, A., & Schramek, T. E. (2007). The effects of stress and stress hormones on human cognition: Implications for the field of brain and cognition. *Brain and Cognition*, *65*, 209–237.
- Lupien, S. J., Wilkinson, C. W., Brière, S., Ménard, C., Ng Ying Kin, N. M. K., & Nair, N. P. V. (2002). The modulatory effects of corticosteroids on cognition: Studies in young human populations. *Psychoneuroendocrinology*, *27*, 401–416.
- Neumann, I. D. (2008). Brain oxytocin: A key regulator of emotional and social behaviours in both females and males. *Journal of Neuroendocrinology*, *20*, 858–865.
- Olick, J. K., & Robbins, J. (1998). Social memory studies: From “collective memory” to the historical sociology of mnemonic practices. *Annual Review of Sociology*, *24*, 105–140.
- Payne, J. D., Jackson, E. D., Hoscheidt, S., Ryan, L., Jacobs, W. J., & Nadel, L. (2007). Stress administered prior to encoding impairs neutral but enhances emotional long-term episodic memories. *Learning & Memory*, *14*, 861–868.
- Preuss, D., & Wolf, O. T. (2009). Post-learning psychosocial stress enhances consolidation of neutral stimuli. *Neurobiology of Learning and Memory*, *92*, 318–326.
- Roozendaal, B. (2000). Glucocorticoids and the regulation of memory consolidation. *Psychoneuroendocrinology*, *25*, 213–238.
- Roozendaal, B. (2002). Stress and memory: Opposing effects of glucocorticoids on memory consolidation and memory retrieval. *Neurobiology of Learning and Memory*, *78*, 578–595.
- Roozendaal, B., McEwen, B. S., & Chattarji, S. (2009). Stress, memory and the amygdala. *Nature Reviews Neuroscience*, *10*, 423–433.
- Roozendaal, B., Okuda, S., de Quervain, D. J.-F., & McGaugh, J. L. (2006). Glucocorticoids interact with emotion-induced noradrenergic activation in influencing different memory functions. *Neuroscience*, *138*, 901–910.
- Scholz, U., La Marca, R., Nater, U. M., Aberle, I., Ehlert, U., Hornung, R., . . . Kliegel, M. (2009). Go no-go performance under psychosocial stress: Beneficial effects of implementation intentions. *Neurobiology of Learning and Memory*, *91*, 89–92.
- Schoofs, D., & Wolf, O. T. (2009). Stress and memory retrieval in women: No strong impairing effect during the luteal phase. *Behavioral Neuroscience*, *123*, 547–554.
- Schwabe, L., Römer, S., Richter, S., Dockendorf, S., Bilak, B., & Schächinger, H. (2009). Stress effects on declarative memory retrieval are blocked by a beta-adrenoceptor antagonist in humans. *Psychoneuroendocrinology*, *34*, 446–454.
- Schwabe, L., & Wolf, O. T. (2009). The context counts: Congruent learning and testing environments prevent memory retrieval impairment following stress. *Cognitive, Affective, & Behavioral Neuroscience*, *9*, 229–236.
- 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. *Hormones and Behavior*, *55*, 507–513.
- Smeets, T., Otgaar, H., Candel, I., & Wolf, O. T. (2008). True or false? Memory is differentially affected by stress-induced cortisol elevations and sympathetic activity at consolidation and retrieval. *Psychoneuroendocrinology*, *33*, 1378–1386.
- Takahashi, T., Ikeda, K., Ishikawa, M., Tsukasaki, T., Nakama, D., Tanida, S., & Kameda, T. (2004). Social stress-induced cortisol elevation acutely impairs social memory in humans. *Neuroscience Letters*, *363*, 125–130.
- Tollenaar, M. S., Elzinga, B. M., Spinhoven, P., & Everaerd, W. A. M. (2008). The effects of cortisol increase on long-term memory retrieval during and after acute psychosocial stress. *Acta Psychologica*, *127*, 542–552.
- van Stegeren, A. H. (2008). The role of the noradrenergic system in emotional memory. *Acta Psychologica*, *127*, 532–541.
- van Stegeren, A. H. (2009). Imaging stress effects on memory: A review of neuroimaging studies. *The Canadian Journal of Psychiatry*, *54*, 16–27.
- Wolf, O. T. (2006). Effects of stress hormones on the structure and function of the human brain. *Expert Review of Endocrinology and Metabolism*, *1*, 623–632.
- Wolf, O. T. (2008). The influence of stress hormones on emotional memory: Relevance for psychopathology. *Acta Psychologica*, *127*, 513–531.
- Wolf, O. T. (2009). Stress and memory in humans: Twelve years of progress. *Brain Research*, *1293*, 142–154.
- Wolf, O. T., Convit, A., McHugh, P. F., Kandil, E., Thorn, E. L., de Santi, S., . . . de Leon, M. J. (2001). Cortisol differentially affects memory in young and elderly men. *Behavioral Neuroscience*, *115*, 1002–1011.

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