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The Impact of Stress on Odor Perception

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Abstract
The olfactory system and emotional systems are highly intervened and share common neuronal structures. The current study investigates whether emotional (e.g., anger and fear) and physiological (saliva cortisol) stress responses are associated with odor identification ability and hedonic odor judgments (intensity, pleasantness, and unpleasantness). Nineteen men participated in the modified Trier Social Stress Test (TSST) and a control session (cycling on a stationary bike). The physiological arousal was similar in both sessions. In each session, participants' odor identification score was assessed using the University of Pennsylvania Smell Identification Test, and their transient mood was recorded on the dimensions of valence, arousal, anger, and anxiety. Multivariate regression analyses show that an increase of cortisol in the TSST session (as compared with the control session) is associated with better odor identification performance ($\beta = .491$) and higher odor intensity ratings ($\beta = .562$). However, increased anger in the TSST session (as compared with the control session) is associated with lower odor identification performance ($\beta = -.482$). The study shows divergent effects of the emotional and the physiological stress responses, indicating that an increase of cortisol is associated with better odor identification performance, whereas increased anger is associated with poorer odor identification performance.

Keywords
odor identification, olfaction, cortisol, anger, Trier Social Stress Test, stress

Introduction

In evolutionary terms, the olfactory system might have evolved as a warning system to detect potential harmful substances or situations (Stevenson, 2010). In line with this hypothesis, the olfactory system and emotional systems are highly intervened and share common neuronal

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structures (e.g., the orbitofrontal cortex, amygdala and hippocampus formation; see Patin & Pause, 2015).

Stress activates the hypothalamic–pituitary–adrenal axis, leading to the release of cortisol into the bloodstream, which modulates olfactory perception via the central nervous system. Patients with adrenal cortical insufficiency have a markedly reduced cortisol production and show an increased olfactory sensitivity (reduced olfactory perception thresholds; Henkin & Bartter, 1966). However, other studies with nonclinical samples show that increased cortisol levels in women are associated with improved odor detection abilities (Pause, Sojka, Krauel, Fehm-Wolfsdorf, & Ferstl, 1996) and mothers with higher cortisol levels were more able to recognize their infants' odors (Fleming, Steiner, & Corter, 1997).

The experience of uncontrollable (psychosocial) stress is often related to feelings of anxiety, fear (Hellhammer & Schubert, 2012; Rodrigues, LeDoux, & Sapolsky, 2009), and anger (Lupis, Lerman, & Wolf, 2014). The main function of cortisol during physiological or psychological stress responses is related to an increase of energy release within the central nervous system, whereas the emotional reaction to stress is related to cognitive appraisal strategies (Lazarus & Folkman, 1984; Lupien, Maheu, Tu, Fiocco, & Schramek, 2007). Therefore, the effects of cortisol as a marker of the physiological stress response on olfactory performances might dissociate from effects of anger and anxiety on olfactory performances (see Lupis et al., 2014).

To our knowledge only one study has investigated the effects of anger on olfactory perception: In war veterans with posttraumatic stress disorder olfactory identification deficits are predictors of aggression and impulsivity (Dileo, Brewer, Hopwood, Anderson, & Creamer, 2008). However, anxiety and related negative emotions in nonclinical samples seem to increase olfactory abilities: Highly anxious individuals (in contrast to low anxious individuals) show faster response times to positive and negative valenced odors (La Buissonnière-Ariza, Lepore, Kojok, & Frasnelli, 2013), and individuals scoring high on emotionality (neuroticism) show better odor discrimination (Havlíček et al., 2012), odor identification abilities (Larsson, Finkel, & Pederson, 2000), and increased olfactory sensitivity (Pause, Ferstl, & Fehm-Wolfsdorf, 1998; but for null results see Croy, Springborn, Lötsch, Johnston, & Hummel, 2011). Similarly, extremely shy individuals show lower olfactory thresholds than sociable individuals (Herberner, Kagan & Cohen, 1989). Furthermore, olfactory sensitivity for malodors is increased after a stress induction procedure (psychosocial stress and socially evaluated cold pressure test; Pacharra et al., 2016). Only a few studies indicate that anxiety could be associated with reduced olfactory abilities, such as, high state and trait anxiety predicting reduced odor detection sensitivity and odor recognition sensitivity (Takahashi et al., 2015). Furthermore, highly anxious individuals show higher detection thresholds for n-octanol than low anxious individuals (Rovee, Harris, & Yopp, 1973).

The current study investigates whether the physiological stress response (activation of the hypothalamic–pituitary–adrenal axis) and the stress-associated emotional response (anger, anxiety, arousal, and negative mood) differently affect olfactory perception. For instance, experienced anxiety and anger might result in a performance loss, whereas activation of the hypothalamic–pituitary–adrenal axis, which is not necessarily related to the experience of anxiety or anger, might improve performance at early processing stages (Shackman, Maxwell, McMenamin, Greischar, & Davidson, 2011).

Using a modified version of the Trier Social Stress Test (TSST; Kirschbaum, Pirke, & Hellhammer, 1993) and a multivariate regression approach, the current study investigates whether emotional and physiological (by means of saliva cortisol) stress responses affect odor identification ability and hedonic odor judgments.

Method

Participants

A total of 27 men participated in the experiment. An exclusively male sample was chosen in order to increase internal validity of the study. No participant indicated suffering from any neurological, psychiatric, endocrine or immunological disease, or using drugs, and all participants were nonsmokers. None of the participants had to be excluded due to increased state or trait anxiety (in order to avoid extreme stress reactions in the TSST; criterion: >47 points in the State Trait Anxiety Inventory; Laux, Glanzmann, Schaffner, & Spielberger, 1981). Due to technical problems ($n = 2$), contaminated saliva samples ($n = 4$), and discontinuing the TSST ($n = 2$), 8 participants were excluded. The age of the 19 participants in the final sample varied between 20 and 44 years ($M = 25.8$, $SD = 6.5$). All participants reached at least 21 points in the University of Pennsylvania Smell Identification Test (UPSIT), indicating the absence of general anosmia.

The study was conducted in accordance with the Declaration of Helsinki and was approved by the ethics committee of the Faculty of Mathematics and Natural Sciences of the Heinrich-Heine-University Düsseldorf. Participants gave their written informed consent and were compensated with €50. At the end of the experiment, participants received a standard debriefing about the TSST methods.

Stress Induction Procedure

The stress induction procedure was a modified version of the TSST (Kirschbaum et al., 1993; see figure 1) and started with a first (20 min) preparation period, in which participants had to prepare three controversial topics (death penalty, animal experiments, personal strengths, and weaknesses) for a free speech. Subsequently, the participants gave a 5-min free speech about one of the topics and then accomplished a 5-min mental arithmetic task (serially subtracting 17 from 2,043 as quickly and accurately as possible; if a mistake was made, the experimenter interrupted, "Incorrect. Start again."). Both tasks were performed in front of a reserved male and female experimenter. To further enhance the feeling of social evaluative threat, participants were videotaped and they were told that their facial expressions and body language would be monitored and evaluated. The odor evaluation was thereafter included. The participants were then instructed that they had to prepare a difficult neurophilosophical text for an oral exam 20 min later. This second preparation period ended 40 min after the end of the arithmetic task.

In the control session, participants cycled on a stationary bicycle (model: E433, Tunturi Fitness GmbH, Germany) instead of completing the preparation periods, the free speech, and the arithmetic task. Cycling was adjusted in order to obtain a heart rate similar to the TSST

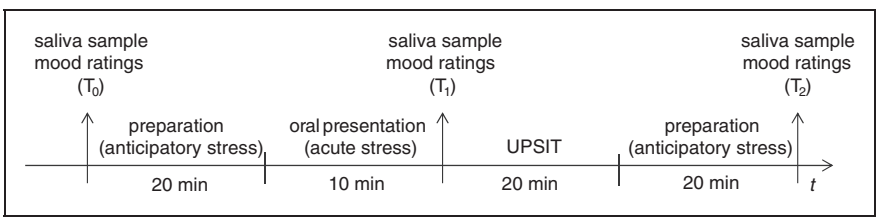

Figure 1. Sequence of the TSST session. In the control session, the three stress blocks were replaced by an ergometer training.

(heart rate TSST session: $M = 76.6$ bpm, $SD = 7.1$ bpm; heart rate control session: $M = 78.1$ bpm, $SD = 5.6$ bpm). Heart rate was assessed using a soft strap heart rate monitor (Polar S810, Polar Electro GmbH, Germany).

Materials

Assessment of odor identification ability and odor quality ratings. The ability to identify odors was determined using the UPSIT (Sensonics Inc., NJ), a 40-item scratch and sniff forced choice test with four options per item (Doty et al., 1984). The UPSIT odors' hedonics were rated regarding intensity, and separately for pleasantness and unpleasantness using computerized 9-point Likert-type scales (1 = *not perceivable* or *not pleasant* or *not unpleasant*; 9 = *very intense* or *very pleasant* or *very unpleasant*).

Emotion ratings. Participants indicated their mood on the dimensions emotional valence (−4 = *negative valence*, 4 = *positive valence*) and arousal (1 = *low arousal*, 9 = *high arousal*) using the language free, computerized Self-Assessment Manikin (Bradley & Lang, 1994). Furthermore, participants indicated their stress-related emotions (anger and anxiety) via computerized visual analog scales (length: 21 cm, range: 0 [*no anger* or *no anxiety*] – 100 [*very strong anger* or *very strong anxiety*]).

Saliva sampling and biochemical analysis of cortisol. Participants refrained from meals, alcoholic beverages, coffee, or tea for at least 2 h prior to the beginning of the session. To avoid arbitrary results due to the periodic secretion patterns of cortisol, saliva samples were collected from each participant at the same time of day in both sessions. Passive drooling devices (Salicaps, Tecan Trading AG, Switzerland) were used for sampling and samples were frozen at −20°C. Prior to analysis, samples were centrifuged at 3000 g for 10 min. Analysis was conducted by means of commercially available enzyme-linked immunosorbent assays with chemiluminescence detection (Tecan Trading AG, Switzerland). Intra-assay coefficients of variation were below 20% and inter-assay coefficients of variation were below 15%. Analytical sensitivity was 0.003 µg/dl.

Procedure

The study consisted of three sessions, carried out on three separate days: an initial session, followed by the TSST session and then the control session. All sessions took place in air-conditioned rooms (mean temperature: 22.4°C, $SD = 0.6$°C) between 9:00 am and 17:00 pm. To control for circadian variations within each participant, the TSST and control sessions were matched for the time of day that they took place.

In an initial session, participants were instructed regarding the perquisites for the saliva sampling, and inclusion criteria were checked. Participants were informed that they will take part in an assessment center like simulation, which most likely will be experienced as stressful. They were also asked to take part in a nonstressful control condition.

At the beginning of the modified TSST session, saliva samples were obtained and participants indicated their emotional status using the Self-Assessment Manikin and visual analog scales (baseline, T_0). Then, the first preparation period started, followed by the free speech and the mental arithmetic task. Afterwards, saliva samples were obtained and participants indicated their emotional status a second time (T_1). Participants then completed the UPSIT and assessed the odors' hedonics, odor by odor. The second preparation period after the UPSIT ratings was stopped 40 min after the T_1 saliva samples

had been obtained and participants were asked to indicate their emotional status and saliva samples were obtained a third time (T_2). During the control sessions, saliva samples, emotional status, the UPSIT score, and odors' hedonics were obtained at time points matching to the TSST session.

Statistical analysis

For all analyses, the odors' hedonic ratings were collapsed across all 40 odors. Cortisol levels were baseline corrected (subtraction of cortisol levels at T_0 from cortisol levels at T_1 and T_2), and cortisol levels at T_1 and T_2 were collapsed because they were highly correlated (TSST session: $r = .858$, control session: $r = .854$).

Effects of emotion on odor hedonics and odor identification ability were assessed using linear multivariate regressions. Regression criteria were the differences between the TSST session and control sessions of the UPSIT score, odor intensity, odor unpleasantness, and odor pleasantness. As a valid prediction of verbal stress reports through cortisol was only observed at time point T_2, the predictors were selected from T_2 only (see Table 1). Predictors were the difference values between TSST session and control session at time point T_2 of mood (emotional valence), arousal, anxiety, anger, and cortisol level (mean of T_1 and T_2). Predictors were successively entered in the regression model using a bidirectional elimination algorithm. Predictors were entered if they significantly altered the model ($p < .050$) and were excluded if they did not alter the model anymore ($p > .100$) when a new predictor was added. To correct for multiple tests, the significance level for the regression models was Bonferroni corrected to $\alpha = .050/4 = .013$.

To validate the TSST paradigm, the effects of the TSST procedure on emotion (mood, arousal, anxiety, anger) and cortisol level were analyzed using separate 3×2 repeated measurement ANOVAs with the factors time (baseline, T_1, T_2) and session (TSST, control). Bonferroni-corrected *t*-tests were used as post hoc tests ($\alpha = .050/3 = .017$).

Results

Validation of the TSST Paradigm

Participants indicated a more negative mood (emotional valence) after the oral presentation (T_1) and at the end of the TSST session (T_2) than in the control session (session within T_1:

Table 1. Mean Values and Standard Deviation (in Parentheses) of the Emotion Ratings in the TSST and Control Session.

		Valence	Arousal	Anxiety	Anger	Cortisol (μg/dl)
TSST	T_0	1.1 (1.6)	4.7 (1.7)	22.0 (24.4)	12.2 (16.7)	0.510 (0.315)
	T_1	−0.3 (1.6)	5.9 (1.5)	27.0 (22.3)	26.5 (30.1)	0.921 (0.426)
	T_2	−0.6 (1.5)	4.9 (1.9)	27.3 (25.7)	24.7 (27.2)	0.778 (0.336)
	Mean	0.1 (1.2)	5.2 (1.5)	25.4 (20.0)	21.1 (21.4)	0.736 (0.299)
Control	T_0	1.7 (1.9)	4.0 (1.9)	5.7 (7.8)	8.4 (12.2)	0.399 (0.175)
	T_1	1.9 (1.8)	4.5 (2.2)	6.4. (9.3)	7.9 (12.4)	0.399 (0.261)
	T_2	2.1 (1.3)	3.4 (1.7)	3.8 (5.8)	5.6 (8.3)	0.347 (0.216)
	Mean	1.9 (1.5)	4.0 (1.8)	5.3 (7.3)	7.3 (10.6)	0.382 (0.189)

Note. Mean values and standard deviation (in parentheses).
TSST = Trier Social Stress Test.

$F(1, 18) = 15.03$, $p = .001$; session within T_2: $F(1, 18) = 27.35$, $p < .001$; interaction session × time: $F(2, 36) = 16.72$, $p < .001$; see Table 1).

In general, participants felt more aroused in the TSST session than in the control session (main effect session: $F(1, 18) = 7.87$, $p = .012$) and more aroused at T_1 than at T_0 ($t(18) = 3.69$, $p < .001$) and T_2 ($t(18) = 4.02$, $p < .001$; main effect time: $F(1, 18) = 10.64$, $p < .001$; see Table 1).

Furthermore, participants felt slightly more anxious in the TSST session than in the control session (main effect session: $F(1, 17) = 24.55$, $p < .001$; see Table 1).

Participants experienced more anger after the oral presentation (T_1) and at the end of the TSST session (T_2) than in the control session (session within T_1: $F(1, 18) = 10.26$, $p = .005$; session within T_2: $F(1, 18) = 10.59$, $p = .004$; interaction session × time: $F(2, 36) = 4.51$, $p = .018$; see Table 1).

Cortisol levels were higher after the oral presentation (T_1) and at the end of the TSST session (T_2) than in the control session (session within T_1: $F(1, 18) = 34.41$, $p = .001$; session within T_2: $F(1, 18) = 24.99$, $p < .001$; interaction session × time: $F(2, 36) = 13.40$, $p < .001$; see Table 1).

Validation of the Relationship Between Cortisol and Emotion

Due to the intimate association between cortisol and negative emotions (but not positive emotions) during psychosocial stress, correlations between cortisol values and experienced emotions were tested one sided (for a review: Campbell & Ehlert, 2012). The higher the cortisol level of the participants (mean of T_1 and T_2), the more negative their mood was (emotional valence), and the higher their scores on arousal, anger, and anxiety at the end of the TSST session were (T_2; all rs > .300, all ps$_{\text{one-sided}} \leq .100$).

Relationship Between Odor Perception, Cortisol and Emotion

Variance in the UPSIT score differences (TSST minus control session) could be explained by a model with cortisol and anger differences as predictors (49.2% (R^2); $F(2, 18) = 7.75$, $p = .004$). The higher participants scored in the UPSIT in the TSST session (relative to the control session), the higher their cortisol level in the TSST session (relative to the control session) was ($\beta = .491$, $t(18) = 2.75$, $p = .014$), and the less angry they felt ($\beta = -.482$, $t(18) = 2.70$, $p = .016$). In the regression model, no case with a DFBeta > 0.5 was observed, indicating that the individual cases have no undue influence over the regression parameters. Individual correlations of the cortisol differences and anger differences with the UPSIT score differences resemble the results of the regression analyses (see Figures 2 and 3).

The variance in odor intensity differences could be explained by cortisol differences (mean of T_1 and T_2; TSST minus control session; 31.6 % (R^2); $F(1, 18) = 7.84$, $p = .012$). Participants who indicated higher intensities of the UPSIT odors in the TSST session (relative to the control session) had higher cortisol levels ($\beta = .562$, $t(18) = 2.80$, $p = .012$). In the regression model, no case with a DFBeta > 0.75 was observed, indicating that the cases have no undue influence over the regression parameters. Individual correlations of the cortisol differences with the intensity differences resemble the results of the regression (see Figure 4).

Models predicting pleasantness and unpleasantness of the UPSIT odors could not be established.

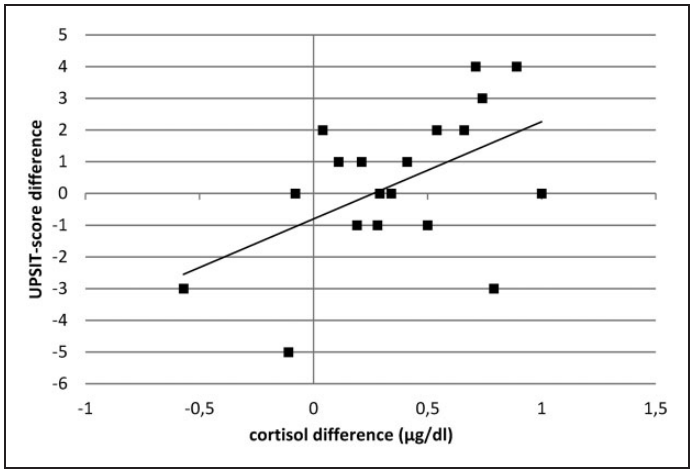

Figure 2. Relationship between cortisol differences (TSST minus control) and the respective UPSIT score difference. The higher in the UPSIT score in the TSST session (relative to the control session), the higher was the cortisol level in the TSST session (relative to the control session; $r = .510$).

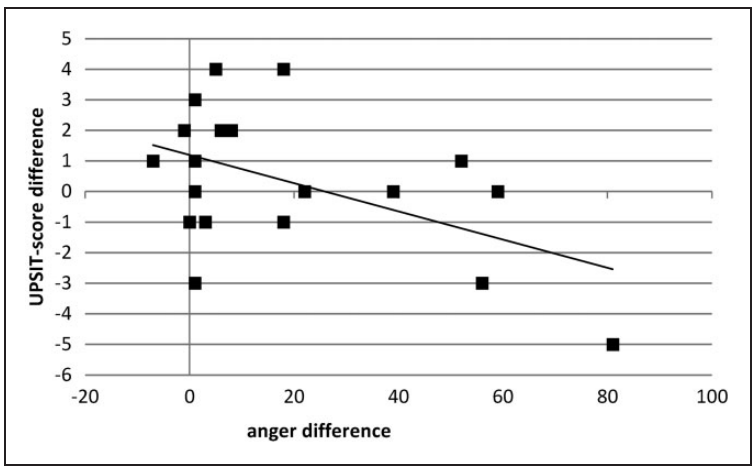

Figure 3. Relationship between anger differences (TSST minus control) and the respective UPSIT score differences. The higher in the UPSIT score in the TSST session (relative to the control session), the less anger was indicated in the TSST session (relative to the control session; $r = -.501$).

Discussion

The results show that increased cortisol levels are associated with a better odor identification performance and higher odor intensity ratings. This is in line with studies showing better odor detection and odor recognition abilities in women with increased cortisol levels (Fleming et al., 1997; Pause et al., 1996). In addition, anxious personality traits, which are associated with increased cortisol levels (Vreeburg et al., 2010), are associated with better odor discrimination abilities (Havlíček et al., 2012), better odor identification abilities (Larsson et al., 2000), and increased olfactory sensitivity (Pause et al., 1998). Furthermore,

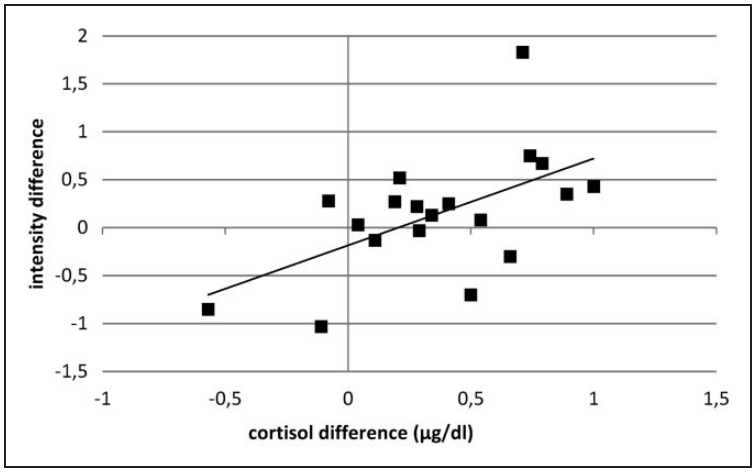

Figure 4. Relationship between cortisol differences (TSST minus control) and the respective intensity rating differences. The higher the odor intensity ratings in the TSST session (relative to the control session), the higher was the cortisol level in the TSST session (relative to the control session; $r = .562$).

previous studies showed that olfactory sensitivity for malodors is increased after a stress induction procedure (Pacharra et al., 2016). The enhanced olfactory abilities might be explained by a shift to a state of sensory hypervigilance and increased excitability of the amygdala during stress (Arnsten, 2009). Indeed, amplified functional connectivity between the primary olfactory cortex, amygdala, and hippocampus in anxious individuals can be shown for negative valenced odors (Krusemark & Li, 2012). The amygdala and hippocampus are part of the secondary olfactory cortex, processing odor intensity and odor identification (Anderson et al., 2003; Kjelvik et al., 2014; Lemogne et al., 2006; Rolls, 2010; Schoenbaum, Chiba, & Gallagher, 1999; Small, Schobel, Buxton, Witter, & Barnes, 2011; Vermetten, Bremner, Skelton, & Spiegel, 2007). This argument is in line with studies showing that individuals with a high emotional reactivity (neuroticism) associated with strong activation of the limbic system have enhanced olfactory abilities (Larsson et al., 2000; Pause et al., 1998).

In contrast to cortisol being associated with better odor identification abilities, anger is associated with poorer odor identification. A similar association between aggression and olfactory identification performance has been reported for veterans with posttraumatic stress disorder (Dileo et al., 2008). Further, this result is in line with a study showing that anger reduces cognitive performance and explicit memory, whereas cortisol increases cognitive performance and explicit memory (Kazén, Kuenne, Frankenberg, & Quirin, 2012). The negative association between anger and odor identification performance can be explained by anger interfering with attentional control: anger attenuates activity within attentional parietal cortices and impairs semantic decision making (Garfinkel et al., 2016), which might lead to poorer performance in odor identification tasks.

It seems contradictory that in the current study, anger is associated with poor odor identification and high cortisol levels are associated with good odor identification, even though anger and cortisol are positively correlated. However, despite the fact that both, cortisol and anger vary with stressor strength, both variables represent mechanisms independent from each other: the cortisol response is related to an increase of energy release within the central nervous system, whereas anger is related to cognitive appraisal

strategies (Lazarus & Folkman, 1984; Lupien et al., 2007). Therefore, the effects of cortisol and anger on olfactory performances might dissociate.

In the current study, the control session always took place after the TSST session. However, sequence effects are ruled out because group mean comparisons were avoided. Instead, differences between sessions in olfactory performance were correlated with differences between sessions in the emotional state and cortisol level. A sequence effect could cause an additive effect, but cannot affect the correlations.

As sex differences of the emotional response to the TSST (Kelly, Tyrka, Anderson, Price, & Carpenter, 2008) as well as of the TSST on cognitive performances (e.g., Smeets, Dziobek, & Wolf, 2009; Wolf, Schommer, Hellhammer, McEwen, & Kirschbaum, 2001) have been reported, a generalization of the present results to female participants should be deduced very cautiously.

Conclusion

To our knowledge, this is the first study investigating the association of emotional and physiological stress responses with individual olfactory perception. An increase of cortisol is associated with better odor identification performance, whereas increased anger is associated with worse odor identification performance. The divergent effects of the emotional and the physiological stress responses might explain the mixed results of previous studies.

Author's Note

Bettina M. Pause is now affiliated to Heinrich Heine University Düsseldorf, Düsseldorf, Germany.

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Declaration of Conflicting Interests

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References

Anderson, A. K., Christoff, K., Stappen, I., Panitz, D., Ghahremani, D. G., Glover, G., . . . Sobel, N. (2003). Dissociated neural representations of intensity and valence in human olfaction. *Nature Neuroscience*, *6*, 196–202.

Arnsten, A. F. (2009). Stress signalling pathways that impair prefrontal cortex structure and function. *Nature Reviews Neuroscience*, *10*, 410–422.

Bradley, M. M., & Lang, P. J. (1994). Measuring emotion: The self-assessment manikin and the semantic differential. *Journal of Behavior Therapy and Experimental Psychiatry*, *25*, 49–59.

Campbell, J., & Ehlert, U. (2012). Acute psychosocial stress: does the emotional stress response correspond with physiological responses? *Psychoneuroendocrinology*, *37*, 1111–1134.

Croy, I., Springborn, M., Lötsch, J., Johnston, A. N., & Hummel, T. (2011). Agreeable smellers and sensitive neurotics–correlations among personality traits and sensory thresholds. *PLoS One*, *6*, e18701.

Dileo, J. F., Brewer, W. J., Hopwood, M., Anderson, V., & Creamer, M. (2008). Olfactory identification dysfunction, aggression and impulsivity in war veterans with post-traumatic stress disorder. *Psychological Medicine*, *38*, 523–531.

Doty, R. L., Shaman, P., & Dann, M. (1984). Development of the University of Pennsylvania Smell Identification Test: a standardized microencapsulated test of olfactory function. *Physiology & Behavior*, *32*, 489–502.

Fleming, A. S., Steiner, M., & Corter, C. (1997). Cortisol, hedonics, and maternal responsiveness in human mothers. *Hormones and Behavior*, *32*, 85–98.

Garfinkel, S. N., Zorab, E., Navaratnam, N., Engels, M., Mallorquí-Bagué, N., Minati, L., … Critchley, H. D. (2016). Anger in brain and body: The neural and physiological perturbation of decision-making by emotion. *Social Cognitive and Affective Neuroscience*, *11*, 150–158.

Havlíček, J., Nováková, L., Vondrová, M., Kuběna, A. A., Valentová, J., & Roberts, S. C. (2012). Olfactory perception is positively linked to anxiety in young adults. *Perception*, *41*, 1246–1261.

Hellhammer, J., & Schubert, M. (2012). The physiological response to Trier Social Stress Test relates to subjective measures of stress during but not before or after the test. *Psychoneuroendocrinology*, *37*, 119–124.

Henkin, R. I., & Bartter, F. C. (1966). Studies on olfactory thresholds in normal man and in patients with adrenal cortical insufficiency: The role of adrenal cortical steroids and of serum sodium concentration. *Journal of Clinical Investigation*, *45*, 1631.

Herberner, E. S., Kagan, J., & Cohen, M. (1989). Shyness and olfactory threshold. *Personality and Individual Differences*, *10*, 1159–1163.

Kazén, M., Kuenne, T., Frankenberg, H., & Quirin, M. (2012). Inverse relation between cortisol and anger and their relation to performance and explicit memory. *Biological Psychology*, *91*, 28–35.

Kelly, M. M., Tyrka, A. R., Anderson, G. M., Price, L. H., & Carpenter, L. L. (2008). Sex differences in emotional and physiological responses to the Trier Social Stress Test. *Journal of Behavior Therapy and Experimental Psychiatry*, *39*, 87–98.

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.

Kjelvik, G., Saltvedt, I., White, L. R., Stenumgård, P., Sletvold, O., Engedal, K., … Håberg, A. K. (2014). The brain structural and cognitive basis of odor identification deficits in mild cognitive impairment and Alzheimer's disease. *BMC Neurology*, *14*, 1.

Krusemark, E. A., & Li, W. (2012). Enhanced olfactory sensory perception of threat in anxiety: An event-related fMRI study. *Chemosensory Perception*, *5*, 37–45.

La Buissonnière-Ariza, V., Lepore, F., Kojok, K. M., & Frasnelli, J. (2013). Increased odor detection speed in highly anxious healthy adults. *Chemical Senses*, *38*, 577–584.

Larsson, M., Finkel, D., & Pedersen, N. L. (2000). Odor identification influences of age, gender, cognition, and personality. *The Journals of Gerontology Series B: Psychological Sciences and Social Sciences*, *55*, 304–310.

Laux, L., Glanzmann, P., Schaffner, P., & Spielberger, C. D. (1981). *STAI:* Das State-Trait-Angstinventar. Theoretische Grundlagen und Handanweisung. Weinheim, Germany: Beltz.

Lazarus, R. S., & Folkman, S. (1984). *Stress, appraisal, and coping*. New York, NY: Springer publishing company.

Lemogne, C., Piolino, P., Friszer, S., Claret, A., Girault, N., Jouvent, R., … Fossati, P. (2006). Episodic autobiographical memory in depression: Specificity, autonoetic consciousness, and self-perspective. *Consciousness and Cognition*, *15*, 258–268.

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.

Lupis, S. B., Lerman, M., & Wolf, J. M. (2014). Anger responses to psychosocial stress predict heart rate and cortisol stress responses in men but not women. *Psychoneuroendocrinology*, *49*, 84–95.

Pacharra, M., Schäper, M., Kleinbeck, S., Blaszkewicz, M., Wolf, O. T., & van Thriel, C. (2016). Stress lowers the detection threshold for foul-smelling 2-mercaptoethanol. *Stress*, *19*, 18–27.

Patin, A. & Pause, B. M. (2015). Human amygdala activations during nasal chemoreception. *Neuropsychologia*, *78*, 171–194. DOI:10.1016/j.neuropsychologia.2015.10.009.

Pause, B. M., Ferstl, R., & Fehm-Wolfsdorf, G. (1998). Personality and olfactory sensitivity. *Journal of Research in Personality*, *32*, 510–518.

Pause, B. M., Sojka, B., Krauel, K., Fehm-Wolfsdorf, G., & Ferstl, R. (1996). Olfactory information processing during the course of the menstrual cycle. *Biological Psychology*, *44*, 31–54.

Rodrigues, S. M., LeDoux, J. E., & Sapolsky, R. M. (2009). The influence of stress hormones on fear circuitry. *Annual Review of Neuroscience*, *32*, 289–313.

Rolls, E. T. (2010). A computational theory of episodic memory formation in the hippocampus. *Behavioural Brain Research*, *215*, 180–196.

Rovee, C. K., Harris, S. L., & Yopp, R. (1973). Olfactory thresholds and level of anxiety. *Bulletin of the Psychonomic Society*, *2*, 76–78.

Schoenbaum, G., Chiba, A. A., & Gallagher, M. (1999). Neural encoding in orbitofrontal cortex and basolateral amygdala during olfactory discrimination learning. *Journal of Neuroscience*, *19*, 1876–1884.

Shackman, A. J., Maxwell, J. S., McMenamin, B. W., Greischar, L. L., & Davidson, R. J. (2011). Stress potentiates early and attenuates late stages of visual processing. *Journal of Neuroscience*, *31*, 1156–1161.

Small, S. A., Schobel, S. A., Buxton, R. B., Witter, M. P., & Barnes, C. A. (2011). A pathophysiological framework of hippocampal dysfunction in ageing and disease. *Nature Reviews Neuroscience*, *12*, 585–601.

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.

Stevenson, R. J. (2010). An initial evaluation of the functions of human olfaction. *Chemical Senses*, *35*, 3–20.

Takahashi, T., Itoh, H., Nishikawa, Y., Higuchi, Y., Nakamura, M., Sasabayashi, D., . . . Suzuki, M. (2015). Possible relation between olfaction and anxiety in healthy subjects. *Psychiatry and Clinical Neurosciences*, *69*, 431–438.

Vermetten, E., Bremner, J. D., Skelton, L., & Spiegel, D. (2007). PTSD and Vietnam veterans. *Science*, *315*, 184–187.

Vreeburg, S. A., Zitman, F. G., van Pelt, J., DeRijk, R. H., Verhagen, J. C., van Dyck, R., . . . Penninx, B. W. (2010). Salivary cortisol levels in persons with and without different anxiety disorders. *Psychosomatic Medicine*, *72*, 340–347.

Wolf, O. T., Schommer, N. C., Hellhammer, D. H., McEwen, B. S., & Kirschbaum, C. (2001). The relationship between stress induced cortisol levels and memory differs between men and women. *Psychoneuroendocrinology*, *26*, 711–720.