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Odours as context cues of emotional memories – The role of semantic relatedness

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A R T I C L E I N F O

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A B S T R A C T

Odours constitute effective context cues, facilitating memory retrieval. Identifying factors which modulate the effectiveness of olfactory context cues can advance the understanding of processes underlying this effect. We hypothesized that the interplay of subjective stress and semantic relatedness between the odour and the learning material would modulate the effectiveness of an olfactory context cue. We further explored the effect of the odorant Hedione, which is a ligand for a putative human pheromone receptor (VN1R1). To this end, 120 participants watched a video of a stressful episode in which visual objects were present, that were either manipulated in the video (central objects) or not (peripheral objects). Participants rated their subjective stress afterwards. After 24 h, recognition and spatial memory of the objects in the video were tested. Ambient during encoding and recall was an odour related to the episode, an unrelated odour, Hedione or no odour. As a result, we observed a narrowing of recognition memory with increased subjective stress elicited by the video - but only if a semantically related odour was ambient. Moreover, higher subjective stress predicted enhanced spatial memory in the no odour condition, but not in presence of a semantically related or unrelated odour. When exposed to Hedione, higher subjective stress predicted impaired recognition and spatial memory of peripheral objects. Our findings stress the importance of considering semantic relatedness between the olfactory context and the encoded episode when applying odours as context cues for emotional or stressful memories.

1. Introduction

Imagine you immerse yourself into an enthralling novel in a cosy library. When, after some time, you return to this place thinking back to what you last read there, you will likely retrieve details of the novel better than elsewhere. According to the encoding specificity principle, memory is enhanced when contextual information encoded along with the target information is available at retrieval (Tulving, 1983). This is referred to as *environmental context effect*, when contextual information is extrinsic – i.e., related to arbitrary aspects of the situation. The environmental context effect was demonstrated in numerous studies, which reported enhanced memory performance when the learning context is reinstated during retrieval (Smith & Vela, 2001). Contextual information can further be intrinsic, i.e., related to aspects of the learning material and thus a determinant of what is encoded (Hewitt, 1977). For context effects to arise, context cues being present during encoding and retrieval may suffice: If you find yourself exposed to exactly that smell of old books, wooden shelves, and warm lights that you sensed while reading, this may be enough to facilitate retrieval of the novel.

Ambient odours constitute effective context cues. One of the first experimental studies in this field was conducted by Cann and Ross (1989), using a recognition memory paradigm. In the encoding session, they presented slides of female faces to male college students, who rated their attractiveness while being exposed to a pleasant, an unpleasant or no odour. Recognition of the faces was tested 48 h later. Participants exposed to the same odour during encoding and recognition performed better than those with different or no odours. Evidence for olfactory context effects was amplified since then, showing that olfactory information can be integrated in a memory representation of a specific episode and act as trigger of this episode (Larsson et al., 2017). The olfactory context effect appears to be independent of the way olfactory information is presented, since odours were found to be effective context cues when presented unconsciously (Holland et al., 2005), ambiently in the background or directly via an olfactometer (Hackländer & Bermeitinger, 2018).

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A targeted use of olfactory context cues is promising – given that the retrieval of learned material is desired. However, olfactory context effects may also be detrimental. For instance, odours can evoke craving and relapse of maladaptive behaviour in addiction (Taylor et al., 2009) or trigger emotionally arousing intrusions related to a traumatic event in posttraumatic stress disorder (PTSD; Daniels & Vermetten, 2016; Vermetten & Bremner, 2003). Thus, when aiming for control over olfactory context effects or for prediction of their occurrence under varying conditions, knowledge about modulating factors is essential.

One such factor is the nature of the memory test. Extrinsic context manipulations can affect intentional retrieval –as measured by free and cued recall on the one hand, and as measured in recognition memory tests on the other hand (Smith & Vela, 2001). However, while being fairly robust for recall tests, environmental context effects could not always be demonstrated in recognition memory tests (Godden & Baddeley, 1980). Godden and Baddeley postulated that for context effects on recognition memory to arise, intrinsic context cues would be more effective than extrinsic manipulations, due to their relatedness to the learning material. In line with this idea, Smith and colleagues argued that an extrinsic context manipulation may leave recognition memory – especially familiarity – unaffected when it is not robust enough (Smith et al., 2018). The importance of a robust manipulation of extrinsic context could be shown specifically for olfactory context cues by Herz, 1997a. In this study, the more distinctive an odour was, the better it served as an extrinsic context cue. Distinctiveness was defined as a combination of novelty and contextual incongruence. The assumption underlying this finding is that a deeper processing due to more attention paid to the odour facilitates memory for the situation.

Another factor that modulates the potency of olfactory context cues is subjective stress during encoding. It was shown that an olfactory context cue facilitated retrieval of a word list more strongly when participants encoded the list in an anxious state (either induced by a laboratory stressor or naturally before an exam) as compared to a neutral state (Herz, 1997b). Further, it was previously demonstrated that an odour can be an effective context cue for remembering aspects of a stressful situation (Wiemers et al., 2014). In this study, recognition of central and peripheral objects that were present in a stressful situation was tested. When exposed to the same odour during encoding and retrieval of a stressful situation, participants showed better recognition of central objects than participants in a non-stressful control condition.

Such interactive effects of odours, subjective stress, and memory are commonly attributed to a close neuroanatomical interrelation between olfactory and emotional processing (Soudry et al., 2011). Olfactory information is directly related to brain areas, which are crucially involved in emotional processing. For instance, the amygdala is only two synapses away from the olfactory mucosa (Buck, 2000). Another part of the olfactory cortex receiving direct sensory input from the olfactory bulb is the entorhinal cortex (Doty, 2001), which closely interacts with the hippocampus. Both are critically involved in spatial memory formation (Moser et al., 2017), and were acknowledged for their differential roles in recognition memory with the hippocampus being crucial for detailed recollection of events and the entorhinal cortex for assessing stimulus familiarity (Yonelinas, 2002). Despite the close olfactory-emotional interrelations, affective congruence (or incongruence) between the odour and the learned material did not appear to modulate the potency of olfactory context cues in two experiments conducted by Hackländer and Bermeitinger (2017).

One aspect that has not been considered in research investigating olfactory context-dependent memory so far is semantic relatedness between the olfactory cue and the learned material. Semantic relatedness/cohesion is well-investigated with regard to emotional memory enhancement, with enhanced retrieval when semantic relatedness among the encoded objects is high (Buchanan et al., 2006; Maratos et al., 2000; Talmi et al., 2007; Talmi & Moscovitch, 2004). However, it remains open whether semantic relatedness between an olfactory context cue and the encoded objects would affect memory retrieval in a similarly enhancing way. This question is especially meaningful when considering research that is concerned with odour-evoked autobiographical memory. The central finding in this field is that odours have a unique potential to spontaneously trigger vivid and emotional autobiographical memories – the so-called Proust phenomenon (Chu & Downes, 2002; Hackländer et al., 2019; Larsson et al., 2014; Saive et al., 2014). Typically, in these cases, the olfactory cue is an inherent component of the retrieved autobiographical episode and therefore semantically related. The same holds true for odours triggering intrusions of a traumatic event, i.e., smell of blood or petrol (Daniels & Vermetten, 2016; Vermetten & Bremner, 2003). This could suggest that semantic relatedness between the olfactory context cue and the emotional learning material might promote reinstatement of the learning context during retrieval – and thus, facilitate the context effect. It would further be in line with the above-mentioned suggestion of Godden and Baddeley (1980) that an intrinsic context cue can facilitate context effects (especially on recognition memory), since it is related to the learning material and thus, a determinant of what is encoded.

Besides, we explored whether the odorant Hedione in interaction with subjective stress during encoding would modulate memory retrieval. Hedione is a synthetically created aroma with a floral smell. It was identified as a ligand of the VN1R1 receptor (Wallrabenstein et al., 2015). This receptor belongs to the vomeronasal-type 1 receptor family, which is expressed in the vomeronasal organ (VNO) of most mammals, being involved in pheromone detection (Boschat et al., 2002). Although the human VNO is not functional (Smith et al., 2014), five of the vomeronasal-type 1 receptors were detected on the human nasal mucosa (Rodriguez et al., 2000; Wallrabenstein et al., 2015). They have the same functional attributes and signalling mechanism as common olfactory receptors (Precone et al., 2020). The exact function of these receptors is still unclear, and it is subject to investigation, whether they might be involved in human chemosensory communication. An investigation using fMRI demonstrated that exposure to Hedione, as compared with a common floral odour (phenylethyl alcohol), elicited stronger limbic (amygdala, hippocampus) and hypothalamic activation, especially in female participants (Wallrabenstein et al., 2015). This led the authors to consider a potential effect on hormonal regulation mediated by Hedione binding to the VN1R1 receptor. Further, the odorant seems to exert behavioural effects, such as enhanced reciprocity (Berger et al., 2017) and reduced subjective vicarious stress when observing another person in a stressful situation (Pützer et al., 2020). Thus, as an exploratory question we investigated whether Hedione would affect memory retrieval in interaction with subjective stress during encoding.

In the present study, we investigated whether semantic relatedness of an olfactory context cue and the encoded episode modulates retrieval of this episode in interaction with subjective stress during encoding. Additionally, we explored potential effects of the odorant Hedione as an olfactory context cue. We hypothesized that with increased subjective stress perceived during encoding, an odour being semantically related to the encoded episode would constitute a better cue for spatial and recognition memory than an unrelated or no odour. In line with the findings of Wiemers et al. (2014), we expected this to apply especially to central aspects of the episode. We were particularly interested in recognition and spatial memory. As outlined above, both depend on the conjunction of entorhinal cortex and hippocampus, which receives direct olfactory input and may thus be sensitive to olfactory cueing of emotional memory. To this end, 120 participants watched a video of a participant in a modified version of the Trier Social Stress Test (TSST; Kirschbaum et al., 1993) and provided ratings of subjectively perceived stress after watching the video. After 24 h, they recalled objects presented during the TSST by means of an object recognition test and a spatial memory test. During encoding and retrieval, an odour that was semantically related to the video, an unrelated odour, Hedione, or no odour was dispersed in the experimental chamber.

2. Materials and methods

2.1. Participants

We recruited 120 healthy female participants, which were randomly assigned to the four odour conditions – 31 to the control group, 29 to the related odour group, 30 to the unrelated odour group and 30 to the Hedione group. This number was inferred from a power analysis for linear multiple regression (fixed model, R^2 deviation from zero) using G-power 3.1.9.2 (Faul et al., 2007). For our model including three predictors, 119 participants were required to detect a medium effect of $f^2 = 0.15$ with a power of 95% and an alpha error probability of 5%.

Our choice of a female sample was based on meta-analytic evidence for sex differences in human olfaction showing better olfactory abilities in women than men (Sorokowski et al., 2019), and the finding of sex-specific activation of the hypothalamus in response to Hedione, with a ten times stronger activation in women (Wallrabenstein et al., 2015). Sex differences further modulate the effects of stress effects on memory performance (Merz & Wolf, 2017). We checked for a similar composition of the odour conditions with respect to oral contraceptive intake, because women show different sensitivities to olfactory stimuli depending on reproductive state and oral contraceptive intake. For instance, women in their follicular phase were shown to be more sensitive to social odours, whereas a higher sensitivity to environmental odours was found in non-fertile phases of their cycle or during oral contraceptive intake (Lundström et al., 2006; Renfro & Hoffmann, 2013).

Participants were aged between 18 and 35 years ($M = 23.71$, $SD = 3.92$). Before being invited to our study, participants underwent a standardized screening via email or telephone. They were excluded from participation in case they reported a history of mental disorders, chronic or current illnesses, current psychological or medical treatment, the intake of psychoactive drugs, alcohol consumption exceeding the recommendations of the German Centre for Addiction Issues (Seitz & Bühringer, 2007), as well as prior participation in a TSST. Further exclusion criteria were factors relevant for a functional sense of smell including a running nose, allergies, asthma, smoking or self-reported deficits of the sense of smell. Additionally, each participant was instructed to refrain from utilizing fragrant cosmetics at the two test days.

2.2. Design

To test our hypothesis, we used a randomized mixed design, measuring recognition and spatial memory performance as dependent variables. As predictors, odour condition was manipulated by a random assignment of participants to one out of four experimental conditions (control/peppermint/cherry/Hedione). Further, object type was manipulated within subjects, using objects that were either interacted with in the encoding session (central objects), or not (peripheral objects). Subjective stress during encoding was the third predictor, which was not experimentally manipulated, but measured for each participant via a visual analogue scale. To control for potential confounds, we statistically checked for group differences with respect to age, subjective stress, state empathic concern and personal distress, alertness, perceived odour valence, and oral contraceptive intake.

2.3. Materials

2.3.1. Odours

As an odour that was semantically related to the learned material, peppermint aroma oil (Baldini, TAOASIS GmbH, Detmold, Germany) was chosen due to the utilization of mint tea in the Video of the TSST. We selected wild cherry aroma oil (v03 Trading, Willich, Germany) as a control odour that was semantically unrelated to learned material. This choice was based on a previous study (Sulmont-Rossé et al., 2002), in which familiarity and valence ratings of cherry and peppermint odour were highly similar. In the third group, Hedione (order # 947325, Firmenich, Meyrin, Switzerland, used as 5% solution in propylene glycol) was used. The odours were diffused in the experimental chamber (1.70x2x3 m^3) by application of 5 ml on an Aroma Stream (Aroma-Stream, TAOASIS GmbH, Detmold, Germany). The Aroma stream was switched on 15 min before each experimental session. In the odour-free control chamber, the aroma stream was on but unfilled.

2.3.2. Video of the TSST and stress measurement

All participants watched the same pre-recorded 10-minute video of a female participant undergoing a modified version of the TSST (Kirschbaum et al., 1993). The video was recorded from the perspective of the interviewed person by means of SMI Eye Tracking Glasses 2.0 (Senso-Motoric Instruments GmbH, Teltow, Germany).

In this version of the TSST, developed by Wiemers et al. (2013) and further adapted by Bierbrauer et al. (in revision), after a 2-min instruction, the participant was exposed to an 8-minute mock job interview. She was video-taped and observed by a panel, consisting of a male and a female member. The panel members were trained to behave in a neutral way, to refrain from any facial or non-verbal feedback, and to give standardized verbal instructions. The room was equipped with 24 objects of which 12 were defined as central objects and another 12 as peripheral objects. Central objects (see Table 1) were manipulated by the committee during the task and thus, bound to the stressful situation (Wiemers et al., 2013). Peripheral objects were similar types of objects (e.g., rubber, book, hole puncher, plastic cup) but not manipulated by the committee. Among the central objects were a box containing peppermint tea bags, a teapot, and a mug. One minute after the start of the interview, the male committee member used these three objects to infuse the tea bag in hot water. Further actions of the committee are listed in Table 1. To assess subjective stress in response to watching the video, participants completed a visual analogue scale reaching from 0 (not stressed) to 100 (extremely stressed). Further, we used the German version of the Positive Affect Negative Affect Scale (PANAS; Watson et al., 1988), which captures positive and negative affect. The Emotional Response Scale (Batson et al., 1997) served as a state measure of empathic concern and personal distress.

2.3.3. Recognition and spatial memory tests

Recognition of the central and peripheral objects was assessed using a picture recognition test. To this end, images of the 24 objects from the video and a second set of 48 distractor objects were presented. As distractor objects, 24 objects were chosen to be similar to one of the central and peripheral objects (e.g., rooibos tea box as distractor for peppermint tea box, blue paper tray as distractor for black paper tray) and 24 objects were dissimilar (e.g., watering can, scissors). Each object was presented for 2 s. Participants then rated for each object on a six-point scale whether they had seen it in the video or not (from 1 = very sure I have not seen this object to 6 = very sure I have seen this object). After a 1-second fixation cross, the next picture was presented.

Table 1
Actions of the panel members including the manipulation of central objects.

Panel member	Min after onset	Object	Action
Both	0	Stopwatch, pencils, clipboards	Started stopwatch, wrote down names and time
Male	1	Teabox, teapot, mug	Infused tea bag in hot water
Female	2	Handkerchief	Used to wipe nose
Male	4	Pencil sharpener	Used to sharpen pencil
Female	6	Ruler	Used to underline text
Male	8	Text marker	Used to mark text
Female	10	Stopwatch, stapler, paper tray	Stopped stopwatch, used stapler to staple papers, put papers in tray

A spatial memory test was adapted from Bierbrauer et al. (in revision), to capture spatial memory of the episode. In this computerized task, programmed with the Unreal Engine version 4.11 (Epic Games, Inc., North Carolina, US), a virtual copy of the room in which the video had been recorded was visible. It was centred around a 3D replica of the table that was placed in front of the panel during the TSST with the objects aligned on both sides of the table. Participants were instructed to reconstruct the arrangement of objects on the table that they had seen in the TSST video by dragging the objects to their respective position.

2.3.4. Control variables

Previous research has indicated that peppermint odour may enhance alertness (Moss et al., 2008; Raudenbush et al., 2009). Thus, we intended to ensure that a potential effect of the olfactory cues on memory performance would not be due to enhanced alertness in one of the conditions. To test for differences in alertness between the groups in the retrieval session, the alertness test of the Testbatterie zur Aufmerksamkeitsprüfung (TAP; version 2.2) was conducted (Zimmermann & Fimm, 2002). It consists of four blocks with 20 trials each in which participants respond as soon as a cross is presented on the screen. In two blocks, an acoustic signal precedes the cross. The blocks are presented in an ABBA order (A = no acoustic signal; B = acoustic signal). To quantify phasic alertness, denoting an elevated preparedness to respond to trials with a warning signal, an index is calculated by subtracting the median of reaction times in the B trials from the A trials and dividing this by the total reaction time in all trials. A value close to 0 signifies similar reaction times in A and B trials.

In the follow-up questionnaire, participants stated whether they were aware of the experimental condition that they had been assigned to. If they indicated that they had perceived an ambient odour, they were asked to specify which one it was and their associations with the odour. Further, they rated how pleasant it was on a nine-point valence subscale of the Self-Assessment Manikin (SAM; Bradley & Lang, 1994) reaching from unpleasant to pleasant. To exclude potential smelling deficits, we used the Screening 12 Test® (Burghart Messtechnik, Wedel, Germany). In this test, 12 Sniffin' Sticks containing familiar odorants were presented to the participants for 3 s each. By choosing one out of four possible answers, participants identify the odour. All participants gave 10 or more out of 12 correct answers.

2.4. Procedure

The study consisted of an encoding session and a retrieval session, scheduled 24 h later. In the encoding session, participants signed informed consent and were guided to the experimental chamber, which was scented with one of the odours or an odour-free control chamber. In this chamber, they watched the pre-recorded video of a female participant in the TSST. Participants were informed that the video contained a recording of the TSST with a real participant. They were instructed to watch the video attentively, so that they would be able to rate their feelings afterwards and their empathy with the person interviewed in the video. They were not informed about the memory tests in the second experimental session (incidental encoding). After the video, participants completed the visual analogue scale, the German version of the Positive Affect Negative Affect Scale (PANAS; Watson et al., 1988) and the Emotional Response Scale (Batson et al., 1997). At the end of the session, they were reminded of the retrieval session on the next day.

The retrieval session took place 24 h later in the same chamber with the same ambient odour. It started with the object recognition test, followed by the spatial memory test. After the tests were completed, participants completed the alertness test of TAP and the follow-up questionnaire. Eventually, the olfactory screening was conducted in a separate, odourless chamber. Participants were reimbursed with 10€.

2.5. Statistical analysis

To test for group differences with respect to age, subjective stress, state empathic concern and personal distress, alertness, and perceived odour valence, we applied one-factorial ANOVAs with the factor odour condition (control/peppermint/cherry/Hedione). Further, the non-parametric Kruskal-Wallis test was used to compare the number of participants taking oral contraceptives between the groups.

As an index for recognition memory performance, the discrimination index d', was calculated (Snodgrass & Corwin, 1988). It can be interpreted as a measure of participant's ability to discriminate between old and new objects in the recognition memory test. Higher values of d' indicate better discrimination performance. To quantify spatial memory performance, the coordinates of each object placed on the table by a participant were compared with the coordinates of its original position via the Euclidean distance. Lower values indicate lower deviation of the object positions reconstructed by the participant from their original position – and thus, better spatial memory performance.

For a statistical analysis of the modulation of recognition and spatial memory by odour group, object type and subjective stress, linear regression models were fitted to the data. These models predicted d' and the Euclidean distance based on the two categorical predictors odour condition (control/peppermint/cherry/Hedione) and object type (central/peripheral). Subjective stress during encoding as measured by the visual analogue scale was centred and inserted as a continuous predictor. When interactions between the predictor variables emerged, they were followed up by separate regressions for the respective odour condition including object type and stress as predictors. To quantify the model fit, R^2 is reported. To check whether performance in the recognition and spatial memory test were associated, the Pearson correlation coefficient was determined.

3. Results

3.1. Descriptive results

The experimental groups did not differ with respect to age, subjective stress, positive and negative affect, state empathic concern and personal distress, alertness, and perceived odour valence. In total, one third of the participants ($n = 40$) reported taking oral contraceptives, which was equally distributed between the experimental conditions. Characteristics of the sample are summarised in Table 2.

3.2. Recognition memory performance

The linear regression model for the discrimination index d', including object type, odour condition, and stress as predictors, accounts for 12% of variance in the observed data. This is indicated by the determination coefficient ($R^2 = 0.12$). As a reference, the intercept ($b = 0.29$, $SE = 0.10$, $t = 2.85$, $p < .01$) denotes d' estimated for participants with mean stress levels in the control group for peripheral objects.

Object type emerged as a significant predictor of d' ($b = 0.47$, $SE = 0.15$, $t = 3.20$, $p < .01$), meaning that a participant in the control group with mean subjective stress would show higher values of d' for central than peripheral objects. The effect of object type did not vary by odour condition, which can be inferred from the insignificant interactions between object type*peppermint ($b = -0.18$, $SE = 0.21$, $t = -0.85$, $p = .40$), object type*cherry ($b = -0.36$, $SE = 0.21$, $t = -1.71$, $p = .09$), and object type*Hedione ($b = -0.30$, $SE = 0.01$, $t = -1.38$, $p = .17$). Likewise, d' for peripheral objects and mean ratings of subjective stress was not predicted by group, neither for peppermint ($b = -0.03$, $SE = 0.15$, $t = -0.17$, $p = .87$), nor cherry ($b = -0.04$, $SE = 0.15$, $t = -0.30$, $p = .77$), nor Hedione ($b = 0.01$, $SE = 0.15$, $t = 0.08$, $p = .94$). To summarise, no differences between the odour conditions emerged, neither for central, nor for peripheral objects when assuming mean subjective stress during encoding. In line with previous findings, across all odour conditions, d'

Table 2
Sample characteristics displayed by experimental condition.

	Control	Peppermint	Cherry	Hedione	Group comparison		
	M (*SD*)	*M* (*SD*)	*M* (*SD*)	*M* (*SD*)	*F*	*p*	η^2
Age (years)	23.5 (3.9)	24.7 (3.9)	23.0 (3.6)	23.6 (4.3)	0.19	.67	0.0
Stress (VAS)	48.5 (27.0)	47.4 (25.0)	49.5 (27.3)	44.3 (22.9)	0.23	.61	0.0
PA (PANAS)	25.0(6.6)	25.3 (5.9)	23.1 (5.9)	25.5 (7.3)	0.03	.87	0.0
NA (PANAS)	20.8 (7.6)	19.3 (6.9)	24.6 (9.1)	21.4(9.1)	1.15	.29	0.0
PD (ERS)	32.1 (10.3)	32.5 (7.4)	35.8 (10.3)	31.8 (9.4)	0.11	.74	0.0
EC (ERS)	26.5 (7.1)	25.1 (8.5)	24.7 (8.5)	24.8 (6.9)	0.86	.36	0.0
Phasic alertness	0.00 (0.04)	−0.03 (0.07)	0.01 (0.09)	−0.02 (0.10)	0.15	.70	0.0
Odour valence	6.5 (2.2)	6.3 (2.5)	6.6 (2.4)	6.2 (2.2)	0.00	.97	0.0
	n (%)	*n* (%)	*n* (%)	*n* (%)	χ^2	*p*	ε^2
OC intake	10 (32.3)	10 (34.5)	11 (36.7)	9 (30.0)	0.33	.95	0.0

Note. Positive affect (PA) and negative affect (NA) by means of the Positive Affect Negative Affect Scale (PANAS; Watson et al., 1988). Personal distress (PD) and empathic concern (EC) by means of the Emotional Response Scale (ERS; Batson et al., 1997). Phasic alertness by means of the Testbatterie zur Aufmerksamkeitsprüfung (TAP; Zimmermann & Fimm, 2002). Odour valence rated on a 9-point pictorial scale (from 1 = unpleasant to 9 = pleasant) of the Self-Assessment Manikin (SAM; Bradley & Lang, 1994). OC = oral contraceptive.

was higher for central than peripheral objects.

When considering subjective stress as a predictor, notable differences between the odour conditions became evident. Higher subjective stress did neither predict changes in d' for peripheral objects in the control group ($b = 0.01$, $SE = 0.00$, $t = 1.67$, $p = .10$), nor in the cherry (unrelated odour) group ($b = -0.01$, $SE = 0.01$, $t = -1.04$, $p = .30$). Neither was an effect of stress on d' significantly modulated by object type in the control group ($b = -0.01$, $SE = 0.01$, $t = -1.23$, $p = .22$), nor in the cherry group ($b = 0.01$, $SE = 0.01$, $t = 0.64$, $p = .52$). Thus, in the control and cherry groups, subjective stress did not predict d'– neither for central, nor for peripheral objects.

In the peppermint (related odour) group, in contrast, a prediction of d' by subjective stress was revealed for peripheral objects ($b = -0.01$, $SE = 0.01$, $t = -2.41$, $p = .02$) and central objects ($b = 0.02$, $SE = 0.01$, $t = 2.39$, $p = .02$). In the Hedione group, subjective stress emerged as a significant predictor for peripheral objects ($b = -0.02$, $SE = 0.01$, $t = -2.88$, $p = .01$) and central objects ($b = 0.02$, $SE = 0.01$, $t = 2.06$, $p = .04$). To follow up these interactions, separate regressions for each of the two groups including stress and object type as predictors were conducted. In the peppermint group, object type ($b = 0.29$, $t(54) = 2.22$, $p = .03$), stress ($b = -0.01$, $t(54) = -2.02$, $p < .05$) and object type*stress ($b = 0.01$, $t(54) = 2.43$, $p = .02$) significantly predicted d', in a way that

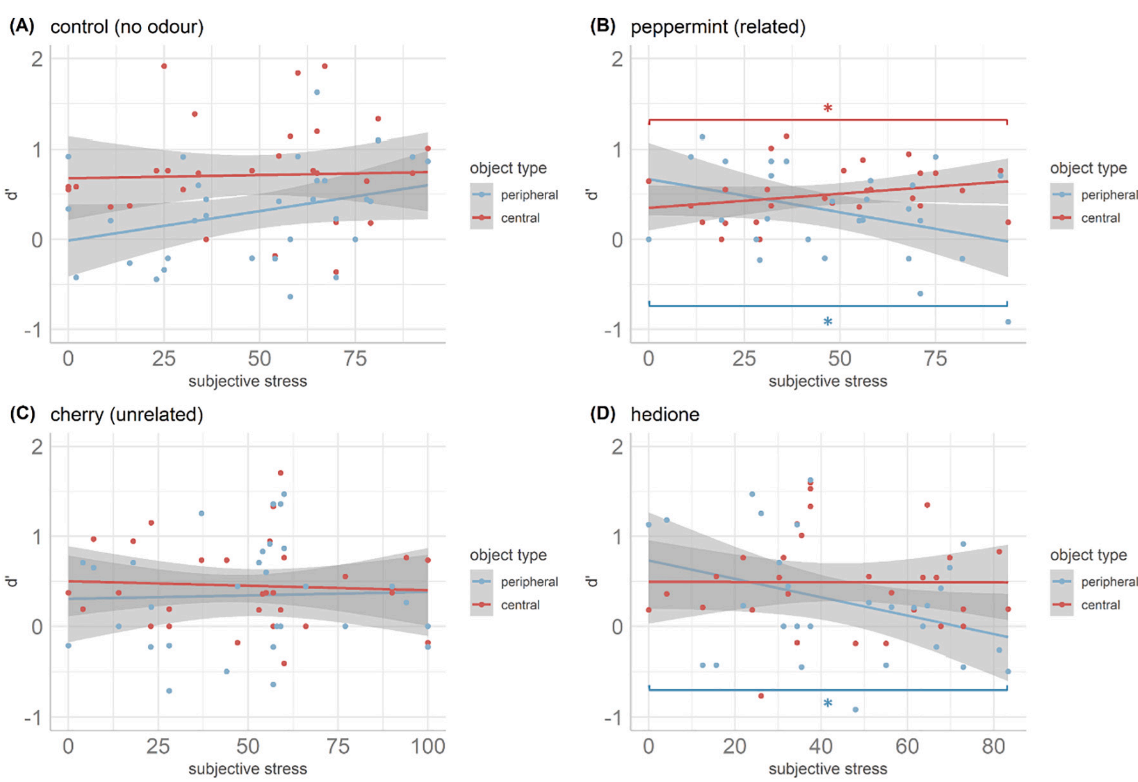

Fig. 1. Recognition memory performance (d') varying by subjective stress ratings for central and peripheral objects displayed by odour condition.
Overall, d' did not differ between the groups for participants with mean subjective stress during encoding. D′ for central objects (red) was higher than for peripheral objects (blue) across groups for participants with mean subjective stress. In the control group (A) and the cherry (unrelated odour) group (C), d' was not predicted by subjective stress. In the peppermint (related odour) group (B), higher subjective stress predicted higher d' for central objects and lower d' for peripheral objects. When exposed to Hedione (D), higher subjective stress predicted lower d' for peripheral objects.
Note. To facilitate readability of the figure, the uncentred values of subjective stress are displayed. * = p < .05. Shaded errors denote the 95% CI. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

stronger subjective stress predicted increased d' for central objects and decreased d' for peripheral objects. In the Hedione group, higher subjectve stress predicted lower d' for peripheral objects ($b = -0.01$, $t(56) = -2.11$, $p = .04$), but neither object type ($b = 0.18$, $t(56) = 1.07$, $p = .29$), nor stress*object type ($b = 0.01$, $t(56) = 1.48$, $p = .14$) emerged as significant predictors.

In sum, whereas no prediction of recognition memory performance by stress was found in the control and cherry (unrelated odour) group, higher subjective stress was predictive of higher recognition memory performance for central objects in the peppermint (related odour) group and lower performance for peripheral objects in the peppermint and Hedione groups. Results for d' are shown in Fig. 1.

3.3. Spatial memory performance

Overall, performance in the recognition and spatial memory task were significantly correlated ($r = -0.20$, $t(116) = -2.21$, $p = .03$) in a way that higher d' in the recognition memory test (= better recognition memory performance) was associated with a lower Euclidean distance in the spatial memory task (= better spatial memory performance).

The linear regression model for Euclidean distances, including object type, condition, and stress as predictors, accounts for 33% of variance in the observed data ($R^2 = 0.33$). As a reference, the intercept ($b = 334.62$, $SE = 14.87$, $t = 22.50$, $p < .001$) denotes Euclidean distances estimated for participants with mean stress levels in the control group for peripheral objects.

Object type emerged as a significant predictor of Euclidean distances ($b = -109.00$, $SE = 21.04$, $t = -5.18$, $p < .01$), meaning that a participant in the control group with mean subjective stress would show lower Euclidean distances for central than peripheral objects. The effect of object type did not vary by odour condition, which can be inferred from the insignificant interactions between object type*peppermint ($b = 13.33$, $SE = 30.53$, $t = -0.44$, $p = .66$), object type*cherry ($b = 9.21$, $SE = 30.03$, $t = 0.31$, $p = .76$), and object type*Hedione ($b = 14.65$, $SE = 30.35$, $t = 0.48$, $p = .63$). Likewise, Euclidean distance for peripheral objects was not predicted by group, neither for peppermint ($b = -18.42$, $SE = 21.59$, $t = -0.85$, $p = .39$), nor cherry ($b = 9.92$, $SE = 21.24$, $t = -0.47$, $p = .64$), nor Hedione ($b = -17.01$, $SE = 21.46$, $t = -0.79$, $p = .42$), assuming mean ratings of subjective stress. To summarise, no differences between the odour conditions emerged, neither for central, nor for peripheral objects when assuming mean subjective stress during encoding. Across all odour conditions, Euclidean distance was lower for central as compared to peripheral objects.

When considering subjective stress as a predictor, variations between the odour conditions became evident. Euclidean distances for peripheral objects were predicted by subjective stress in the control group ($b = -1.63$, $SE = 0.56$, $t = -2.92$, $p < .01$). This effect was not significantly modulated by object type ($b = 1.35$, $SE = 0.79$, $t = 1.71$, $p = .09$), indicating that it also applies to central objects. Accordingly, a follow-up regression separately for the control group, including object type and subjective stress as predictors, revealed a prediction of Euclidean distances by object type ($b = -109.00$, $SE = 16.50$ $t = -6.61$, $p < .001$), by stress ($b = -1.63$, $SE = 0.4381$, $t = -3.721$, $p < .001$), and by stress*object type ($b = 1.35$, $SE = 0.62$, $t = 2.18$, $p = .04$). Thus, higher subjective stress predicted higher spatial memory performance for both object types in the control group.

This result pattern was not resembled in the odour conditions, as indicated by significant interactions in the cherry (unrelated odour) group ($b = 1.84$, $SE = 0.7931$, $t = 2.32$, $p = .02$), in the Hedione group ($b = -3.25$, $SE = 0.87$, $t = 3.72$, $p < .001$), and a trend-significant interaction in the peppermint (related odour) group ($b = 1.53$, $SE = 0.85$ $t = -1.80$, $p = .07$). To follow up these interactions, separate regressions were conducted for each odour condition, including subjective stress and object type as predictors. In the peppermint group, object type emerged as a significant predictor ($b = -95.68$, $t(52) = -5.0$, $p < .001$), but neither stress ($b = -0.10$, $t(52) = -0.19$, $p = .85$), nor object type*stress ($b = 0.17$, $t(52) = 0.22$, $p = .83$). The same was revealed in the cherry group with object type ($b = -99.79$, $t(56) = -3.94$, $p < .001$) as a significant predictor, but neither stress ($b = 0.21$, $t(56) = 0.32$, $p = .75$), nor object type*stress ($b = -1.10$, $t(56) = -1.17$, $p = .25$). In the Hedione group, object type ($b = -94.35$, $t(54) = -3.86$, $p < .001$) and stress ($b = 1.62$, $t(54) = 2.17$, $p = .03$) emerged as significant predictors, but not object type*stress ($b = -0.69$, $t(54) = -0.65$, $p = .52$).

Our results show that higher subjective stress predicted increased spatial memory performance for both object types in the control group. In contrast, subjective stress was not predictive of spatial memory performance in the peppermint (related odour) and cherry (unrelated odour) groups – for neither of the two object types. In the Hedione group, as opposed to the control group, higher subjective stress predicted lower spatial memory for peripheral objects (Fig. 2).

4. Discussion

In the present study, we investigated interacting effects of semantic relatedness and subjective stress in olfactory context cueing. To this end, participants rated their subjective stress elicited by watching a video of a modified version of the TSST. They conducted a recognition memory and a spatial memory test 24 h later, related to objects presented during the TSST video. During encoding and retrieval, an odour that was semantically related to the video, an unrelated odour, or no odour was dispersed in the experimental chamber. An additional group of participants was exposed to Hedione, which is a ligand for a putative human pheromone receptor (VN1R1). Across groups, better spatial and recognition memory was found for central rather than peripheral objects. This is in line with research comparing recognition of objects presented during the TSST between participants exposed to the stressful situation or a non-stressful control condition (Herten et al., 2016; Herten et al., 2017; Wiemers et al., 2013; Wiemers et al., 2014; Wolf, 2019). Further, for both, recognition and spatial memory, no substantial differences emerged between the groups. When considering subjective stress experienced during encoding as a predictor, differential patterns were revealed between the groups. While subjective stress did not predict recognition memory performance in the control and unrelated odour group, higher subjective stress predicted better recognition of central and poorer recognition of peripheral objects in the related odour group. Regarding spatial memory performance, higher subjective stress was associated with improved spatial memory performance in the control group, whereas it did not predict spatial memory performance in the related and unrelated odour group. For participants exposed to Hedione, higher subjective stress was associated with lower recognition and spatial memory for peripheral objects.

Our results show that recognition memory is differentially modulated, depending on the odour condition and subjective stress elicited by the TSST video. If encoded and retrieved in the presence of a semantically related odour, we observed a narrowing of memory when subjective stress experienced during encoding is high. This became manifest in enhanced memory of central objects presented during the episode at the cost of peripheral detail. Thus, in accordance with the suggestion of Godden and Baddeley (1980), we demonstrated a modulation of recognition memory by a manipulation of intrinsic context. Our main finding could indicate that a semantically related odour enhances the focus on relevant aspects of an episode, when the processing capacity is limited due to the demanding character of the stressful episode (Christianson, 1992). It is of particular significance, when considering that a comparable narrowing of memory depending on perceived stress was not observed in presence of an unrelated odour or no odour, and that no overall group differences in memory performance were observed. This stresses the important functional role of a semantically related olfactory context during encoding and retrieval for an efficient adaptation to the situational demands. Odours becoming potent triggers of aspects that are bound to the emotional or stressful situation is a finding that translates well to olfactory cueing of autobiographical memories, which

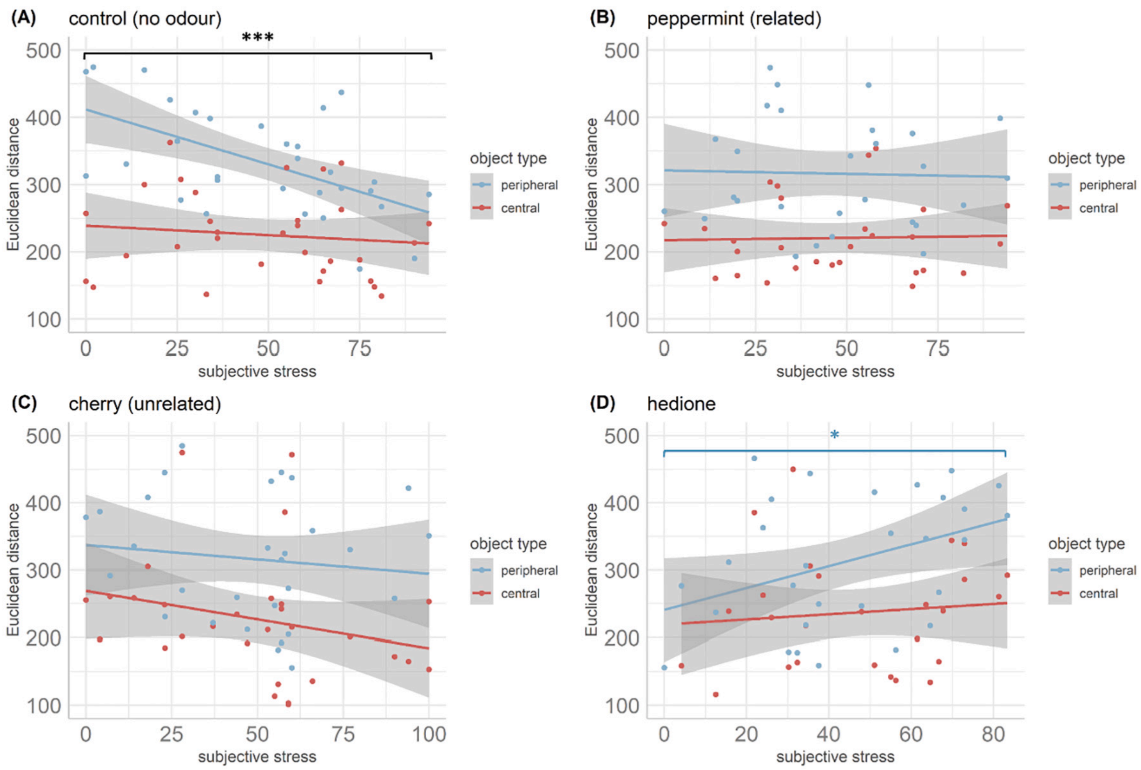

Fig. 2. Spatial memory performance (Euclidean distances) varying by subjective stress ratings for central and peripheral objects displayed by odour condition. Overall, mean Euclidean distances did not differ between the groups for participants with mean subjective stress during encoding. Euclidean distances for central objects (red) were lower than for peripheral objects (blue) across groups for participants with mean subjective stress. In the control group (A), higher subjective stress predicted decreased Euclidean distances for central and peripheral objects. In the peppermint (related odour; B) and cherry (unrelated odour; C) groups, no prediction by subjective stress was observed. When exposed to Hedione (D), higher subjective stress predicted higher Euclidean distances for peripheral objects. Note. Higher Euclidean distances denote lower spatial memory performance. To facilitate readability of the figure, the uncentred values of subjective stress are displayed. * = p < .05. *** = p < .001. Shaded errors denote the 95% CI. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

is essentially characterized by its emotional nature (Larsson et al., 2014).

A similar enhancement of recognition of central objects under stress was reported in the above-mentioned studies using a similar version of the object TSST (Herten et al., 2016; Herten et al., 2017; Wiemers et al., 2013; Wiemers et al., 2014; Wolf, 2019). It has been ascribed to restricted cue utilization in emotionally arousing situations (Easterbrook, 1959), and focused attention on emotionally arousing elements of an episode (Mather, 2007), resulting in enhanced memory binding of these central elements. Such a modulation of emotional memory by stress is mainly attributed to the joint effects of glucocorticoids (GC) and noradrenergic activation in brain areas relevant for emotion and memory, such as the amygdala, the hippocampus, and the PFC (Joëls et al., 2018; McEwen et al., 2015; Roozendaal et al., 2009). It was not resembled in associations with higher subjective stress (Wiemers et al., 2013), which is in accordance with our result that higher subjective stress in the odour-free control group was not associated with recognition memory performance, neither for central nor for peripheral objects. Although the stress measurement in our study was limited to subjective stress, we assume that besides increasing subjective stress, watching the video did not elicit robust activation of the HPA axis, as this would be in accordance with a study that we previously conducted (Pützer et al., 2020) using a similar video tape of the TSST. Further, subjective and physiological stress measures are not always positively correlated (Campbell & Ehlert, 2012). Therefore, mechanisms underlying the stress-related narrowing of recognition memory by a semantically related odour observed in the present study are likely different from the interplay of GCs and noradrenergic activation. To clarify these mechanisms, a starting point for future studies could be enhanced memory binding of the central objects to the olfactory context due to semantic relatedness (Talmi et al., 2007).

The second important finding revealed by our results is the blocking of a beneficial effect of subjective stress on spatial memory performance in the related and unrelated odour condition. In contrast, better spatial memory of central and peripheral objects of the episode was predicted by higher subjective stress in the odour-free control group. Thus, despite close connections of the olfactory system with brain regions processing spatial (Moser et al., 2017) and stress-related (McEwen et al., 2015) information, olfactory cues did not reinstate the spatial allocation of the objects any better under conditions of higher subjective stress. A potential explanation for this result relates to the difficulty for humans to infer spatial information from olfactory cues. Although it was shown that humans possess the ability to track scent trails (Porter et al., 2007), it remains unclear whether we use olfactory cues for spatial orientation or are able to follow an odour plume to its source (Stevenson, 2010). Based on our findings, we suggest that an odour, serving as retrieval cue for memory of a stressful episode, is less prone to convey spatial information of the stressful episode. Instead, it fosters the recognition of central aspects over peripheral detail of the situation. The blocking of spatial memory enhancement in the related and unrelated odour conditions when subjective stress is high needs to be addressed in future research. At this point, the result pattern observed in the recognition and spatial memory tasks diverge; though overall, performance in both tasks was significantly correlated (i.e., better recognition performance was associated with better performance in the spatial memory task). It will be necessary to confirm the robustness of this finding via replication of the study – especially since for the Hedione group, impairing effects of high subjective stress were similar for recognition and spatial memory.

When exposed to Hedione, higher subjective stress was associated with a lower spatial and recognition memory performance for peripheral objects. Performance for central objects was not associated with subjective stress ratings. To explain the negative association of subjective stress and recognition/spatial memory of peripheral objects when exposed to Hedione, a discussion of potential mechanisms is necessary. The odorant was found to exert strong activations of brain areas relevant for stress and emotional memory (hypothalamus, amygdala, hippocampus; Wallrabenstein et al., 2015). Via these pathways, it might exert detrimental effects on recognition of peripheral detail of a subjectively stressful episode. We can only speculate about the adaptive significance of this effect. Since Hedione affected reciprocity (Berger et al., 2017), and subjective vicarious stress (Pützer et al., 2020), its function might be to shift the focus to social aspects of a stressful episode. This could be at the cost of memory for peripheral detail of the episode. To test this, studies focusing on the social aspects of the TSST, for instance the social interaction between the participant and the panel, are warranted.

Another consideration worth discussing is fuelled by our findings. Our experimental procedure differs from the previous studies mentioned above in the sense that participants were not directly exposed to the TSST. Instead, they observed another person in this situation, which is a common paradigm in studies investigating empathic stress (Buchanan et al., 2012; Engert et al., 2014; Erkens et al., 2019). Our findings could therefore be viewed from the perspective of vicarious memory (Pillemer et al., 2015). This phenomenon has received little attention in previous research despite its clinical significance for conditions of vicarious trauma (Cohen & Collens, 2013). One study has shown that vicarious memories resembled direct personal memories with respect to emotionality, vividness or physiological reaction, despite being weaker and more often retrieved from an observer perspective (Pillemer et al., 2015). Odour-evoked vicarious memories have not been investigated in previous research. Thus, our study may be a first indicator that vicarious odour-evoked memories appear to be characterized by a similar enhancement for central objects of a stressful situations than direct memories of this situation (Wiemers et al., 2014). Peripheral detail might, however, be differentially affected in odour-evoked vicarious and direct memory of a stressful situation.

One limitation of the present study is that we cannot completely rule out that the peppermint odour per se instead of semantic relatedness is the driver of the effects. Although we confirmed that the odours did not differentially affect alertness, a better way to support our interpretation of the results would be to apply a cross-over design including multiple odours. As another limitation, we did not check for the occurrence of an extrinsic context effect, since participants in all groups were exposed the same odour during encoding and retrieval. Thus, studies including inconsistent odour conditions will be of particular importance. Moreover, the fact that subjective stress during encoding was measured instead of manipulated allows for correlative conclusions, only. Future studies should therefore experimentally manipulate stress by introducing a non-stressful control group, and characterize differential effects of physiological and psychological stress.

5. Conclusions

In conclusion, our results demonstrate that exposure to a semantically related odour during encoding and retrieval of a stressful episode narrows the memory of this episode depending on how stressful it was perceived. This manifests in a better recognition of central elements of the episode at the expense of peripheral detail when subjective stress is high. Such an effect was neither observed in the absence of an olfactory context cue nor with a semantically unrelated odour. With respect to spatial memory, beneficial effects of subjective stress in the odour-free control group were not resembled in the presence of any of the olfactory context cues. We therefore propose that an odour that is semantically related to a stressful episode is less prone to convey spatial information of the stressful episode. Rather, it fosters the recognition of central aspects over peripheral detail of the situation. This could signify a facilitated adaptation to increased cognitive demands of the stressful situation. Exploring the effect of Hedione as a context cue of a stressful episode, we observed detrimental effects on recognition and spatial memory of peripheral objects. Hedione might thus be functionally related to other aspects of a stressful situation (i.e., social interaction in the TSST), which comes at the cost of exact memory of the episode. Our findings are especially relevant when aiming for control over olfactory context effects or for prediction of their occurrence under varying conditions. Further, they attract notice to odour-evoked vicarious memory, which has received only little attention so far. With the help of future studies, it is necessary to characterize differential effects of the physiological and psychological processes of stress, to further specify the mechanisms and functional significance underlying our findings.

CRediT authorship contribution statement

Anika Pützer: Conceptualization, Methodology, Data analysis, Writing, Original draft preparation. **Oliver T. Wolf**: Conceptualization, Supervision, Reviewing, and Editing.

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Ethics statement

This study was designed and conducted in accordance with the Declaration of Helsinki and the recommendations of the German Psychological Society (DGPs). The local ethics committee of the Faculty of Psychology at Ruhr University Bochum approved all procedures. All individual participants, as well as the participant and panel members that were visible in the video of the TSST, provided informed consent.

Declaration of competing interest

None.

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