Pleasant and unpleasant odour-face combinations influence face and odour perception: an event-related potential study.

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Abstract

Odours alter evaluations of concurrent visual stimuli. However, neural mechanisms underlying the effects of congruent and incongruent odours on facial expression perception are not clear. Moreover, the influence of emotional faces on odour perception is not established. We investigated the effects of one pleasant and one unpleasant odour paired with happy and disgusted faces, on subjective ratings and ERP responses to faces.

Participants rated the pleasantness of happy and disgusted faces that appeared during 3 second pleasant or unpleasant odour pulses, or without odour. Odour pleasantness and intensity ratings were recorded in each trial. EEG was recorded continuously using a 128-channel system.

Happy and disgusted faces paired with pleasant and unpleasant odour were rated as more or less pleasant, respectively, compared to the same faces presented in the other odour conditions. Odours were rated as more pleasant when paired with happy faces, and unpleasant odour was rated more intense when paired with disgusted faces. Unpleasant odour paired with disgusted faces also decreased inspiration. Odour-face interactions were evident in the N200 and N400 components.

Our results reveal bi-directional effects of odours and faces, and suggest that odour-face interactions may be represented in ERP components. Pairings of unpleasant odour and disgusted faces resulted in stronger hedonic ratings, ERP changes, increased odour intensity ratings and respiratory adjustment. This finding likely represents heightened adaptive responses to multimodal unpleasant stimuli, prompting appropriate behaviour in the presence of danger.

Keywords: Odours, emotion, ERP, perception

1. Introduction

Previous research has shown that odours modulate face processing and recognition (Walla, 2008; Steinberg *et al.*, 2012), subjective ratings of faces (Bensafi *et al.*, 2002; Dematte *et al.*, 2007; Li *et al.*, 2007; McGlone, 2013; Seubert *et al.*, 2014; Cook *et al.*, 2015), and perceptions of facial expression (Leppanen & Hietanen, 2003; Pause *et al.*, 2004; Zhou & Chen, 2009; Seubert *et al.*, 2010; Leleu *et al.*, 2015a). The effects of odours on perception of facial expressions are often driven by affective congruency between odours and faces. For example, Leppanen and Hietanen (2003) observed that happy faces were recognised faster than disgusted faces in the presence of a pleasant odour. Moreover, Leleu *et al.* (2015a) observed that the minimum amount of visual information required to perceive an expression was lowered when the odour context was emotionally congruent. However, neural mechanisms underlying such effects are not established, and visual-olfactory combinations have rarely been addressed in the context of evaluative priming (Herring *et al.*, 2013). Further, the influence of emotional faces on odour perception has not been investigated.

The effect of odours on neural responses to facial expressions has been investigated using EEG, but the influence of congruency in such effects is less clear. One study showed that both neutral and unpleasant chemosensory signals modulated N170 amplitudes in responses to fearful facial expressions (Adolph *et al.*, 2013). Another observed that stress sweat odour enhanced the late LPP in responses to neutral and ambiguous faces (Rubin *et al.*, 2012). Leleu *et al.* (2015b) found that an aversive olfactory context modulated the P200 by amplifying the difference in response to neutral versus happy and disgusted facial expressions. Moreover, these previous experiments involved no explicit tasks regarding the facial expressions or olfactory stimuli. Therefore, whether the effects of congruent and incongruent odour-face interactions on EEG activity are comparable with subjective ratings of facial expressions has yet to be investigated. In doing so, we contribute to the understanding of the neural mechanisms underlying olfactory-visual influences on behaviour.

Effects of non-face visual stimuli on odour perception are well documented (Gottfried & Dolan, 2003; de Araujo *et al.*, 2005; Pollatos *et al.*, 2007; Dematte *et al.*, 2009; Seo *et al.*, 2010; Olofsson *et al.*, 2012; Hummel *et al.*, 2017), where studies have demonstrated that visual information

can affect odour pleasantness and intensity perception. Neutral odours were rated less pleasant and more intense following unpleasant picture presentation, and more pleasant after viewing positive images (Pollatos *et al.*, 2007). Another study showed that congruent symbol-odour pairs increased perceived pleasantness and intensity of a pleasant odour, and increased the unpleasantness of an unpleasant odour. A recent study by Hummel *et al.* (2017) showed that emotionally positive visual stimuli increased perceived pleasantness of pleasant odours. Such effects were reflected in the activation of brain structures relevant for reward processing. It is clear that visual information can affect odour perception and that olfactory-visual congruency plays a role, however, the effects of facial expressions on evaluations of odour pleasantness and intensity have not yet been investigated. Both face and odour processing almost always involve some aspect of emotion (Walla, 2008). Investigating bidirectional cross-modal effects of odours and emotional faces will provide further understanding of olfactory-visual integration in the context of emotion.

The aim of the present study was to investigate the effects of a pleasant and an unpleasant odour paired with happy and disgusted faces on evaluations of the facial expressions and odour pleasantness and intensity. Our study is the first of its kind to observe effects of olfactory-visual interactions on perceptions of both the visual and odour stimuli, using ERP analysis. Given the previous findings (Leppanen & Hietanen, 2003; Seo *et al.*, 2010; Leleu *et al.*, 2015a), we hypothesised that congruent odour-face pairings would shift face and odour pleasantness ratings further in the direction of the given odour-face valence, and increase intensity ratings of odours. Moreover, in line with previous results (Rubin *et al.*, 2012; Cook *et al.*, 2015; Leleu *et al.*, 2015b), we expected odour-face interactions to affect the P200 and LPP components of the ERP during face processing. The present study contributes to the more general concept of evaluative priming (Herring *et al.*, 2013). Using odours and faces as both primes and targets, we aimed to extend the current understanding of the mechanisms underlying evaluative priming by examining the phenomenon in a cross-modal sense, using ERP analysis.

2. Methods and Materials

2.1 Participants

A total of 25 (11 male) healthy participants aged 18−30 years (mean ± standard deviation: 23.28 ± 3.58) took part in the experiment after giving written informed consent in accordance with the Declaration of Helsinki. The study was approved by the Research Ethics Committee at the University of Liverpool. Two participants withdrew from the study, and data from a further three participants were subsequently excluded from the EEG analysis due to excessive amounts of artifacts. Hence, behavioural data from 23 (10 male) participants, and EEG data from 20 (9 male) participants were used in the analysis. All participants were initially screened in a separate session using the Sniffin'Sticks (Hummel *et al.*, 1997) test battery to ensure adequate odour identification ability. Participants were asked not to smoke, drink coffee or chew gum for two hours prior to the experiment, and were asked to minimise their use of fragranced products on the day. Participants were reimbursed for their time and travel expenses.

2.2 Visual and olfactory stimuli

Face-images of 30 actors (15 male) showing happy and disgusted expressions were used in the experiment, for a total of 60 faces. These were selected from the NimStim Set of Facial Expressions (Tottenham *et al.*, 2009). All face images were frontal views, in colour, with a consistent light background and similar dimensions.

Odours were administered through two tubes approximately 2 centimetres away from the nostrils, using a custom-built, continuous airflow, computer-controlled olfactometer with 8 channels (Dancer Design Ltd., UK). Odour pulses were embedded within a constant flow of clean air, in order to avoid effects of a sudden increase in airflow associated with presentation of an odour (Huart *et al.*, 2012). Airflow was kept constant at 2.5 l/min.

There were three odour conditions in the experiment; pleasant, unpleasant and a neutral, 'clean air' control. Methylmercaptan (1% dilution in Propylene Glycol), a rotten cabbage-like odour,

was selected for the unpleasant condition. Jasmine odour (no dilution) was selected for the pleasant condition. These dilutions were matched on perceived intensity based on data from previous experiments (Cook *et al.*, 2015; Cook *et al.*, in preparation). Odours were supplied by Symrise Ltd. (Netherlands). Propylene Glycol (1,2-Propanediol 99%, Sigma-Aldrich Ltd., UK) was used for dilution, the clean air control and constant flow.

Both presentation of the experimental task stimuli and triggering of the odour valves were achieved using the Cogent 2000 v. 1.32 program (Wellcome Department of Imaging Neuroscience, United Kingdom) running in Matlab v. R2011a (The MathWorks, Inc., USA). In between experimental blocks and sessions, a Blueair 203 air purifier (Blueair Ltd., Sweden) was used to minimise any residual odour that may have carried into the next experimental block or session.

2.3 Recordings

EEG was recorded continuously using a 128-channel Geodesics EGI System (Electrical Geodesics, Inc., Eugene, Oregon, USA) with a sponge-based Geodesic Sensor Net. The sensor net was aligned with respect to three anatomical landmarks; two pre-auricular points and the nasion. Electrode-to-skin impedances were kept below 50 kΩ and at equal levels across all electrodes. The recording band-pass filter was 0.01−1000 Hz, and the sampling rate was 1000 Hz. Electrode Cz was used as the reference.

Participants' respiration and pulse rate were recorded continuously throughout the experiment with a piezo-electric respiratory belt transducer worn around the chest at the level of the epigastrium, and a finger pulse oximeter transducer worn on the index finger of the left hand (ADInstruments Ltd., Oxford, UK). Signals were transduced and extracted using LabChart 7 (ADInstruments Ltd., Oxford, UK).

2.4 Procedure

After application of the EEG cap, participants were seated in a dimly lit, sound attenuated room facing a 19 inch LCD monitor (60 Hz refresh rate) placed approximately 0.7 m in front of them.

First, the respiratory and pulse monitoring equipment was fitted onto participants and the signals were checked. Following this, the olfactometer head piece was fitted, and participants were given instructions. The experimental session lasted around 1.5 hours in total, including baseline odour ratings and the experimental task. Ratings of odour pleasantness, intensity, and familiarity were recorded before and after the task. Each odour was administered individually, in a four-second pulse manually triggered to coincide with the onset of inspiration. After each odour pulse, on-screen visual analogue scales prompted participants to rate the pleasantness (from 0 – very unpleasant to 100 – very pleasant), intensity (0 – no odour to 100 – very intense odour) and familiarity (0 – not familiar at all to 100 – extremely familiar) of the odour.

The experimental task was split into four blocks of 45 trials (180 trials in total). Trials were pseudo-randomly ordered such that each of the 30 actors appeared 6 times: showing a happy and a disgusted expression under each of the three odour conditions. A given actor never appeared showing the same expression more than once in each block. Odour presentation was also pseudo-random, such that all three odours were presented across all four blocks, but no two consecutive trials used the same odour. Figure 1 shows a flowchart of the trial procedure. Each trial began with a resting interval during which participants viewed a white cross on a black background. The duration of this interval was dependent upon the triggering of the odour pulse; the experimenter observed participants' respiratory waveforms, and manually triggered the odour pulses at the very onset of inspiration. Odour pulses were 3000 ms in duration. At a random time point between 1000–2000 ms of the odour pulse, a happy (half of the trials) or disgusted face was displayed on-screen for 300 ms. Following the odour pulse, a 3000 ms resting interval with a black screen preceded a rating scale prompting participants to rate the pleasantness of the facial expression (from 0 – very unpleasant to 100 – very pleasant). Once they had responded, a second screen with two scales prompted participants to rate the pleasantness (from 0 – very unpleasant to 100 – very pleasant) and the intensity (0 – no odour to 100 – very intense odour) of the odour administered in that trial. After their response, the next trial began.

2.5 Behavioural analysis

Ratings of odour pleasantness, intensity and familiarity taken before and after the experimental task were collapsed and analysed using paired t-tests. Data from the experimental task were analysed using 2 × 3 repeated measures ANOVAs, observing differences in face pleasantness ratings, and odour pleasantness and intensity ratings with odour condition (pleasant, unpleasant, neutral) and face type (happy or disgusted) as the independent variables. Significant main effects were investigated using pairwise comparisons; significant interactions were followed up with post-hoc t-tests and one-way ANOVAs, using Bonferroni correction for multiple comparisons. P values in all ANOVA effects were adjusted using the Greenhouse-Geisser □ □method. All behavioural data was analysed using SPSS v. 22 software package (IBM Inc., USA).

2.6 ERP analysis

EEG recordings were pre-processed using BESA v. 6.0 (MEGIS GmbH, Germany). Data were first referenced to a common average using the common averaging method (Lehmann, 1987). The oculographic and, when necessary, electrocardiographic artifacts were removed by principal component analysis (Berg & Scherg, 1994). Data were visually inspected for the presence of any movement or muscle artifacts, and trials contaminated with artifacts were excluded. The mean number of accepted trials across all subjects and all conditions was 161 (± 17.02). Participants were excluded from the analysis if the number of trials accepted was less than 127 (2 standard deviations from the mean). The mean numbers of accepted trials for each condition were as follows: Clean air + happy face: 27, Clean air + disgusted face: 27, Jasmine + happy face: 27, Jasmine + disgusted face: 26, Methylmercaptan + happy face: 26, Methylmercaptan + disgusted face: 26.

Data were band-pass filtered from 2−35 Hz and down-sampled to a rate of 256 Hz, and exported from BESA into the SPM12 software package (Statistical Parametric Mapping, UCL, England; http://www.fil.ion.ucl.ac.uk/spm/software/spm12/). Event-related potentials (ERPs) in response to faces were computed separately for each odour and face condition by averaging respective epochs in the intervals ranging from 300 ms before photo onset to 1000 ms after photo onset. The baseline period ranged from -300 ms to 0 ms relative to the onset of the visual stimulus.

We applied an omnibus analysis of the effects of odours on ERPs involving all time points from 0 ms to 1000 ms and all scalp sites, allowing us to explore the effects of odours on ERPs without applying a priori knowledge of peak latencies. The SPM12 toolbox combines advanced statistical models with robust control for Type I error (Poline *et al.*, 1997; Kiebel & Friston, 2004). In contrast to alternative approaches, such as permutation analysis of clusters of ERPs over the epoch time (Maris & Oostenveld, 2007), SPM applies the theory of random fields to volumes of space-time data. This allows for calculation of the degrees of freedom in the evaluation of statistical test results based on the spatial and temporal complexity of data (Worsley, 2003).

The statistical analysis was performed in two steps. In the initial exploratory step, EEG data were converted into three-dimensional scalp-time images using SPM. The electrodes were mapped onto a standardised scalp grid sized 32 × 32 pixels (pixel size 4.25 × 5.3 mm^2), representing the field potential planes stacked over the time axis. Images were smoothed with a Gaussian kernel of 9 × 9 × 20 mm^2 .ms (full width at half maximum). Data from over the whole epoch (385 time samples) and all standardised scalp points were screened for statistically significant effects of odours and face-valence using a flexible factorial ANOVA for repeated measures. The flexible factorial model in SPM allows for the inclusion of the subject factor as an independent variable. We applied an uncorrected threshold of $P < 0.001$, and a cluster size of 20 contiguous space-time voxels to detect clusters affected by odours and face-valence. The data were masked such that only clusters occurring later than 100 ms following face onset were analysed. The amplitude data from these clusters were subsequently analysed using further repeated measures ANOVAs in SPSS v. 22 (IBM Inc., USA). The statistical threshold of this confirmatory analysis was $P < 0.05$.

2.7 Analysis of respiratory movements

Respiratory movement signals were low-pass filtered, and averaged separately for each of the six conditions in the epoch of interest, then analysed statistically using a 2 × 3 repeated measures ANOVA (2 face types, 3 odours). The 7 s analysis epoch ranged from odour onset (t = 0 s) to 7 s after odour onset. Therefore, the interval 1–3 s coincided with the ERP analysis epoch. To control for Type I error due to the large number of ANOVAs, given that one ANOVA was computed on each time

sample, a permutation analysis with 500 permutations was used to correct the P values (Maris & Oostenveld, 2007). Data from the interval showing a significant effect of condition on respiratory movements were analysed using confirmatory repeated measures ANOVA in SPSS. We used a 2 × 3 ANCOVA for repeated measures in BMDP 2V program (Biomedical Data Package, Cork, Ireland) to analyse whether changes in respiratory movement patterns contributed to the effects of experimental condition observed in ERP clusters.

3. Results

3.1 Baseline odour ratings

Mean ratings of odour pleasantness, intensity and familiarity taken before and after the experimental task were collated and are shown in Table 1. A paired t-test confirmed that jasmine was rated as significantly more pleasant than methylmercaptan ($t(22) = 21.55$, $P < 0.001$). A further paired t-test showed there was no significant difference between intensity ratings of jasmine and methylmercaptan ($t(22) = -1.58$, $P = 0.13$). A third t-test confirmed that there was no significant difference in familiarity ratings of jasmine and methylmercaptan $t(22) = 1.14$, $P = 0.27$).

Table 1: Mean (± standard deviation) ratings of odour pleasantness, intensity and familiarity that were taken before and after the experimental task and concatenated.

	Pleasantness	Intensity	Familiarity
Jasmine	79.28 (± 6.97)	71.95 (± 7.67)	71.67 (± 15.48)
Methylmercaptan	15.7 (± 11.94)	76.34 (± 13.08)	66.59 (± 19.23)

3.2 Face and odour ratings during experimental task

3.2.1 Face ratings under each odour condition

Figure 2A shows the mean ratings of the happy and disgusted faces under each odour and face condition. A repeated-measures ANOVA revealed a significant main effect of odour on ratings of faces overall ($F(2, 44) = 30.4$, $\eta_p^2 = 0.58$, $P < 0.001$). Pairwise comparisons indicated that all faces presented in the methylmercaptan odour condition were rated as less pleasant (44.68 ± 26.49) in

comparison to faces presented in both the clean air (48 ± 25.47) and jasmine (49.2 ± 26.43) conditions ($P < 0.001$), and faces in the jasmine condition were rated as significantly more pleasant than those in the clean air condition ($P = 0.01$). There was a significant main effect of face type on ratings of faces ($F(1, 22) = 886.37$, $\eta_p^2 = 0.98$, $P < 0.001$), confirming that happy faces were rated as significantly more pleasant (72.55 ± 1.1) than disgusted faces (22.04 ± 1.09). There was also a significant interaction between odours and face type affecting face ratings ($F(2, 44) = 4.28$ $\eta_p^2 = 0.16$, $P = 0.02$). Post-hoc one-way ANOVAs were employed to investigate this interaction, by observing the effects of odours on face ratings of happy and disgusted faces separately. For happy faces, a one-way ANOVA revealed a significant effect of odour ($F(2, 44) = 18.83$, $\eta_p^2 = 0.46$, $P < 0.001$). Pairwise comparisons indicated that happy faces presented in the jasmine odour condition were rated as more pleasant (74.78 ± 5.77) in comparison to the same faces presented in both the clean air (72.64 ± 5.31, $P = 0.002$) and methylmercaptan (70.24 ± 5.89) odour conditions ($P < 0.001$), and happy faces in the methylmercaptan condition were rated as significantly less pleasant than those in the clean air condition ($P = 0.001$). For disgusted faces, a one-way ANOVA revealed a significant effect of odour ($F(2, 44) = 28.29$, $\eta_p^2 = 0.56$, $P < 0.001$). Pairwise comparisons indicated that disgusted faces in the methylmercaptan condition were rated significantly less pleasant (19.12 ± 5.85) than the same faces in both the clean air (23.38 ± 5.52) and jasmine (23.62 ± 5.26) odour conditions ($P < 0.001$). There was no significant difference in ratings of disgusted faces between the jasmine and clean air conditions ($P > 0.05$).

3.2.2 Odour pleasantness ratings

Figure 2B shows the mean odour pleasantness ratings from experimental trials for each odour and face condition. A repeated-measures ANOVA revealed a significant main effect of odour type on odour pleasantness ratings ($F(2, 44) = 323.76$, $\eta_p^2 = 0.94$, $P < 0.001$). Pairwise comparisons confirmed that the jasmine odour was rated as more pleasant (74.56 ± 7.75) than both clean air (51.87 ± 3.19) and methylmercaptan (20.55 ± 7.45, $P < 0.001$); and that methylmercaptan was also rated as

significantly less pleasant than clean air ($P < 0.001$). There was also a significant main effect of face type on odour pleasantness ratings ($F(1, 22) = 12.29$, $\eta_p^2 = 0.36$, $P = 0.003$), indicating that all odours were rated as more pleasant (49.67 ± 23.15) when presented with happy faces in comparison to when presented with disgusted faces (48.31 ± 23.27). The interaction between odours and face type affecting odour pleasantness ratings did not reach statistical significance ($F(2, 44) = 2.34$ $\eta_p^2 = 0.1$, $P = 0.11$).

3.2.3 Odour intensity ratings

Figure 2C shows the mean odour intensity ratings from experimental trials for each odour and face condition. A repeated-measures ANOVA revealed a significant main effect of odour type on intensity ratings ($F(2, 44) = 219.26$ $\eta_p^2 = 0.91$, $P < 0.001$). Pairwise comparisons confirmed that methylmercaptan was rated as more intense (58.25 ± 15.45) than both jasmine (49.94 ± 13.67, $P = 0.003$) and clean air (2.63 ± 2.49, $P < 0.001$); and that jasmine was also rated as significantly more intense than clean air ($P < 0.001$). There was no significant main effect of face type ($P > 0.05$); however, there was a significant interaction between odour and face type affecting odour intensity ratings during experimental trials ($F(2, 44) = 6.89$, $\eta_p^2 = 0.24$, $P = 0.003$). Post-hoc t-tests confirmed that this effect was driven by intensity ratings of methylmercaptan: when presented in combination with disgusted faces, methylmercaptan was rated as significantly more intense (60.11 ± 16.38) than the same odour presented with happy faces (56.39 ± 14.96, $t(22) = -3.34$, $P = 0.003$). There were no significant effects of face type on intensity ratings of clean air or jasmine ($P > 0.05$).

3.3 ERP components

Figure 3 illustrates the event-related potentials in response to faces across all trials and all conditions in the form of a butterfly plot and topographic maps of selected potential components. The topography of the first component showed bilateral positivity over the occipital electrodes and negativity over frontal electrodes, peaking around 95 ms (see Figure 3B). This is consistent with characteristics of the P1 component, which is related to early processing of visual stimuli (Hopf *et al.*,

2002). The second component, peaking around 145 ms (Figure 3C), showed negative potential over parietal and temporal electrodes, consistent with characteristics of the N170 face-processing component (Bentin *et al.*, 1996). The next component peaked around 200 ms (Figure 3D), showing positive potential in parietal-occipital, and strong negative potential in central-frontal electrodes, consistent with typical characteristics of the N200 component (Folstein & Van Petten, 2008). The fourth component peaked at 395 ms (Figure 3E) and showed weak positivity in occipital electrodes. The final component was a long-latency component peaking around 500 ms (Figure 3F), showing a strong negative potential over occipital and parietal electrodes, and a positive potential over central midline electrodes. These components are consistent with characteristics of the N400 component, implicated in the processing of meaningful stimuli, including faces (Kutas & Federmeier, 2011), and the late positive potential (LPP), which is sensitive to the emotional content of pictures, words and faces (Cacioppo *et al.*, 1993; Cuthbert *et al.*, 2000; Hajcak *et al.*, 2006; Hajcak *et al.*, 2007).

3.4 Effects of odours and face-valence on ERPs

SPM12 was used to compute a 2 × 3 (face valence × odour) repeated measures ANOVA on smoothed scalp-time images of data from 0−1000 ms relative to the onset of the faces. The ANOVA revealed scalp-time clusters showing significant main and interaction effects of face-valence and odour on the ERP response to faces. Figure 4 illustrates these significant scalp-time clusters. The corresponding topographic maps from each odour/face condition for each significant cluster are shown with bar graphs representing the mean EEG scalp-amplitude (μV).

3.4.1 Main effects of happy and disgusted faces on the ERP response to faces

There was a significant main effect of face valence on the ERP response to faces peaking at 192 ms and 704 ms after face onset (uncorrected $P < 0.001$), coinciding with the N170 latency window and the late-LPP, respectively (see Figure 4A). Subsequent t-tests performed on EEG amplitude data from these two clusters showed that happy faces yielded stronger EEG amplitude than disgusted faces in both the 192 ms cluster ($t(19) = -5.01$, $P < 0.001$), and the 704 ms cluster ($t(19) = -2.91$, $P = 0.009$).

3.4.2 Main effect of odour on the ERP response to faces

Another statistically significant scalp-time cluster represented a main effect of odour on ERP response to faces peaking at 165 ms following face onset (unc. $P < 0.001$), in frontal electrodes during the N170 time-window (see Figure 4B). A confirmatory one-way ANOVA in this cluster showed a significant effect of odour ($F(2, 38) = 16.84$, $\eta_p^2 = 0.47$, $P < 0.001$). Pairwise comparisons indicated that there were significant differences in EEG amplitude between all three odour conditions ($P < 0.05$): irrespective of face-valence, faces in the clean air condition produced a small negative amplitude (-0.24 ± 0.76), faces in the pleasant odour condition produced a very small negative amplitude (-0.1 ± 0.68), and faces in the unpleasant odour condition produced a positive amplitude (0.27 ± 0.95).

3.4.3 Odour-face interactions affecting the ERP response to faces

An interaction between odour and face-valence yielded a significant effect on ERP response to faces in two scalp-time clusters (unc. $P < 0.001$, see Figure 4C). One such interaction peaked at 259 ms following face onset ($F(2, 38) = 7.77$, $\eta_p^2 = 0.29$, $P = 0.003$). Post-hoc t-tests were employed to further investigate this interaction. These showed that happy faces produced a significantly greater negative potential at right frontal electrodes (-0.42 ± 0.58) than disgusted faces (-0.02 ± 0.79) in the clean air condition ($t(19) = -3.63$, $P = 0.002$), and that disgusted faces produced a significantly greater negative potential (-0.32 ± 0.48) than happy faces (-0.06 ± 0.81) in the unpleasant odour condition ($t(19) = 2.19$, $P = 0.04$). There was no significant difference in the amplitude produced by happy and disgusted faces in the pleasant odour condition ($P > 0.05$). An interaction between odour and face valence also occurred at 352 ms following face onset ($F(2, 38) = 5.98$, $\eta_p^2 = 0.24$, $P = 0.01$). Post-hoc t-tests showed that disgusted faces produced a greater positive potential at left frontal-parietal electrodes (0.29 ± 0.68) than happy faces (-0.01 ± 0.48) in the clean air condition ($t(19) = -2.78$, $P = 0.01$), and that happy faces produced a greater positive potential (0.21 ± 0.5) than disgusted faces (-0.76 ± 0.52) in the unpleasant odour condition ($t(19) = 2.76$, $P = 0.01$). There was no significant

difference in ERP amplitudes produced by happy and disgusted faces in the pleasant odour condition ($P > 0.05$).

3.5 Respiratory movements

Figure 5A shows averaged respiratory waveforms for each condition in a 7 s interval, beginning at odour onset. A repeated-measures ANOVA (2 face-types, 3 odours) showed a statistically significant effect of odour during the interval 1530–2215 ms ($P < 0.05$), and a significant interaction between face valence and odour during the interval 1434–1796 ms ($P < 0.05$). Given that these intervals overlapped, it is likely that the main effect in the interval 1530–2215 ms was driven by the interaction during the interval 1434–1796 ms. To analyse these effects further, respiratory movement data from these intervals were subjected to repeated measures ANOVAs in SPSS. This confirmed a significant effect of odour on respiratory movements during the interval 1530–2215 ms, ($F(2, 38) = 3.53$ $\eta_p^2 = 0.16$, $P = 0.05$), where pairwise comparisons confirmed a significant difference in respiratory movements between the jasmine and methylmercaptan odour conditions ($P = 0.04$). Inspiration was reduced during stimulation with methylmercaptan, compared to jasmine odour (see Figure 5A & 5B). Further analysis confirmed the interaction between odour and face valence during the interval 1434–1796 ms ($F(2, 38) = 3.44$, $\eta_p^2 = 0.15$, $P = 0.05$), and post hoc t-tests revealed that this interaction was representative of a marginally significant difference between respiratory movements in trials presenting happy faces compared to those presenting disgusted faces in the unpleasant odour condition only ($t(19) = 1.8$, $P = 0.09$). Inspiration was reduced during presentation of disgusted faces compared to presentation of happy faces in the unpleasant odour condition (see Figure 5A & 5C).

Intervals showing significant effects of odour and face valence on respiratory movements overlapped with the period in which ERPs were recorded and analysed. However, repeated measures ANCOVA showed that there were no statistically significant covariate effects of respiratory movements on ERP data from any of the five significant scalp-time clusters ($P > 0.05$). Therefore, it is

unlikely that differences in respiratory movements directly affected odour- or face-related ERP changes.

4. Discussion

Results showed that odour-face priming effects were bidirectional: Pleasant and unpleasant odours influenced evaluations of happy and disgusted facial expressions, and happy and disgusted faces also affected perceptions of odour pleasantness and intensity. In particular, unpleasant odour paired with disgusted faces resulted in shifts in face evaluation, increased odour intensity ratings and a reduction in respiratory movement. Such bidirectional priming effects are instances of a multi-modal integration that may be driven by a negative bias induced by the relevance for threat detection, or hedonic congruency of unpleasant odours and faces. Effects of odour-face interactions manifested in changes in cortical potentials during the N200 and N400 components of face ERPs.

4.1 Effects of odour-face combinations on perception

Happy faces in the pleasant odour condition were rated as most pleasant, happy faces in the unpleasant odour condition were rated as least pleasant, and happy faces in the clean air condition were rated between the two. This finding corresponds with previous results showing that odour valence linearly modulated evaluations of neutral faces (Seubert *et al.*, 2014; Cook *et al.*, 2015). Disgusted faces were rated as significantly less pleasant when they were presented with an unpleasant odour, compared to the same faces paired with a pleasant odour or no odour. The lack of difference between ratings of disgusted faces in the clean air and pleasant odour conditions may be attributable to the stronger influence of a negative odour on evaluations. This is consistent with the negative bias hypothesis, which states that the influence of negative stimuli is often greater than the influence of positive stimuli of the same intensity (Ito *et al.*, 1998; Smith *et al.*, 2003; Smith *et al.*, 2006). Indeed, previous studies have shown that unpleasant odours increase aversion to other unpleasant events, whereas pleasant odours had no effect (Stancak *et al.*, 2015). The increase and decrease in pleasantness ratings of happy and disgusted faces paired with pleasant and unpleasant odours, respectively, suggests that the congruency of odour-face valence may play a role in the subjective

evaluation of facial expressions (Leppanen & Hietanen, 2003; Leleu *et al.*, 2015b). In particular, stronger subjective reactions to disgusted faces in the presence of an unpleasant odour may be characteristic of an evolutionarily adaptive response to combined aversive stimuli from visual and olfactory modalities.

Interestingly, regardless of valence, all odours were rated as more pleasant when paired with happy faces compared to when they were paired with disgusted faces. The unpleasant odour was also rated as more intense when it was paired with disgusted face stimuli. These findings are consistent with previous studies showing effects of various visual stimuli on odour perception (Pollatos *et al.*, 2007; Seo *et al.*, 2010; Hummel *et al.*, 2017), and novel in the respect that emotional faces were also able to induce such effects. Our results demonstrate not only that pleasant and unpleasant odour can influence continuous subjective evaluations of happy and disgusted faces, but also that emotional faces can affect perceptions of odour pleasantness and intensity. The hedonic congruency of faces and odours may contribute to these effects.

4.2 Effects of odour-face combinations on electrophysiological responses

Odour-face interactions were observed during the N200 component of face ERPs. The N200 has been implicated in the analysis, discrimination and classification of visual stimuli (Ritter *et al.*, 1983; Naatanen & Picton, 1986). In the clean air condition, happy faces produced greater negative potential amplitude than disgusted faces. In the unpleasant odour condition, disgusted faces produced greater negative potential amplitude than happy faces. In the pleasant odour condition, face valence did not differentiate the potential amplitude. A similar, but reversed effect was found in the N400 component, which is known to be involved in processing contextual information about faces (Kutas & Federmeier, 2011): Disgusted faces produced greater positive potential amplitude than happy faces in the clean air condition, and happy faces produced a greater positive potential amplitude than disgusted faces in the unpleasant odour condition. Again, there was no difference in the amplitude produced by happy and disgusted faces in the pleasant odour condition.

Pleasant odour appeared to induce a moderate response to faces in both components, regardless of the face valence. A possible explanation for this is that the hedonic state induced by the pleasant odour was strong enough to mask any interactions with faces valence. Happy and disgusted faces may have been perceived as congruent or incongruent with clean air or unpleasant odour, and vice versa, resulting in increased cortical potentials for such congruent and incongruent pairings. These findings are consistent with those of Castle *et al.* (2000), who showed significant differences in the N400 for congruent versus incongruent stimuli in an unpleasant odour condition, but not in a pleasant odour condition. Our results are also partially consistent with those of Leleu *et al.* (2015b), who found odour-face interactions during the P200, and showed that unpleasant odour context amplified the difference in responses to neutral versus happy and disgusted faces. However, their results suggested that unpleasant odour context increased responses to emotional faces in general, regardless of the face valence. On the other hand, our results suggest that unpleasant and no odour contexts amplified the difference between happy and disgusted faces, whilst pleasant odour eliminated effects of face valence in N200 and N400 components.

Recent studies from the more general evaluative priming literature suggest that evaluative incongruity is represented in the LPP and N400 components (Zhang *et al.*, 2010; Herring *et al.*, 2011). Herring *et al.* (2011) argued that the N400 may be more specifically involved in semantic, rather than evaluative incongruity, and cross-modality priming. Our results show a possible incongruity effect during the N400, and may therefore lend support to the finding that the N400 represents effects of congruency in cross-modal priming (Zhang *et al.*, 2010). Encoding perspectives of evaluative priming suggest that primes activate object-evaluation associations in memory that make the valence of targets more accessible, thus facilitating evaluative priming. On the other hand, response perspectives suggest that primes influence the ease with which a person can generate a response to the target. A recent meta-analysis of evaluative priming studies argued that both encoding and response processes are involved in most cases, depending on the task (Herring *et al.*, 2013). The present study observed effects of odours on face-ERPs, likely involved in encoding, as well as in subjective behavioural responses. Our results therefore support the findings of Herring *et al.* (2013), and contribute that both

encoding and response mechanisms were involved in evaluative priming where odours and faces served as cross-modal primes and targets.

An interesting odour-face interaction was also observed in the respiratory movement data. In the unpleasant odour condition, the amplitude of inspiratory movements was significantly reduced during presentation of disgusted faces compared to happy faces. Decreased inspiration when an unpleasant olfactory stimulus was simultaneously paired with a congruent unpleasant visual stimulus is another example of the adaptive role of olfactory-visual integration in our multisensory environment. Indeed, aversive odours act as a warning about dangers in our surroundings and evoke withdrawal reflexes (Stevenson, 2010). Evidently, this warning is heightened when an odour is accompanied by a congruent visual stimulus, resulting in decreased inspiration in the case of the present study. Such a finding is in keeping with the notion that our senses work together to enhance the salience of biologically meaningful events, increasing the speed at which responses can be generated (Stein & Stanford, 2008). Indeed, previous studies showed enhanced skin conductance responses for unpleasant images combined with unpleasant odour (Banks *et al.*, 2012), and decreased inspiratory time and breath duration for high arousal and unpleasant stimuli (Ritz *et al.*, 2000; Gomez *et al.*, 2004).

A main effect of odour, irrespective of face valence, was observed in the N170 component of face ERPs. The unpleasant odour produced the greatest, positive potential amplitude, the pleasant odour produced very small negative amplitude, and clean air produced negative amplitude. The findings are partially consistent with those of Leleu *et al.* (2015b), who showed a generic enhancement of the EEG response to faces, regardless of their emotional content, between 130 and 180 ms after face onset when faces were presented with an odour. Moreover, results from our previous study showed an increase in N170 amplitude when faces were presented in the presence of an odour (Cook *et al.*, in preparation). It is likely that faces presented in the unpleasant odour condition produced the largest N170 amplitude due to greater salience of the unpleasant odour. This is consistent with the aforementioned negative bias hypothesis (Ito *et al.*, 1998), and may further represent an evolutionary adaptive response to aversive stimuli.

An effect of face valence, regardless of odour condition, was observed in the N170 and late-LPP components of face ERPs. Happy faces produced a stronger amplitude potential across all odour conditions than disgusted faces. Whilst previous studies have suggested that the N170 response is similar across faces, irrespective of emotional expression (Eimer *et al.*, 2003; Eimer & Holmes, 2007), others have found differential effects depending on emotional expression (Batty & Taylor, 2003). The LPP is also known to be sensitive to the valence of pictures, words and faces (Cacioppo *et al.*, 1993; Cuthbert *et al.*, 2000; Hajcak *et al.*, 2006; Hajcak *et al.*, 2007). It is possible that happy faces resulted in increased cortical amplitude potentials due to a boosting effect of positive valence, in the same way that the pleasant odour context masked effects of congruency in odour-face interactions. We argue that happy faces may have had a greater activation effect on reward circuitry or valuation structures in the brain (Lebreton *et al.*, 2009). This may apply in particular to the cluster in the N170, as it was located in frontal electrodes and is thus more likely to represent activity of reward structures such as the orbitofrontal cortex.

4.3 Multisensory negative bias

A key theme emerging across our results is the accumulation of negative stimuli across olfactory and visual modalities to affect perception of both odours and faces, and even respiratory movements. Specifically, unpleasant odour paired with disgusted faces resulted in stronger face and odour unpleasantness ratings, increased odour intensity ratings and decreased respiratory amplitude. These findings correspond with the aforementioned negative bias hypothesis (Ito *et al.*, 1998; Smith *et al.*, 2003; Smith *et al.*, 2006).

Given the effect of aversive odour-face combinations evidenced in the present results, it is important to consider the multisensory nature of this negative bias effect. From an evolutionary perspective, odours serve as warnings about threats in our environment (Paustenbach & Gaffney, 2006; Stevenson, 2010), allowing us to respond quickly and correctly to potential adverse events (Taylor, 1991). Unpleasant odour contexts may therefore heighten awareness and increase attention to stimuli from other modalities, particularly if these other stimuli also signal a negative event. Supporting this idea, a very recent study showed that exposure to an unpleasant odour increased the

sense of presence in virtual reality (Baus & Bouchard, 2017). Another showed that unpleasant odour increased responses to painful stimuli relative to pleasant odour (Villemure *et al.*, 2003). Moreover, another recent study found that unpleasant odour increased aversion and related skin conductance responses to monetary losses. It was argued that unpleasant odour likely primes avoidance behaviour, and consequently boosts existing avoidance responses to negative events (Stancak *et al.*, 2015). Such findings combined with the present results indicate increased attention to negative stimuli when an aversive, unpleasant odour is also present. These effects likely relate to an evolutionarily adaptive mechanism where cross-modal stimuli interact and accumulate in the brain to produce an appropriate behavioural response when aversive stimuli signal danger.

4.4 Limitations

A limitation of the present study was the use of only one pleasant and one unpleasant odour. The odours used were selected on the basis that they were generically very pleasant and very unpleasant (avoiding food and body specific odours). The large differences in odour pleasantness ratings observed suggest that they were indeed hedonically distinct. However, the findings may relate to specific characteristics of these two odours, and caution should be exercised before generalising across all pleasant and unpleasant odours. Future studies should endeavour to include a variety of olfactory and visual stimuli to further investigate cross-modal effects on perception, since specific odours (e.g. perfume fragrances, food odours) may interact differently with faces as well as other types of visual stimuli.

4.5 Summary

In summary, the results show that pleasant and unpleasant odours are able to influence evaluations of both happy and disgusted facial expressions, and that these facial expressions are also able to modulate evaluations of odour pleasantness and intensity. Olfactory-visual congruency may have a role in these effects. A key finding was that pairings of unpleasant odour and disgusted faces resulted in stronger shifts in face evaluation, increased odour intensity ratings and a decrease in inspiration. It is likely that the multisensory combination of congruent aversive olfactory and visual

stimuli strengthens hedonic responses and produces withdrawal behaviours as part of an adaptive mechanism. Olfactory-visual interactions were represented in the N200 and N400 components of face ERPs. Differences in ERP amplitude evoked by happy and disgusted faces were apparent in clean air and unpleasant odour conditions, whilst such differences were masked by a pleasant odour context. It is possible that the hedonic state induced by the pleasant odour was able to mask effects of face valence. In a wider context, our results also suggest that both encoding and response mechanisms are involved in cross-modal evaluative priming.

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References

Adolph, D., Meister, L. & Pause, B.M. (2013) Context counts! social anxiety modulates the processing of fearful faces in the context of chemosensory anxiety signals. *Front Hum Neurosci*, **7**.

Banks, S.J., Ng, V. & Jones-Gotman, M. (2012) Does good+good=better? A pilot study on the effect of combining hedonically valenced smells and images. *Neuroscience letters*, **514**, 71-76.

Batty, M. & Taylor, M.J. (2003) Early processing of the six basic facial emotional expressions. *Cognitive Brain Research*, **17**, 613-620.

Baus, O. & Bouchard, S. (2017) Exposure to an unpleasant odour increases the sense of Presence in virtual reality. *Virtual Reality*, **21**, 59-74.

Bensafi, M., Pierson, A., Rouby, C., Farget, V., Bertrand, B., Vigouroux, M., Jouvent, R. & Holley, A. (2002) Modulation of visual event-related potentials by emotional olfactory stimuli. *Clin. Neurophysiol.*, **32**, 335-342.

Bentin, S., Allison, T., Puce, A., Perez, E. & McCarthy, G. (1996) Electrophysiological studies of face perception in humans. *Journal of cognitive neuroscience*, **8**, 551-565.

Berg, P. & Scherg, M. (1994) A multiple source approach to the correction of eye artifacts. *Electroencephalography and Clinical Neurophysiology*, **90**, 229-241.

Cacioppo, J.T., Crites, S.L., Berntson, G.G. & Coles, M.G.H. (1993) If attitudes affect how stimuli are processed, should they not affect the event-related brain potential? *Psychol Sci*, **4**, 108-112.

Castle, P.C., Van Toller, S. & Milligan, G.J. (2000) The effect of odour priming on cortical EEG and visual ERP responses. *International journal of psychophysiology : official journal of the International Organization of Psychophysiology*, **36**, 123-131.

Cook, S., Fallon, N., Wright, H., Thomas, A., Giesbrecht, T., Field, M. & Stancak, A. (2015) Pleasant and Unpleasant Odors Influence Hedonic Evaluations of Human Faces: An Event-Related Potential Study. *Front. Hum. Neurosci.*, **9**, 661.

Cook, S., Kokmotou, K., Soto, V., Wright, H., Fallon, N., Thomas, A., Giesbrecht, T., Field, M. & Stancak, A. (in preparation) Effects of stimulus onset asynchrony on odour induced hedonic evaluations of faces: an event-related potential study.

Cuthbert, B.N., Schupp, H.T., Bradley, M.M., Birbaumer, N. & Lang, P.J. (2000) Brain potentials in affective picture processing: covariation with autonomic arousal and affective report. *Biological psychology*, **52**, 95-111.

de Araujo, I.E., Rolls, E.T., Velazco, M.I., Margot, C. & Cayeux, I. (2005) Cognitive modulation of olfactory processing. *Neuron*, **46**, 671-679.

Dematte, M.L., Osterbauer, R. & Spence, C. (2007) Olfactory cues modulate facial attractiveness. *Chem Senses*, **32**, 603-610.

Dematte, M.L., Sanabria, D. & Spence, C. (2009) Olfactory discrimination: when vision matters? *Chem Senses*, **34**, 103-109.

Eimer, M. & Holmes, A. (2007) Event-related brain potential correlates of emotional face processing. *Neuropsychologia*, **45**, 15-31.

Eimer, M., Holmes, A. & McGlone, F.P. (2003) The role of spatial attention in the processing of facial expression: an ERP study of rapid brain responses to six basic emotions. *Cognitive, affective & behavioral neuroscience*, **3**, 97-110.

Folstein, J.R. & Van Petten, C. (2008) Influence of cognitive control and mismatch on the N2 component of the ERP: a review. *Psychophysiology*, **45**, 152-170.

Gomez, P., Stahel, W.A. & Danuser, B. (2004) Respiratory responses during affective picture viewing. *Biological psychology*, **67**, 359-373.

Gottfried, J.A. & Dolan, R.J. (2003) The nose smells what the eye sees: crossmodal visual facilitation of human olfactory perception. *Neuron*, **39**, 375-386.

Hajcak, G., Dunning, J.P. & Foti, D. (2007) Neural response to emotional pictures is unaffected by concurrent task difficulty: an event-related potential study. *Behavioral neuroscience*, **121**, 1156.

Hajcak, G., Moser, J.S. & Simons, R.F. (2006) Attending to affect: appraisal strategies modulate the electrocortical response to arousing pictures. *Emotion*, **6**, 517.

Herring, D.R., Taylor, J.H., White, K.R. & Crites Jr, S.L. (2011) Electrophysiological responses to evaluative priming: the LPP is sensitive to incongruity. *Emotion*, **11**, 794.

Herring, D.R., White, K.R., Jabeen, L.N., Hinojos, M., Terrazas, G., Reyes, S.M., Taylor, J.H. & Crites, S.L. (2013) On the automatic activation of attitudes: a quarter century of evaluative priming research. *Psychological bulletin*, **139**, 1062-1089.

Hopf, J.-M., Vogel, E., Woodman, G., Heinze, H.-J. & Luck, S.J. (2002) Localizing visual discrimination processes in time and space. *Journal of Neurophysiology*, **88**, 2088-2095.

Huart, C., Legrain, V., Hummel, T., Rombaux, P. & Mouraux, A. (2012) Time-frequency analysis of chemosensory event-related potentials to characterize the cortical representation of odors in humans. *PloS one*, **7**, e33221.

Hummel, T., Fark, T., Baum, D., Warr, J., Hummel, C.B. & Schriever, V.A. (2017) The Rewarding Effect of Pictures with Positive Emotional Connotation upon Perception and Processing of Pleasant Odors—An FMRI Study. *Frontiers in Neuroanatomy*, **11**, 19.

Hummel, T., Sekinger, B., Wolf, S.R., Pauli, E. & Kobal, G. (1997) 'Sniffin'Sticks': Olfactory Performance Assessed by the Combined Testing of Odor Identification, Odor Discrimination and Olfactory Threshold. *Chem Senses*, **22**, 39-52.

Ito, T.A., Larsen, J.T., Smith, N.K. & Cacioppo, J.T. (1998) Negative information weighs more heavily on the brain: The negativity bias in evaluative categorizations. *Journal of personality and social psychology*, **75**, 887-900.

Kutas, M. & Federmeier, K.D. (2011) Thirty years and counting: finding meaning in the N400 component of the event-related brain potential (ERP). *Annual review of psychology*, **62**, 621-647.

Lebreton, M., Jorge, S., Michel, V., Thirion, B. & Pessiglione, M. (2009) An automatic valuation system in the human brain: evidence from functional neuroimaging. *Neuron*, **64**, 431-439.

Lehmann, D. (1987) Principles of spatial analysis. In Gevins, A.S., Remond, A. (eds) *Handbook of Electroencephalography and Clinical Neurophysiology: Methods of Analysis of Brain Electrical and Magnetic Signals* Elsevier, Amsterdam, pp. 309-354.

Leleu, A., Demily, C., Franck, N., Durand, K., Schaal, B. & Baudouin, J.Y. (2015a) The Odor Context Facilitates the Perception of Low-Intensity Facial Expressions of Emotion. *PloS one*, **10**, e0138656.

Leleu, A., Godard, O., Dollion, N., Durand, K., Schaal, B. & Baudouin, J.Y. (2015b) Contextual odors modulate the visual processing of emotional facial expressions: An ERP study. *Neuropsychologia*, **77**, 366-379.

Leppanen, J.M. & Hietanen, J.K. (2003) Affect and Face Perception: Odors Modulate the Recognition Advantage of Happy Faces. *Emotion*, **3**, 315-326.

Li, W., Moallem, I., Paller, K.A. & Gottfried, J.A. (2007) Subliminal smells can guide social preferences. *Psychol Sci*, **18**, 1044-1049.

Maris, E. & Oostenveld, R. (2007) Nonparametric statistical testing of EEG-and MEG-data. *Journal of Neuroscience Methods*, **164**, 177-190.

McGlone, F.Ö., R. A.; Demattè, L. M.; Spence, C. (2013) The Crossmodal Influence of Odor Hedonics on Facial Attractiveness: Behavioural and fMRI Measures. In Signorelli, F. (ed) *Functional Brain Mapping and the Endeavor to Understand the Working Brain*. InTech, pp. 209-225.

Naatanen, R. & Picton, T.W. (1986) N2 and automatic versus controlled processes. *Electroencephalography and clinical neurophysiology. Supplement*, **38**, 169-186.

Olofsson, J.K., Bowman, N.E., Khatibi, K. & Gottfried, J.A. (2012) A time-based account of the perception of odor objects and valences. *Psychol. Sci.*, **23**, 1224-1232.

Pause, B.M., Ohrt, A., Prehn, A. & Ferstl, R. (2004) Positive emotional priming of facial affect perception in females is diminished by chemosensory anxiety signals. *Chem Senses*, **29**, 797-805.

Paustenbach, D.J. & Gaffney, S.H. (2006) The role of odor and irritation, as well as risk perception, in the setting of occupational exposure limits. *International archives of occupational and environmental health*, **79**, 339-342.

Poline, J.B., Holmes, A.P., Worsley, K.J. & Friston, K.J. (1997) Statistical inference and the theory of random fields. *SPM short course notes*, 1-27.

Pollatos, O., Kopietz, R., Linn, J., Albrecht, J., Sakar, V., Anzinger, A., Schandry, R. & Wiesmann, M. (2007) Emotional stimulation alters olfactory sensitivity and odor judgment. *Chem Senses*, **32**, 583-589.

Ritter, W., Simson, R. & Vaughan, H.G., Jr. (1983) Event-related potential correlates of two stages of information processing in physical and semantic discrimination tasks. *Psychophysiology*, **20**, 168-179.

Ritz, T., George, C. & Dahme, B. (2000) Respiratory resistance during emotional stimulation: evidence for a nonspecific effect of experienced arousal? *Biological psychology*, **52**, 143-160.

Rubin, D., Botanov, Y., Hajcak, G. & Mujica-Parodi, L.R. (2012) Second-hand stress: inhalation of stress sweat enhances neural response to neutral faces. *Social cognitive and affective neuroscience*, **7**, 208-212.

Seo, H.S., Arshamian, A., Schemmer, K., Scheer, I., Sander, T., Ritter, G. & Hummel, T. (2010) Cross-modal integration between odors and abstract symbols. *Neuroscience letters*, **478**, 175-178.

Seubert, J., Gregory, K.M., Chamberland, J., Dessirier, J. & Lundström, J.N. (2014) Odor Valence Linearly Modulates Attractiveness, but Not Age Assessment, of Invariant Facial Features in a Memory-Based Rating Task. *PloS one*, **9**, e98347.

Seubert, J., Kellermann, T., Loughead, J., Boers, F., Brensinger, C., Schneider, F. & Habel, U. (2010) Processing of disgusted faces is facilitated by odor primes: a functional MRI study. *NeuroImage*, **53**, 746-756.

Smith, N.K., Cacioppo, J.T., Larsen, J.T. & Chartrand, T.L. (2003) May I have your attention, please: Electrocortical responses to positive and negative stimuli. *Neuropsychologia*, **41**, 171-183.

Smith, N.K., Larsen, J.T., Chartrand, T.L., Cacioppo, J.T., Katafiasz, H.A. & Moran, K.E. (2006) Being bad isn't always good: Affective context moderates the attention bias toward negative information. *Journal of personality and social psychology*, **90**, 210-220.

Stancak, A., Xie, Y., Fallon, N., Bulsing, P., Giesbrecht, T., Thomas, A. & Pantelous, A.A. (2015) Unpleasant odors increase aversion to monetary losses. *Biological psychology*, **107**, 1-9.

Stein, B.E. & Stanford, T.R. (2008) Multisensory integration: current issues from the perspective of the single neuron. *Nat Rev Neurosci*, **9**, 255-266.

Steinberg, C., Dobel, C., Schupp, H.T., Kissler, J., Elling, L., Pantev, C. & Junghofer, M. (2012) Rapid and highly resolving: affective evaluation of olfactorily conditioned faces. *J Cogn Neurosci*, **24**, 17-27.

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

Taylor, S.E. (1991) Asymmetrical effects of positive and negative events: the mobilization-minimization hypothesis. *Psychological bulletin*, **110**, 67.

Tottenham, N., Tanaka, J.W., Leon, A.C., McCarry, T., Nurse, M., Hare, T.A., Marcus, D.J., Westerlund, A., Casey, B.J. & Nelson, C. (2009) The NimStim set of facial expressions: Judgments from untrained research participants. *Psychiatry Res*, **168**, 242-249.

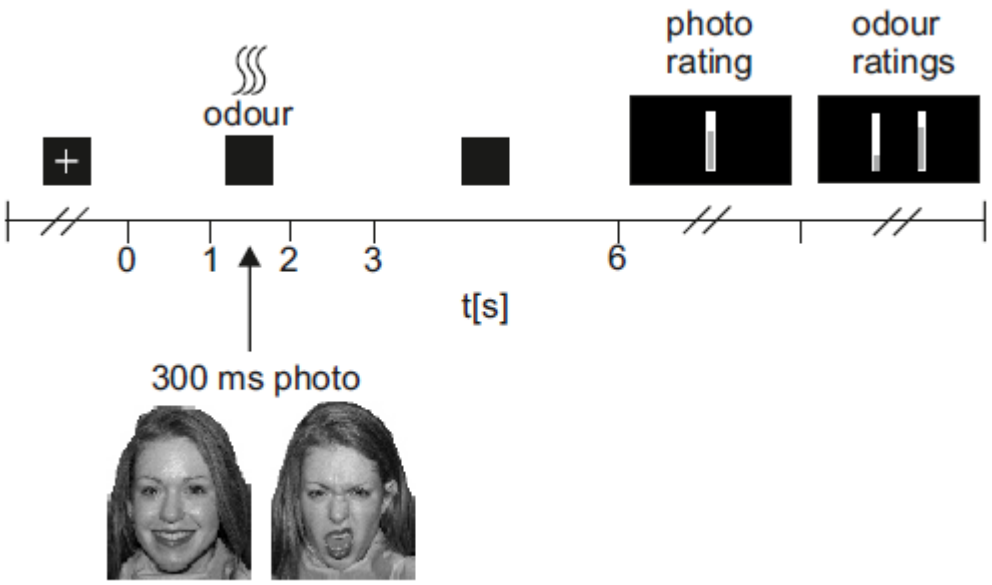
Villemure, C., Slotnick, B.M. & Bushnell, M.C. (2003) Effects of odors on pain perception: deciphering the roles of emotion and attention. *Pain*, **106**, 101-108.

Walla, P. (2008) Olfaction and its dynamic influence on word and face processing: cross-modal integration. *Progress in neurobiology*, **84**, 192-209.

Worsley, K.J. (2003) Developments in random field theory. *Hum. Brain. Func.*, **2**, 881-886.

Zhang, Q., Li, X., Gold, B.T. & Jiang, Y. (2010) Neural correlates of cross-domain affective priming. *Brain Res.*, **1329**, 142-151.

Zhou, W. & Chen, D. (2009) Fear-related chemosignals modulate recognition of fear in ambiguous facial expressions. *Psychol Sci*, **20**, 177-183.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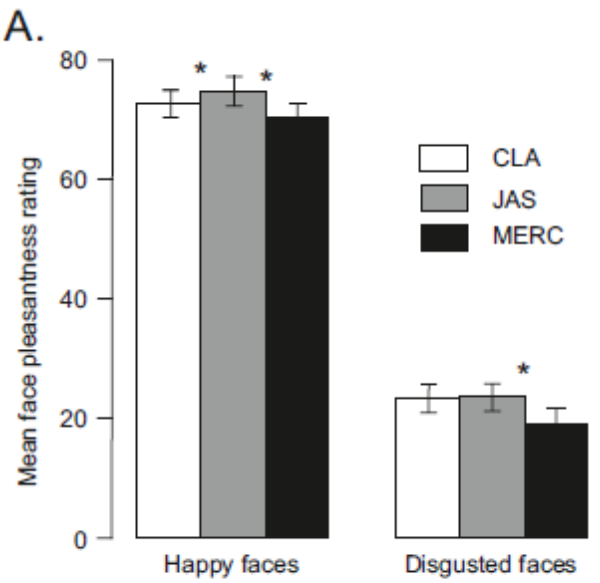
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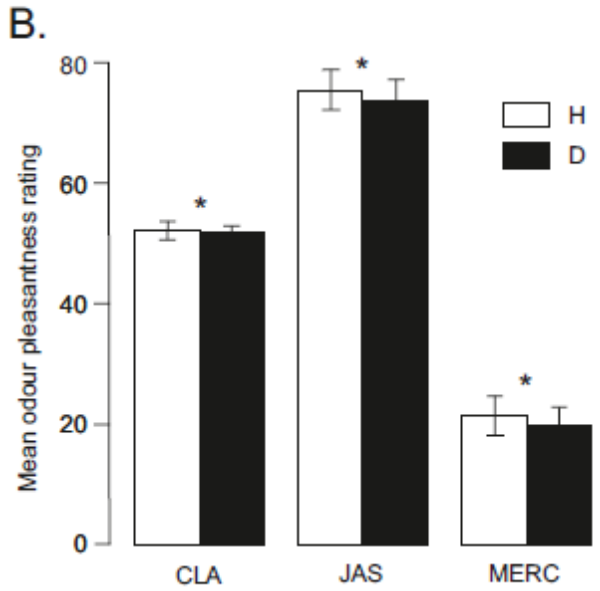
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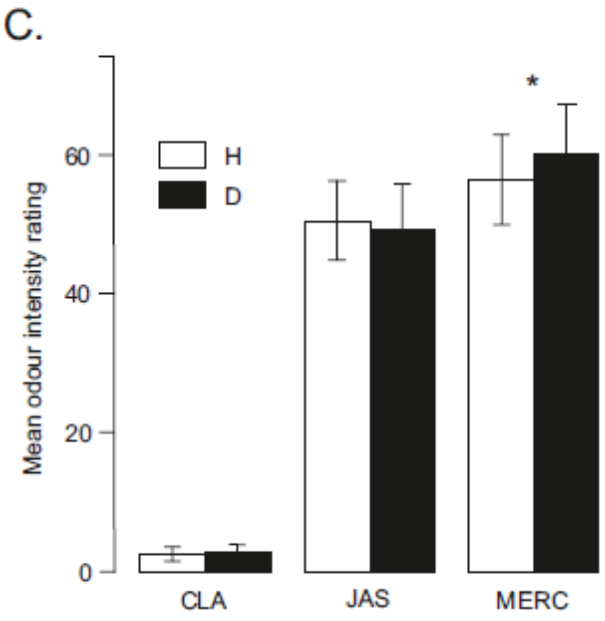
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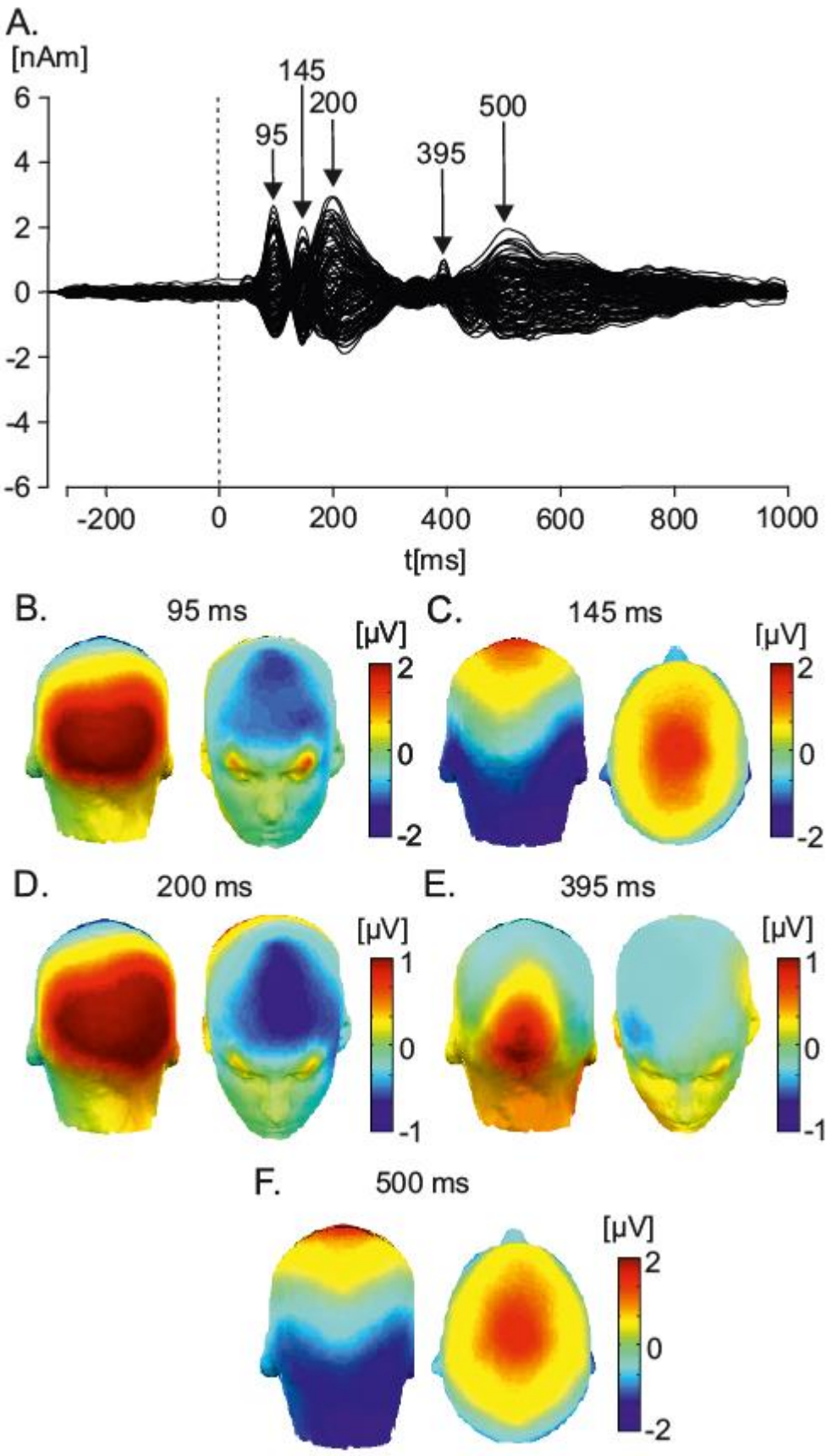
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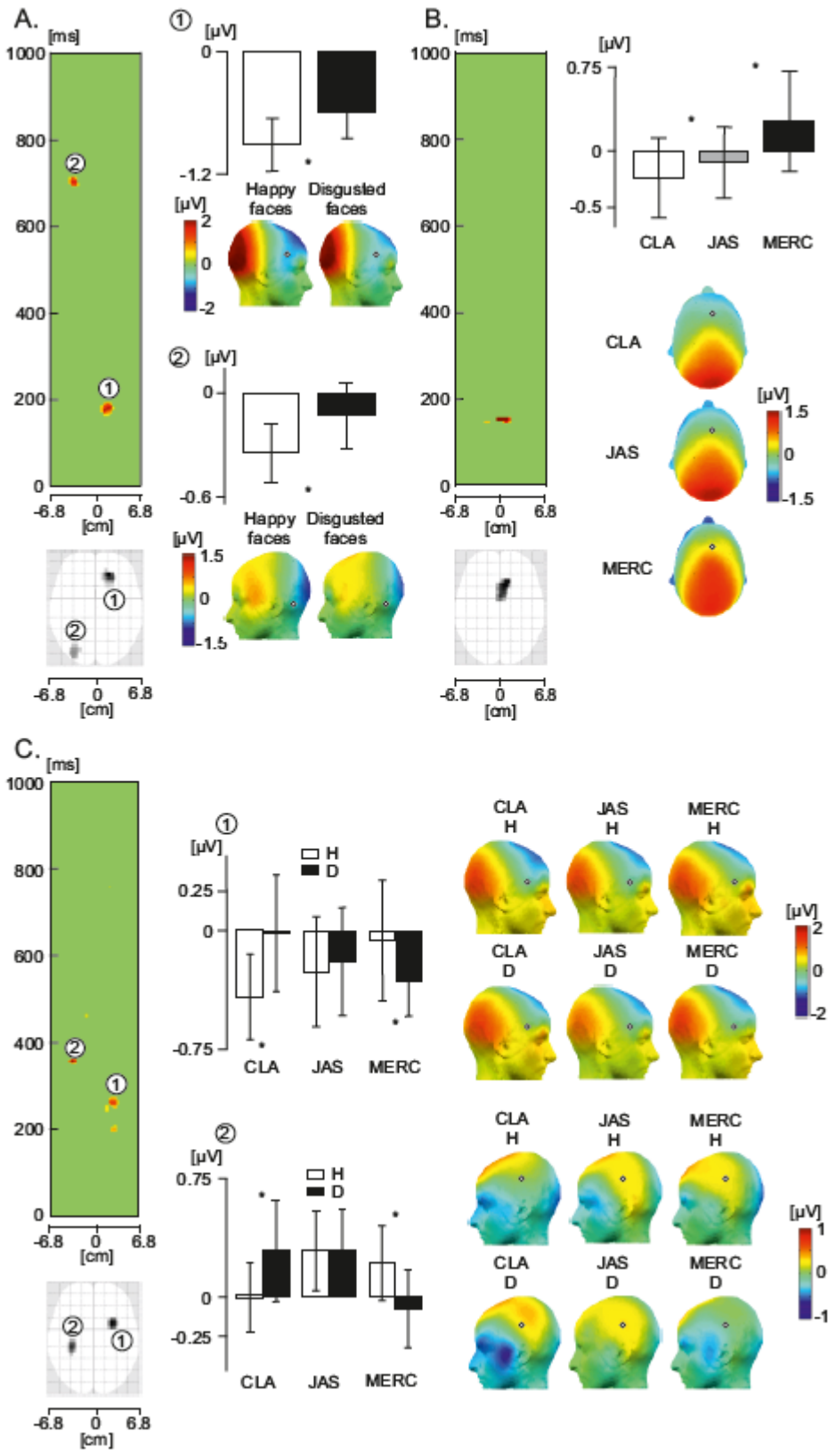
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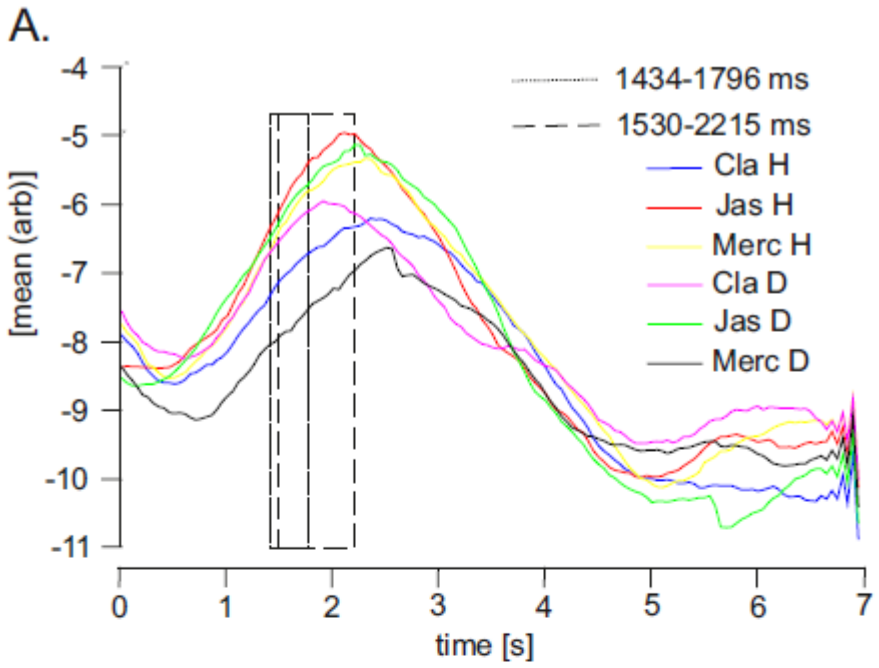
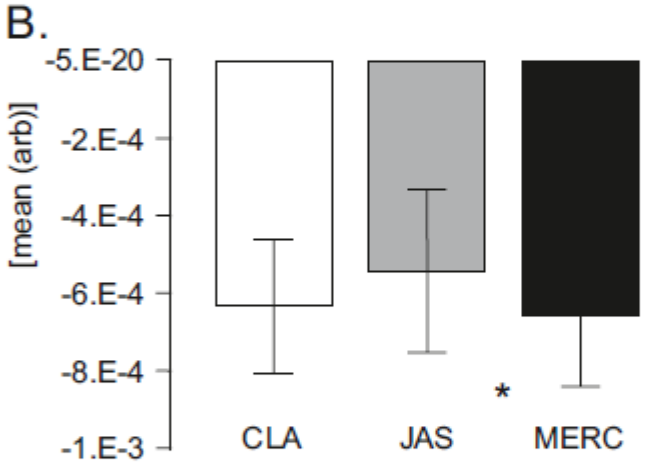
0.75
-0.5
CLA
JAS
MERC
1.5
C.
0.25
-0.75
H
D
-0.25
CLA H
JAS H
MERC H
CLA D
JAS D
MERC D


A.
1434-1796 ms
1530-2215 ms
Cla H
Jas H
Merc H
Cla D
Jas D
Merc D
[mean (arb)]
-4
-5
-6
-7
-8
-9
-10
-11
0
1
2
3
4
5
6
7
time [s]


B.
[mean (arb)]
-5.E-20
-2.E-4
-4.E-4
-6.E-4
-8.E-4
-1.E-3
*
CLA
JAS
MERC

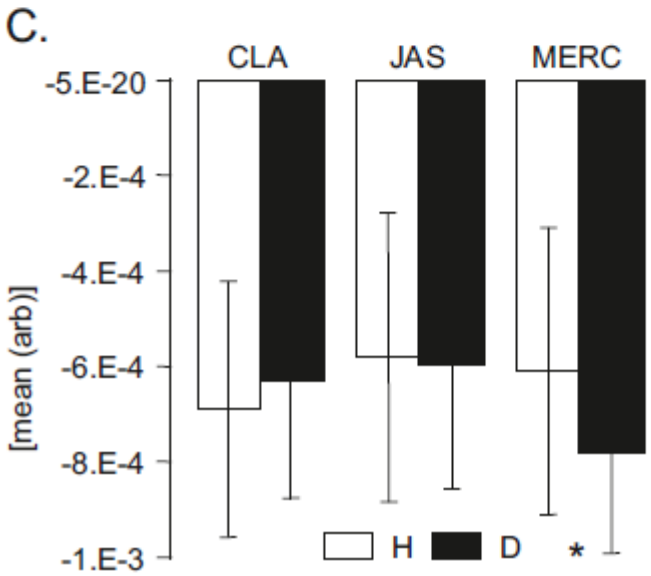

C.
CLA
JAS
MERC
[mean (arb)]
-5.E-20
-2.E-4
-4.E-4
-6.E-4
-8.E-4
-1.E-3
H
D
*

Figure legends

Figure 1: Flowchart of experimental trial procedure. At the start of each trial, participants viewed a white fixation cross on a black background. Participants were instructed to relax and breathe normally during this time. At the very onset of a participant's inspiration, the experimenter triggered a three-second odor pulse. At a random time-point between 1–2 s of the odour pulse, a photograph of either a happy or a disgusted face was displayed for 300 ms. After a 3 s resting interval with a black screen, a visual-analogue scale prompted participants to rate the pleasantness of the photograph (very unpleasant – very pleasant), 6 seconds after odour onset. Following this, a second screen with two scales then prompted participants to rate the pleasantness (very unpleasant – very pleasant) and intensity of the odour (no odour – very intense odour). Once participants had completed these ratings, the next trial began.

Figure 2: Mean ratings of face pleasantness, odour pleasantness and odour intensity. (A) Bar graph illustrating the mean ratings of face pleasantness in each odour and face condition. White bars represent clean air trials (labelled CLA), grey bars represent trials using jasmine odour (labelled JAS), and black bars represent trials using methylmercaptan (labelled MERC). Asterisks indicate statistically significant differences. (B) Bar graph illustrating mean ratings of odour pleasantness in each odour and face condition. White bars represent trials where happy faces were presented (labelled H), and black bars represent trials where disgusted faces were presented (labelled D). Odour conditions are labelled CLA, JAS, MERC. Asterisks indicate significant effects. (C) Bar graph illustrating mean ratings of odour intensity in each odour and face condition. White bars represent trials where happy faces were presented (labelled H), and black bars represent trials where disgusted faces were presented (labelled D). Odour conditions are labelled CLA, JAS, MERC. Asterisks indicate statistically significant differences.

Figure 3: Butterfly plot of grand average ERP response to faces and corresponding scalp topographies. (A) Butterfly plot of grand average ERPs in response to faces. Peak latencies of distinct ERP components (95 ms, 145 ms, 200 ms, 395 ms and 530 ms) are highlighted with arrows. (B) Latency component 95 ms (P1). The topographic maps of grand average ERPs overlaid on the volume rendering of the human head are shown. (C) Latency component 145 ms (N170). (D) Latency component 200 ms. (E) Latency component 395 ms (N400). (F) Latency component 500 ms (LPP).

Figure 4: Repeated-measures ANOVA showing the effects of the three odour conditions and two face conditions on ERP response to faces. . (A) Main effect of face-valence on ERP response to faces across all odour conditions. The green panel shows statistically significant latency periods (uncorrected $P < 0.001$) in the scalp-time plot where F values represent the strength of variance between SOA conditions over the horizontal axis of the scalp in every time sample from 0 ms and 1000 ms relative to the onset of the face photograph. The scalp values over the horizontal axis of the scalp are averages of F values occurring at each vertical point for a given horizontal point in the standardized scalp map (from -6.8 cm to +6.8 cm). There were two spatio-temporal clusters showing a statistically significant effect of face-valence. Below the green panel is the standard scalp map of statistically significant clusters using ERPs. The first significant cluster, labelled 1, peaked at 192 ms and had negative amplitude. The second, labelled 2, peaked at 704 ms and also had

negative amplitude. Bar graphs illustrate the mean EEG amplitude for each cluster under each face condition (μV). White bars represent trials with happy faces, and black bars represent trials with disgusted faces. Asterisks indicate statistically significant differences ($P < 0.05$). Corresponding topographic maps of the numbered significant clusters for the two SOA conditions are shown. White circles with a black outline pinpoint the centre of significant electrode clusters. (B) Main effect of odour condition on ERP response to faces across both face conditions. The green panel shows statistically significant latency periods ($P < 0.05$ FWE) in the scalp-time plot where F values represent the strength of variance between odour conditions. One spatio-temporal cluster showed a statistically significant effect of odour during the N170 time-window. Below the green panel is the standard scalp map of the statistically significant cluster. Bar graphs illustrate the mean EEG amplitude at this cluster under each odour condition (μV). The white bar represents the clean air condition (labelled CLA), the grey bar represents the pleasant odour condition (labelled JAS) and the black bar represents the unpleasant odour condition (labelled MERC). Asterisks indicate statistically significant differences ($P < 0.05$). Corresponding topographic maps of the significant cluster for the three odour conditions are shown. (C) Interaction between odour and face-valence condition affecting ERP response to faces. The green panel shows statistically significant latency periods ($P < 0.001$ uncorrected) in the scalp-time plot. Two spatio-temporal clusters during the LPP showed were significantly affected by an interaction between odour and face-valence conditions. Below the green panel is the standard scalp map of the statistically significant clusters. The first significant cluster, labelled 1, peaked at 259 ms and had negative amplitude. The second, labelled 2, peaked at 352 ms and had positive amplitude. Bar graphs illustrate the mean EEG amplitude for each cluster under each condition (μV). White bars represent trials with happy faces, and black bars represent trials with disgusted faces. Odour conditions are labelled CLA, JAS, and MERC. Asterisks indicate statistically significant differences ($P < 0.05$). Corresponding topographic maps of the numbered significant clusters for all conditions are shown.

Figure 5: Average respiratory waveforms for each condition. Respiratory movement signals from every subject across all trials were averaged over a period of 7 seconds, beginning at odour onset (Time 0). The blue line represents clean air trials using happy faces (denoted as ‘Cla H’), the red line represents pleasant odour trials using happy faces (‘Jas H’) and the yellow line represents unpleasant odor trials using happy faces (‘Merc H’). The pink line represents clean air trials using disgusted faces (‘Cla D’), the green line represents pleasant odour trials using disgusted faces (‘Jas D’) and the black line represents unpleasant odour trials using disgusted faces (‘Merc D’) The grey rectangle indicates the time interval where respiratory movement signals differed significantly according to a two-way ANOVA for repeated measures ($P < 0.05$). Upwards deflection of respiratory signals corresponds to inspiration.