Odor-evoked hedonic contexts influence the discrimination of facial expressions in the human brain

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Short title: Valenced odors influence expression discrimination

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Abstract

The influence of odor valence on expressive-face perception remains unclear. Here, three "valenced" odor contexts (pleasant, unpleasant, control) were diffused while scalp electroencephalogram (EEG) was recorded in 18 participants presented with expressive faces alternating at a 6-Hz rate. One facial expression (happiness, disgust or neutrality) repeatedly arose every 6 face pictures to isolate its discrimination from other expressions at 1 Hz and harmonics in the EEG spectrum. The amplitude of the brain response to neutrality was larger in the pleasant vs. control odor context, and fewer electrodes responded in the unpleasant odor context. The number of responding electrodes was reduced for disgust in both odor contexts. The response to happiness was unchanged between odor conditions. Overall, these observations suggest that valenced odors influence the neural discrimination of facial expressions depending on both face and odor hedonic valence, especially for the emotionally ambiguous neutral expression.

Keywords: Fast Periodic Visual Stimulation, EEG, facial expression of emotion, valenced odor, multisensory integration

Introduction

Efficient social interaction relies on the rapid and accurate decoding of others' emotional signals, mainly communicated through facial expressions. In particular, some patterns of facial actions have been well identified, based on the assumption that facial expressions communicate universal basic emotions: anger, disgust, fear, happiness, sadness and surprise (Ekman & Friesen, 1978; Ekman, 1992; but see Jack et al., 2012; Sauter & Eisner, 2013 for discussions on the universality of facial expression recognition). Nevertheless, the perception of emotional expressions from the face is strongly mediated by contextual information (e.g., body posture, gaze direction, surrounding visual scenes; for reviews see Wieser & Brosch, 2012; Barrett et al., 2011; Hassin et al., 2013; Aviezer et al., 2017), including cues from other sensory modalities (e.g., auditory cues, de Gelder and Vroomen, 2000; Dolan et al, 2001; Pourtois et al., 2005; Hagan et al., 2009).

Mounting evidence indicates that the multisensory context provided by the integration of odor and visual cues exerts a substantial influence on the processing of facial information. For instance, odors modulate face encoding and recognition (Steinberg et al., 2012; Walla, 2008; Walla et al., 2003, 2005; Cecchetto et al., 2020), as well as ratings of face attractiveness (Demattè et al., 2007; Parma et al., 2012; but see Lundström and Olsson, 2005), likeability/pleasantness (Li et al., 2007; Cook et al., 2015, 2017, 2018) or confidence, trustworthiness, and competence levels (Dalton et al., 2013). Modulation of face perception by odor cues is already observed in young infants (Durand et al., 2013, 2020; Godard et al., 2016; Jessen, 2020; Leleu et al., 2020; Rekow et al., 2020), and in children (Cavazzana et al., 2018). For the recognition of facial expressions in particular, several studies revealed the influence of body odors (Mujica-Parodi et al., 2009; Rocha et al., 2018; Zernecke et al., 2011; Zhou & Chen, 2009; Wudarczyk et al., 2016; Kamiloglu et al., 2018). Overall, these studies showed that compared with odors collected from sweat after physical exercise, stress/anxiety sweat odors facilitate the recognition of congruent facial expressions, namely fearful (threatened) faces (Zhou & Chen, 2009; Wudarczyk et al., 2016; Kamiloglu et al., 2018) or angry (threatening) faces (Mujica-Parodi et al., 2009). For instance, compared to odors collected after physical exercise, stress odors lead to increased expressiveness ratings (Wudarczyk et al., 2016) or decreased reaction times (Kamiloglu et al., 2018) to congruent expressions. When the facial expression is ambiguous (i.e., morphed with a neutral expression), the presence of a stress odor increases the number of "fear" or "anger" responses (Mujica-Parodi et al., 2009; Zhou & Chen, 2009). By contrast, it decreases the number of "happy" responses (Zernecke et al., 2011).

In recent years, there has been a growing interest in the influence of non-body odors on the evaluation of facial expressions, yet with more inconsistent results across studies. Some studies have reported that valence-contrasted ("valenced") odors influence the perception of expressive faces

according to the emotional congruency between odors and expressions. When the odor context is congruent, happy and disgusted faces are respectively rated as more pleasant and unpleasant (Cook et al., 2017). Furthermore, the amount of expressivity needed to match low-intensity happy and disgusted faces with their full-blown versions is lower when presented with an emotionally congruent odor (Leleu et al., 2015a). Another study observed an odor-expression congruency effect for happiness, but no effect for disgust (Leppänen & Hietanen, 2003). Seubert and collaborators (2010) rather found greater recognition of disgusted faces when paired with both pleasant and unpleasant odor contexts vs. a no-odor context, and no difference for happy faces. A general effect of odor unpleasantness was also reported, with faster recognition (Syrjänen et al., 2017), and more negative valence ratings (Syrjänen et al., 2018) of happy, disgusted, and neutral facial expressions compared with control and pleasant odors. More specifically for neutral faces, Cook et al. (2015, 2018) observed less positive ratings in an unpleasant odor context, but also more positive ratings in a pleasant odor context (Cook et al., 2015).

It is worth noting that the discrepancy between studies may come from the use of various tasks and measurements, which may have biased participants' explicit behavior toward faces. More generally, behavioral performance can be impacted by many factors beyond perceptual abilities, such as understanding of instructions, motivation, decisional and attentional processes. This makes it difficult to determine whether the valence of odors directly modulates the perception of facial expressions, that is, the automatic ability (i.e., without explicit intention) to visually categorize a pattern of facial actions as a specific emotional expression.

To dissociate processing stages and gain more direct access to perceptual operations, several studies used electroencephalographic (EEG) recordings and examined the influence of valenced odors on the event-related potentials (ERPs) evoked by facial expressions (Forscher and Li, 2012; Leleu et al., 2015b; Cook et al., 2015, 2017, 2018; Syrjänen et al., 2018). However, as for behavioral responses, findings were largely inconsistent across studies. Some studies reported an early (i.e., around 160 ms post face-onset) modulation of the ERPs recorded for every facial expression (i.e., anger, disgust, fear, happiness, sadness and neutrality depending on the study) by the mere presence of valenced odorants vs. a control odorant (Forscher & Li, 2012; Leleu et al., 2015b; Cook et al., 2017). Yet, this general odor effect was observed over variable scalp locations (i.e., occipito-temporal: Forscher & Li, 2012; parietal and central: Leleu et al., 2015b; frontal: Cook et al., 2017), and as a lower (Forscher & Li, 2012) or larger (Leleu et al., 2015b; Cook et al., 2017) ERP amplitude. Interactions between odors and the emotion expressed by the face were also described, mainly over occipito-temporal sites (Forscher & Li, 2012; Leleu et al., 2015b; Syrjänen et al., 2018; but see Cook et al., 2017 for interactions over parietal and frontal regions). However, strongly different modulation patterns between odors and expressions were observed, as well as variable latencies after face

stimulus-onset (i.e., around 100 ms: Forscher & Li, 2012; 160 ms: Syrjänen et al., 2018; 210 ms: Leleu et al., 2015b; 260 and 350 ms: Cook et al., 2017).

These inconsistencies across studies may well be accounted for by some limitations of the standard ERP approach that make it inappropriate to isolate the specific processes elicited by a given facial expression (see Dzhelyova et al., 2017; Leleu et al., 2018; Poncet et al., 2019 for discussions). Since scalp ERPs reflect an absolute brain response to the sudden onset of a stimulus against a blank background, many low- and high-level visual processes shared by all (expressive) face stimuli contribute to the response. Hence, reliable differences between expressions are difficult to observe from the simple post-hoc comparison of their respective ERPs. Accordingly, despite two decades of research on the ERP signatures of facial expression processing, no robust and systematic differences between facial expressions have been evidenced, except for neutral vs. any expressive face (Calvo & Nummenmaa, 2016 for review). In addition, the ERP approach suffers from a low signal-to-noise ratio (SNR) which strongly hampers the ability to analyze individual brain responses. Taken together, these limitations are challenging for who wants to precisely delineate the impact of valenced odors on facial expression processing using EEG.

Here we circumvent these issues and report an EEG measurement of the influence of valenced odors on facial expression processing using fast periodic visual stimulation (FPVS-EEG). FPVS-EEG is based on the old observation (Adrian & Matthews, 1934) that a stimulus presented at a rapid periodic rate (e.g., 6 stimuli per second) elicits an EEG response at the exact same frequency (i.e., 6 Hz) and its harmonics (i.e., integer multiples). Frequency-domain analysis of such periodic brain activity allows quantifying an objective signature of the automatic processes elicited by the stimulation with high SNR (Norcia et al., 2015 for review). This approach has been recently adapted to investigate perceptual abilities for faces (e.g., Liu-Shuang et al., 2014; Rossion et al., 2015; Zimmermann et al., 2019), including facial expression processing in healthy (Dzhelyova et al., 2017; Leleu et al., 2018; Poncet et al., 2019) and clinical populations (Leleu et al., 2019; Favre et al., 2019; Van der Donck et al., 2019).

In the current study, we presented visual streams of variable facial expressions at a 6-Hz base stimulation frequency, and inserted a given facial expression every 6 stimuli, i.e., at a 1-Hz expression-specific frequency (Figure 1). The brain response recorded at the base frequency thus reflects the general visual processing of all (expressive) face stimuli (i.e., an absolute brain response to stimulus-onset as for the standard ERP approach) while the expression-specific frequency isolates the differential processing of the periodically-inserted facial expression against all the other expressions. This latter response is thus a direct neural signature of the visual discrimination of a specific facial expression excluding all processes shared with the other expressions. We quantified the expression-specific response to three facial expressions (happiness, disgust, neutrality) recorded

in three valence-contrasted odor contexts (pleasant, unpleasant, control). We hypothesized an effect of valenced odors on the expression-specific response according to the congruency between the valence of the odor and the valence of the emotional expression (i.e., a larger response to happiness and disgust in the pleasant and unpleasant odor contexts, respectively). Moreover, because no clear-cut valence is associated with the neutral expression, we also predicted differential effects of odors on the response to neutrality, according to their valence.

Participants, materials and methods

Participants

Eighteen participants (12 females, mean age = 25.8 ± 7.2 (SD) years, range 19–39 years) were included in the experiment and received financial compensation. Sample size was estimated a priori by considering a moderate odor effect on facial expression discrimination (i.e., Cohen's d = +0.65), a significance level α = .05 (two-tailed) and a standard power 1-β = .80. They reported normal or corrected-to-normal vision and none reported history of psychiatric, neurological or olfactory disorders. All of them provided written informed consent prior to the experiment and testing was conducted in accordance with the Declaration of Helsinki and approved by the French ethics committee (CPP Sud-Est III - 2016-A02056-45).

Visual stimuli

Images from 6 individual faces depicting 5 emotional facial expressions (disgust, happiness, anger, fear, sadness) and neutrality were taken from the KDEF database (identities #: 05F, 09F, 21F, 14H, 32H, 34H, Lundqvist, Flykt & Öhman, 1998) according to a high recognition performance for each facial expression (between 75% and 100% as evaluated by another group of 40 independent adult raters (20 females): mean age = 24.9 ± 4.9 (SD) years, range 18–37 years). Surprise was not included due to its ambiguity in terms of emotional valence (Kim et al., 2004), and the lack of evidence for categorical boundaries between surprise and other expressions (Etcoff & Magee, 1992). Stimuli were equalized in terms of luminance and cropped in a medallion-shape window to discard information from the background and hairstyle (Figure 1). They were displayed on a mid-level grey background (i.e., 128/255 in greyscale) in the center of a screen at an approximate viewing distance of 57 cm. Images were set to a size of 6.8 × 5.2 cm (6.8 × 5.2 ° of visual angle at a viewing distance of 57 cm).

Odor stimuli

To exclude confounding a specific odorant with its hedonic valence, 3 odorants were used for each valence-contrasted context. These odorants were selected among a set of 52 odorants that

were previously evaluated for their hedonic valence by 38 participants (mean age: 24.8 ± 3.78 (SD), range: 20-35, 22 females) using a 10-point scale (ranging from 0 = very unpleasant to 9 = very pleasant) (Vieillard et al., 2020). The three unpleasant odorants were: isovaleric acid bearing a smell of vomit (Aldrich, Steinheim, Germany) rated 1.71 ± 1.74, ethylmethylsulfide bearing a rotten-cabbage quality (96%, Aldrich, CAS: 624-89-5, Steinheim, Germany) rated 2.21 ± 2.07, and triethylamine giving off a rotten fish odor (TEA, Aldrich, CAS: 121-44-8, Steinheim, Germany) rated 2.45 ± 1.59. The three pleasant odorants were: "peppermint essential oil" (Mentha piperita, Pranarôm, Ghislenghien, Belgium) rated 6.79 ± 1.68 (SD), "sweet orange essential oil" (Citrus sinensis, Orange douce, Nature & Découverte, Laboratoire Sirius, Cambounet-sur-le-sor, France) rated 6.97 ± 1.30, and "pear aroma" (Arôme Poire, Meilleur du Chef, Bassussary, France) rated 7.18 ± 1.37. During their initial evaluation, these odorants were presented in glass containers with different dilutions in mineral oil. Eight additional participants evaluated the selected odorants using the experimental display designed in the present EEG experiment (see Procedure) to equate detectability and intensity across odorants, and to determine which quantity was needed to maintain their intensity throughout the experiment. The final concentrations were: "peppermint essential oil" 10^{-3}, "sweat orange essential oil" 10^{-2}, "pear aroma" $10^{-1.4}$, "vomit smell" 10^{-4}, "rotten-cabbage" 10^{-4}, "rotten fish"10^{-2}. The control odor condition was the mineral oil in which the odorants were solved. Every participant received the three odorants in each hedonic condition.

Procedure

The procedure for the visual stimulation was similar to the experiment of Poncet et al. (2019). Fast periodic visual stimulation (FPVS) was designed with a base rate stimulation of 6 Hz (i.e. 6 images/s), and an expression-specific rate of 1 Hz (same emotional expression every 6 pictures, see below). Using a 24-inch LED monitor (refresh rate: 60 Hz, resolution: 1920 × 1080 pixels), stimuli were displayed at the base frequency (6 Hz) without inter-stimulus interval. At this rate, each stimulus is presented for about 167ms, implying that processing occurs at a glance. To avoid low-level repetition effects, the size of the images randomly varied at every stimulus onset, between 95 % and 105 % (i.e., 6.5 × 4.9 ° and 7.1 × 5.5 ° of visual angle respectively). Each stimulation sequence presented one individual face, and tested the processing of one specific facial expression periodically inserted at the expression-specific rate (i.e., 6 Hz / 6 images = 1 Hz, 1 s between two target expressive faces) among the other expressions randomly displayed at the base frequency (Figure 1). Two brain responses are thus elicited within a single stimulation sequence and tagged in the EEG frequency spectrum, reflecting two distinct processes. The brain response recorded at 6 Hz and its harmonics (i.e., integer multiples: 12 Hz, 18 Hz, etc.) reflects the general visual processing of the rapid stream of face stimuli changing in size and expression. By contrast, the brain response elicited

at 1 Hz and harmonics is a direct marker of the automatic discrimination of a given facial expression compared with all the other expressions; i.e., a differential neural activity to a specific expression. In other words, this paradigm directly contrasts every expression category within a single stimulation sequence and thus isolates specific neural responses to one facial expression against the others. The discrimination of three facial expressions was tested in the experiment: happiness, disgust and neutrality. Happiness and disgust were chosen due to their respective congruency with the pleasantness and unpleasantness of the odor stimuli. Neutrality was included to determine whether a neutral face is differentially processed according to the hedonic valence of the odor context.

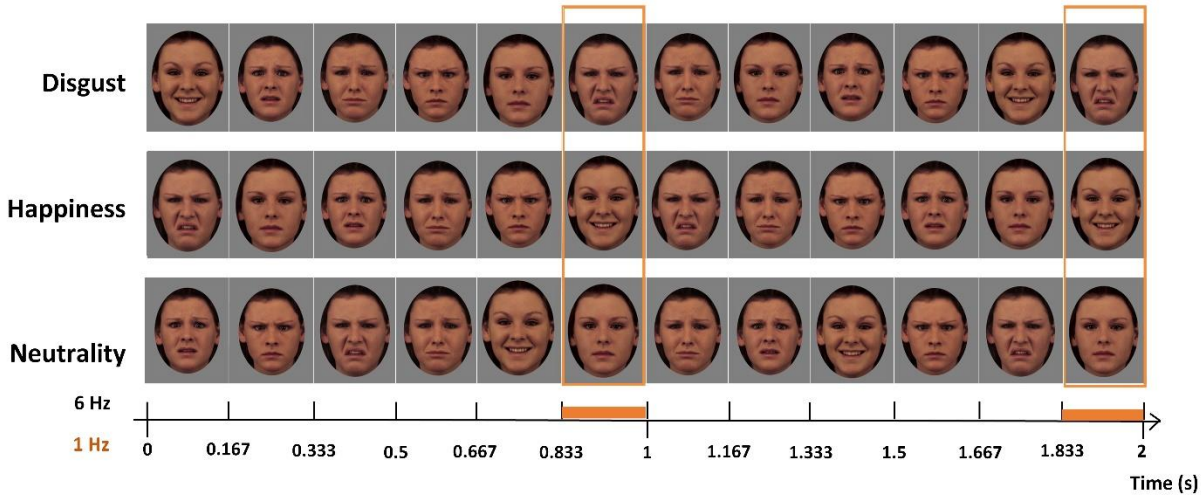

Figure 1. *Visual stimuli and experimental design*. Example of one individual female face with a neutral expression or expressing 5 basic emotions (i.e., anger, disgust, fear, happiness and sadness). All emotions were randomly displayed at a 6 Hz base rate (1 cycle ≈ 167ms) except for one (disgust, happiness or neutrality) which was periodically inserted at a lower rate of 1 Hz (every 6th cycle ≈ 1s between each onset). Every type of sequence was presented with the 3 valenced odor contexts. Images were presented without inter-stimulus interval with a 10 % randomized size variation. This design isolates the specific response to the expression displayed at 1 Hz regardless of the rapid expression changes occurring at 6 Hz.

The procedure for the olfactory stimulation was similar to the one used in Leleu et al. (2015b). Odorants were spiked on a scentless adsorbent material (P100, Powersorb, 3M) and put in dedicated 250-ml polypropylene bottles. Bottles were connected to a constant air-delivering device (0.1 bar). The airflow was purified on charcoal filters, and delivered at room temperature. The main airflow was directed to each bottle using hand-activated valves. Downstream to the bottles, independent tubes were connected to a chinrest, positioned just under the nose of the participants during the experiment. At such low pressure, the airflow was undetectable during testing. We also ensured that the airflow was not detectable from auditory cues. Throughout the experiment, rotation between the different odorants was performed manually using the valves. Since each experimental condition (i.e., a combination between an odor context and a facial expression) was repeated 6 times, each odorant was used for two sequences of the same experimental condition

(e.g., for the condition “pleasant odor – happiness”, each pleasant odorant was used 2 times). For the control odor context, only scentless mineral oil was repeated 6 times. In sum, we evaluated the brain response to three facial expressions (disgust, happiness, neutrality) in 3 odor contexts (pleasant, unpleasant, control) for a total of 9 experimental conditions. Six sequences were presented per condition for a total of 54 sequences per participant. Thus, for each participant, 1/3 of the sequences were associated with pleasant odor contexts, 1/3 with unpleasant odor contexts, and the last 1/3 with the control odor context. Odorants were delivered to the participants during a whole visual stimulation sequence. In addition to being used as the control odor context, the odorless mineral oil was also diffused after each stimulation sequence for a minimum 30-s break before the next sequence, bringing a pause to the olfactory receptors before receiving the odorous molecules of the next sequence.

After EEG-cap placement, participants seated in a light- and sound-isolated cabin and held their head on a chinrest placed at 57 cm from the screen. Each participant was presented with 54 sequences (3 odor conditions x 3 facial expressions × 6 individual faces). For each sequence, the stimulation lasted 26.5 s with a pre-stimulation interval of 0.5 s of a blank screen, followed by a gradual fade-in of increasing contrast modulation depth (1.833 s), and then by the stimulation (23.167 s). Afterward, a gradual fade-out lasted 0.833 s before a blank post-stimulation interval (0.167 s). The 54 sequences were pseudo-randomized (the same identity, odor context, or expression were not presented successively) to define 18 orders (one per participant) divided in 2 blocks of 27 sequences. The presentation order of the 5 non-target expressions at the base frequency followed cycles of the 5 expressions (e.g., anger, disgust, fear, sadness, and neutrality when happiness was presented at the expression-specific frequency; Figure 1) whose order was randomized at each cycle. During each sequence, participants were asked to detect brief (200 ms) changes of the color of a fixation cross (i.e., blue to red) located at the center of the screen 5 random times within every sequence by pressing the space bar with both index fingers. A minimum interval of 3 s between two color changes was introduced. When asked at the end of the experiment, all participants reported having noticed expressive faces during the stimulation, but none detected that a given expression periodically appeared at 1 Hz.

At the end of the experiment, the odorants were evaluated by each participant. Participants were first asked whether they noticed something special during the experiment. All reported having noticed the rapid presentation of expressive faces. In contrast, only 11 participants spontaneously reported that they noticed odors during testing, but none detected all the odorants. Five participants mentioned odors once they were specifically asked for, and two participants did not notice anything. Afterward, each participant evaluated each odorant and the control odor in the experimental display.

They were diffused one by one in a pseudo-random order across participants, i.e., for each individual, pleasant and unpleasant odorants were alternated, each being randomly selected from their respective sets. A 30-s interval of the control odor was introduced between odorants. Half of the participants began with a pleasant odorant, and the other half with an unpleasant odorant. For each odorant, participants were asked whether they smelled something, and if so, they evaluated both the intensity (from 0 no intense to 9 very intense) and valence (from 0 very unpleasant to 9 very pleasant) using 10-point scales. Every participant was able to detect some to all odorants (at least 4/6 with at least one for each valence), and none detected something for the control condition. Mean intensity ratings did not differ between the pleasant (4.40 ± 0.36 [SEM]) and unpleasant (3.68 ± 0.43) odorants ($t(17) = 1.43$, $p = .17$). In contrast, the difference was significant for the valence ratings ($t(17) = 7.22$, $p < .0001$), with a more positive evaluation of the pleasant (6.15 ± 0.38) than of the unpleasant odorants (2.76 ± 0.25).

EEG acquisition

Electroencephalographic (EEG) activity was continuously recorded from a BioSemi Active-Two amplifier system (BioSemi, The Netherlands) with 64 Ag/AgCl electrodes placed according to the 10-10 classification system. During acquisition, the Common Mode Sense (CMS) active electrode was used as reference and the Driven Right Leg (DRL) passive electrode as ground. Electrode offset was reduced between ± 15 µV for each channel and EEG was digitalized at a 1024 Hz sampling rate.

EEG preprocessing

EEG processing was conducted using Letswave 6 (https://www.letswave.org/), running on Matlab 2017 (Mathworks, USA), and largely followed analysis steps described in previous studies (Dzhelyova et al., 2017; Leleu et al., 2018; Poncet et al., 2019). EEG data were first high-pass filtered at 0.1Hz (Butterworth filter, 4^{th} order) and then resampled to 200 Hz to reduce file size and processing time. They were cropped into 27-s segments for each sequence (at the beginning of the fade-in and 1.167 s after the fade-out). We applied an Independent Component Analysis (ICA) (e.g., Makeig et al., 1996) to remove components corresponding to eye blinks (recorded over Fp electrodes) and artifacts recorded over frontal and temporal electrodes. Remaining noisy or artifact-ridden electrodes (i.e., with amplitude exceeding ± 100 µV) were rebuilt using linear interpolation from the four neighboring channels (mean number across participants: 2.5 channels, range: 0–5). EEG epochs were finally re-referenced to a common average reference.

EEG frequency-domain analysis

Preprocessed data were cropped down into 24-sec epochs beginning just after the fade-in and corresponding exactly to twenty-four 1 Hz cycles (for a total of 4800 time bins). The 6 epochs for

each facial expression (i.e., 6 individual faces) were then averaged in the time domain for all participants to reduce EEG activity non-phase-locked to the stimuli. The resulting 9 averaged segments (i.e., 3 odor contexts × 3 expressions) were finally transformed using a fast Fourier transform (FFT) and amplitude spectra were extracted for all channels with a high frequency resolution of 1/24 ≈ 0.0417 Hz. Individual FFT data were grand-averaged across participants for group analysis.

To determine the significant harmonics (i.e., integer multiples) for both general visual (i.e., elicited by the rapid 6-Hz stimulation frequency) and expression-specific (i.e., elicited by the 1-Hz presentation of a given facial expression) responses, FFT grand-averaged data were pooled across conditions and electrodes, and Z-scores were calculated at each frequency bin by subtracting the amplitude of the mean surrounding noise (i.e., estimated from the 20 surrounding frequency bins, 10 on each side, excluding the 2 immediately adjacent and the 2 most extreme bins, e.g. Dzhelyova et al., 2017; Leleu et al., 2018; Poncet et al., 2019) and dividing by the standard deviation of the noise. Harmonics were considered significant until Z-scores were no longer above 1.64 ($p < .05$, one-tailed, signal > noise). For the general visual response, harmonics were significant until the 8th harmonic (i.e., 48 Hz, harmonics were not considered after the 50 Hz response elicited by AC power). For the expression-specific response, harmonics were significant until the 13th harmonic (i.e., 13 Hz).

To quantify the overall magnitude of each brain response in a single value (Retter & Rossion, 2016) expressed in amplitude (µV), individual FFT data for each condition were first baseline corrected by subtracting the mean noise amplitude (see above) and harmonics were summed until the 8th harmonic for the general visual response, and until the 13th harmonic for the expression-specific response, excluding the 6th and 12th harmonics corresponding to the base frequency (i.e., 6 and 12 Hz). These summed baseline-corrected amplitudes (BCA) were then used as a data-driven whole-scalp approach to identify the electrodes over which the responses were the largest. According to previous studies with a similar design (Dzhelyova et al., 2017; Leleu et al., 2018; Poncet et al., 2019), the topography of the general visual response is not different between facial expressions while the topography of the expression-specific response depends on the emotion expressed. Hence, relevant electrodes were identified from all conditions combined for the general visual response whereas electrodes were identified separately for each facial expression (averaged across odor contexts) for the expression-specific response. For the latter response, the three electrodes with the largest BCA (found in the right hemisphere [RH] for each expression) and their homologous channels in the left hemisphere (LH) were selected to determine two regions-of-interest (ROI). ROIs comprised lateral occipito-temporal and occipito-parietal sites for each facial expression (disgust: O1/2, PO7/8, P7/8; happiness: O1/2, PO3/4, PO7/8; neutrality: O1/2, PO7/8, P9/10). For the

general visual response, only one medial occipital ROI was established including the 4 channels with the largest BCA: O1, Oz, O2, and PO8.

Repeated-measures ANOVAs were conducted on the summed BCA for the base response with *Expression* (disgust, happiness and neutrality) and *Odor context* (pleasant, unpleasant and control) as within-subject factors, and for the expression-specific response with *Expression* (disgust, happiness and neutrality), *Odor context* (pleasant, unpleasant and control) and *Hemisphere* (LH, RH) as within-subject factors. Mauchly's test for sphericity violation was performed and Greenhouse-Geisser correction for degrees of freedom was applied whenever sphericity was violated. Post-hoc comparisons were conducted using Tukey's HSD test. For visualization of the brain responses, SNR were calculated as summed uncorrected amplitudes divided by the mean noise amplitude.

To determine whether the different odor contexts may also impact which electrodes present a significant expression-specific response for each facial expression, an additional analysis was conducted on grand-averaged data by computing Z-scores as previously. We explored the 29 posterior electrodes (i.e., behind the midline: CP1, CP2, CP3, CP4, CP5, CP6, CPz, P1, P2, P3, P4, P5, P6, P7, P8, P9, P10, Pz, PO3, PO4, PO7, PO8, POz, O1, O2, Iz, Oz, TP7, TP8) and considered a Bonferroni-corrected p-value to test for the significance of the response compared with mean surrounding noise ($Z > 2.92$, $p < .0017$, one-tailed, signal > noise).

To assess the difference between the odor contexts at an individual level, we calculated Z-scores in every participant and for each posterior electrode (see above). Summed uncorrected amplitudes for two odor conditions were first subtracted and Z-scores were computed as previously using a two-tailed significance threshold for pairwise comparisons between the odor contexts ($Z > 1.96$ or < -1.96, $p < .05$).

Results

Expression-specific response and influence of the odor context

In line with previous studies (Dzhelyova et al., 2017; Leleu et al., 2018; Poncet et al., 2019), the periodic presentation of a specific facial expression at 1 Hz among all the other expressions randomly displayed at 6 Hz triggers a brain response at the same frequency and its harmonics. This response directly reflects single-glance discrimination of the expression against the others. Visual inspection (Figure 2) reveals a clear expression-specific response for the three expressions tested (i.e., disgust, happiness and neutrality). These responses are mainly recorded over lateral occipito-temporal and occipito-parietal regions, with a right-hemispheric dominance. Slightly different spatial distributions of the responses are also visible between the three expressions, especially a more dorsal topography for

happiness than disgust and neutrality. The expression-specific response is of high SNR for all expressions, albeit larger for happiness (SNR ≈ 1.45, 45 % of signal increase) than disgust (SNR ≈ 1.3, 30 % of signal increase) and neutrality (SNR ≈ 1.2, 20 % of signal increase).

The repeated-measures ANOVA confirmed visual inspection with a significant main effect of *Expression,* F(2,34) = 6.13, η^2_p = 0.27, *p* = .005, indicating a larger expression-specific response for happiness (0.52 ± 0.07 [SEM] µV) than for disgust (0.37 ± 0.05 µV, *p* = .02) and neutrality (0.36 ± 0.04 µV, *p* = .01). The main effect of *Hemisphere* was also significant, F(1,17) = 10.41, η^2_p = 0.13, *p* = .005, indicating a larger response over the RH (0.48 ± 0.06 [SEM] µV) than the LH (0.36 ± 0.04 µV) for the three expressions combined.

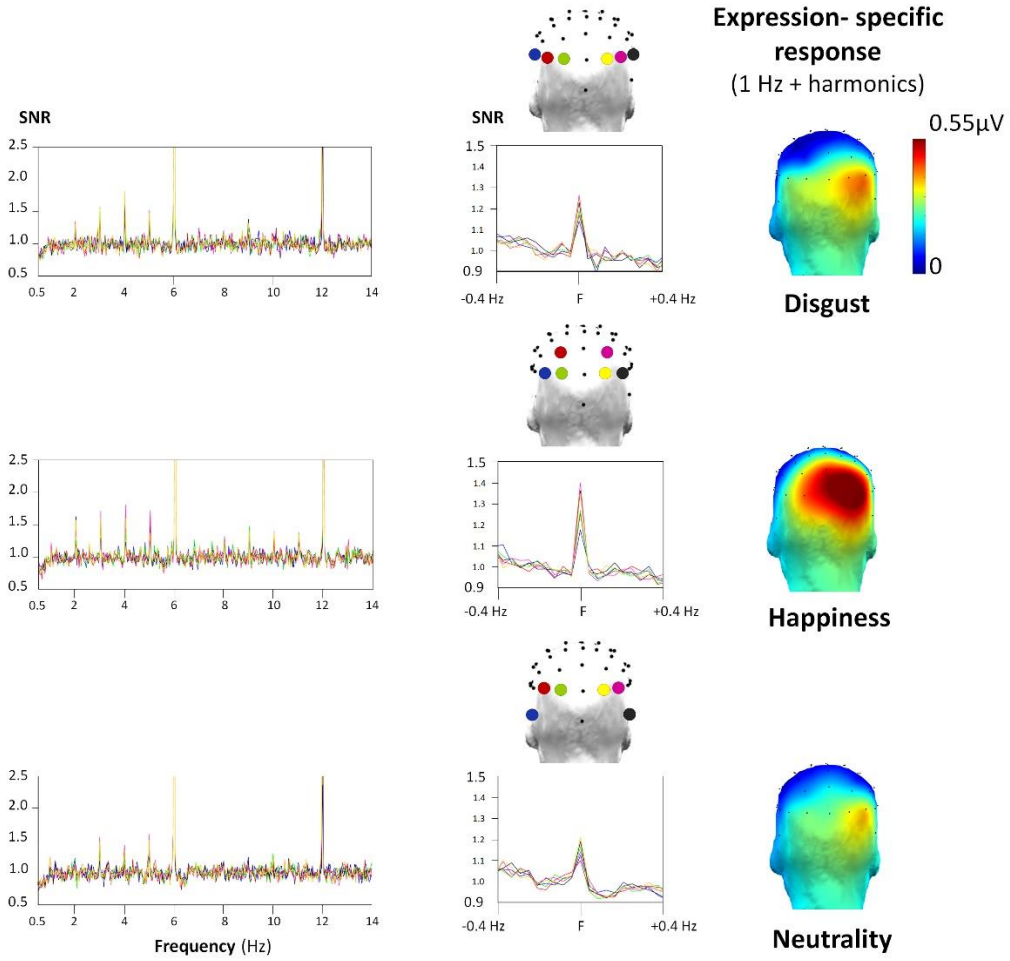

Figure 2. *Expression-specific response for each facial expression.* Left: FFT signal-to-noise ratio (SNR) spectra averaged across the channels included in the regions-of-interest (ROIs) for each of the three facial expressions. SNR for the expression-specific response are visible at 1 Hz and harmonics (i.e., integer multiples, e.g., 2 Hz, 3 Hz) while SNR for the general visual response are visible at 6 Hz and harmonics (only 12 Hz is displayed). Middle: SNR calculated on the sum of significant harmonics of the 1 Hz expression-specific rate (F: until the 13th harmonic, i.e. 13 Hz, excluding the 6 Hz base frequency and its 12-Hz harmonic) and surrounding frequency bins (± 0.4 Hz) for each channel included in the ROIs and for each facial expression. Right: 3D-topographical maps (posterior view) of summed baseline-corrected amplitudes for the expression-specific response to each facial expression.

Most importantly for our purpose, visual inspection of the expression-specific responses depending on the odor context (Figure 3) suggests an influence of the hedonic valence of odors on the rapid discrimination of facial expressions. This modulation by the odor context is more clearly visible for neutrality, with a response larger in the pleasant odor context and lower in the unpleasant odor context compared to the control context. In the unpleasant context, the expression-specific response to neutrality also appears larger over medial parietal sites, suggesting a topographic change rather than a mere modulation of amplitude. For disgust, the expression-specific response is visually reduced in both hedonically contrasted odor contexts compared with the control context, this reduction being more clearly visible in the unpleasant context. Finally, the expression-specific response to happiness does not seem to be strongly modulated by the odor context.

Supporting the observations from visual inspection of the expression-specific response to neutrality, we found a marginally significant interaction between *Expression* and *Odor* ($F(4,68) = 2.48$, $\eta^2_p = 0.13$, $p = .052$), explained by a significant *Odor context* effect on the response to neutrality ($F(2,34) = 3.41$, $p = .045$), but not to disgust ($F(2,34) = 2.06$, $p = .14$) and happiness ($F(2,34) = 0.04$, $p = .96$). Post-hoc comparisons revealed a significantly larger amplitude in the pleasant (0.47 ± 0.06 (SEM) µV) than the control odor context (0.29 ± 0.04 µV, p = .006), and a trend for a significant difference with the unpleasant odor context (0.33 ± 0.05 µV, p = .067). No difference appeared between the responses obtained in the unpleasant and control odor contexts (p = .46).

To further determine whether the expression-specific response varies as a function of the valence of the odor context, we explored the significance of the response over the 29 posterior channels (Figure 3 and Supplementary Table) using Bonferroni-corrected Z-scores ($Z > 2.92$, $p < .0017$, one-tailed, signal > noise). This analysis revealed that every condition led to a significant expression-specific response, except for the response to neutrality in the unpleasant odor context. However, note that a high Z-score of 2.88 ($p < .002$) was found over POz in this context compared with the pleasant ($Z = 1.77$, $p = .038$) and control ($Z = 0.78$, $p = .22$) odor contexts, and several medial parietal channels (P1, P2, P3, P5, CP3) crossed the standard threshold of $Z > 1.64$ ($p < .05$) only for the unpleasant context (pleasant context: $Zs < 1.42$, control context: $Zs < 0.57$). This suggests a topographic change toward medial parietal regions associated with a reduced response over occipito-temporal sites in the unpleasant context, as noted during visual inspection. In addition, Z-scores confirmed the main analysis with 6 vs. only 2 significant electrodes in the pleasant vs. the control odor context. These electrodes were mainly located over the occipito-temporal (OT) region for both contexts.

For the expression-specific response to disgust, Z-scores also supported visual inspection, with 8 significant electrodes in the control odor context vs. only 3 and 2 in the pleasant and unpleasant

contexts, respectively. In both hedonically contrasted contexts, the response is centered over occipito-temporal sites while more diffuse over right parietal and medial occipital regions in the control context. Hence, the significance of the expression-specific response revealed a variable strength depending on the odor context. Finally, as visual inspection suggested for happiness, the expression-specific response was not substantially different depending on the odor context since 8 (control context) or 9 (pleasant and unpleasant contexts) electrodes were significant over occipito-temporal and occipito-parietal scalp regions in every odor context.

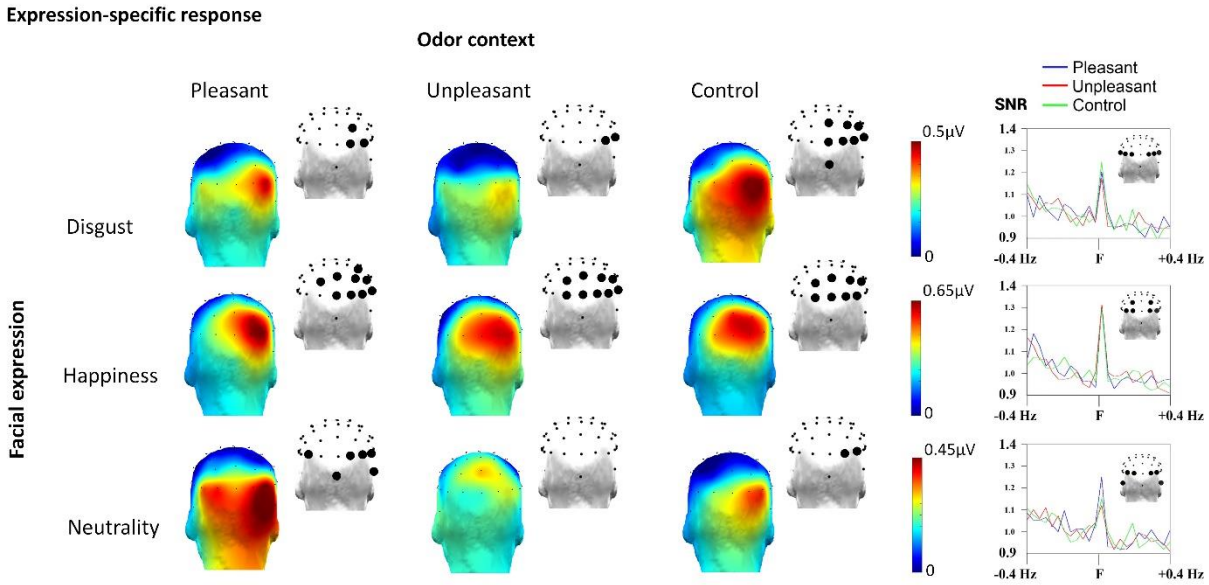

Figure 3. *Expression-specific response according to the odor context.* 3D-topographical maps (posterior view) of summed baseline-corrected amplitudes for the expression-specific response to a disgusted, happy or neutral face in the pleasant, unpleasant and control odor contexts. The smaller topographical maps illustrate which electrodes present a significant response compared with mean surrounding noise ($Z > 2.92$, $p < .0017$, one-tailed, signal > noise). Right: SNR calculated on the sum of significant harmonics of the 1 Hz expression-specific rate and surrounding frequency bins (± 0.4 Hz) in the pleasant, unpleasant and control odor contexts for each facial expression. The amplitude was averaged over all the electrodes that constitute the ROIs for each expression (illustrated on small topographical maps).

Individual odor effects

To explore whether the sensitivity of the expression-specific response to the odor context is reliable across participants, we considered the response to neutrality for which the main analysis revealed a significant odor effect (i.e., larger amplitude in the pleasant than in the control odor context). For every participant (Figure 4), we subtracted the uncorrected response obtained in the control context from the one obtained in the pleasant context, and we determined the significance of individual odor effects using Z-scores calculated for each posterior electrode ($Z > 1.96$ or < -1.96, $p < .05$, two-tailed, pleasant ≠ control).

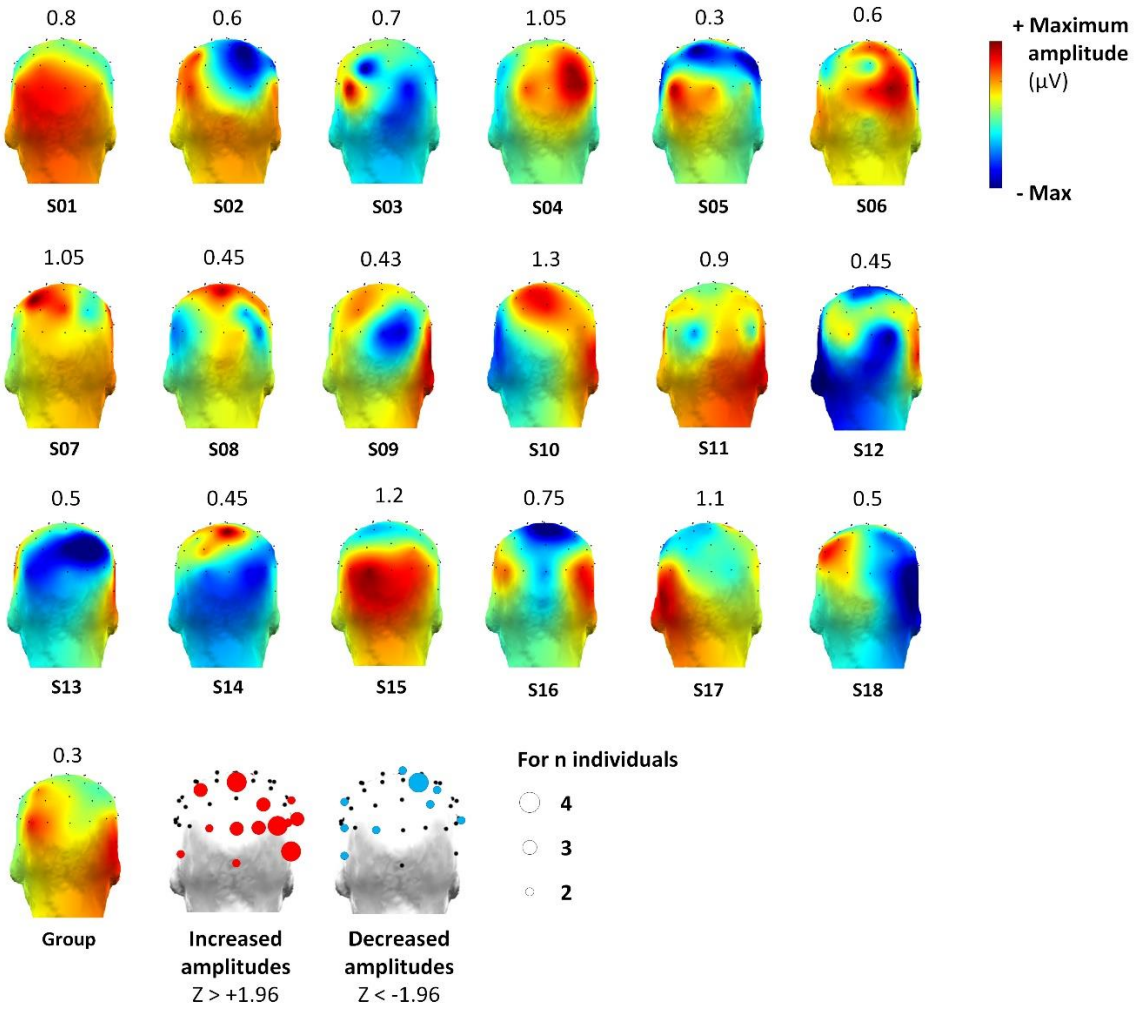

Figure 4. *Group and individual amplitude differences between the pleasant and control odor contexts for the expression-specific response to neutrality.* 3D-topographical maps (posterior view) of summed baseline-corrected amplitudes for the difference between the pleasant and control odor contexts on the neutrality-specific response (color-coded maps) obtained for the group and each individual participant. The value above each map indicates the maximum amplitude of individual color scales (both positive and negative amplitudes). White topographical maps (bottom right) illustrate individual significant differences over the posterior electrodes with color circles (blue: decreased amplitude; red: increased amplitude) when at least 2 individuals presented a difference (circle size at each electrode represents the number of participants with a significant difference).

Among the 18 participants, 16 presented at least one significant differential response between the pleasant and the control contexts over the posterior electrodes, with 15 participants presenting at least one electrode with a larger response in the pleasant context, as observed for the group. Interestingly, 11 participants presented a significant difference between the two odor contexts over at least one electrode belonging to the ROIs defined for the expression-specific response to neutrality (i.e., O1/2, PO7/8, P9/10). Seven out of those 11 participants presented a significantly larger response in the pleasant odor context. The distribution of individual odor effects over the posterior scalp region

(Figure 4) shows a majority of positive effects (i.e., larger amplitude in the pleasant context) with a right occipito-temporal dominance that mirrors the effect observed for grand-averaged data.

General visual response and behavioral data

The brain response recorded at the base frequency and its harmonics reflects the processes elicited by low- and high-level visual cues rapidly changing in the stream of stimulation (e.g., contrast, expression-change). In line with previous studies (Dzhelyova et al., 2017; Leleu et al., 2018; Poncet et al., 2019), we found a clear medial occipital response of high amplitude (Figure 5). This brain response was insensitive to the facial expression displayed at 1 Hz (main effect of *Expression*: $F < 1$) and to the odor context in which the visual stimulation occurred (main effect of *Odor context*: $F < 1$), and these two factors did not interact, $F(2.51,42.64) = 1.44$, $\varepsilon = 0.63$, $\eta^2_p = 0.08$, $p = .25$. Hence, differences in low-level visual processing or attentional level that generally modulate such periodic brain activities (e.g., Kim et al., 2007) cannot account for the effects observed on the expression-specific response.

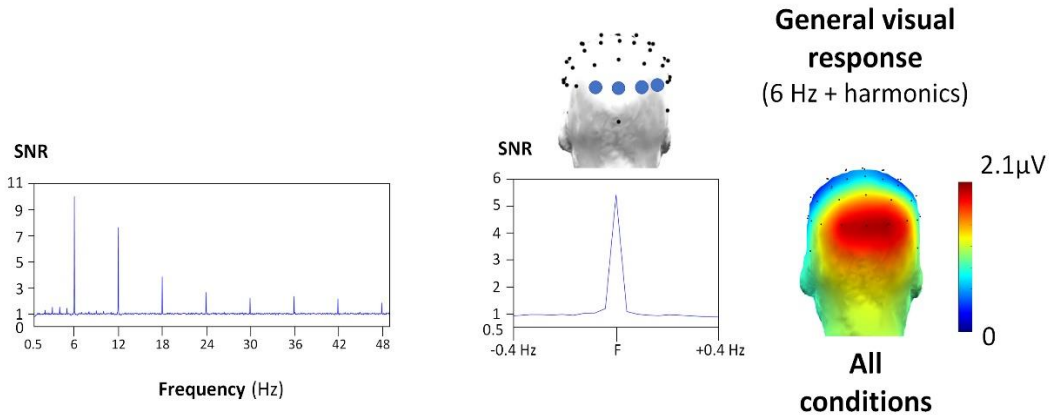

Figure 5. *General visual response.* Left: FFT signal-to-noise ratio (SNR) spectra averaged across the channels included in the region-of-interest (ROI: O1, Oz, O2, PO8) and across facial expressions and odor contexts. High SNR are visible at the 6 Hz base frequency and its harmonics (i.e., integer multiples, e.g., 12 Hz, 18 Hz). Middle: same data depicted for the sum of significant harmonics (F: until the 8th harmonic, i.e., 48 Hz) showing that the overall brain response elicited at the base rate is of high SNR (SNR ≈ 5, 400 % of signal increase). Right: 3D-topographical maps (posterior view) of summed baseline-corrected amplitudes for the general visual response averaged across facial expressions and odor contexts.

Finally, behavioral data for the color-change detection task performed by participants during the visual stimulation showed that the mean accuracy for detecting the blue-to-red cross changes was near ceiling (99.3 ± 0.2 [SEM] %) with a mean correct response time of 371 ± 6 ms. No differences appeared between facial expressions, odor contexts or the *Odor context* × *Expression*

interaction for both accuracy and response times (all Fs < 2.1, all ps > .14), indicating that participants paid similar attention to the stimulation across conditions.

Discussion

By using FPVS-EEG, a highly effective approach for isolating a direct brain marker of rapid (i.e., at a glance) and automatic (i.e., without explicit intention) visual discrimination (Norcia et al., 2015 for review), the present study reveals that contextual valenced odors influence the discrimination of a neutral face, and to a lesser extent of a disgust face, as indexed by an occipito-temporal expression-specific brain response. In particular, the brain response to neutrality is respectively larger and lower in pleasant and unpleasant odor contexts compared with the control odor context. Although not significantly different when considering the mean amplitude of the response over the ROIs, the expression-specific response to disgust is weaker for both valence-contrasted odor contexts compared with the control odor context, as shown by fewer significant electrodes over posterior scalp regions. By contrast, the discrimination response to happiness is not modulated by the presence of valenced odors. In addition, individual expression-specific responses revealed a significant odor context effect on the brain response to a neutral face in a majority of participants.

A main conclusion of the study is that valenced odors do not influence the discrimination of facial expressions through a direct association between discrete basic emotions and odors. Pleasant odors do not specifically improve the discrimination of happiness (nor hinder the discrimination of disgust), and unpleasant odors do not improve the discrimination of disgust (nor hinder the discrimination of happiness). In our design, the expression-specific response is a direct differential brain response to a given facial expression, larger and lower responses respectively indexing more or less efficient discrimination from the other expressions displayed in the stimulation sequence (Poncet et al., 2019). As a result, the amplitude of the expression-specific response can reflect the discrimination of one expression from the others as a function of several discrimination levels, such as the differentiation between discrete basic emotions (i.e., specific patterns of facial actions), but also according to the hedonic valence (i.e., positive or negative). Regarding that latter case, we used 4 negative expressions (anger, disgust, fear and sadness), 1 positive expression (happiness), and 1 hedonically ambiguous expression (neutrality). Happiness is thus the only positive expression among mostly negative expressions, neutrality is an ambiguous expression among mostly negative expressions, and disgust is one negative expression among other mostly negative expressions. Hence, our observations reveal that neutrality is more readily discriminated from mostly negative expressions (anger, disgust, fear, sadness and happiness) in the pleasant odor context while being

more difficult to discriminate from the same expressions in the unpleasant context. By contrast, a disgusted face tends to be less discriminated from other mostly negative expressions (anger, fear, sadness, happiness and neutrality) in both valenced odor contexts. For happiness, discrimination from mostly negative expressions (anger, disgust, fear, sadness and neutrality) is similar across odor conditions.

In light of these findings, we suggest that valenced odors influence the processing of facial expressions as a function of the hedonic valence (positive/pleasant vs. negative/unpleasant) of both expressions and odors (depending on the ambiguity of the expression, see below), whereas expressions are more discriminated as discrete basic emotions without valenced odors (i.e. in the control odor condition). For unambiguous facial expressions (happiness and disgust), the presence of any valenced odor, either congruent or incongruent, would orient their processing toward their own valence. Disgust would be processed more as a negative expression, and its discrimination from other mostly negative expressions would be hindered. Happiness would be processed more as a positive expression readily discriminated from other mostly negative expressions. However, happiness, as a basic emotion, is already efficiently discriminated from other expressions (i.e., the "happy face advantage" generally attributed to the high saliency of its distinctive features, e.g. the smile; Feyereisen et al., 1986; see Calvo & Nummenmaa, 2016 for review). This would explain why there is no difference between odor contexts for this expression, in line with the large, perhaps saturated, expression-specific response we observed for happiness in every odor condition. By contrast, for neutrality, the valence of the facial expression is ambiguous, such that the processing of a neutral face would depend more on the odor valence (i.e., pleasant or unpleasant). In other words, neutrality may be processed as more positive in the pleasant odor context, and as more negative in the unpleasant context, respectively leading to facilitated and hampered discrimination from other mostly negative expressions (the trend for a sparser topographical distribution of the response to neutrality in the unpleasant context further suggests less reliable processing). The strong and opposite odor effects of pleasant vs. unpleasant odors for neutrality would thus mainly rely on the ambiguity of this expression in terms of hedonic valence.

Supporting the interpretation of an odor-driven perceptual bias toward the valence of the odor for the ambiguous neutral expression, previous behavioral tasks showed that neutral faces are judged as more negative in an unpleasant odor context, and as more positive in a pleasant context (Cook et al., 2015; Li et al., 2007). The fact that neutrality is sensitive to valenced odor contexts, certainly because there is no straightforward interpretation of the emotion it expressed, suggests that odors more strongly mediate facial expression processing for ambiguous stimuli. This view is in accordance with many previous studies showing the largest effects of stress-related and valence-

contrasted odors when facial expressions are ambiguous (Forscher & Li, 2012; Leleu et al., 2015a; Mujica-Parrodi et al., 2009; Novak et al., 2015; Rubin et al., 2012; Zernecke et al., 2011; Zhou & Chen, 2009; but see Wudarczyk et al., 2016 for a larger odor effect with full-blown expressions). However, the current findings are also difficult to reconcile with previous studies showing inconsistent effects of valenced odors on facial expression perception. Behavioral studies reported odor-expression valence congruency effects (Cook et al., 2017; Leleu et al., 2015a; Leppänen & Hietanen, 2003), better recognition of disgust in both pleasant and unpleasant odor contexts (Seubert et al., 2010), or a general effect of unpleasant odors on happiness, disgust and neutrality (Syrjänen et al., 2018). Previous ERP studies also reported various interaction patterns between valenced odors and facial expressions (Cook et al., 2017; Forscher & Li, 2012; Leleu et al., 2015b; Syrjänen et al., 2018), but none relates to our findings. This could well be explained by the nature of ERPs, which are absolute brain responses that do not directly reflect facial expression discrimination, contrary to the expression-specific response we isolated.

One may also suggest that the valenced odor effect reported here is specific to the present experimental design, when facial expressions must be rapidly discriminated within fast trains of stimuli while participants perform an orthogonal task. Future studies should obviously explore this possibility, but we note that it would strengthen the view that facial expression perception largely depends on contextual information (for reviews see Wieser & Brosch, 2012; Barrett et al., 2011; Hassin et al., 2013; Aviezer et al., 2017). More generally, the strong dependency on contextual cues could account for the discrepancy across reviewed studies. For instance, it has been reported that the effect of valenced odors on the visual matching of facial expressions is influenced by the presence of verbal labels (Leleu et al., 2015a). Low-intensity angry and disgust faces are better matched with their full-blown versions in an unpleasant odor context when no verbal information is displayed, while the effect becomes restricted to disgust when emotional labels are associated with the faces. Such context-driven perception is consistent with the view that facial expressions are not always categorized as discrete entities signaling basic emotions (Jack et al., 2012; Sauter & Eisner, 2013). It also supports the recent claim that one facial expression is not always associated with the same emotion, and one emotion is not always expressed by the same facial movements (Barrett et al., 2019). Following this claim, valenced odors could likely modify which emotion (or emotional property) is attributed to a given facial expression. Thus, a possibility is that the expression-specific response might reflect a mixture of categorization processes (e.g., as a basic discrete expression, as a positive/negative expression), each with different weights depending on the valenced odor context.

What could be the underlying neural substrates of the valenced odor effect? Facial expressions are processed in the ventral occipito-temporal cortex (VOTC; e.g., Haxby et al., 2000;

Kawasaki et al., 2012), and in the posterior part of the superior temporal sulcus (pSTS; e.g., Puce et al., 2003; Srinivasan et al., 2016). They also recruit a large network of regions dedicated to emotional processing such as the amygdala (e.g., Harris et al., 2014, Whalen et al., 2013), the insula (e.g., Chen et al., 2009; Wicker et al., 2003), and the orbitofrontal cortex (OFC; e.g., Adolphs, 2002; Whalen et al., 2013). Similarly, olfactory neural pathways involve the amygdala, the insula, and the OFC (Anderson et al., 2003; Rolls & Baylis, 1994; Royet et al., 2000; Wicker et al., 2003; Zald & Pardo, 1997; Zald, 2003; Zatorre et al., 2000). Therefore, the valenced odor context may induce modulations in these "emotional" brain regions during the processing of facial expressions. Though precise neural sources cannot be easily estimated from EEG, the scalp location of the expression-specific response over posterior cortical regions suggests a main generator in the visual system. Odor-driven modulation of the "emotional" structures may thus directly influence the visual processing of facial expressions through reentrant connections with visual areas. Accordingly, a functional neuroimaging study observed that associations between odor inputs and facial expressions elicit increased activity in the insula and the VOTC (Seubert et al., 2010). Another study found strengthened connectivity between the amygdala, the OFC and the pSTS (Novak et al., 2015), the latter being a hub for multisensory integration of socio-emotional signals (e.g., Hagan et al., 2009; Watson et al., 2014). Considering that odor valence is mainly coded in the OFC (Anderson et al., 2003), and that the OFC and the VOTC actively communicate during visual perception (Bar et al., 2006), an interaction between those two brain regions may particularly subtend the odor-related valence effect we observed in the present study. However, strong conclusions about neural underpinnings cannot be drawn from EEG and further studies are needed.

Finally, contrary to the expression-specific response, the general visual response elicited by the rapid stream of expressive faces is not affected by valenced odor contexts. Similarly, the explicit response of the participants during the orthogonal task is not different between odor conditions. These results suggest that valenced odors had no attentional effect on a simple behavioral task and on the absolute neural activity elicited by the visual stream of expressive faces. By using the standard ERP approach in EEG, previous studies found that valenced odors have a general effect on the absolute brain response to facial expressions as early as 160 ms after face-onset (Forscher & Li, 2012; Leleu et al., 2015b; Cook et al., 2017). However, our study presents methodological specificities such as the use of a rapid stimulation rate (i.e., 6 images per second; stimulus duration ≈ 167 ms) and facial expression changes at each stimulus-onset with forward- and backward-masking from surrounding stimuli. This experimental design puts the visual system under tight constraints that may have reduced/abolished any general influence of valenced odors. Future studies using FPVS-EEG to investigate the influence of valenced odors on visual processing should disentangle this issue.

In conclusion, the present study brings novel evidence about the influence of valenced odors on facial expression processing by using an original EEG approach, which isolates and quantifies a neural marker of rapid and automatic discrimination of facial expression in every participant with high validity (i.e., by measuring a direct differential response to a given expression contrasted with other expressions), high SNR (i.e., the response is confined in a tiny portion of the EEG spectrum), and objectivity (i.e., frequencies are pre-experimentally defined). Admittedly, future studies should bolster the current findings in larger samples and investigate the numerous (contextual) factors that could mediate how valenced odors influence facial expression discrimination. FPVS-EEG provides a unique opportunity to further address this issue, and more generally to explore how information is integrated across the senses during (a)typical processing.

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Open Practices Statement

None of the data or materials for the experiments reported here is available, and none of the experiments was preregistered.

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