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Highlights

- We explored whether contextual odors modulate facial expression processing with ERPs
- The odors modulated the ERPs in response to facial expressions in two phases
- First, ERPs around 160 ms were enhanced by odors regardless of the expression
- Second, the aversive odor interacted with the content of expressions around 200 ms

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Contextual odors modulate the visual processing of emotional facial expressions: An ERP study

(Running title: Odor effects on expression processing)

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Abstract

1
2 We studied the time course of the cerebral integration of olfaction in the visual
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4 processing of emotional faces during an orthogonal task asking for detection of red-colored
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6 faces among expressive faces. Happy, angry, disgust, fearful, sad, and neutral faces were
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8 displayed in pleasant, aversive or no odor control olfactory contexts while EEG was recorded
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10 to extract event-related potentials (ERPs). Results indicated that the expressive faces
11
12 modulated the cerebral responses at occipito-parietal, central and central-parietal electrodes
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14 from around 100 ms and until 480 ms after face onset. The response was divided in different
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16 successive stages corresponding to different ERP components (P100, N170, P200 and N250
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18 (EPN), and LPP). The olfactory contexts influenced the ERPs in response to facial
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20 expressions in two phases. First, regardless of their emotional content, the response to faces
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22 was enhanced by both odors compared with no odor approximately 160 ms after face-onset at
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24 several central, centro-parietal and left lateral electrodes. The topography of this effect clearly
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26 depended on the valence of odors. Then, a second phase occurred, but only in the aversive
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28 olfactory context, which modulated differentially the P200 at occipital sites (starting
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30 approximately 200 ms post-stimulus) by amplifying the differential response to expressions,
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32 especially between emotional neutrality and both happiness and disgust. Overall, the present
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34 study suggests that the olfactory context first elicits an undifferentiated effect around 160 ms
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36 after face onset, followed by a specific modulation at 200 ms induced by the aversive odor on
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38 neutral and affectively congruent/incongruent expressions.
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48 **Key-words:** Facial expression, Olfaction, Inter-sensory integration, Multisensory processes,
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1. Introduction

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2 The perception of facial expressions of emotions is not an encapsulated mechanism
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4 only involving the processing of visual cues from faces, but it also integrates information
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6 from the context (for reviews, see Barrett et al., 2011; Hassin et al., 2013; Wieser & Brosch,
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8 2012). Various types of contextual information influence facial expression perception. For
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10 example, gaze direction (e.g., Adams et al., 2003; Sander et al., 2007) and body posture (e.g.,
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12 Aviezer et al., 2008; Meeren et al., 2005) modulate the way we perceived emotions in faces.
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14 External features such as surrounding visual scenes (Righart & de Gelder, 2006, 2008), verbal
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16 labels (e.g., Gendron et al., 2012) or sentences describing the situation encountered by the
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18 perceived face (Diéguez-Risco et al., 2013) are also integrated in expression perception.
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20 Likewise, the perception of emotions in faces also depends on the perceiver's internal states
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22 such as facial mimicry (Niedenthal et al., 2001; Oberman et al., 2007), emotional state (e.g.,
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24 Niedenthal et al., 2001) or social bias (e.g., Bijlstra et al., 2014). Studies using event-related
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26 potentials (ERPs) indicated that contextual integration could arise at different processing
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28 stages reflected by the N170 (Righart & de Gelder, 2006, 2008) or the late positive potential
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30 (LPP) (Diéguez-Risco et al., 2013).
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39 The above-reviewed literature deals with the integration of the visual context but
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41 contextual influences are also multisensory. For instance, the modulation of facial expressions
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43 perception by auditory cues from the voice, especially affective prosody, has been largely
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45 described (e.g., de Gelder & Vroomen, 2000; Dolan et al., 2001). At the cerebral level, it has
46
47 been shown that the activity of the amygdala and the fusiform gyrus is enhanced when a
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49 fearful face is displayed with a congruent vocal intonation (e.g., Dolan et al., 2001).
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51 Moreover, greater activation for expressive faces presented with affective voices has been
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53 found in the posterior part of the superior temporal sulcus (STS) and in the middle temporal
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55 gyrus (e.g., Pourtois et al., 2005a), two regions involved in multisensory integration. The
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1 face-voice integration in the posterior STS occurs within the first 250 ms of processing as
2 revealed by a MEG study (Hagan et al., 2009).
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4 In this respect, affective information carried by odors may be able to modulate the
5 perception of emotions in expressive faces. An increasing number of studies indicate that
6 olfaction does not play as minor a role as was previously believed in human behavior and
7 cognition (see Zucco et al., 2012, 2014, for reviews). In particular, olfaction modulates the
8 processing of information by the senses considered as “major” (e.g., Robinson et al, 2013;
9 Seigneuric et al., 2010) and is strongly involved in multisensory social interactions (for
10 reviews, cf. Schaal & Porter, 1991; Semin & de Groot, 2013). In visual scenes and in social
11 objects as well, faces are stimuli for which the processing appears especially sensitive to the
12 olfactory context. The odor context modulates visual processing in face encoding and
13 recognition (Steinberg et al., 2012; Walla, 2008; Walla et al., 2003, 2005) and in the rating of
14 attractiveness (Demattè et al., 2007; Lundstrom & Olsson, 2005), likeability (Li et al., 2007),
15 stress level or confidence (Dalton et al., 2013). This odor context effect on face processing is
16 already fully active in early infancy (Durand et al., 2013).
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36 Odors also influence the perception of facial expressions (Leppänen & Hietanen,
37 2003; Mujica-Parodi et al., 2009; Pause et al., 2004; Seubert et al., 2010a, 2010b; Zernecke et
38 al., 2011; Zhou & Chen, 2009). For example, Leppänen and Hietanen (2003) identified faster
39 and more accurate recognition of happy faces in pleasant (lemon, strawberry, or vanilla) than
40 in aversive (pyridine) or no-odor contexts. Conversely, Seubert et al. (2010b) identified
41 slower and less accurate recognition of smiling faces with odor priming regardless of the
42 valence of the odor (vanillin vs. hydrogen sulfide), but enhanced speed and accuracy for
43 disgust faces. An fMRI study demonstrated that odorants activate the primary olfactory
44 cortex, the anterior insula and the superior temporal gyrus during the perception of facial
45 expressions (Seubert et al., 2010a). Hypoactivation for disgust faces in the fusiform, middle
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1 frontal and middle cingulate gyri was interpreted as reflecting the priming effect of both
2 aversive and pleasant odorants. This priming effect was also noted in the anterior insula, but
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4 only with an aversive odor.
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7 Thus, odors clearly influence how facial expressions are processed. However, little is
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9 known regarding the dynamic interactions between olfaction and vision in the modulation of
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11 the cerebral response to emotional facial expressions. Several recent studies have revealed
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13 that compared with a control odor, the odor of sweat (collected either after physical exercise
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15 or after an anxiogenic situation) enhances the amplitudes of both the P100/N100 and N170
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17 components of the event-related potentials (ERPs) in response to fearful faces, with a
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19 diminished late LPP (Late Positive Potential, Adolph et al., 2013). These results were
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21 interpreted as reflecting the effects of sweat odor to enhance the allocation of visual attention
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23 toward faces. It has also been reported that stress sweat enhances the late LPP (400-600 ms
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25 post-stimulus-onset) to neutral and ambiguous faces, but not to angry faces (Rubin et al.,
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27 2012). The same authors also reported an earlier effect of stress odor on the early LPP (250-
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29 400 ms), which was not specific of neutral, ambiguous, or angry expressions. Though mixed,
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31 these results suggest at least two phases in the olfactory modulations of visual processing of
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33 facial expressions: first, a global odor effect on any facial expression and then an interactive
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35 odor-vision effect that depends on the emotional content of the facial expression.
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43 These ERPs studies, however, concerned biological odorants emitted by the body
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45 which convey potential information regarding the emitter's emotional state. Much less is
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47 known regarding the time course of the effect of environmental odorants (e.g., related to food
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49 or to non-specific surroundings) that concurrently influence the emotional state of both the
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51 emitter and the perceiver. In a recent study, Forscher and Li (2012) reported that aversive
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53 odors (valeric and hexanoic acids) reduce the spatial attention bias to low-intensity fearful
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55 faces in a dot-probe task, and this behavioral effect was accompanied by a reduced P100
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1 amplitude for fearful faces compared with neutral ones. The N170 amplitude was
2 subsequently decreased in the negative odor context, but without selective interference
3 according to expressions. Hence, these results suggest that environmental odorants may
4 influence early visual processing of emotional faces through the congruency between the
5 emotional valences of both cues. However, this effect might also be due to an undifferentiated
6 effect of the presence of an odor irrespective of its valence. Remember that behavioral data
7 have shown inconsistent results, either congruency effects between odors and
8 happiness/disgust (e.g., Leppänen & Hietanen, 2003) or a global effect of odors for disgust
9 and happiness whatever the affective valence of the olfactory cues (e.g., Seubert et al.,
10 2010b). As far as we know, no ERP study has attempted to assess whether hedonically
11 contrasted odors differentially modulate the early processing of facial expressions. An
12 additional explanation of the discrepant results may be a task-dependent integration of
13 olfactory and visual information, as the modulation of facial emotion processing by odors
14 may depend on decisional and goal-directed mechanisms. Thus, the task-unrelated influence
15 of odors on the early visual processing of emotional faces needs to be investigated to dismiss
16 any contribution of such mechanisms.

17 Accordingly, the present study aimed to clarify the nature and time course of olfactory
18 influences on the processing of facially-expressed emotions, when no bodily emitted odorants
19 are used and when the task performed is orthogonal to facial expression processing (i.e.,
20 pleasant/aversive/control olfactory contexts alternated with happy/disgust/other expressions).
21 The participants were engaged in a detection task of neutral red-faces among expressive and
22 neutral non-red faces displayed in hedonically contrasted odor contexts (butyric acid as an
23 aversive context and strawberry as a pleasant context) or in a no odor control context. The
24 non-red faces were expressive faces, which valence was congruent/incongruent with the
25 olfactory context (i.e., happy and disgust expression). They were also composed of different

1 control conditions with expressive faces unrelated to both odors (i.e., angry, fearful, and sad
2 faces) and neutral faces. Based on previous ERP studies (Forscher & Li, 2012; Rubin et al.,
3 2012), we hypothesized that the odor context would modulate the ERPs to facial expressions
4 in two phases: An early global effect of the olfactory context on the cerebral processing of
5 faces should first emerge whatever the expressions, followed by a subsequent interactive
6 odor-vision effect with the valence of the olfactory context differentially modulating ERPs
7 according to the congruent/incongruent relation with the perceived facial expression.
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10 11 12 13 14 15 16 17 18 **2. Methods**

19 20 21 *2.1. Participants*

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24 Twenty-nine participants were recruited by advertisements and remunerated for their
25 participation. All of the participants provided informed consent, and testing was conducted
26 according to the Declaration of Helsinki (BMJ 1991; 302: 1194). Five participants were
27 excluded because their EEG recordings were too noisy (less than 60% of signals kept after
28 artefact rejection, see below). The final sample was composed of 24 participants (12 women;
29 mean age \pm SD: 22 ± 2.9 years; range: 18-30 years). They were all right-handed (mean
30 laterality quotient \pm SD: $0.78 \pm .14$; range: + 0.52 to +1; Dorte et al., 1995). At the moment
31 of the experiment, no participant reported any problem regarding their vision and olfaction
32 (no allergies or infections). At the end of the experiment, the participants were interviewed
33 with a standardized set of questions regarding their degree of awareness of odors in the
34 environment. Twelve participants spontaneously reported having smelled an odor when they
35 were asked if they noticed anything unusual, and ten other participants only reported smelling
36 an odor when they were asked. None of the participants noticed the exact source of the
37 odorants (chinrest), nor any somesthetic stimulation related to the flow of odor, but reported
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their impression that some odor stimuli (perfume/body odor) were linked to the room or the experimenter.

2.2. Stimuli

2.2.1. Face stimuli

The participants were required to detect neutral red-colored faces among sets of emotional and neutral distractor faces. Six different facial identities were chosen from the NimStim set of facial expressions (Models F01, F02, F05, F07, F09 and F10; Tottenham et al., 2009); for each model, neutral pictures and 5 different emotions (angry, happy, sad, fear and disgust) were selected. An additional set of 6 neutral faces was used to create the “red faces”. The faces were cropped and mounted on a gray background of medium luminance (gray level = 128) and scaled to an image size of 385×513 pixels. The “red faces” were created by increasing the intensity of red to 175-189 in the RGB properties.

2.2.2. Olfactory stimulation

Two odor stimuli were selected for their contrasted hedonic valence: a pleasant strawberry odor (“Meilleur du Chef”, Maignon, France) and butyric acid (Sigma, Saint-Quentin-Fallaviers, France), which conveys a cheese odor that is strongly aversive (Soussignan & Schaal, 1996; Schaal et al., 1997). The strawberry odor was used in undiluted form, while butyric acid was diluted in mineral oil (concentration: $5 \cdot 10^{-4}$ v/v). We used 20 μ L strawberry and 40 μ L butyric acid solutions that were spiked on pieces of an odorless adsorbent material (P100, Powersorb, 3M). These concentrations were chosen due to a pilot study that was performed with 4 judges to determine the subjective intensity and detectability of both odor stimuli and equilibrate them. Each judge was tested with the same experimental display as in the main experiment (see below). Different concentrations were presented for each odor stimulus and the judges should say whether they detected an odor and which odor it

1 was. The lowest concentrations for an accurate detection were kept for the main experiment.
2 The pieces of absorbent material were introduced into 20-ml polypropylene bottles. The
3 control stimulus consisted of a bottle that contained the scentless adsorbent material without
4 any odorant. These bottles were connected to an air-delivering device through which a
5 constant flow of scentless air was passed (at 0.5 bars). This continuous flow of air originated
6 from a tank of pressured air which was purified on charcoal filters and set at room
7 temperature. The main air-stream was directed to one of the 3 20-ml polypropylene bottles
8 through a hand-activated valve so that it could entrain the odor-saturated air developed over
9 the adsorbent material within each bottle. Downstream of each bottle, an independent tube
10 was connected to a chinrest on which the participants applied their heads during the whole
11 experiment. Although it was extremely weak, the air-flow was not directed toward the
12 participants' face to ensure that it could not be detected through somesthetic stimulation. The
13 odor-laden or control airflows were thus conveyed under the participants' noses in the absence
14 of visual or auditory cues. The odor-delivery device was hidden from the participants' visual
15 field.

16 ***2.3. Procedure***

17 After the electrode-cap placement, the participants were seated in a light-attenuated
18 room in front of a screen where the stimuli were displayed at a viewing distance of 57 cm.
19 The sequence of a trial started with a fixation cross lasting 400 ms, followed by the
20 presentation of a face stimulus for 700 ms (see figure 1). A blank screen then followed for a
21 random interval between 300 and 500 ms. Participants were asked to detect when a face
22 stimulus was red-colored by pressing as quickly as possible the "space bar" of a computer
23 with both forefingers. Each block was composed of 42 trials: 36 trials with non-red faces
24 expressing neutrality or one emotional expression among the five used and 6 trials with
25

1 neutral red-faces. The participants were trained during 7 blocks (without any air-flow
2 delivery). The test was subsequently initiated and consisted of 21 blocks of 42 trials. Each
3 block was associated with one odor. The order of odor stimuli was counterbalanced across
4 participants for the 3 first blocks (for example: butyric acid – strawberry – control). The same
5 sequence of olfactory context was then repeated for the 6 remaining sets of 3 blocks. The 6
6 possible orders (with 3 olfactory contexts) were balanced across participants. Participants
7 could rest between blocks, with minimal inter-block intervals of 1 minutes. Finally, in each
8 odor context, the entire procedure comprised 252 trials for non-red faces (five expressions and
9 neutrality) and 42 trials for neutral red faces. Only trials containing non-red faces were
10 analyzed (42 for each emotional expression, 42 for neutrality) as we aimed to examine
11 olfactory-visual interactions during the passive viewing of facial expressions. The unrelated
12 “red-face” detection task was performed to ensure that participants paid attention to the
13 stimuli.

31 Insert figure 1 here

34 ***2.4. EEG recording and analysis***

35 EEG was continuously recorded from 32 Ag/AgCl electrodes mounted in an electrode
36 cap (Waveguard, ANT, Enschede, The Netherlands) according to the 10-10 classification
37 system with respect to a reference electrode placed in a fronto-central position (AFz). It was
38 digitalized at a sampling rate of 1024 Hz (band-pass filter: 0.1–100 Hz) and electrode
39 impedance was maintained below 10 k Ω . EEG data were analyzed with the ASA software
40 (version 4.6, ANT). A 30 Hz low-pass filter was applied off-line and all electrodes were re-
41 referenced to a common average reference. ERPs were then averaged for 600 ms, including a
42 100-ms baseline prior to the stimulus-onset and a 500-ms interval after the stimulus-onset,
43 and trials contaminated with eye movements or other artifacts were rejected (any activity
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1 exceeding $\pm 75 \mu\text{V}$ relative to the baseline). After artefact rejection, all conditions (i.e., for
2 each expression in each olfactory context) contained at least 27 trials (range: 27-42) for the
3 remaining participants. Only trials containing non-red expressive and neutral faces were
4 analyzed.
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9 Inferential analyses were performed on mean amplitudes for distinct components that
10 have been shown to be involved in face and facial expression processing (e.g., Williams et al.,
11 2006). At occipital and parietal sites, the P100, N170, P200 and N250 components were
12 analyzed (electrodes O1/2, P3/4, and P7/8). The P100 was tested by averaging the signal in
13 the 80-110-ms window, the N170 in the 130-180-ms window, the P200 in the 180-240-ms
14 window, and the N250 in the 240-320-ms window. These time windows were chosen by
15 visually inspecting the time course of each component. In the 130-180-ms time-window, the
16 vertex positive potential (VPP) was also analyzed at central sites (electrodes C3/4, Cz; George
17 et al., 1996). Finally, the LPP was analyzed at central-parietal sites (electrodes C3/4, CP5/6;
18 e.g., Schupp et al., 2004) in the 320-480 ms time-window.
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34 The data were analyzed by computing ANOVAs for the different components.
35 Analyses on P100, N170, P200 and N250 included four within-subjects factors: Expression
36 (anger vs. disgust vs. happiness vs. neutrality vs. fear vs. sadness), Olfactory context (aversive
37 vs. pleasant vs. control), Hemisphere (right vs. left), and Site (O1/2, P3/4, and P7/8). Another
38 Site factor was used for the VPP analysis (C3, Cz, C4) and the Hemisphere factor was not
39 included due to the central site (Cz). The LPP was analyzed with the Expression, Olfactory
40 context and Hemisphere factors, and another Site factor (C3/4, CP5/6). Greenhouse-Geisser
41 corrections were performed for each main effect and interaction. Post-hoc analyses were
42 performed using the Tukey's one-factor HSD procedure. In order to improve readability, main
43 effects or interactions involving the Site and Hemisphere factors will be described only if they
44 interacted with the Expression and/or Olfactory context factors.
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3. Results

Results regarding the main effect of facial expression (regardless of olfactory contexts) for each component will be presented first to consider the different stages of expression processing. Then, results regarding the modulations induced by the olfactory context will be presented in detail.

3.1. Different phases of facial expression processing

The modulations of cerebral response induced by the expressions at electrodes O1/2, P3/4, P7/8 are illustrated in figure 2. The modulations at electrodes CP5/6, C3/4 and Cz are illustrated in figure 3. Distinct patterns emerged for the different components (P100, N170, VPP, P200, N250 and LPP), which indicate different phases in the visual processing of emotional faces.

Insert figure 2 here

For the **P100**, figure 2 shows an early effect of fear at central parietal sites (P3/4) and, both anger and disgust at the more lateral parietal sites (P7/8). The main effect of Expression was not significant ($F(4,89)=1.06$), but it interacted significantly with Site ($F(6,135)=6.79$, $\epsilon=.59$, $p<.0001$, $\eta^2=.23$) with a significant effect of Expression at both P3/4 and P7/8 ($F(4,96)=5.67$, $\epsilon=.84$, $p<.001$, $\eta^2=.20$ and $F(5,104)=4.73$, $\epsilon=.90$, $p<.001$, $\eta^2=0.17$) but not at O1/2 ($F<1$). At P3/4, post-hoc comparisons indicated that the P100 was significantly more positive for fear than anger ($p<.01$), sadness ($p<.001$) or happiness ($p<.0001$), whereas at P7/8 the P100 was significantly larger for anger and disgust than neutrality ($p<.01$ and $p<.001$, respectively).

At central sites in the 130-180-ms time-window, a main effect of Expression emerged in the **VPP** amplitude ($F(4,95)=8.38$, $\epsilon=.83$, $p<.0001$, $\eta^2=.27$) with a pattern close to the one found for the P100 (see figure 3). VPP was reduced for neutrality compared with disgust, anger and fear (all p values $<.01$), but no difference emerged with happiness and sadness. VPP

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2 amplitude was also more positive for disgust than for happiness and sadness (all p
3 values $<.01$), and for anger than for happiness ($p<.05$).

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Insert figure 3 here

The **N170** was measured in the same time-range at occipital and lateral parietal sites but a different pattern appeared. Indeed, figure 2 suggests that dissociations emerged in N170 amplitude between the emotional and neutral expressions and between disgust and the other emotional expressions. The analysis revealed that the main effect of Expression was significant ($F(3,77)=10.85$, $\epsilon=.67$, $p<.0001$, $\eta^2=.32$) and was significantly qualified by Site ($F(5,124)=11.66$, $\epsilon=.54$, $p<.0001$, $\eta^2=.34$). The effect of Expression was significant at both O1/2 and P7/8 ($F(3,64)=12.02$, $\epsilon=.56$, $p<.0001$, $\eta^2=.34$ and $F(4,88)=17.06$, $\epsilon=.76$, $p<.0001$, $\eta^2=.43$) but not at P3/4 ($F(4,81)=2.02$). Post-hoc comparisons indicated a quite similar pattern at O1/2 and P7/8. At both sites, the N170 amplitude was significantly enhanced for disgust as compared with any other emotional expression (all p values $<.0001$, with the exception of fear at P7/8) and reduced for neutrality as compared with any other emotional expression (all p values $<.0001$). At P7/8, the N170 was also significantly greater for fear than for the other expressions (all p values $<.05$, with the exception of disgust as described above).

The **P200** mirrored, to some extent, the pattern reported for the N170 by distinguishing expressive faces from neutral faces and disgust faces from most other expressions. The main effect of Expression was significant ($F(4,92)=2.84$, $\epsilon=.80$, $p<.05$, $\eta^2=.11$) and interacted with Site ($F(6,138)=3.40$, $\epsilon=.60$, $p<.01$, $\eta^2=.13$). The effect of Expression was significant at both O1/2 and P7/8 ($F(4,85)=3.59$, $\epsilon=.74$, $p<.05$, $\eta^2=.14$ and $F(4,92)=3.03$, $\epsilon=.80$, $p<.05$, $\eta^2=.12$) but not at P3/4 ($F(4,86)=1.76$). Post-hoc comparisons revealed that at O1/2, the P200 was of higher amplitude for neutrality than for any other emotional expression (all p values $<.05$), with the exception of sadness. At P7/8, the amplitude

1
2 was higher for neutrality than for anger, disgust, and fear (all p values $<.01$), but not for
3 happiness or sadness.

4
5 The **N250** component primarily resembled the patterns reported at the level of the
6
7 P200, but it was not modulated by Expression ($F(3,78)=1.46$). In contrast, Expression
8
9 significantly interacted with Site ($F(6,132)=3.75$, $\epsilon=.57$, $p<.01$, $\eta^2=.14$). Further analyses
10
11 demonstrated that the effect of Expression was significant at O1/2 only ($F(3,70)=3.01$, $\epsilon=.61$,
12
13 $p<.05$, $\eta^2=0.12$; at P3/4: ($F(3,79)=1.54$; at P7/8: $F<1$). Post-hoc tests indicated that most
14
15 emotional expressions elicited more negative N250 compared with neutrality, at the occipital
16
17 site. This effect was significant for anger ($p<.05$), disgust ($p<.0001$), happiness ($p<.0001$), and
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19 fear ($p<.001$), but not for sadness. Finally, disgust elicited also a more negative component
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21 than sadness ($p<.001$).
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26
27 For the **LPP** component, a significant main effect of Expression was observed
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29 ($F(4,83)=4.87$, $\epsilon=.72$, $p<.01$, $\eta^2=.17$). It was driven by greater amplitudes for disgust and
30
31 fear as compared to sadness (both p values $<.05$) and neutrality (both p values $<.01$). As
32
33 suggested by figure 3, different patterns emerged according to the recording sites. Indeed, a
34
35 significant Expression \times Site interaction was found ($F(4,88)=2.76$, $\epsilon=.77$, $p<.05$, $\eta^2=.11$) and
36
37 further analyses indicated a significant main effect of Expression for both CP5/6
38
39 ($F(4,87)=4.22$, $\epsilon=.76$, $p<.01$, $\eta^2=.16$) and C3/4 electrodes ($F(4,86)=3.59$, $\epsilon=.75$, $p<.05$, $\eta^2=$
40
41 $.17$). Post-hoc tests showed that the enhanced amplitudes for disgust were only observed at
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43 the CP5/6 electrodes with a significant difference with neutrality ($p<.01$). Conversely, at the
44
45 level of the C3/4 electrodes, amplitudes for fear were greater than those for sadness ($p<.01$).
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51 ***3.2. Different phases of the effect of the olfactory context in the processing of facial*** 52 ***expression*** 53 54

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56 The olfactory context modulated the brain response to facial expressions in two
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58 sequential phases: 1) an enhanced response regardless of the emotional content of faces when
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1 an odor was present, which especially occurred at central sites in the 130-180-ms time-
2 window (VPP), but also at different centro-parietal and temporal scalp locations in the same
3
4 time-window (see section 3.3); and 2) an interaction effect between the olfactory context and
5
6 the type of facial expression initiated at the level of the occipital P200.
7
8

9 For the first phase, the modulations of the visual responses by the olfactory contexts
10 are illustrated in figure 4. No main effect of Olfactory context was noted on the VPP, despite a
11 strong trend ($F(2,41)=2.85$, $\epsilon=.89$, $p=.075$), but it significantly interacted with Site
12
13 ($F(4,82)=3.27$, $\epsilon=.89$, $p<.05$, $\eta^2=.12$). The main effect of Olfactory context was further
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15 significant at Cz ($F(2,45)=4.16$, $\epsilon=.97$, $p<.05$, $\eta^2=.15$) and C4 ($F(2,46)=3.98$, $\epsilon=1$, $p<.05$,
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17 $\eta^2=.15$), but not at C3 ($F<1$). For Cz, post-hoc comparisons indicated a larger amplitude for
18
19 the pleasant odor context than for the control and aversive odor contexts (both p values $<.01$).
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21 However for electrode C4, no effects were found after post-hoc corrections, despite an
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23 apparent effect of the aversive context in figure 4. No other effects or interactions involving
24
25 the Olfactory context were noted at the level of VPP. Because the effect of the olfactory
26
27 context irrespective of the content of facial expressions was detected only at central sites, and
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29 because no post-hoc comparisons were significant at electrode C4 despite a significant main
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31 effect, we performed complementary analyses to more precisely characterize the timing and
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33 topography of this effect in this time-window. Details and results from these analyses are
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35 provided in section 3.3.
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46 Insert figure 4 here
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48 For the second phase, the interaction between Expression and Olfactory context is
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50 illustrated for electrodes O2 and P8 in figure 5. The data in this figure suggest that the
51
52 previous effects of Expression described at the levels of P200 and N250 were larger in the
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54 aversive odor context than in the control and pleasant odor contexts, with an exaggeration
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1
2 enhancement in the ERP differences between neutrality and both happiness and disgust in the
3 aversive odor context.

4
5 At the level of the P200, the analyses that included the 3 sites (O1/2, P3/4, and P7/8)
6
7 suggested hemispheric differences in the interaction between Expression and Olfactory
8
9 context, but the interaction between the three factors did not reach significance after
10
11 Greenhouse-Geisser correction ($F(7,153)=1.89$, $\epsilon=.67$, $p=.078$). A similar analysis restricted to
12
13 each site where the main effect of Expression was significant (i.e., O1/2 and P7/8) indicated
14
15 that the interaction between Expression, Olfactory context, and Hemisphere was significant at
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17 O1/2 ($F(6,137)=2.26$, $\epsilon=.60$, $p<.05$, $\eta^2=.09$), but not at P7/8 ($F(7,155)=1.54$).

18
19 Complementary analyses at O1/2 indicated that the interaction between Expression and
20
21 Olfactory context was significant in the right hemisphere ($F(6,138)=2.44$, $\epsilon=.60$, $p<.05$,
22
23 $\eta^2=.10$), but not in the left hemisphere ($F(7,152)=1.11$). Interestingly, in the right hemisphere
24
25 (electrode O2), the effect of Expression was not significant in the control or pleasant odor
26
27 contexts ($F(4,89)=1.94$ and $F(4,84)=.50$, respectively), but it was significant in the aversive
28
29 odor context ($F(4,97)=5.30$, $\epsilon=.84$, $p<.001$, $\eta^2=.19$), with significantly greater amplitudes for
30
31 neutrality than for the other emotional expressions (all p values $<.05$), except fear. P200
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33 amplitudes were also lower for disgust and happiness than for the other emotional expressions
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35 (all p values $<.001$). Considering the effect of the Olfactory context, P200 amplitudes for
36
37 disgust and happiness were lower in the aversive odor context than in the control and pleasant
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39 odor contexts (all p values $<.01$). Conversely for neutrality, the P200 component was more
40
41 positive in the aversive odor context than in the control ($p<.05$) and pleasant ($p<.01$) odor
42
43 contexts. Regarding the other expressions, the amplitude was larger for anger in both the
44
45 pleasant and aversive odor contexts compared with the control context (both p values $<.0001$),
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47 with no difference between these two last olfactory contexts. For fear, there was only a
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49 significant difference between the control and aversive odor contexts, with a higher positive
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1 component in the aversive odor context ($p < .0001$). No difference was detected for sadness.

2 Finally, analyses of the N250 and LPP components indicated that the Olfactory context by

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4 Expression interaction vanished around 240 ms after face onset.

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7 Insert figure 5 here

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10 ***3.3. Complementary analyses on the first phase of undifferentiated influence of***
11 ***odors in facial expression processing***

12 Because the results indicated a main effect of the Olfactory context regardless of the
13 emotional content of facial expressions only at central sites (VPP amplitude), and because this
14 effect was not clearly identified with post-hoc comparisons at electrode C4, we performed
15 complementary analyses to precisely characterize the timing and topography of this effect in
16 ERPs. We first computed the F values for the main effect of Olfactory context at each
17 electrode and at each time sample in the 130-180-ms time-window. To control for false
18 positives when performing such a high number of comparisons, a criterion of consecutive
19 significance (e.g., Guthrie & Buchwald, 1991) was used for each electrode to determine the
20 time course of the effect: at least 15 consecutive significant time points should be obtained to
21 indicate the onset of the effect, followed by at least 15 consecutive non-significant samples to
22 determine when it stopped. Due to this criterion, we included the 30-time samples
23 surrounding the time-window (15 before and 15 after) to compute the F values (complete
24 time-window: 115-195 ms). Further, we restricted a similar analysis with t-tests between the
25 different olfactory contexts in the same time-window for the electrodes that showed a
26 significant main effect. For both analyses, p values were translated in color-codes to illustrate
27 the results. For the main effect of Olfactory context, significant effects are represented in
28 green, with the darker points indicating the lower p values. For the t-tests comparing each
29 olfactory context, significant effects are represented in red for positive differences, and in blue

1
2 for negative differences. Again, the darker points indicate the lower p values. Results from
3 these analyses are depicted in figure 6.

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5 Insert figure 6 here
6

7 For the main effect of the Olfactory context, results from the analysis of the VPP
8 amplitude were confirmed with a significant effect between 135 and 185 ms at electrode Cz
9 and between 155 and 185 ms at electrode C4, but no effect at electrode C3. At the Cz
10 electrode, significant differences were further confirmed between the pleasant and both the
11 aversive and the no odor contexts. Critically, whereas post-hoc comparisons did not
12 previously show significant differences between odors at C4 electrode, consecutive
13 significance rather indicates that both the aversive and the pleasant odors elicited more
14 positive VPP amplitudes than the no odor olfactory context. Interestingly, the main effect of
15 the Olfactory context was also found for centro-parietal and temporal sites. It started as soon
16 as 130 ms after face-onset at electrodes T7 and CP6, 20 ms later at electrode M1 and 40 ms
17 later at electrode CP1. T-tests indicated significant differences between the pleasant odor and
18 the no odor contexts at T7 and CP1. Significant differences between the aversive and the no
19 odor contexts mainly appeared at M1 and CP6, but a short early effect was also noted at T7.
20 Finally, only CP6 also showed a short significant difference between the aversive and the
21 pleasant odor contexts at early latencies. Note that the sign of the significant differences
22 mainly reflects greater amplitudes for the odor vs. no odor conditions, as a positive
23 component was recorded at central and centro-parietal sites, and a negative component at
24 temporal sites. In sum, both pleasant and aversive odor contexts elicited enhanced amplitudes
25 compared with the no odor context in the 115-195-ms time-window, but these effects were
26 found at different sites depending on the odor (Cz, C4, T7 and CP1 for the pleasant odor; C4,
27 M1, T7 and CP6 for the aversive odor).
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57 In order to explore more precisely the different topographies elicited by the effects of
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1 the pleasant and aversive odors compared to no odor control condition, we performed two
2 principal component analyses (PCAs) including the six electrodes showing a significant odor
3 effect as variables and each time point in the 115-195 ms time-window as observations. The
4 first analysis was performed for the differences between pleasant and no odor conditions, the
5 second analysis was performed for the differences between aversive and no odor conditions.
6 Both analyses were computed according to the effect sizes (Cohen's d). Varimax rotation was
7 applied to minimize component overlap and the number of components was decided
8 according to a minimal eigenvalue of 1.
9

10 The first PCA indicated two principal components (PC1 and PC2) with eigenvalues of
11 4.28 and 1.13 respectively (variance explained: 71.4 % for PC1 and 18.9 % for PC2).
12 Electrodes M1, T7, CP1, Cz and C4 loaded in PC1 whereas electrode CP6 loaded in PC2.
13 Thus, PC1 included all electrodes showing a significant effect of the pleasant odor but M1.
14 PC2 only included electrode CP6 that did not show any significant effect of the pleasant odor.
15 The second PCA also indicated two PCs with respective eigenvalues of 3.05 and 2.69
16 (variance explained: 50.8 % for PC1 and 44.8 % for PC2). PC1 included three recording sites
17 (T7, C4 and CP6) whereas PC2 included the three others (M1, CP1 and Cz). In other words,
18 three electrodes showing a significant effect of the aversive odor loaded in the first
19 component whereas the three electrodes loading in the second component did show any
20 significant effect of the aversive odor, except M1. In sum, the PCAs confirmed that the two
21 effects of odors compared to no odor in the 115-195 ms time-window developed over
22 different recording sites, despite slight differences with the topographies suggested by the
23 previous analysis of consecutive significance.
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25 **4. Discussion**

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1 Using a technique (ERPs) with high temporal resolution, this study was designed to
2 investigate the time-course of the modulations induced by contextual odors valence on the
3 processing of emotionally expressive faces. Odorants convey indeed influential cues that can
4 concurrently influence the emotional state of both the emitter and the perceiver of facial
5 indices, and may affect how expressions of the emitter are perceived. Here, we used an
6 orthogonal task to assess how odor-vision interactions affect early visual processing
7 uncontaminated by explicit goal-directed mechanisms. Based on previous ERP studies (e.g.,
8 Williams et al., 2006), we predicted an early odor-based modulation of brain responses to
9 expressive faces from 80 to 480 ms after stimulus onset in several occipital, parietal and
10 central ERP components (P100, VPP, N170, P200, N250 and LPP). Moreover, based on
11 previous studies investigating odor-vision interactions (e.g., Rubin et al., 2012), we expected
12 that the odor context would have a general effect before interacting with the decoding of
13 facial expressions depending on whether odors and faces convey congruent/incongruent
14 affective information. Our main results fit well with this prediction and cast some new light
15 on the time course of odor-vision integration in the early processing of facial expression.
16 Three main phases were evidenced in odor-vision interactions in face reading: a main effect of
17 face expressions occurring from 80 to 480 ms after face-onset at posterior and central
18 topographies, a main effect of odors globally modulating the early stages of face processing
19 between 130 and 180 ms at several central, centro-parietal and temporal scalp locations, and
20 an interaction between expressions and odors around 200 ms after face-onset at occipital sites.

21 ***4.1. The different phases of facial expression processing***

22 First, the emotional content of some expressions (e.g., fear, anger, and disgust),
23 enhanced the cerebral responses at the level of the P100, starting around 80 ms after stimulus-
24 onset. Such emotional modulations corroborate prior studies (e.g., anger: Brosch et al., 2008;
25 Kolassa & Miltner, 2006; disgust: Utama et al., 2009; fear: Eimer & Holmes, 2002; Li et al.,
26

1 2008; Pourtois et al., 2004a, 2005b) which consider that they derive from the stronger
2 mobilization of attention orienting or alerting mechanisms for these expressions and have
3
4 been interpreted in terms of higher relevance to the perceiver (e.g., signaling an immediate
5 danger) compared with the other expressions (i.e., happiness, sadness, and neutrality). This
6
7 early sensitivity may index fast cortical pathways (Pessoa & Adolphs, 2010) or influences
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9 from the amygdala (Vuilleumier et al., 2001, 2004) through the processing of coarse visual
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11 information from magnocellular inputs (Pourtois et al., 2005b). The same emotional
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13 expressions also enhanced VPP amplitudes approximately 130 ms after face-onset at central
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15 sites, corroborating previous reports of expression-sensitive positive responses at central and
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17 anterior topographies (Ashley et al., 2004; Eger et al., 2003; Eimer & Holmes, 2002; Luo et
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19 al., 2010; Smith et al., 2013; Williams et al., 2006). It has been suggested that these activities
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21 may reflect emotional enhancement of visual processing (e.g., Eimer & Holmes, 2002; Smith
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23 et al., 2013), maybe larger for expressions that previously elicited larger responses at the level
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25 of the P100. This interpretation fits well with the extraction of the affective content of visual
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27 objects in this time-range (Barrett & Bar, 2009). Hence, VPP amplitudes in response to facial
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29 expressions may reflect a response to alerting emotions following the first emotional
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31 relevance detection observed in the posterior P100.
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41 The emotional content of expressions also modulated the occipito-temporal N170
42 component where emotional expressions, especially disgust, gave rise to a differential
43 response compared with neutrality. The N170 is known to be involved in the perceptual
44 coding of facial information (Bentin et al., 1996; George et al., 1997; Rossion & Jacques,
45
46 2011) and is sensitive to facial expressions (Ashley et al., 2004; Campanella et al., 2002; Eger
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48 et al., 2003; Luo et al., 2010; Sprengelmeyer & Jentzsch, 2006; Utama et al., 2009; Williams
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50 et al. 2006). Because the N170 reflect the encoding of facial configuration, it has been
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52 suggested that it is sensitive to the intensity of facial expressions but not indicative of emotion
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1 categories (Sprengelmeyer & Jentzsch, 2006; Utama et al., 2009). As we mainly observed
2 enhanced amplitudes for disgust, and in a lesser extent for fear, this interpretation suggests
3 that these expressions were the most intense in our set of stimuli (i.e., with the greatest
4 difference in facial configuration compared with neutrality). Another explanation could be
5 that the diagnostic features for perceiving disgust and fear were more salient, as it has been
6 suggested that the N170 indicates the integration of diagnostic features for the perceptual
7 categorization of facial expressions (e.g., Joyce et al., 2006; Schyns et al., 2007, 2009). Future
8 studies are needed to evaluate these interpretations. Nonetheless, both suggest that the
9 expression effect at the level of the N170 is not related to the specific affective content of the
10 expressions. Note that it has been shown that the VPP and the N170 index the same
11 mechanisms during face categorization (Joyce & Rossion, 2005). However, in line with
12 previous findings (Ashley et al., 2004; Smith et al., 2013; Williams et al., 2006), we noted
13 different patterns for both components in the present study. This likely suggests that at least
14 some different generators may be involved during facial expression processing, perhaps
15 reflecting differential perceptual coding and sensitivity to emotional relevance.

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36 Concerning the P200 and the N250, we found increased negativities for all facial
37 expressions except sadness. Previous studies showed increased negativity for emotional
38 expressions at posterior sites in the P200 time-range (Schupp et al., 2004; Williams et al.,
39 2006; see also Eimer & Holmes, 2002). Previous evidence also showed modulations by facial
40 expressions at the level of the subsequent N250 component or in the same time-window
41 (Ashley et al., 2004; Dennis & Chen, 2007; Williams et al., 2006). Increased negativities
42 appearing in the P200 and N250 time-ranges (around 200 to 350 ms after stimulus-onset)
43 have been previously reported for emotional expressions relative to neutral faces, and often
44 called early posterior negativities (EPN; e.g., Schupp et al., 2004; Smith et al., 2013). These
45 are interpreted as enhanced processing for affective information (Schupp et al., 2004; Smith et
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1 al., 2013), which may index projections from the amygdala (Sato et al., 2001) or the insula
2 (Ashley et al., 2004) on the visual system. This interpretation has also been more generally
3 provided for all kinds of emotional stimuli (e.g., Foti et al., 2009). Thus, EPN may index the
4 first integration of the specific emotional meaning in the visual processing of stimuli sharing
5 emotional content through connections between the visual system and the amygdala, the OFC,
6 the insula, and the somatosensory cortices (Adolphs, 2002). For example, the OFC and
7 posterior structures in the visual system interact as soon as 215 ms after stimulus onset (Bar et
8 al., 2006). Because we observed increased EPN for all emotional expressions except sadness,
9 our results fit well with this interpretation. After different stages reflecting the initial
10 attentional capture by emotional relevance (P100, VPP) and the perceptual coding of
11 expressive faces (N170), the EPN observed in the P200 and N250 time-windows indexes the
12 first stage sensitive to the emotional meaning conveyed by the expressions, maybe through
13 connections between the emotional brain and the visual system.

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31 Finally, our results showed increased amplitude of the LPP, especially for disgust and
32 fear compared with other expressions. The LPP has been interpreted as reflecting sustained
33 attention to motivationally salient stimuli, and/or elaborative processing (Schacht & Sommer,
34 2009; Schupp et al., 2004). Whereas some studies report larger LPP for all expressions (e.g.,
35 Luo et al., 2010), other observed larger LPP only for fearful and angry faces (Schupp et al.,
36 2004; Williams et al., 2006). In the present study, we found the effect for fear but not for
37 anger, whereas disgust also elicited a larger LPP. The present evidence suggests that faces
38 expressing fear and disgust were especially motivationally relevant compared with other
39 expressions. Interestingly, it may be related to their higher salience and/or intensity as
40 indicated by the effects observed at the level of the N170. Note that because we used an
41 orthogonal task designed to avoid any influence from decisional and goal-directed
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1 mechanisms, modulation of the LPP may have been reduced for some emotions in the present
2 study because participants were not explicitly motivated to process facial expressions.
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4 Altogether, the above-mentioned results indicate that between 80 and 480 ms after
5 face onset, emotional expressions elicit different ERP modulations associated with different
6 mechanisms which allow an elaborate representation of the perceptual and emotional contents
7 of expressive faces. We will now describe the results according to the main goal of the present
8 study, namely determine which mechanism in the reading of facial expressions are sensitive to
9 the olfactory context and its affective value.
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18 ***4.2. Different phases of olfactory context effects on the processing of facial*** 19 ***expression*** 20 21 22 23

24 Our results indicate a biphasic influence of the odor context on facial expression
25 processing. The first phase concerned an early enhancement of EEG responses between 130
26 and 180 ms after face onset in the presence of odor contexts, regardless of the emotional
27 content of the faces. This effect is consistent with previous studies and with our own
28 hypotheses indicating at least one phase in odor-vision integration with an unspecific effect on
29 facial expression processing (Forscher & Li, 2012; Rubin et al., 2012). Our main analyses
30 have shown this effect only for the pleasant odor context in the VPP component. However,
31 complementary analyses also revealed this effect for both odor contexts in several central,
32 centro-parietal and temporal scalp locations in the same time-range, with differential
33 topographies for the pleasant odor (T7, CP1, Cz, C4) and the aversive odor (M1, T7, C4,
34 CP6), further confirmed by two PCAs.
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51 Different hypotheses can be suggested regarding the nature of these odor-based
52 modulations of facial processing. Olfactory and visual inputs activate common or interactive
53 brain structures. The olfactory system has close connections with the emotional brain (e.g.,
54 amygdala, insula, and OFC; Carmichael, Clugnet, & Price, 1994; Gottfried, 2006; Rolls &
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1 Baylis, 1994). Smelling disgusting odorants and seeing disgust faces both activate the insula
2 (Wicker et al., 2003). The amygdala (for a review, see Zald, 2003) and the OFC (e.g., Royet et
3 al., 2000) are also activated by odor stimulations and emotional facial expressions. Thus, the
4 odor context may pre-activate these brain structures and subsequently influence their
5 responses when a face appears in the visual field, possibly boosting the processing of faces.
6 Remember that the extraction of the affective content of visual objects occurs in this time-
7 range (Barrett & Bar, 2009). Note that the separable topographies discriminating both odors
8 likely indicate recruitment of distinct neural substrates, possibly because of the difference in
9 affective valence between them and/or intrinsic differences in the nature of the odorants, as
10 the chemical structure of an odorant often determine its affective value (e.g., Khan et al.,
11 2007). In sum, according to our previous interpretation of VPP amplitudes, the response to
12 alerting emotions may be enhanced by concurrently presented odors, with different
13 topographies (and probably underlying neural activations) depending on the valence of the
14 odors.
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34 Alternatively, the odor context may provoke facial micro-reactions in the perceiver.
35 Facial reactions to odors were already reported, notably with the odorants we used in the
36 present study (Godard, Baudouin, Schaal, & Durand, in press; Soussignan Schaal Marlier &
37 Jiang, 1997; Soussignan & Schaal, 1996). Since automatic facial reactions were also reported
38 when participants have to recognize facial expressions and influence the “reading” of the face
39 (e.g., Aguado et al., 2013; Soussignan et al., 2013), the odor context may have acted as
40 mimicking-like responses or priming effects and facilitate the recognition of facial
41 expressions (see Lundqvist & Dimberg, 1995; Niedenthal, 2007; Hess & Fischer, 2013, for a
42 review). Likewise, it may intervene through embodiment by simulating emotional reactions
43 and allowing the matching between an individual’s own emotional states and the states
44 perceived by other individuals (Adolphs, 2002; Wicker et al., 2003). Both interpretations are
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1 not incompatible. Indeed, the neural structures involved in the embodiment of facial
2 expressions partly overlap with emotional structures, as emotion is intrinsically an embodied
3 mechanism. For instance, the insula is a visceral sensorimotor structure, explaining its
4 involvement in both the feeling of disgust and the perception of disgust in others (Wicker et
5 al., 2003). Likewise, the OFC is well-known for its presumable role in reactivating the
6 affective value of any kind of object/context through somatic modulations or simulations
7 further coded in cortical somatosensory areas (Damasio, 1998). As a matter of fact,
8 somatosensory cortices are also of great importance in facial expression recognition (Adolphs,
9 2002; Pourtois et al., 2004b). Finally, despite some differences in theoretical considerations,
10 both interpretations suggest that the odor context may mobilize emotional and sensorimotor
11 areas to modify the responses to subsequent facial expressions. Future investigations must be
12 designed to precisely determine whether the above-mentioned cerebral regions are involved in
13 olfactory influences on the visual processing of emotional faces within the time-window
14 identified in the present study.

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34 Following this first phase, we also observed that odors interacted with the content of
35 expressions between 180 and 240 ms after face onset (P200) at a right occipital site (O2), but
36 no more after 240 ms (N250). The main finding here is that the aversive odor context
37 amplified the differences between the facial expressions primarily through an increase in the
38 EEG differentiation between i) neutrality and all expressions (except fear) and ii) between
39 disgust/happiness and other emotional expressions. Compared with the two other olfactory
40 contexts, the aversive odor mainly induced increased negativities for faces expressing disgust
41 and happiness and reduced negativities for neutral faces. Overall, whereas these results were
42 significant only for the aversive odor context, they support our hypothesis of an interacting
43 mechanism depending on the congruent/incongruent relations between odors and the
44 perceived facial expressions. In any way, these results exclude interpretations suggesting that

1 the mere presence of an odor suffices to provoke a global effect on facial processing
2 regardless of its affective value.
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4 Previous reports on odor-vision interactions during the processing of expressive faces
5 have yielded inconsistent results. Some authors found that reaction times to recognize
6 happiness depend on the congruency with the olfactory context, an effect they did not notice
7 for disgust face, however (Leppänen & Hietanen, 2003). In contrast, others showed that
8 disgust is processed faster and happiness more slowly in the presence of odor contexts,
9 irrespective of their emotional valence (Seubert et al., 2010b). When considering ERPs, some
10 studies evidenced early effects of odors on visual processing of facial expressions (e.g., at the
11 level of P100 and N170 components; Adolph et al., 2013; Forscher & Li, 2012), while others
12 found later effect (e.g., between 250 and 600 ms; Rubin et al., 2012). Moreover, a global
13 effect of odors regardless of the emotional content of expressions was noticed sometimes
14 before (e.g., Rubin et al., 2012) and sometimes after (e.g., Forscher & Li, 2012) an interaction
15 between the affective values of both cues. These discrepancies may originate from several
16 methodological differences, such as the nature of the task. For instance, contrary to the
17 present study, Forscher and Li (2012) used a dot-probe task where attentional resources are
18 explicitly solicited and found early interactive effects. Even earlier effects were observed by
19 Steinberg et al. (2012) when a strong associative learning between odors and faces was
20 previously engaged. Hence, future studies are needed to disentangle this issue and to
21 determine whether the present findings may differ according to the depth of processing and/or
22 goal-directed mechanisms by manipulating the task performed. Note that we precisely chose
23 an orthogonal task to examine odor-vision interactions uncontaminated by these processes, in
24 order to provide a frame for further studies. Another explanation for the discrepant results
25 between the present and earlier studies may come from the nature of the odorants. It seems
26 conceivable that body odors do not elicit the same neural responses than 'conventional', non-

1 social odors, such as those of foods. Following this view, the specific effect observed here for
2 the aversive odor may have arisen due to intrinsic differences between the odorants. However,
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4 this kind of effect would have been observed for every emotional expression. The specific
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6 results found only for some expressions suggest an interaction between the affective contents
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8 of both olfactory and visual cues.
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11 The time-window of the interactive modulation of facial expression processing by the
12 odor context, namely the P200 between 180 and 240 ms after face onset, corresponds to the
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14 first part of the EPN. Our findings on the main effect of facial expressions at this level
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16 suggested that it is the first processing stage of specific affective information. Accordingly, it
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18 is also the first stage where the influence of odors depends on the specific emotional content
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20 of facial expressions. EPN are classically interpreted as enhanced processing of affective
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22 information (e.g., Schupp et al., 2004). Hence, the fact that the aversive odor increased the
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24 EPN for disgust and happiness, and conversely reduced the EPN for neutrality, likely suggests
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26 that its emotional value elicits enhanced processing of affective information for disgust and
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28 happiness, but also reduced affective processing during the perception of neutral faces. In
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30 other words, the aversive odor context may be able to modulate the processing of all emotions
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32 related to its affective meaning, either congruent or incongruent. It may thus facilitate their
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34 processing by increasing their relevance through the perceived difference between them and
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36 neutrality, while leaving unaffected other emotions unrelated to the “aversive” emotional
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48 Previous studies using ERPs did not find an influence of contextual information on
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50 facial expression processing at the same latency. Some of them found an earlier effect with
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52 enhanced amplitude of the N170 in response to fearful faces when a congruent visual scene
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54 was concomitantly displayed (Righart & de Gelder, 2006, 2008). Another one observed a later
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56 influence with congruency effects between the perceived expression and a previously
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1 presented sentence arising at the level of the LPP (Diéguez-Risco et al., 2013). However, the
2 integration of face-voice emotional meanings was shown within the first 250 ms of processing
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4 by a MEG study (Hagan et al., 2009). This discrepancy between studies may be first
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6 explained by the nature of contextual information. Indeed, when a visual scene surrounds a
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8 face (Righart & de Gelder, 2006, 2008), both cues are visual and this unisensory contextual
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10 influence may be processed faster. In contrast, when an auditory or an olfactory context is
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12 presented, multisensory integration may be slower, depending on the activity of specific brain
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14 regions (see below). Moreover, even when contextual information is visual in nature, physical
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16 objects (Righart & de Gelder, 2006, 2008) vs. verbal information (Diéguez-Risco et al.,
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18 20013) may differentially influence the onset of the integration. Methodological factors might
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20 also explain these discrepant results. Indeed, in Diéguez-Risco et and collaborators' study, the
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22 context is displayed before the expressive face. This sequential contextual “priming” may
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24 trigger different mechanisms such as expectations for example. However, because the
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26 olfactory context in the present study was presented along an entire block, it could have
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28 elicited expectations as well. Another explanation would be that the LPP is modulated by
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30 affective congruency only during an explicit task, as it is particularly sensitive to task-related
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32 motivation. As previously discussed, the orthogonal task in the present study may have
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34 reduced the sensitivity of the LPP to various effects. Nonetheless, future studies should further
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36 investigate the time-course of contextual integration in the visual processing of facial
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38 expressions and its variability depending on several factors.
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48 At the neural level, the contextual effect we found may be mediated by feedback from
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50 “emotional” structures in multisensory or sensorimotor areas (Adolphs, 2002; Ashley et al.,
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52 2004; Sato et al., 2001) that may have been pre-activated during the early global modulation
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54 induced by the odors. Accordingly, both the insula (Chen et al., 2009) and the somatosensory
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56 cortices (Pourtois et al., 2004b) intervene approximately 200 ms after stimulus-onset during
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1 emotional face processing. Likewise, the OFC and the visual system start to interact around
2 215 ms after stimulus onset (Bar et al., 2006). Moreover, multisensory integration of affective
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4 prosody and emotional face occurs in the posterior STS with the same time-course (Hagan et
5
6 al., 2009). Hence, the affective value computed by emotional structures may have been
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8 modulated by the odor input and may subsequently modulate the visual processing of
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10 expressions. However, we acknowledge that ERPs do not allow precise conclusions on brain
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12 regions involved and further studies are needed to solve this issue.
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16 17 **4.3. Conclusion** 18

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20 In conclusion, the results of the present study show that non-social odors (food odors)
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22 influence the brain responses during facial expression processing. A first effect started 130 ms
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24 after face-onset at several central, centro-parietal and temporal locations depending on the
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26 valence of the contextual odors and elicited enhanced activation regardless of the emotional
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28 content of expressions. Then, an interaction between odors and expression occurred around
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30 200 ms with an occipital location, showing that the aversive odor context increased the
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32 differentiation between facial neutrality and emotional displays, especially of happiness and
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34 disgust. Collectively, these results suggest a global effect of olfaction on face processes
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36 around 160 ms, followed by an interaction between the aversive odor and
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38 congruent/incongruent facial expressions. This interaction may reflect enhanced affective
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40 processing and is presumably due to feedback from emotional or multisensory or
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42 somatosensory structures to the visual cortices. Because these results were evidenced without
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44 any explicit task toward the facial expressions and toward the presence of olfactory stimuli,
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46 future studies must be designed to investigate whether the time course of olfactory-visual
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48 interactions depend on the task performed. Nonetheless, the present study offers a promising
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50 frame to explore the functional properties of odor-vision integration over time.
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Figure captions

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Figure 1. Time sequence of the experimental trials. The stimuli were displayed for a duration of 700 ms following the appearance of a fixation cross for 400 ms. A blank screen then appeared for a random duration ranging from 300 and 500 ms. In each block, 36 expressive faces were randomly intermixed with 6 neutral red faces. The participant's task was to press the "space" bar each time a red face was perceived¹.

Figure 2. Main effect of expression at the occipito-parietal electrodes for P100, N170, P200 and N250. The black-lined brackets indicate the time-windows for analysis. Mean amplitudes (and SEs) for each expression are indicated within boxes.

Figure 3. Main effect of expression at the central and parietal electrodes for VPP and LPP. The black-lined brackets indicate the time-windows for analysis. Mean amplitudes (and SEs) for each expression are indicated within box.

Figure 4. Main effect of odor context at the central electrodes for VPP. The black-lined brackets indicate the time-windows for analysis. Mean amplitudes (and SEs) for each olfactory context are indicated within boxes.

Figure 5. Interaction of expression and odor context at the right occipito-parietal electrodes O2 and P8 for P200 and N250. The black-lined brackets indicate the time-windows for analysis. Mean amplitudes (and SEs) for each expression are indicated within boxes.

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Figure 6. (A) Time course of the main effect of the odor context at each electrode in the 115- to-195-ms time-window computed with a criterion of consecutive significance of 15 time samples. *P* values are color-coded in green with the darker areas indicating the lower values. LH: left hemisphere; RH: right hemisphere. (B) Time course of the differences between each odor context in the same time-window for the electrodes that showed a significant main effect (the same criterion of consecutive significance was applied). *P* values are color-coded in red for positive differences, and in blue for negative differences, with the darker points indicating lower *p* values.

Footnote

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5¹ Note that for image authorization purposes, the second “no-go” face was not used in the
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7 course of the present experiment; however, the model provided informed consent for the
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9 publication of her picture. The other models used did not agree to publication of their pictures,
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11 but they can be seen on <http://www.macbrain.org/resources.htm>.
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Figure 1

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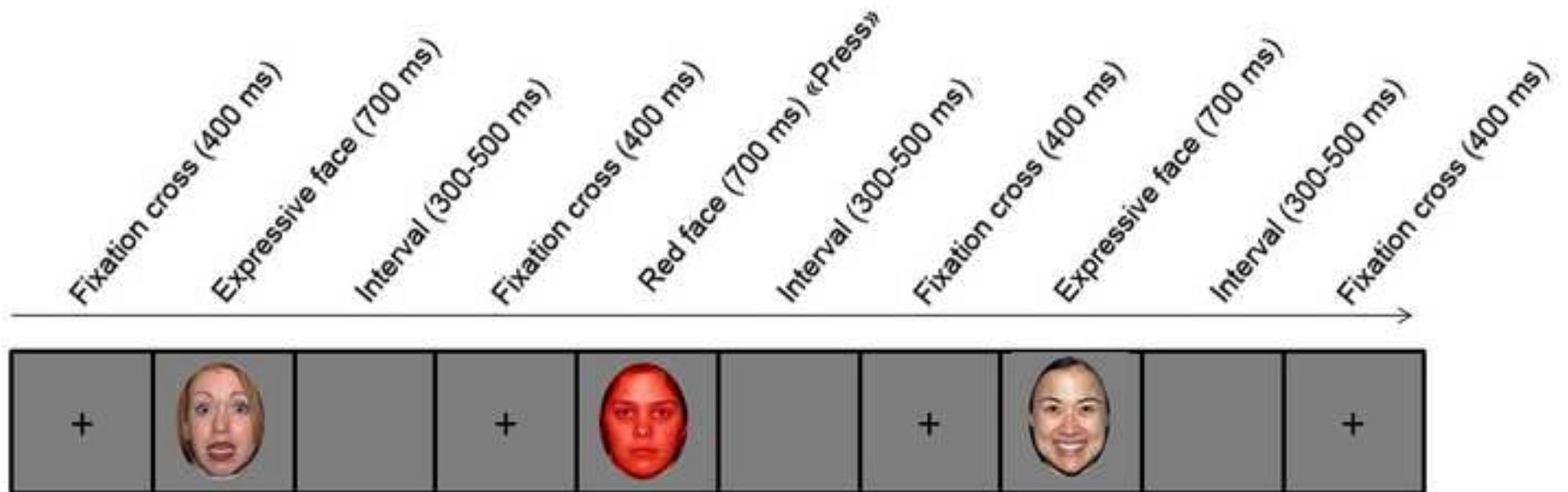


Figure2

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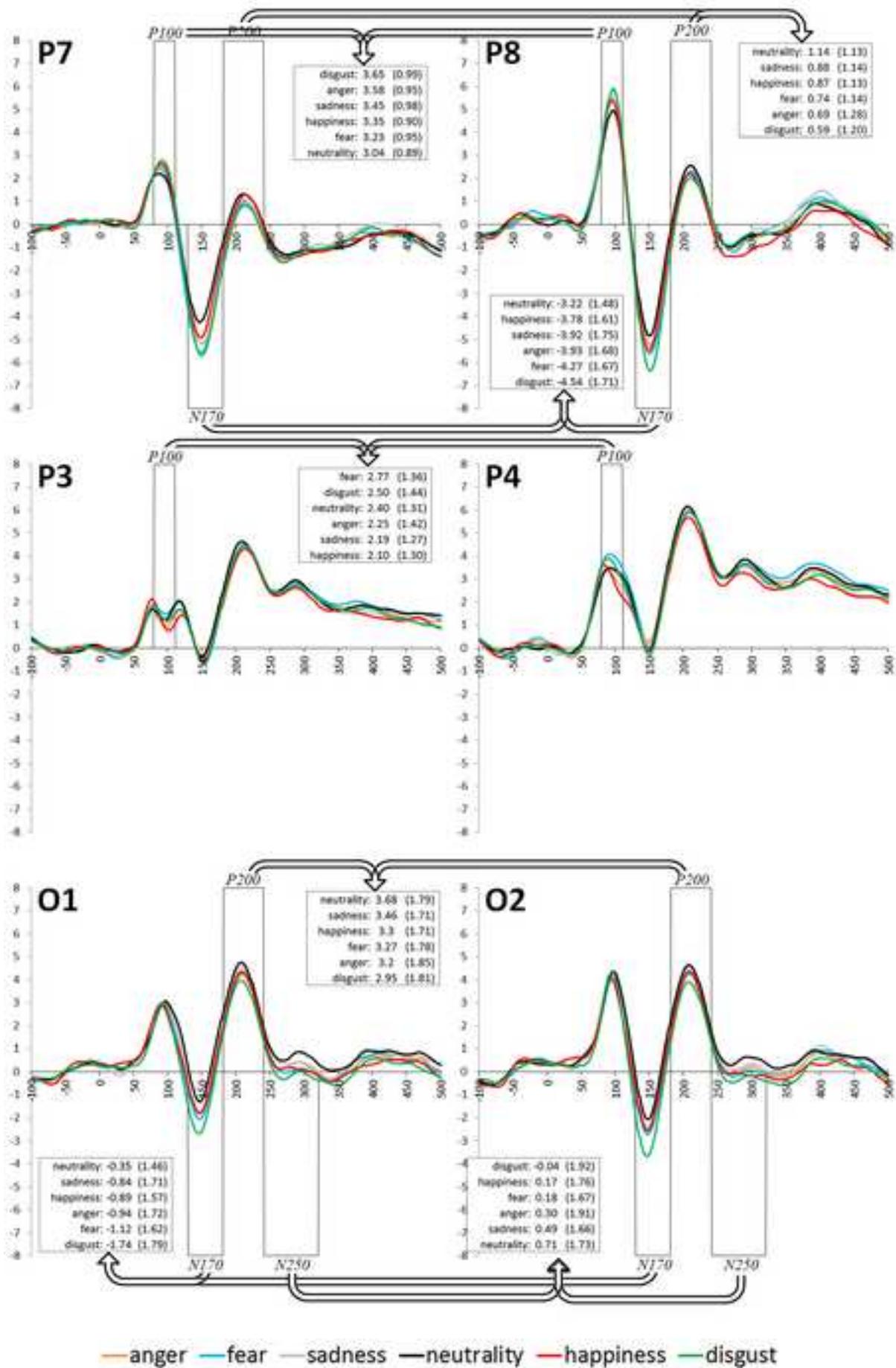


Figure3

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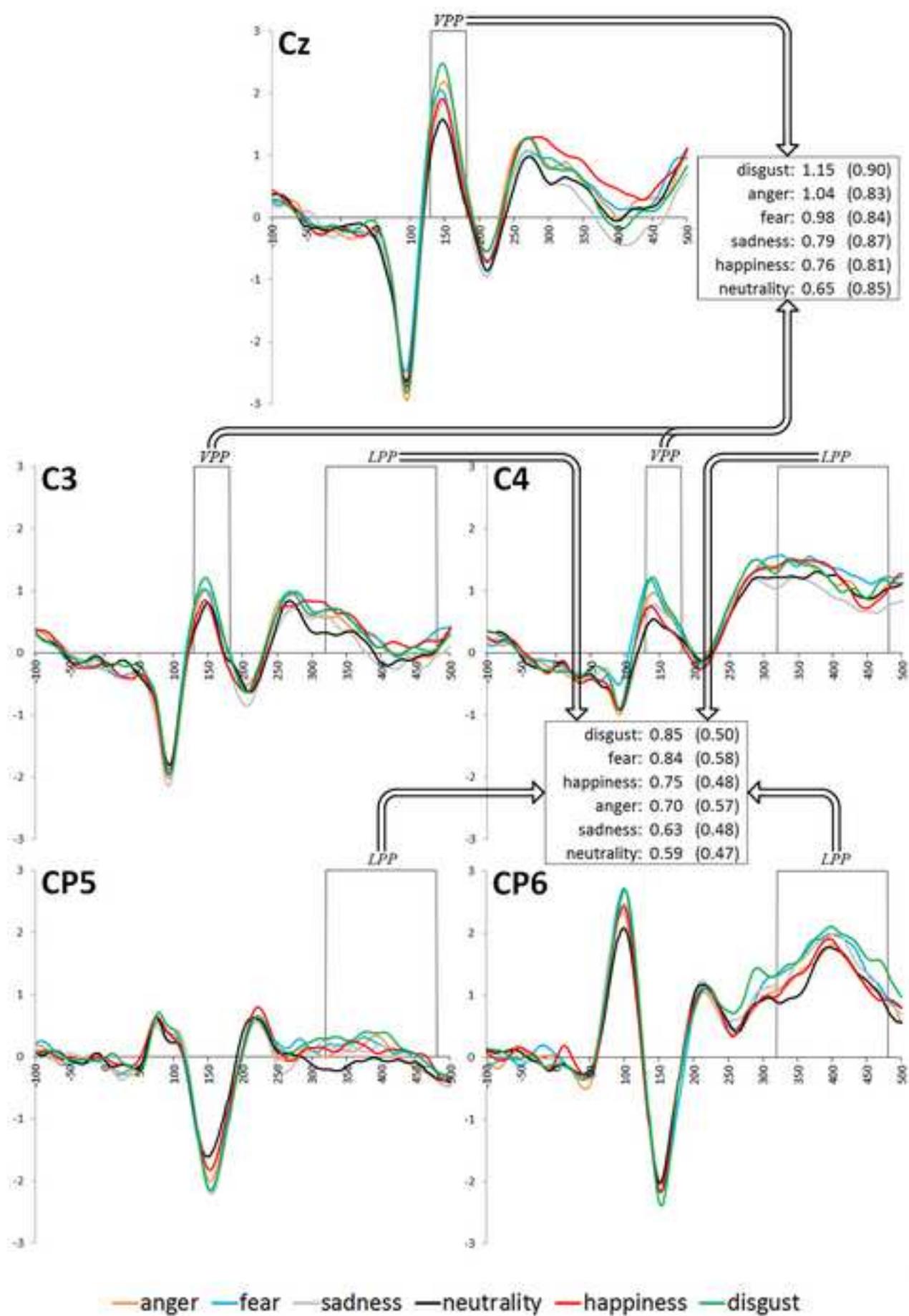


Figure4

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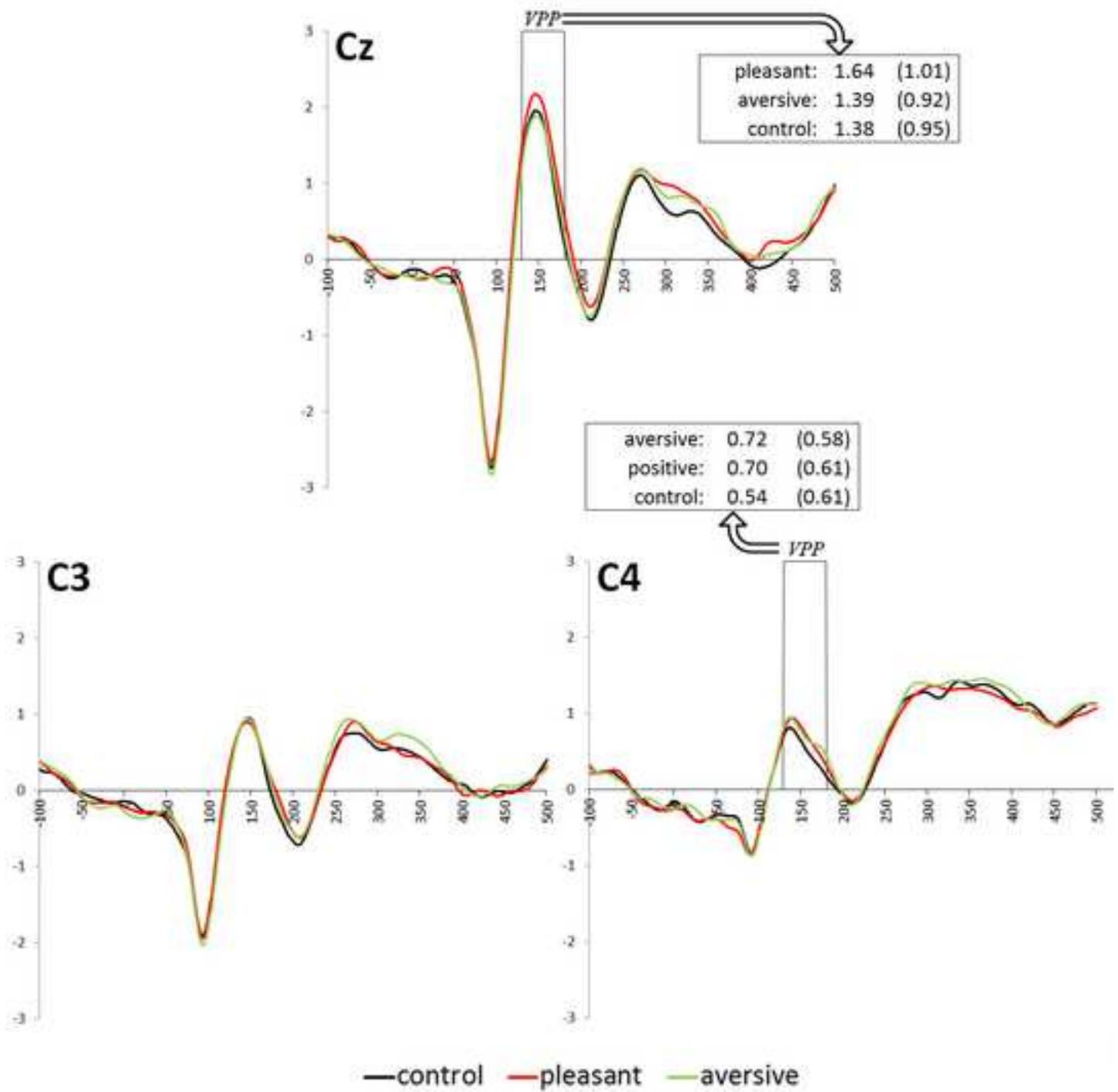


Figure 5
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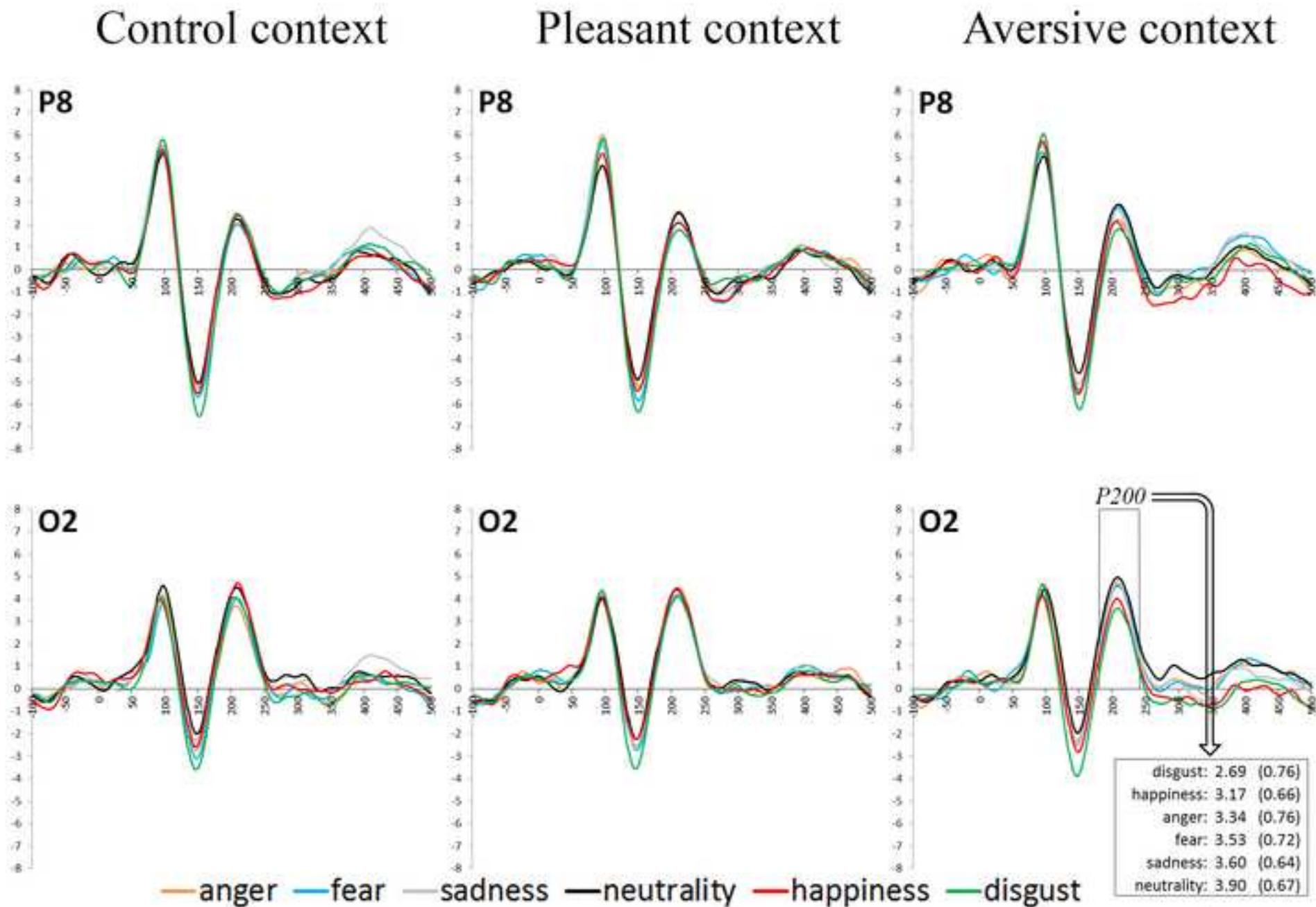
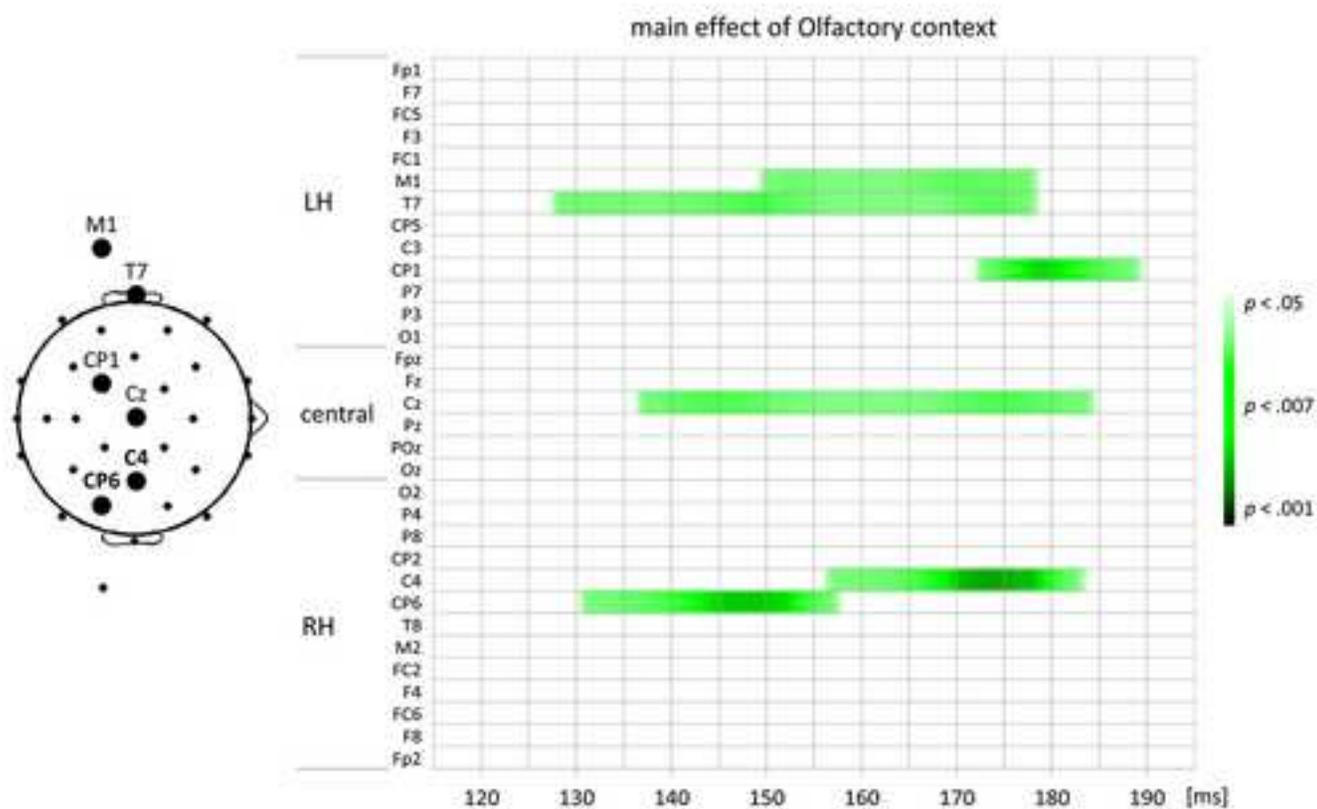


Figure6
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A.



B.

