Irritancy Expectancy Alters Odor Perception: Evidence From Olfactory Event-Related Potential Research

Patricia J. Bulsing,1 Monique A. M. Smeets,1 Christian Gemeinhardt,2 Martin Laverman,1 Benno Schuster,2 Marcel A. Van den Hout,1 and Thomas Hummel2
1Department of Clinical and Health Psychology, Utrecht University, Utrecht, The Netherlands; and 2Smell and Taste Clinic, Department of Otorhinolaryngology, University of Dresden Medical School, Dresden, Germany

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INTRODUCTION

Evidence has accumulated supporting top-down influence of experiential factors on olfactory perception (for an overview see Wilson and Stevenson 2006). For example, in a functional magnetic resonance imaging (fMRI) study, Li et al. (2008) showed that aversive conditioning induces plasticity in the primary olfactory (piriform) cortex, resulting in enhanced discriminability of previously indistinguishable odors. Furthermore, labeling an identical test odor as “body odor” versus “cheddar cheese” resulted not only in the evaluation of that odor as more unpleasant, but also resulted in significant differences in activation of the medial orbitofrontal/anterior cingulate cortex and amygdala (De Araujo et al. 2005). The combined findings from these studies reinforce the conclusions from earlier psychophysical studies (e.g., Herz and Von Clef 2001) that information processing modulates odor perception.

The notion that experience, cognition, and cortical plasticity all combine to modulate our sense of smell facilitates our understanding of why some individuals report health symptoms in reaction to otherwise innocuous odor exposures (Schiffman et al. 2000). Dalton and colleagues (Dalton 1999; Dalton et al. 1997) demonstrated that inducing beliefs about harmful consequences of exposure to certain odorants resulted not only in increased intensity but also in irritancy of those odorants as well as enhanced frequency and intensity of symptom reports. These findings led Dalton to propose that changes in health effects and symptom reporting are modulated by changes in odor perception (Dalton 2002, 2003). Thus the aim of the present research was to test whether the expectations of adverse health consequences following an odor alter the processing of that odor using an olfactory event-related potential (OERP) paradigm. Several of the studies mentioned earlier used fMRI, which has high spatial resolution, thus allowing localization of regions in the brain where experimental manipulations take effect. In contrast, ERPs have high temporal resolution: if cognition exerts top-down influences on perception, correlated activities should not only be encountered in areas of the brain associated with perceptual processing, but they should also occur early during information processing when odor characteristics are encoded. A demonstration of early effects may be considered as converging evidence for earlier findings using fMRI, thus strengthening the same conclusion.

To investigate the effects of odor-related expectation on the olfactory ERP signal, two conditions were compared in a within-subjects design. Although the same odor stimulus was presented on all trials, participants were expecting adverse effects to follow the odor only on half the trials while not expecting any adverse effects from that same odor on the other half of trials. Choice of design was motivated by criticism raised against between-subjects designs in electroencephalographic (EEG) research based on substantial between-subjects variability in ERP signals (Luck 2005) and ERP variability associated with different odors (Kobal and Hummel 1988). Expectation was manipulated presenting a visual cue signaling either danger (irritancy) or safety (no irritancy) presented on the computer screen prior to the onset of the odor. Following the danger signal, the odor was followed by a brief intranasal presentation of CO2, stimulating the nerve endings of the trigeminal nerve in the nose and leading to a sensation of an unpleasant, irritable sting. Sensory irritation (or irritancy) in the nose, characteristic of trigeminal irritants, is among the health symptoms often reported in the context of multiple chemical sensitivity (MCS) or in association with exposure to volatile chemicals in the environment. Following the safety
signal, clean air instead of CO₂ was presented after the odor. In conclusion, participants smelled the same odor under two different expectancy conditions: one where they expected to feel irritancy as soon as they smelled the odor and one where they did not expect any irritancy following perception of the odor.

In the ERP paradigm, a distinction is made between “sensory” or “exogenous” ERPs whose characteristics are controlled by the physical properties of an external event and “endogenous” ERPs, whose characteristics are determined by the interaction between the subjects and the event. Although initially the N1 was considered primarily as reflecting exogenous stimulus characteristics, it is now considered as “mesogenous” in that it reflects not only the processing of physical properties of the stimulus but also the nature of the interaction between subject and event (Fabiani et al. 2000) (time window of 200–700 ms for OERPs). In the OERP, the P2 and P3 have been found to be closely clustered (Olofsson et al. 2008); we will refer to this complex as P3 (time window of 300–800 ms). The P3 has been associated with endogenous processing reflecting stimulus salience, novelty, and odor valence (e.g., Bensafi et al. 2007; Geisler and Murphy 2000; Krauel et al. 1998; Lundström et al. 2006; Nordin et al. 2005). Generally, the P3 component has been interpreted as reflecting amodal rather than modality-specific processing (Olofsson et al. 2008). More specifically, it has been interpreted in terms of updating of the stimulus environment and working memory (Donchin and Coles 1988).

The aim of the studies reported here was to determine whether expectations of irritancy following smelling an odor affected only later cognitive or amodal stages of information processing (P3) or whether they would (also) affect earlier modality-specific stages of odor processing as reflected by the N1 (see Olofsson et al. 2008). If, as in Bulsing et al. (2007), the N1 peak would be affected by the manipulation, it would show that influences of cognition can reach earlier, modality-specific stages of information processing rather than, or in addition to, amodal stages or information processing and thus have more invasive effects than previously believed.

For adults, most naturally occurring odors already have acquired meanings and “neutral” odors are hard to identify. To investigate the influence of preexisting hedonic value on the effect of expectations on perception, we conducted two experiments using an odor generally considered as unpleasant (Study 1: H₂S or rotten egg) and an odor generally considered as pleasant (Study 2: phenyl ethyl alcohol [PEA] or rose).

METHODS

Methods for Study 1 and 2 were identical, with the one difference being the odor compound tested: H₂S in Study 1 and PEA in Study 2. We discuss materials and methods for both studies in this section.

Participants

All participants came to the lab for screening purposes. They were all students at the University of Dresden and recruited by advertisement distributed throughout the university campus. Only women were tested, to exclude as much unrelated variability in brain responses as possible (Lundström and Hummel 2006; Stuck et al. 2006). To examine general olfactory functioning, the identification part of the Sniffin’ Sticks test battery was administered (Kobal et al. 2000).

Participants unable to identify ≥9 of 12 odors from the battery were excluded from further participation. Furthermore, participants unable to detect ≥12 of 15 test odorant presentations administered at unpredictable moments by olfactometer were excluded (odorant concentrations and durations during the screening were the same as those during the experiment; see following text). Additionally, eye-blink behavior in response to these presentations was checked. Participants who blinked in response to >50% of these presentations were also excluded, since too many blinks would distort ERP recordings during the actual experiment. CO₂ sensitivity in response to three CO₂ presentations, again administered at unpredictable moments, was assessed to check whether participants demonstrated a genuinely adverse reaction—a startle or blinking reflex in response to all three CO₂ presentations—which was necessary for the cognitive manipulation (inducing CO₂ expectancy) to succeed. Participants meeting all inclusion criteria were scheduled to participate in the experiment on a separate day.

For Study 1, in which the unpleasant odor of H₂S was used, 60 participants were screened. Reasons for exclusion were low sensitivity to the stimuli (H₂S: 14 participants; CO₂: 6 participants) and blinking in response to the majority of the odor stimuli (4 participants). Five participants did not show up for the experiment. The final H₂S group consisted of 31 participants. Mean age was 22.6 yr (SD = 2.6). For Study 2, in which the pleasant odor of PEA was used, 55 naive, never-screened-before participants were screened. Participants were excluded because they were not sensitive enough to PEA (5 participants) or blinked too often in response to the odor presentations (12 participants). Eight participants did not show up for the experiment. The final group consisted of 30 participants. Mean age was 24.1 yr (SD = 2.8).

Design

For reasons explained earlier, a within-subjects design was used. Participants were led to believe that one and the same odor could be predictive not only of irritation but also of no irritation in the nose. The induction of these expectations was the aim of the first phase of the experiment (Expectancy induction; see Table 1) and was accomplished by introducing a visual cue that was presented prior to the presentation of the odor that predicted whether the odor would be followed by CO₂. The visual cues used were a “98%” sign and a “0%” sign presented on a computer screen, with the former indicating a high chance that the odor would be followed by the irritable sting of CO₂ and the latter indicating that the odor would never be followed by CO₂. We will further refer to these trials as 98%-odor-CO₂ trails and 0%-odor-no CO₂ trials. In Table 1 the frequency of the different trial types in the Expectation induction phase are presented. Trials were semirandomly (i.e., with no more than two identical trials after each other) presented using two different prepared orders.

In agreement with the 98% cue, some trials (i.e., 1 of 10 odor presentations) following the 98% cue remained unreinforced by CO₂ during the Expectation induction phase. That is, no CO₂ pulse was given here, even though the odor was present (to create the impression...
that not 100% but close to 100% of the trials were reinforced; see Test phase in the following text).

In Table 1 the frequency of the different trial types in the Test phase are presented. The procedure during the Test phase was almost identical to the Expectation induction phase. Since the intention was to conduct a within-subjects comparison of the perception of the odor across the two expectancy conditions (without contamination with CO2), 16 98% trials remained unreinforced, that is, no CO2 was presented after presenting the odor, even though the visual cue indicated a high chance on irritancy.1 These 16 98%-odor-no CO2 trials were compared with 16 0%-odor-no CO2 trials. In this manner, only participants’ cognitive state between the two crucial trial types differed (e.g., expecting irritancy vs. expecting no irritancy).

To maintain high expectations of irritancy following the combination of the 98% cue and the odor, 24 reinforced 98%-odor trials followed by CO2 were presented (see Table 1). All trial types (98%-odor-CO2, 98%-odor- no CO2, and 0%-odor-no CO2) were semirandomly presented using two different prepared orders. After the experiment, participants were asked if they were aware of the purpose of the experiment.

Composition of one trial

Each separate trial in the Expectation induction phase took about 40 s and consisted of the following events (see Table 2).

1 Expectation cueing, involving the presentation of the visual cue (either “0%” or “98%”) for 4 s. Following the offset of this cue participants were given maximally 6 s to rate the extent to which they expected to experience irritancy after the subsequent presentation of odor. The visual cue was then repeated for 6 s. There was a variable period lasting between 3 to 23 s between the offset of the visual cue and the onset of the odor. The exact duration depended on the speed of completing the sensory ratings of a previous trial, as will be explained in the following text.

2 Odor presentation, consisting of the presentation of the odor followed by a CO2 pulse in specific cases, after a delay of 1,500 ms. The entire odor presentation phase always had a duration of 3 s, even if no CO2 pulse was presented.

The term “pain” was used in instructions to the participants because many participants have claimed experiencing the stimulus as painful and because the term “sensory irritation” or “irritancy” may lead to confusion. However, since there is no evidence that the sensation was actually one of pain, we will refer to it as irritancy in the remainder of this study.

TABLE 2. Composition of a single trial

<table>
<thead>
<tr>
<th>Phase + Event</th>
<th>Duration</th>
</tr>
</thead>
<tbody>
<tr>
<td>Expectation cueing</td>
<td>4 s</td>
</tr>
<tr>
<td>Cue presentation (0% or 98%)</td>
<td></td>
</tr>
<tr>
<td>Rating of expectancy (VAS)</td>
<td>6 s (max)</td>
</tr>
<tr>
<td>Cue repetition</td>
<td>6 s</td>
</tr>
<tr>
<td>Expectancy buildup</td>
<td>3–23 s</td>
</tr>
<tr>
<td>Odor presentation</td>
<td></td>
</tr>
<tr>
<td>Odor</td>
<td>250 ms</td>
</tr>
<tr>
<td>Delay between odor offset and CO2 presentation</td>
<td>1,500 ms</td>
</tr>
<tr>
<td>or sensory ratings (CO2 presentation)</td>
<td></td>
</tr>
<tr>
<td>Sensory rating</td>
<td>500–700 ms</td>
</tr>
<tr>
<td>Rating of intensity odor (VAS)</td>
<td>6 s (max)</td>
</tr>
<tr>
<td>Rating of annoyance odor (VAS)</td>
<td>6 s (max)</td>
</tr>
<tr>
<td>Rating of annoyance CO2 (VAS)</td>
<td>6 s (max)</td>
</tr>
</tbody>
</table>

Each separate trial consisted of three different stages: 1) the Expectation cueing phase, where the cue (either 0% or 98%) was presented, irritancy expectancy was rated, and expectations were built up; 2) the Odor presentation phase, where the odor was presented, followed by CO2 in some instances; and 3) the Sensory rating phase, during which odor intensity, odor annoyance, and CO2 annoyance were rated.

3 Sensory rating, where participants rated odor intensity, odor annoyance, and CO2 annoyance. Participants were allowed ≤6 s to complete each of the ratings. If they answered faster than these 6 s, the program automatically moved on to the next rating question and, ultimately, to the next trial. In this manner, variations in duration of the expectation buildup could occur because they depended on individual speed of completing the ratings, with the duration of each trial remaining constant. The purpose of the variation was to maximize uncertainty with respect to the exact time of the next stimulus onset after the second expectation cue on the next trial.

Chemosensory stimuli

In Study 1, the odor of H2S (10 ppm) was used. In Study 2, PEA (40% vol/vol) was used. All odor presentations had a duration of 250 ms. CO2 (60% vol/vol) was used as the aversive reinforcer of irritancy expectations. In a number of pilot studies habituation to CO2 was observed in repeated presentations, as reflected by a reduced startle reflex in response to stimulus presentation. Therefore CO2 pulses had an initial duration of 500 ms, but increased by 50 ms every 10 presentations (from 500 to 550 ms, from 550 to 600 ms, etc.) to ensure that intensity and annoyance (i.e., irritancy expectancies) would remain stable regardless of habituation. Stimulus concentrations and durations were the same as those used in related, previous experiments, with requirements similar to those posed for the present research (i.e., the odor had to be a clearly perceptible, but nonirritating stimulus, whereas the CO2 pulses had to elicit clear and relatively strong irritation that was moderately irritating; Bulsing et al. 2007).

Subjective ratings

Subjective ratings on each trial included the following.

1 Irritancy expectancy, i.e., assessing the expectancy that the CO2 is imminent: “Do you think you will feel a painful sting in your nose after you have smelled the odor?” This was a manipulation check and it was obtained after participants had seen the visual cue. Extreme categories of the visual analog scale (VAS): “I don’t think so” at the left side versus “I think so” at the right side of the scale.

2 Odor intensity: Extreme VAS categories: “Not intense” versus “Very intense.”

3 Odor annoyance: Extreme categories: “Not annoying” versus “Very annoying.”

4 CO2 Annoyance: Extreme categories: “No sting/not annoying” versus “Very annoying.”

ERP recordings

EEG signals were recorded for 2,048 ms per trial, covering a 500 ms prestimulus period (baseline), 250 ms of CS (odor or clean air) presentation, followed by 1,334 ms poststimulus period, which was sufficient to capture all EEG responses to the stimulus. Recordings were obtained from the midline sites Fz (frontal), Cz (central), and Pz (parietal) of the international 10–20 system, referenced to linked earlobes (A1 + A2). Eye-blink artifacts were monitored from Fp2/ (A1 + A2) and single recordings with artifacts >50 μV during the critical recording period were discarded (on average 9 of 32 H2S presentations and 7 of 32 PEA presentations). The records were amplified, filtered (band-pass 0.02–15 Hz), digitized (250 Hz sampling frequency), stored on disk, and averaged off-line separately for the three electrode sites and the two expectancy conditions (Irritancy vs. No irritancy Expectancy). Base-to-peak amplitudes and latencies (the amount of neuronal activation allocated to processing and processing speed, respectively; Hummel and Kobal 2002) of N1 and P3 were examined.

Equipment

Stimuli were presented using a dynamic air-dilution olfactometer (Burghart Instrument, Wedel, Germany) that presented odorants with-
out altering the mechanical or thermal conditions of the mucosa (Kobal 1981). The stimuli were presented in a constantly flowing air stream of 7.2 L/min, with controlled temperature and humidity (36°C, 80% relative humidity). Participants used the velopharyngeal closure breathing technique (Kobal 1981): they were trained to use the levator veli palatini muscle to elevate the soft palate to isolate the pharyngeal cavity from the nasal cavity. This technique prevents intranasal respiratory airflow, ensuring the absence of interference from respiration on stimulus presentation (Kobal 1981) and thus stimuli could be presented nonsynchronously to inhalation. They received white noise through headphones to mask the sound of clicking accompanying the presentation of stimuli.

The olfactometer was connected by means of a cable from the Trigger Out-port of the olfactometer to the parallel port of a laptop running E-Prime (version 1.2, Psychology Software Tools). The experiment was programmed to wait for a trigger (TTL “high” signal) from the olfactometer at two moments during a trial, to guarantee synchronization of the olfactometer and the E-Prime script. The first trigger was the actual odor presentation, after which the script continued with the sensory rating scales. The second trigger (activated by a nondetectable clean air pulse) indicated the end of the intertrial interval (i.e., the start of the next trial), resulting in the script continuing with the expectation cueing of the next trial (see Composition of one trial).

Procedure

On arrival at the lab, participants received information about the experimental procedure before onset. All participants signed informed consent prior to starting the study. The study was described as an investigation of the influence of chemical concentration on brain processing. Participants were told that the visual cue (which was a percentage on a computer screen: 0% or 98%) indicated the chance that they would experience a painful sting in the nose after smelling the odor. 2 At least 8 trials should be averaged to obtain a reliable olfactory ERP (Hummel and Kobal 2002). We chose to average 16 identical trials to improve the signal. Furthermore, it was checked whether the CO₂ pulses remained sufficiently annoying during the entire experiment. Mean VAS ratings of CO₂ annoyance during the first half of the experiment were compared with mean VAS ratings during the second half of the experiment. Mean VAS scores of experienced intensity and annoyance of the 16 98%-odor-no CO₂ (Irritancy Expectancy condition) and the 16 0%-odor-no CO₂ (No irritancy Expectancy condition) were compared, to investigate whether the perception of the odor had changed as a result of irritancy expectancy (all paired-sample t-tests).

RESULTS

Study 1

EXPECTATION INDUCTION PHASE. Irritancy expectancy ratings were significantly higher in the Irritancy Expectancy condition compared with the No irritancy Expectancy condition [M Irr = 76.66, SD = 18.21, M No Irr = 5.28, SD = 6.45; t(30) = 18.75, P < 0.01]. In conclusion, if participants saw the “98%” cue, they indeed expected the CO₂ after smelling the odor, whereas the “0%” cue induced (almost) no expectation of CO₂. This was the case for all participants.

TEST PHASE. Manipulation check and ratings H₂S. Irritancy expectancy awareness remained high during the test phase of the experiment. Ratings were significantly higher in the Irritancy Expectancy condition as opposed to the No irritancy Expectancy condition [M Irr = 80.47, SD = 18.19, M No Irr = 4.70, SD = 5.60; t(30) = 23.59, P < 0.01]. To check whether CO₂ annoyance remained sufficiently high during the experiment, annoyance ratings from the first half of the experiment were compared with ratings from the second half of the experiment. CO₂ habituation during the experiment did not occur. Apparently, the increase in presentation length throughout the experiment helped to avoid this. Annoyance ratings did not change significantly over the course of the experiment [M first half = 63.56, SD = 20.06, M second half = 69.19, SD = 22.48; t(30) = 1.84, P = 0.08]. When asked about the purpose of the study during the debriefing, nobody specifically stated that the purpose was to measure effects of expectations about sensory irritation on the perception of odors or anything resembling this purpose.

Effects of manipulation. Odor intensity ratings were not significantly higher in the Irritancy Expectancy condition compared with the No irritancy Expectancy condition [M Irr = 26.56, SD = 17.26, M No Irr = 24.70, SD = 15.97; t(30) = 1.29, P = 0.21]. Odor annoyance ratings, on the other hand, differed significantly between conditions, where the odor was rated as more annoying in the Irritancy condition compared with the No irritancy condition [M Irr = 24.45, SD = 18.51, M No Irr = 21.64, SD = 17.52; t(30) = −2.19, P = 0.04]. Apparently, expecting a negative consequence following an odor altered the way the odor was evaluated later on.

Event-related potential results H₂S. Mean amplitudes and latencies of the N1 and P3 peaks, recorded at Fz, Cz, and Pz, are presented in the left panel of Table 3. Figure 1 (left panel) shows the grand-average OERPs per electrode site.

N1 peak. On N1 amplitude, a significant main effect of Expectancy Condition was found [F(1,30) = 5.80, P = 0.02], indicating that irritancy expectancies increased the early N1 amplitude (M Irr = −4.47, SD = 4.08; M No Irr = −3.01, SD = 2.90). There was no main effect of Electrode (F < 1.0), but there was an interaction effect between Expectancy Condition and
and Electrode $[F(2,29) = 3.92, P = 0.03]$. Post hoc tests with Bonferroni corrections demonstrated that the difference between the Irritancy and No irritancy Expectancy condition was significant at electrodes Cz ($P < 0.01$) and Pz ($P = 0.01$), but not at Fz. This indicates that different brain areas were activated to different degrees under the two conditions (see also Kettenmann et al. 1996).

On N1 latency, a significant main effect of Expectancy Condition was found $[F(1,30) = 23.48, P < 0.01]$, revealing that latencies were shorter during the Irritancy Expectancy condition compared with the No irritancy Expectancy condition ($M_{\text{irr}} = 327.23$, SD = 62.81; $M_{\text{no irr}} = 393.89$, SD = 75.69). There was no main effect of Electrode $[F(2,29) = 2.53, P = 0.10]$ and no interaction effect between Expectancy Condition and Electrode $[F(2,29) = 1.12, P = 0.34]$.

P3 peak. On P3 amplitude, a significant main effect of Expectancy Condition was found $[F(1,30) = 12.73, P < 0.01]$, showing that irritancy expectancies increased the P3 amplitude ($M_{\text{irr}} = 11.03$, SD = 5.27; $M_{\text{no irr}} = 9.50$, SD = 4.61). Additionally, a significant main effect of Electrode was found $[F(2,29) = 22.35, P < 0.01]$. Post hoc testing with Bonferroni corrections demonstrated that P3 amplitude was generally highest at Pz and lowest at Fz, as expected for olfactory ERPs (Hummel and Kobal 2002; $M_{\text{Fz}} = 7.82$, SD = 4.24, $M_{\text{Cz}} = 10.84$, SD = 5.47, $M_{\text{Pz}} = 12.13$, SD = 5.50; all $P$ values <0.01). No interaction effect between Electrode and Expectancy Condition was found ($F < 1.0$).

The same analysis was conducted for the dependent variable P3 latency. Although P3 latencies were shorter in the Irritancy Expectancy condition ($M_{\text{irr}} = 507.54$, SD = 66.13; $M_{\text{no irr}} = 572.74$, SD = 75.51), this effect was not significant $[F(1,30) = 3.52, P = 0.08]$. There was no main effect of Electrode $[F(2,29) = 1.29, P = 0.29]$ and no interaction between Expectancy Condition and Electrode ($F < 1.0$).

DISCUSSION STUDY 1. Experimental induction of the expectation that an odor would be followed by sensory irritation in the nose under predictable circumstances was effective, as evidenced by the substantial irritancy expectancy in the participants. Apparently, seeing the 98% sign in combination with smelling the odor raised the awareness that irritancy might be imminent, in turn resulting in a more negative evaluation of the odor. Additionally, the N1 peak appeared earlier and both the N1 and P3 peak had larger amplitudes, indicating faster (for N1) and more intensive processing of the odor. This suggests that expectations of aversive (health) consequences from inhaling an odor alter modality-specific stages (as reflected by effects on the N1 peak), as well as amodal stages of odor information processing (as reflected by a changed P3 peak and evaluations). Study 2 tests whether these effects are limited to aversive odors or also occur for pleasant odors.

**Study 2**

EXPECTATION INDUCTION PHASE. Irritancy expectancy ratings were significantly higher in the Irritancy Expectancy condition compared with the No irritancy Expectancy condition ($M_{\text{irr}} = 80.00$, SD = 17.97, $M_{\text{no irr}} = 4.73$, SD = 6.73; $t(29) = 19.23$, $P < 0.01$). Again, the expectancy induction was successful because participants knew to expect irritancy after seeing the “98%” cue in combination with smelling the odor. This was the case for all participants. Again, participants did not demonstrate any awareness about the purpose of the experiment.

TEST PHASE. Manipulation check and ratings PEA. Irritancy expectancy ratings were significantly higher in the Irritancy Expectancy condition as opposed to the No irritancy Expectancy condition ($M_{\text{irr}} = 84.64$, SD = 19.59, $M_{\text{no irr}} = 6.51$, SD = 8.95; $t(29) = -18.79$, $P < 0.01$), again indicating that the induction of expectancies had succeeded (see Fig. 1, right panel). To check whether CO$_2$ annoyance remained significantly high during the experiment, annoyance ratings of the first half of the experiment were compared with ratings of the second half of the experiment. Again, annoyance did not decrease due to habituation ($M_{\text{first half}} = 62.37$, SD = 18.05, $M_{\text{second half}} = 66.13$, SD = 19.05; $t(29) = -1.92$, $P = 0.06$).

Effects of manipulation. PEA intensity ratings did not differ between conditions ($M_{\text{irr}} = 18.96$, SD = 11.36, $M_{\text{no irr}} = 19.41$, SD = 12.92; $t(29) = 0.44$, $P = 0.66$). However, annoyance ratings did, with the odor rated as significantly more annoying in the Irritancy Expectancy condition ($M_{\text{irr}} = 6.95$, SD = 7.18; $M_{\text{no irr}} = 5.61$, SD = 5.82; $t(29) = -2.37$, $P = 0.03$).
0.03], even though on a scale of 1 to 100 overall annoyance was low. Still, this demonstrates that expecting a negative consequence following an odor altered the way the odor was evaluated later on.

Event-related potential results PEA. Mean amplitudes and latencies of the N1 and P3 peaks, recorded at Fz, Cz, and Pz, are presented in the right panel of Table 3. Figure 1 (right panel) shows the grand-average OERPs per electrode site.

N1 peak. On N1 amplitude a significant main effect of Expectancy Condition was found \([F(1,29) = 5.59, P = 0.03]\), indicating that irritancy expectancy increased the early N1 amplitude \([M_{\text{irr}} = 3.97, SD = 3.15; M_{\text{no irr}} = 2.59, SD = 2.51]\). There was no main effect of Electrode \([F(2,28) = 2.08, P = 0.14]\).

On N1 latency no significant main effect of Expectancy Condition was found \([F < 1.0]\). There was no main effect of Electrode \([F(2,28) = 2.84, P = 0.08]\) and no interaction effect between Expectancy and Electrode \([F < 1.0]\).

P3 peak. On the P3 amplitude, no significant main effect of Expectancy Condition was found \([F < 1.0]\); however, a significant main effect of Electrode was found \([F(2,28) = 25.95, P < 0.01]\). Post hoc testing with Bonferroni corrections demonstrated that P3 amplitude was generally highest at Pz and lowest at Fz \([M_{Fz} = 8.89, SD = 4.46, M_{Cz} = 11.68, SD = 4.56, M_{Pz} = 12.13, SD = 4.20; \text{all } P \text{ values } <0.01]\). Additionally, a significant interaction effect between Electrode and Expectancy Condition was found \([F(2,28) = 3.55, P = 0.04]\). Post hoc tests showed that for both the Irritancy and the No irritancy Expectancy condition, amplitudes differed between Pz and Fz (Pz largest, Fz smallest, all \(P \text{ values } <0.01\)), whereas differences between Cz and Pz did not reach statistical significance. Although this may reflect error variance, it could also indicate that the two different conditions produced differential activation of cortical generators of the P3 component (Hummel and Kobal 2002).

On P3 latency, no significant main effect of Expectancy Condition was found \([F < 1.0]\); however, there was a significant main effect of Electrode \([F(2,28) = 4.93, P = 0.02]\). Post hoc testing demonstrated that latencies measured at Cz were shortest and latencies measured at Fz were longest \([M_{Fz} = 508.80, SD = 69.71, M_{Cz} = 493.20, SD = 71.40, M_{Pz} = 497.00, SD = 69.92; \text{only significant between } Cz \text{ and } Fz, P = \ldots\]
OERPs (Krauel et al. 1998; Pause 2002; Pause and Krauel latency components may index anticipation of the aversive outcome. Activation in modality-specific processing, whereas the later components as well as studies demonstrating effects on later components as P3 peak, in the case of H2S. The effects of expectation on the N1 component appear to be fairly robust because similar effects on N1 latency were found in a previous study by our group (Bulsing et al. 2007), which also involved the effects of expectation of irritancy on odor perception. In other words, influences of the expectation of irritancy extended beyond the amodal information processing phase, as reflected by the P3, to modality-specific processing of odor, as reflected by N1 (Olofsson et al. 2008).

Effects of cognition on early components of the ERP have also been found for the visual modality, although not always. Pizzagalli et al. (2003), for example, showed that fearful faces associated with an aversive outcome modulated early exogenous visual ERP components such as N1. They cited a number of other studies, such as that by Baas et al. (2002), demonstrating aversive conditioning effects on early ERP components as well as studies demonstrating effects on later components such as P3 instead (e.g., Skrandies and Jedynak 2000). They interpreted the results from these studies, especially those revealing early effects, as “...consistent with the assumption that adaptive behavior relies on rapid monitoring of potentially salient cues in the environment, a mechanism that may be implemented through enhanced sensory processing” (Pizzagalli et al. 2003). According to these authors, and referring to Baas et al. (2002), the early components may index boosted activation in modality-specific processing, whereas the later component may index anticipation of the aversive outcome.

The process of (selective) attention has been proposed to explain shortened N1 latencies in other studies assessing OERPs (Krauel et al. 1998; Pause 2002; Pause and Krauel 2000). Indeed, expecting an odor to be harmful would cause an individual to be more attentive to that odor, resulting in enhanced or faster perception of the stimulus (see also Bulsing et al. 2007). For the N1 amplitude on the other hand, the role of attentional or cognitive factors seems to be small or even absent (Pause and Krauel 2000). However, we found that when participants expected trigeminal irritation after smelling an odor, N1 amplitudes to that odor were enhanced. This implies that more processing capacity—and perhaps more attention—was devoted to the processing of that odor. Interpretations of the N1 in terms of attention are in line with interpretations in terms of “boosted activation” of olfactory processing referred to earlier.

A comparison of Study 1 with Study 2 revealed that the magnitude of the expectancy effect on brain potentials was smaller for the pleasant odor of roses, i.e., PEA, relative to the unpleasant odor of rotten eggs, i.e., H2S. When the exact same procedure that was applied with H2S as the conditioned stimulus was repeated with PEA as the odor stimulus, only the amplitude of the N1 peak was affected. In both studies, the odorant was evaluated as more annoying when irritancy was expected than when no irritancy was expected.

Our findings with respect to differences between the two odors resemble those reported by Van den Bergh et al. (1995, 1997, 1998), who used classical conditioning to establish learned associations between odors and aversive consequences. Van den Bergh and colleagues demonstrated successful conditioning of unpleasant, but not pleasant, odors to CO2-enriched air, resulting in increased respiratory frequency in response only to the unpleasant odor. The difference in brain activity in the present studies cannot be explained by differences in perceived intensity of these odorants because there was no significant difference in perceived intensity associated with these odors across Studies 1 and 2. Preexisting hedonic evaluations of H2S (“unpleasant and possible implying danger”) may be more difficult to overcome than preexisting liking of PEA (“pleasant smell of flowers”), possibly in relation to the congruency of hedonic evaluations of the former odor and CO2 sensation versus incongruency of the latter odor and CO2 sensation [see also Bradley et al. (2005) for similar findings in the context of pictorial stimuli (either intrinsic pleasant or unpleasant) and physiological responses].

In both Study 1 and Study 2, participants perceived the odors as more annoying, but not more intense, when expecting irritancy compared with not expecting irritancy. This is in contrast with studies conducted by Dalton (e.g., Dalton 1999) who reported increased intensity perception when participants believed the odor of exposure to be potentially harmful as opposed to healthful. These differences may be due to the fact that, in Dalton’s studies, participants received a continuous ambient exposure to the odorant for ≥20 min in an environmental chamber, whereas the participants in the present studies received very brief intermittent exposures to the nose only.

The findings from this study confirm the notion that the expectation that an odor is irritable may change perception of that odor. Consequently, health symptoms attributed to odor exposures could be modulated by these changes as posited by Dalton (1999), although this hypothesis still remains to be fully tested by including endpoints related to health effects (e.g., ocular hyperemia, nasal secretion; Smeets et al. 2002) in studies such as the present one.

Health effects from environmental odor exposure are conventionally construed as reflecting individual differences in interpretations (referring to high-level information processing) but not perceptions (referring to low-level information processing) from verifiable exposures. This perspective can no longer be held, in view of the finding that the neurophysiological basis of perception as much as interpretations are subject to individual variation.


