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Central Processing of Odor Concentration is a Temporal Phenomenon as Revealed by Chemosensory Event-Related Potentials (CSERP)

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Abstract

Chemosensory event-related potentials (CSERP) can be used to examine central nervous odor processing. An important question for understanding odor perception is how different concentrations are processed. In the present study two odors were chosen which activate either the olfactory (linalool) or the trigeminal (menthol) system. Both odors were presented to 11 subjects in four different concentrations. Four subjects had to attend actively to the odors while the others perceived the odors under passive attention. The results showed that increased concentrations of the olfactory stimulus resulted in shorter latencies of the N1 component but did not affect the amplitudes of the CSERP. However, the amplitudes of the stimulus dependent, exogenous components (N1, P2) increased with higher concentrations of the trigeminal stimulus. The amplitude of the late positive complex, which reflects endogenous processes, was usually larger when the odorous stimuli had to be attended to actively. It is concluded that olfactory intensity coding results in a qualitatively different but not in a stronger neuronal response of the human brain. **Chem. Senses 22: 9–26, 1997.**

Introduction

Recent improvements in the recording of chemosensory event-related potentials (CSERPs; Doty and Kobal, 1995) have led to the assumption that many questions about central odor processing may be clarified using this new method (Kobal and Hummel, 1991; Prah and Benignus, 1992; Evans *et al.*, 1993; Lorig *et al.*, 1993; Murphy *et al.*, 1994; Pause *et al.*, 1996b). And, indeed, this method will allow basic and applied aspects of olfactory perception to be explained. For example, it has been shown (Kobal, 1981; Pause, 1994) that the amplitudes of the CSERP decrease strongly with short (<10 s) interstimulus intervals (ISI), reflecting habituation in central odor processing. In another study with CSERPs it has been demonstrated that the olfactory short-term memory expands to >30 s (Pause *et al.*, 1996b). Progress in applied research has been achieved by introducing CSERPs in clinical settings (Becker *et al.*, 1993; Hummel *et al.*, 1991) and by examining the central processing of odors during the human menstrual cycle (Pause *et al.*, 1996a). However, the growing number of papers concerning CSERPs should not lead to the conclusion that the functional significance of the components within the CSERP has been fully established to

date. While most researchers agree that the amplitudes and latencies of the CSERP reflect effects of odor concentration, in the following it will be questioned if this proves to be true for all components of the CSERP and for all odors.

The first study concerning the effects of odor concentration on the CSERP was carried out by Kobal (1981). Five different concentrations of eucalyptol (range 4–6481 p.p.m.) and linalool (range 46–1287 p.p.m.) were presented to the subjects randomly, and after each presentation the subjects had to evaluate the stimulus intensity. When the higher odor concentrations were presented the subjects reported a pungent sensation in their nose. The results revealed that there was a tendency for the higher odor concentrations to evoke CSERPs with larger amplitudes and shorter latencies. Interestingly, the correlations between the amplitudes and the subjective intensity estimates were higher than the correlations between the amplitudes and the objective odor con- centration. Significant results were published by Kobal and Hummel (1991) only for the N1/P2 amplitude evoked by linalool.

Two other studies separated the effects of olfactory and trigeminal stimulation using either H_2S or a CO_2 as stimuli. It has been demonstrated that anosmic subjects only show an electrocortical response to CO_2 but not to H_2S (Doty and Kobal, 1995). Kobal and Hummel (1991) described a study (unpublished data) in which a clear concentration effect of painful CO_2 stimulation (five concentrations, range 32–59% v/v) on the amplitude and latency of the CSERP (N1 and P2 component) was shown. However, using the olfactory stimulus H_2S (five concentrations, range 0.1–32.9 mg/m^3), Thiele and Kobal (1984) could only find a tendency for the CSERP to occur earlier with higher stimulus concentrations, but the amplitudes did not depend on stimulus concentration.

Another group (Prah and Benignus, 1992) used toluene in three concentrations (1600, 8000 and 16 000 p.p.m.). In their study the subjects were required to count the stimulus presentations. They found an enlargement of a positive component within the CSERP when the highest odor concentration was applied to the subjects. However, they failed to find an effect of stimulus concentration on the latency of the CSERP.

It has recently been demonstrated (Pause *et al.*, 1996b) that the CSERP includes components depending on stimulus features (the 'exogenous' components N1 and P2) and components depending on stimulus evaluation (the 'endogenous' component P3). Whereas the amplitude and latency of the components N1 and P2 varied with the concentration of an odorous stimulus (citral, 10 and 844 p.p.b.), the P3 component varied with the subjective stimulus significance.

Summarizing the results indicating a concentration effect on the CSERP, it becomes evident that some studies did not separate effects of olfactory and trigeminal stimulation. Considering the clear concentration effect of CO_2 on the CSERP (Kobal and Hummel, 1991) and the failure to find a concentration effect after stimulation with H_2S (Thiele and Kobal, 1984) it seems likely that the amplitude of the CSERP only increases when the trigeminal system is excited. The finding that eucalyptol and linalool evoked larger amplitudes with higher stimulus concentrations (Kobal, 1981) might be attributed to a response of the trigeminal system because the stimulation was accompanied with trigeminal sensations. In the CSERP study by Prah and Benignus (1991) the concentration effect of toluene was only due to the highest concentration (16 000 p.p.m.). As toluene has been described as having strong trigeminal properties (Doty *et al.*, 1978) this effect might be explained by the properties of high concentrations to stimulate the trigeminal nerve. Finally, the results that citral evokes potentials which vary with the stimulus concentration (Pause *et al.*, 1996b) could again be due to effects of trigeminal stimulation. Even though the stimulus concentrations were low (up to 844 p.p.b.), the study did not control for effects of trigeminal stimulation.

The second effect that could explain some of the concentration effects mentioned in the literature is the subjective stimulus significance of odorous stimuli or the task relevance induced by the experimental setting. With a design requiring stimulus categorization (oddball design) it has been shown that all odorous stimuli evoke a large positive component (P3) which reflects endogenous stimulus processing (Pause *et al.*, 1996b). It is important to note that the exogenous P2 component was usually overlapped by the P3 component and therefore did not appear as a distinct component but as a turning point in the curve. It was concluded from that study that whenever odors have to be attended to, the endogenous component may dominate the CSERP. However, in accordance with the classic P3 research (Donchin and Coles, 1988), the olfactory P3 was larger when the odors were presented with a low probability and had to be counted. In almost all CSERP studies the odors were presented as rare events, because long interstimulus intervals

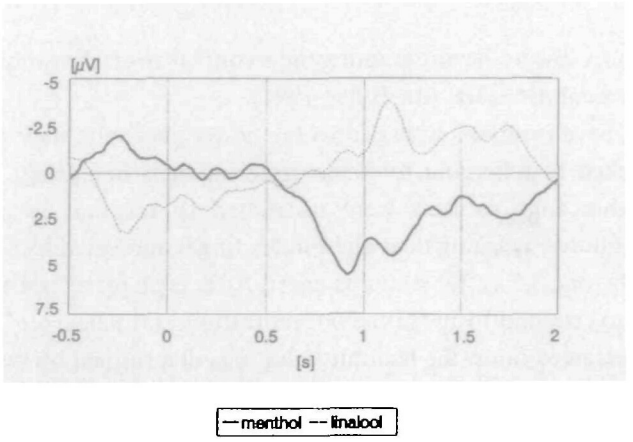

Figure 1 CSERP (Cz) in response to menthol (n = 23) and linalool (n = 23) recorded from an anosmic subject. At time point 0 the odor is supposed to reach the nasal mucosa.

Table 1 Design

Trial set no.	Odor dilution	Linalool concentration (p.p.m.)	Menthol concentration (p.p.m.)
1	odorless air = 8 ml/s no dilution	-/-	-/-
2	odor current = 0.8 ml/s flow dilution = 1:10	0.16	0.10
3	odor current = 1.6 ml/s flow dilution = 1:5	0.33	0.42
4	odor current = 4 ml/s flow dilution = 1:2	not detected	1.44
5	odor current = 8 ml/s no dilution	1.45	4.15

[ISI = 40–50 s in Kobal (1981); ISI = 10–15 s in Prah and Benignus (1992)] were used. In event-related potential (ERP) research it is known that single rare events usually elicit the late positive P3 component (Polich *et al.*, 1994). Furthermore, stimulus intensity estimations were required after each odor presentation (Kobal, 1981; Thiele and Kobal, 1984) and the odors had to be counted (Prah and Benignus, 1992), thereby the odors had to be evaluated and memorized. These experimental conditions suffice to evoke the endogenous late positive complex (Johnson, 1993). It is in line with this consideration that the CSERPs evoked by eucalyptol and linalool (Kobal, 1981) correlated more strongly with the subjective intensity estimates than with the real odor concentration. Finally, the effect that higher odor concentrations evoked larger endogenous components could be due to their emotional valence. It is known that the higher the odor concentration, the more negative the odor is perceived to be (Moskowitz *et al.*, 1976). Since it has been reported that the late positive component varies with the emotional valence of the stimulus (Johnston *et al.*, 1986), the larger amplitude in response to high odor concentrations could be due to the negative valence of high odor concentrations.

The present study was carried out in order to examine the effects of different odor concentrations on the electrical brain activity. [The CSERP recordings as well as the methods for stimulus presentation were carried out in accordance with Evans *et al.* (1993). However, we did not use their suggested conventions for peak labeling (cf. Pause *et al.*, 1996b).] To control for effects of trigeminal stimulation we chose an olfactory (linalool) as well as a trigeminal (menthol) stimulus. The odors were presented in four different concentrations (linalool: 0.16–1.45 p.p.m., menthol: 0.10–4.15 p.p.m.). In accordance with Pause *et al.* (1996b), concentration changes were expected to affect the early components of the CSERP (N1, P2). Moreover, the amount of attention was varied to separate those components of the CSERP which are dependent on endogenous stimulus processing. Some subjects were asked to perform a motor response after each stimulus presentation (active attention) while others were instructed to relax (passive attention) during the EEG recording. The late positive component (P3) of the CSERP was expected to be larger when subjects had to attend to the stimuli actively.

Methods

Subjects

Six male and five female subjects (mean age = 26.5, SD = 5.3) participated voluntarily in the study. They gave their written consent and were paid for participation. The subjects were not under medication and were non-smokers. They did not suffer from any acute or chronic sickness of the respiratory system. Subjects were instructed not to use any perfumed toiletries on the day of the experiment and to refrain from eating 1 h before the test session started. During the session subjects were only allowed to drink water. Sleeping time was at least 5 h during the night prior to the experiment. The female subjects did not take oral contraceptives and reported that they had a regular cycle length. All female subjects were tested within their follicular cycle phase, in the first third of the menstrual cycle but after

menstruation. The study was carried out in accordance with the recommendations of the declaration of Helsinki.

Design

One screening and two EEG sessions were performed. In the screening session the subjects' sensitivity to five odorants (androstenone, citral, isoamylacetate, linalool and menthol) was measured to estimate their average ability to smell. Apart from one subject who was anosmic to androstenone, the subjects could detect 0.15 μg androstenone in 1 ml of an odorless solution (1,2-propanediol). The highest thresholds for the other odorants were 1:600 for citral, 1:60 000 for linalool, 1:200 for menthol and 1:6000 for isoamylacetate (v/v).

During the EEG sessions linalool (±-linalool, 97%, Aldrich, Germany) and menthol (DL-menthol, 99%, Merck-Schuchardt, Germany) were presented in four different concentrations (Table 1). To demonstrate that the linalool concentrations were below the trigeminal threshold, we tested four anosmic subjects suffering from a damaged N. olfactorius (Leplow *et al.*, 1994). After stimulation with 1.45 p.p.m. linalool (the highest concentration used in the present study) the anosmic subjects did not report any subjective sensations and did not show a response within the CSERP, but did respond with large potentials to the presentation of 4.15 p.p.m. menthol. Figure 1 shows an example for one anosmic subject.

In the EEG sessions five sets of 25 trials each were carried out. The trial sets were separated by 10 min breaks. During the first set of trials odorless room air was presented to control for somatosensory artifacts, during the following four sets of trials one of the two odors was presented in ascending concentration. The odor concentrations varied in a ratio of 1:10, 1:5, 1:2 and 1:1. For the highest concentration linalool was dissolved 1:100 in 1,2-propanediol (99%, Merck, Germany) and menthol 1:10 in the same solvent. The lower concentrations were achieved by flow dilution through the olfactometer. Kobal (1981) noted that it is more difficult to obtain concentration effects when the odor concentrations are not presented randomly but in ascending or descending series. However, for technical reasons we could not vary the odor concentrations randomly. To avoid effects of serial presentation we introduced long ISIs (50 s). With an ISI of 50 s, effects of habituation within one set of trials were not expected, therefore each odor was presented as a single stimulus and not within a series of stimuli. Using long ISIs also prevented the subjects having contingency control over the stimulus presentations (cf. van Toller, 1994).

Seven subjects attended to the odors passively; they were asked to relax and to concentrate on their breathing. The other four subjects were instructed to respond to each stimulus by lifting their right index finger, indicated by a 500 Hz tone 3.5 s after stimulus onset. After each set of trials the subjects had to judge the concentration and valence of the perceived odor; the hedonic value was determined by verbal descriptors. However, they were not informed about the variation of the concentration during the sessions and they did not know that the first set of trials only served as a control condition.

All sessions started in the morning between 08.00 and 10.00 a.m.. The sessions began with a threshold test for the odor which was to be presented during the EEG recording; the test was performed separately for each nostril. After the electrodes were fixed, subjects were placed at the olfactometer and practiced a special kind of breathing technique (velopharyngeal closure). This technique was performed in order to avoid the flow of respiratory air within the subjects' nose during odor presentation. A whole session lasted between 5 and 7 h (mean = 6.5 h). Room temperature was always kept between 19 and 21°C.

Stimulus presentation

Olfactory stimuli were presented within a constantly flowing airstream corresponding to the method described by Kobal (1981). With this technique only the chemosensory but not the mechano- or thermosensory receptors in the nasal mucosa are activated. The stimuli were applied for a duration of 200 ms non-synchronously to breathing. They were presented monorhinally to the more sensitive nostril according to the threshold data.

In the olfactometer the odor bottle (either the linalool or the menthol solution) was stored in a warm water chamber and the odor was delivered to the subjects via a Teflon tube. The odor current was 8 ml/s and was added to a carrier stream (92 ml/s). Total flow rate as well as the flow rate of the odorless current presented during the ISI was 100 ml/s. For the dilution of the odor concentrations a flow of either 4, 6.4 or 7.2 ml/s was subtracted from the odor current and added to the carrier current. The temperature of the gas flow at the exit of the olfactometer was 34°C and its humidity was >80%. Switching the current from control air (during the ISI) to odorous air resulted in a flow fluctuation of 5–6 ml/s which was not perceived by the subjects and did

not evoke somatosensory potentials within the ERP (Pause, 1994). The latency between the computer-controlled activation of the switching process and the air flow reaching the nasal mucosa was 75 ms. The total rise time was 35 ms but 70% of the maximum amplitude was reached after 20 ms. White noise of 80 dB was presented binaurally and prevented the subjects from hearing the switching process.

Detection threshold

In the screening and the EEG sessions olfactory detection thresholds were measured according to a three-alternative forced-choice staircase detection threshold procedure (Pause *et al.*, 1996a). Briefly, 14 concentration steps were prepared with 1,2-propanediol as solvent. A 1:2 (v/v) dilution was the highest concentration which was diluted for each consecutive concentration in half decimal log steps (3.162-fold). In the lowest concentration the odor was diluted 1:6 300 000 (v/v). The threshold was defined as the lowest of two consecutive concentrations for which four successive correct identifications were obtained (error probability for a false positive result $P = 0.01$). The results are related to the mean detected dilution step (range = 1–14). Therefore, a higher value indicates a higher sensitivity. Thresholds were determined monorhinally. The left nostril was always measured first while the other nostril was closed with a sterile paper stopper. During the testing period subjects wore opaque glasses, and the room temperature was kept between 19 and 21°C.

Subjective ratings

After each odor concentration presented by the olfactometer, subjects had to judge the hedonic profile and the valence of the odor. The valence was rated on a seven-point scale from –3 to +3: –3 was set to very unpleasant, 0 to neutral and +3 to very pleasant. The hedonic profile of linalool and menthol was measured with a list of verbal descriptors, each of them associated with either a positive or a negative valence (Dravnieks *et al.*, 1984). A German translation of the list was used with 139 verbal descriptors.

The intensity of each odor concentration had to be rated by the subjects twice before and twice after each set of trials. For the statistical calculations the mean values across the four ratings were taken. The second highest concentration was presented as a standard, associated with a value of 0. The concentration of the respective trial set had to be evaluated in comparison to the standard from –10 (not perceivable) to +10 (highest possible concentration).

ERP recording

According to the 10/20 system the EEG data were recorded unipolarily from Fz, Cz and Pz, referred to linked mastoids and Oz was chosen as ground. The electrooculogram (EOG) was measured using three electrode pairs as suggested by Elbert *et al.* (1985). The electrodes (Ag/AgCl) were attached to the cleaned skin (Omniprep, Weaver & Co., USA) with an adhesive electrode cream (EC2-TM, Grass, USA). Electrode impedance was usually <5 kOhm and always <10 kOhm. The low frequency cut-off of the recording system was set to –3 dB at 0.016 Hz (t_c = 10 s) and the upper frequency cut-off was set to –3 dB at 30 Hz. The activity of all channels was A-D converted with a 12-bit resolution and a rate of 125 samples/s.

The recording time per trial was 8 s: after 2 s baseline the odor was presented for 200 ms, the acoustic signal was given 3.5 s after stimulus onset.

Data analysis

The data were checked for artifacts by off-line analysis: single trials contaminated with eye movements or blink artifacts within the time range of 0–1500 ms after stimulus onset were rejected (rejection criterion = deflections within the EOG > 100 μV). The remaining trials were corrected for horizontal and vertical eye movements by means of a multivariate regression model (Elbert *et al.*, 1985). The correction was done to exclude artifacts also in those time ranges which were ignored during the rejection procedure.

Before signal extraction, a phase-true digital low-pass filter (upper cut-off 4.5 Hz) was applied to the raw data (Ruchkin and Glaser, 1978). Low-pass filters of 5 Hz and lower are commonly used in P3 research (e.g. Ruchkin *et al.*, 1982; Johnson and Donchin, 1985). The filter technique was implemented originally to simplify the peak detection on a single-trial basis but has also been used for peak detection in averaged trials (Rösler *et al.*, 1985; Fabiani *et al.*, 1986).

The averaged olfactory potentials were checked for four peaks by determining their positive or negative maximum within a defined latency range. Peaks of the CSERP were labeled N1, P2, P3–1 and P3–2 (Pause *et al.*, 1996b). The following latency windows (all data are related to the activation of the odorous current: to obtain the real latency between stimulus onset and the components of the ERP 75 ms have to be subtracted) were chosen: 350–600 ms for the first negative peak (N1), 450–700 ms for the first positive peak (P2), 700–1000 ms for the second positive peak (P3–1) and 900–1300 ms for the third positive peak (P3–2). Like the

N1 and P2 components of the auditory vertex potential (see e.g. Loveless, 1983), the olfactory N1 and P2 components seem to reflect similar processing stages (Pause *et al.*, 1996b). As both components vary predominantly with stimulus features their amplitudes (μV) were defined as peak-to-peak amplitudes (N1/P2). The amplitudes of the P3–1 and P3–2 components were defined separately as peak-to-baseline amplitudes, because they are related to later processing stages and do not vary with the N1/P2 complex. The baseline was measured as the average electrical brain activity 1000 ms before the switching process commenced until stimulus onset.

Statistical calculations were done by analysis of variance (ANOVA). According to Kirk (1968), RBF designs (randomized block factorial design) were used for within-subject comparisons and SPF designs (split-plot design) were used for mixed designs, including within- and between-subjects comparisons (program no. 34, Fillbrandt, Kiel, Germany). Significance tests included the correction of the degrees of freedom by ε according to Huynh and Feldt (1976). Three kinds of ANOVAs were performed with the data from a total of 22 sessions. A two-way ANOVA including the within-subject factors 'odor concentration' (four steps according to the four different concentrations: the control condition was not included, because no odor-related EEG activity was expected to occur and made it impossible to define the related components) and 'electrode' (Fz, Cz, Pz) was calculated for each odor. The ANOVA 'attention' (between factor with two steps: active, passive) by 'electrode' was calculated separately for each odor and concentration step because no meaningful interaction was expected to occur between odor concentration and the amount of attention. The unweighted-means solution (Kirk, 1968) was used to adjust the unequal group size of the attention condition. To make sure that the odors were perceived as single stimuli and not as a series of odors, effects of habituation were controlled by analyzing effects of trial position within each set of trials. Therefore the ANOVA 'trial position' (2 steps: trial no. 1–10 and no. 11–20) by 'electrode' was calculated for each trial set and odor.

Arithmetic means and standard deviations were calculated across thresholds on the basis of dilution steps (range = 1–14). A *t*-test across all subjects was performed for each odor with the factor 'nostril' (left or right). To evaluate the effect of the different odor concentrations on the intensity and valence ratings, two one-way ANOVAs were calculated for each odor and rating type: one ANOVA across the ratings of all five trial sets, including the control condition, and one ANOVA across the last four trial sets, examining the rating differences between the four odor concentrations, were performed.

Changes in the verbal descriptions due to odor concentration differences were analyzed by determining the degree of agreement (k) between the raters (Fleiss, 1971), separately for each concentration step. The calculation of k incorporates a correction for the extent of agreement expected by chance alone.

The level of significance was set to $P < 0.05$. However, to detect even weak habituation of central odor processing, analyses including habituation effects are presented whenever the P value was <0.10.

Results

Detection thresholds and subjective ratings

Odor thresholds

For linalool and menthol, thresholds were slightly lower for the right nostril than for the left one (linalool left nostril: mean = 10.27, SD = 2.87, right nostril: 10.91, SD = 1.97; menthol left nostril: 8.45, SD = 3.36, right nostril: 8.91, SD = 2.63). However, according to *t*-tests these differences were not significant.

Intensity and valence ratings

The odor intensity during the control condition was judged to be weaker than the intensity of the different odor concentrations [linalool: $F(4,40) = 2.62$, $P = 0.05$; menthol: $F(4,40) = 6.91$, $P < 0.01$). The relation of odor concentration between the last three trial sets was correctly detected by the subjects. However, the lowest odor concentration was judged to be higher than it actually was in relation to the following trial sets. The intensity ratings for menthol varied significantly in relation to the four concentrations [$F(3,30) = 3.45$, $P = 0.03$].

Odorless control air was described to be either more pleasant (linalool) or less pleasant (menthol) than the lowest odor concentration and the valence ratings between all sets of trials (including the control condition) changed significantly [linalool: $F(4,40) = 3.23$, $P = 0.02$; menthol: $F(4,40) = 2.83$, $P = 0.04$]. The emotional valence of both odors decreased with increasing odor concentration. This

Table 2 Odor intensity and valence ratings (mean, ± SD)

Flow dilution	Linalool ratings		Menthol ratings	
	Intensity*	Valence*	Intensity**	Valence*
Control	−3.80 (3.31)	+1.27 (1.01)	−4.23 (2.10)	+0.27 (0.90)
1:10	−1.66 (1.55)	+1.09 (1.70)	−1.45 (2.38)	+0.64 (1.03)
1:5	−1.98 (2.90)	+0.55 (1.75)	−2.30 (2.50)	+0.09 (1.22)
1:2	−1.80 (2.93)	+0.27 (1.56)	−1.36 (1.68)	0.00 (1.26)
None	−1.11 (2.53)	−0.09 (1.70)	+0.18 (2.65)	−0.64 (1.63)

Rating differences between the trial sets are significant with $^{*}P \leq 0.05$ and $^{**}P \leq 0.01$.

Table 3a Hedonic profile, inter-rater agreement (κ) and valence (±) of linalool[a]

Flow dilution							
1:10	*n*	1:5	*n*	1:2	*n*	None	*n*
+ fruity	4	+ fragrant	6	+ aromatic	6	+ floral	5
+ lemon	4	+ aromatic	4	+ lemon	5	+ fragrant	5
+ aromatic	3	+ fruity	4	+ floral	4	+ lemon	5
+ floral	3	+ lemon	4	+ fruity	4	+ aromatic	4
+ fragrant	3	+ floral	3	+ fragrant	3	+ fruity	4
+ light	2	− pungent	2	+ sweet	3	+ light	3
+ spicy	2	+ spicy	2	+ light	2	+ soapy	3
+ sweet	2	+ sweet	2	+ tea leaves	2	+ sweet	3
				+ spicy	2	− cleaning fluid	2
						+ perfumery	2
κ = 0.012		κ = 0.034		κ = 0.066		κ = 0.101	

[a]Only those descriptors are included which were marked by more than one subject.

Table 3b Hedonic profile, inter-rater agreement (κ) and valence (±) of menthol[a]

Flow dilution							
1:10	*n*	1:5	*n*	1:2	*n*	None	*n*
+ eucalyptus	5	+ eucalyptus	6	+ eucalyptus	6	+ eucalyptus	6
+ cooling	3	+ peppermint	5	+ peppermint	5	− pungent	6
+ peppermint	3	− pungent	3	− pungent	5	+ peppermint	4
+ fruity	2	+ cooling	2	+ cooling	3	+ cooling	2
− pungent	2	− heavy	2	+ spicy	3	− medicinal	2
+ sweet	2	+ spicy	2	− heavy	2	+ sweet	2
+ spicy	2			+ sweet	2	+ spicy	2
κ = 0.020		κ = 0.082		κ = 0.131		κ = 0.123	

[a]Only those descriptors are included which were marked by more than one subject

effect is significant for the menthol ratings [$F(3,30) = 3.94$, $P = 0.02$] and near to the significance level for the linalool ratings [$F(3,30) = 2.57$, $P = 0.07$]. For each concentration step menthol was described as less pleasant than linalool. The effects of odor concentration on intensity and valence ratings are shown in Table 2.

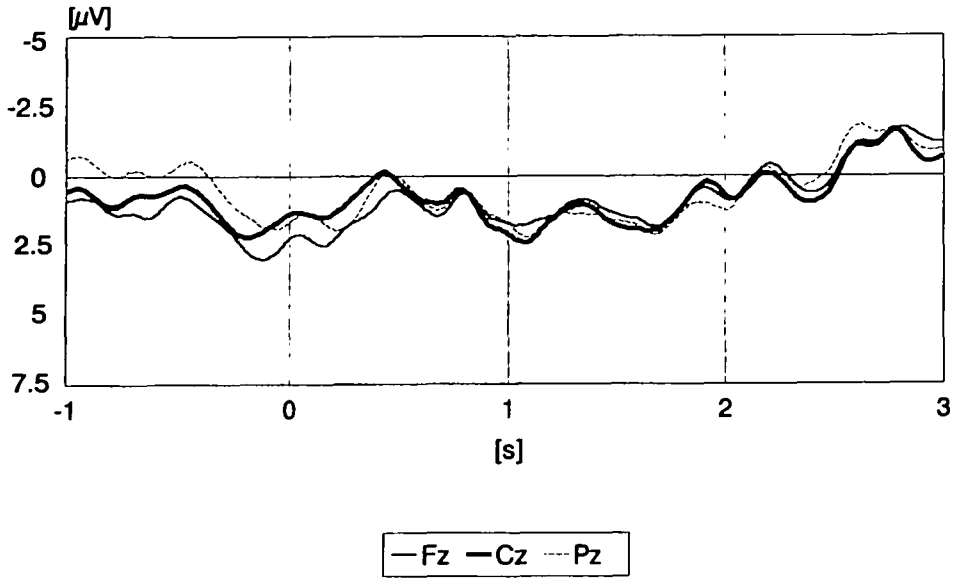

Figure 2 Control condition: grand average across five subjects (eight sessions) in response to odorless control air (n = 159). Time point 0 inidcates the activation of the current switch.

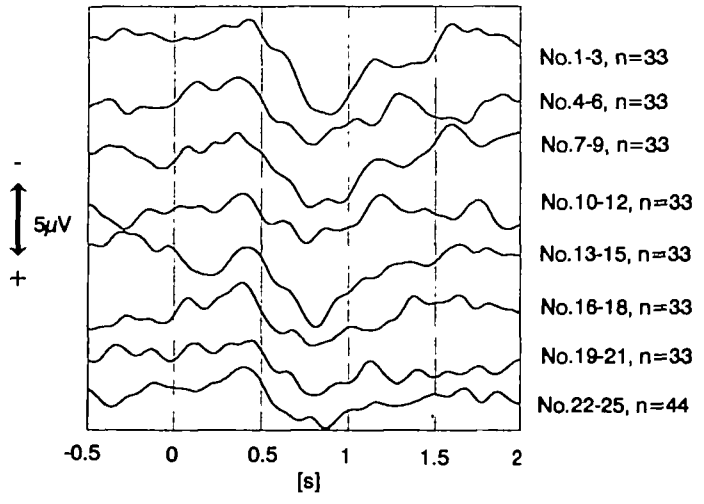

Figure 3 CSERP in reponse to 0.1 p.p.m. menthol, averages across 11 subjects. The 25 trials of the trial set are separated into groups of three or four trials. At time point 0 the odor is supposed to reach the nasal mucosa.

Verbal descriptions

Linalool was mainly described by verbal descriptors with a positive valence (Table 3a). The descriptors most frequently used were 'aromatic', 'fragrant', 'floral' and 'lemon'. The quality of linalool was described differently according to the concentration: The higher the odor concentration, the higher was the inter-rater agreement.

Menthol was correctly identified with descriptors like 'eucalyptus' and 'peppermint' (Table 3b). The use of the descriptors 'cooling' and 'pungent' indicates that menthol was perceived as a trigeminal excitant. The higher the concentration of menthol, the more subjects described the odor as pungent. For each odor concentration descriptors with a negative valence were used to describe menthol ('pungent', 'heavy', 'medicinial'). The inter-rater agreement increased from the lowest to the second highest concentration.

Electrophysiological data

No odor control condition

The grand average for the no odor control condition (trial set 1) included only those subjects who subjectively reported they did not perceive any odorous sensations. Some subjects reported perceiving a weak odor during the first trial set. This was due to the extremely difficult task of cleaning the olfactometer after the sesions. In Figure 2 the grand average across five subjects (eight sessions) for the control condition is shown. The electrical brain activity in response to the current switch is smaller than the spontaneous activity. In accordance with subjective reports that flow fluctuations were not perceivable, the current switch did not evoke somatosensory potentials.

Descriptive component analysis

The four different components appear most clearly when

Table 4 Scalp distribution of amplitudes (μV), means and standard deviations (±)

Component	Linalool			Menthol		
	Fz	Cz	Pz	Fz	Cz	Pz
N1/P2	3.99 (2.35)*	4.91 (2.95)	5.55 (3.78)	4.21 (2.25)	4.78 (2.55)	5.22 (2.77)
P3-1	3.66 (3.09)*	5.33 (4.26)	6.15 (5.91)	4.58 (3.27)*	6.15 (3.49)	6.56 (4.41)
P3-2	2.00 (3.04)**	3.60 (3.64)	4.79 (5.09)	2.94 (2.92)*	4.06 (3.15)	5.03 (3.94)

Main effect 'electrode position' significant at $*P \leq 0.05$ and $**P \leq 0.01$.

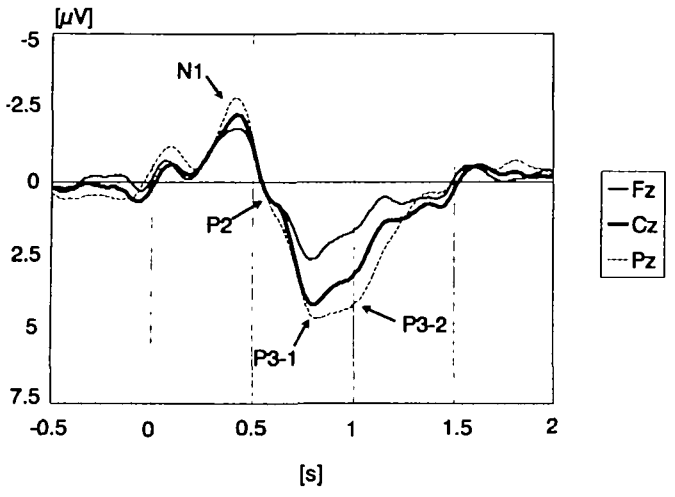

Figure 4 Topographical distribution of the CSERP in reponse to 0.1 p.p.m. menthol, averaged across 11 subjects. At time point 0 the odor is supposed to reach the nasal mucosa.

they are recorded from frontal scalp areas and in averages across trials with constant component latencies. The large P3 complex usually overlaps the small P2 component at parietal recording positions and it also dominates averages across trials with varying component latencies. As an example the CSERP to menthol (0.10 p.p.m.) is separated into smaller averages across three or four trials (according to the trial sequence, Figure 3) and presented for all recording positions (Figure 4).

Scalp distribution

All amplitudes were smallest at frontal and largest at parietal scalp areas, independent of the type of odor (Table 4). This effect was significant for all amplitudes of the CSERP after olfactory stimulation with linalool, the most pronounced effect was found for the P3–2 amplitude [N1/P2: $F(2,110) = 5.56$, $P = 0.03$; P3–1: $F(2,110) = 5.24$, $P = 0.03$; P3–2: $F(2,107) = 8.75$, $P < 0.01$]. After stimulation with menthol the CSERP had a similar scalp distribution, but the N1/P2 amplitude did not change significantly across the midline of the scalp. However, both P3 components were largest at the parietal electrode positions [P3–1: $F(2,110) = 5.12$, $P = 0.03$; P3–2: $F(2,110) = 5.19$, $P = 0.03$]. The latencies of the CSERP components evoked by linalool or menthol did not change with the scalp area. Moreover, for both odors we could not find any interaction between the effects of odor concentration and scalp distribution.

Effects of concentration on amplitudes

The presentation of different concentrations of linalool did not change the amplitudes of the CSERP significantly. The average N1/P2 amplitude evoked by the different concentrations varied between 4.4 and 5.2 μV and the smallest amplitude (4.4 μV) was related to the highest odor concentration. The same independence between amplitude and linalool concentration was observed for the P3–1 and P3–2 amplitudes. The P3–1 amplitude was largest (5.4 μV) when the lowest odor concentration was applied and smallest (4.7 μV) in response to the highest odor concentration. In contrast to the P3–1, the P3–2 amplitude was smallest (2.8 μV) when the lowest odor concentration was applied and largest (3.9 μV) in response to the second highest concentration.

For the trigeminal stimulus menthol a clear concentration effect on the amplitudes of the CSERP was observable. The difference amplitude N1/P2 [$F(3,110) = 6.32$, $P = 0.02$] and the P3–1 amplitude [$F(3,110) = 4.17$, $P = 0.05$] were significantly enlarged by higher odor concentrations. Both amplitudes became systematically larger with increasing odor concentrations (N1/P2: 3.7 μV for the lowest and 5.8 mV for the highest odor concentration; P3–1: 4.6 μV for the lowest and 7.2 μV for the highest odor concentration). However, the P3–2 amplitude did not change corresponding to the odor concentration and was greatest when the lowest (4.2 μV) and the highest (4.5 μV) concentration of menthol

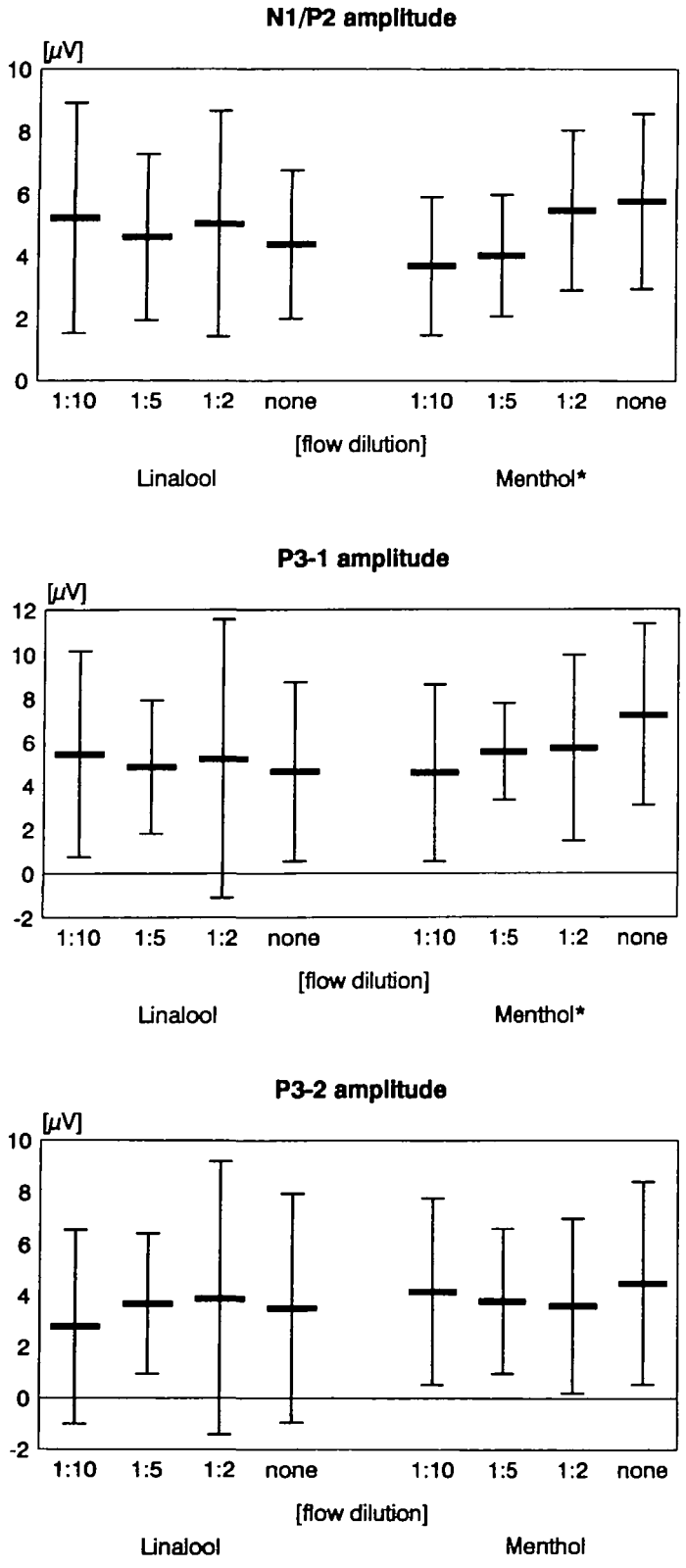

Figure 5 Amplitudes of the CSERP separated for the different odors and odor concentrations. When menthol was presented the amplitudes of the N1/P2 and P3–1 components significantly changed with odor concentration (*$P \leq 0.05$).

was applied. The effects of odor concentration on the amplitudes of the CSERP are summarized in Figure 5.

Effects of concentration on latencies

The higher the concentration of the olfactory stimulus linalool the shorter the latencies of the early component N1 were [$F(3,110) = 4.03$, $P = 0.05$]. The N1 latency was systematically reduced from 484 ms (lowest linalool concentration) to 443 ms (highest linalool concentration). The latencies of the other components were not significantly affected by the different linalool concentrations. However, the administration of the highest concentration always resulted in reduced latencies (latencies in response to the highest linalool concentration: P2: 626 ms; P3–1: 880 ms; P3–2: 1142 ms).

An increase in the menthol concentration did not change the latencies of the early components N1 and P2 signifcantly. The N1 latency was longest in response to the second highest odor concentration (499 ms) and shortest in response to the highest concentration (463 ms). The P2 latency was also longest for the second highest concentration (663 ms) but shortest for the lowest odor concentration (641 ms). The latencies of the late P3 components were significantly reduced after application of the highest menthol concentration [P3–1: $F(3,110) = 10.28$, $P < 0.01$; P3–2: $F(3,110) = 31.01$, $P < 0.01$; latencies in response to the highest menthol concentration: P3–1: 854 ms; P3–2: 1088 ms]. However, they were not reduced systematically by the three lower concentrations. The effects of odor concentration on the latencies of the CSERP are shown in Figure 6.

Effects of habituation

None of the CSERP parameters changed consistently across the four trial sets within one session (see Table 5). After presentation of linalool the N1/P2 amplitude only habituated [$F(1,50) = 4.98$, $P = 0.04$] when the second highest concentration was presented, but not in response to the other concentrations. The latencies of the early components became longer during the first 20 trials when the highest [N1 latency: $F(1,50) = 4.19$, $P = 0.06$] or the lowest [P2 latency: $F(1,50) = 3.65$, $P = 0.08$] concentration of linalool was presented. Whereas neither the amplitude nor the latency of the P3–1 component changed within either trial set, the amplitude of the P3–2 component was affected by the trial position during three of the four trial sets. The amplitude became smaller during the first 20 trials

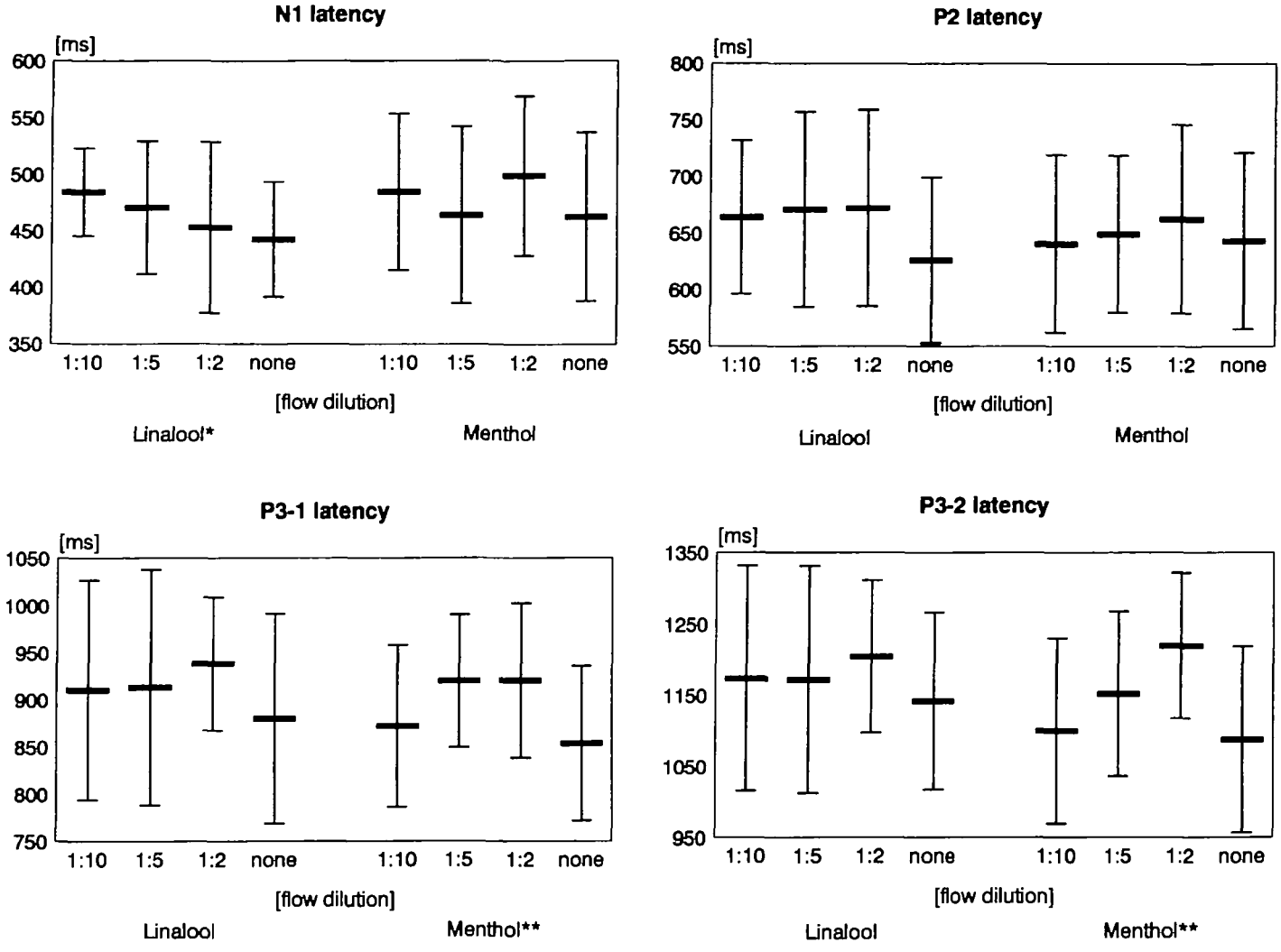

Figure 6 Latencies (related to the activation of the current switch) of the CSERP separated for the different odors and odor concentrations. When menthol was presented the latencies of the P3–1 and the P3–2 components significantly changed with odor concentration (**$P \leq 0.001$). When linalool was presented the latency of the N1 component significantly changed with the odor concentration (*$P \leq 0.05$).

of each trial set when the second lowest [$F(1,50) = 7.08$, $P = 0.02$] or the highest [$F(1,50) = 6.35$, $P = 0.02$] concentration of linalool was applied, but when the second highest concentration was applied it became larger [$F(1,50) = 6.32$, $P = 0.02$]. The latency of the P3–2 component was only enlarged during the first 20 trials when the lowest linalool concentration was presented [$F(1,50) = 15.76$, $P < 0.01$].

The amplitude of the early components (N1/P2) evoked by stimulation with menthol did not habituate, in contrast it became larger during the fourth trial set [flow dilution = 1:2, $F(1,50) = 11.32$, $P < 0.01$]. Whereas the latency of the N1 component did not change within either trial set, the P2 latency was prolonged when the lowest [$F(1,50) = 6.75$, $P = 0.02$] or the highest concentration [$F(1,50) = 7.42$, $P = 0.01$] of menthol was applied. The amplitude of the P3–1 component was reduced twice during the course of a trial set [lowest menthol concentration: $F(1,50) = 5.69$, $P = 0.03$; second highest menthol concentration: $F(1,50) = 21.50$, $P < 0.01$] and its latency was prolonged during the course of a third trial set [second lowest menthol concentration: $F(1,50) = 23.18$, $P < 0.01$]. The amplitude of the P3–2 component was reduced when the lowest menthol concentration was presented [$F(1,50) = 11.05$, $P < 0.01$] and its latency was prolonged in response to the lowest [$F(1,50) = 11.17$, $P < 0.01$], the second lowest [$F(1,50) = 6.11$, $P = 0.03$] and the highest [$F(1,50) = 4.41$, $P = 0.05$] concentration of menthol.

There was no interaction between habituation effects and scalp distribution.

Table 5a Linalool: effects of habituation for amplitudes (μV) and latencies (ms)

Parameter	Flow dilution	Trial no. 1–10	Trial no. 11–20
N1/P2 (A)*	1:2	6.66 (3.92)	5.38 (3.18)
P3–2 (A)*	1:5	5.72 (4.15)	3.84 (2.86)
P3–2 (A)*	1:2	3.60 (4.24)	5.93 (6.19)
P3–2 (A)*	none	4.02 (3.56)	1.79 (4.40)
N1 (L)†	none	436 (45)	456 (67)
P2 (L)†	1:10	648 (53)	672 (96)
P3-2 (L)**	1:10	1087 (100)	1140 (104)

A = amplitude, L = latency (related to the activation of the current switch), means (standard deviations, ±) for the main effect 'trial position': †$P \leq 0.10$, *$P \leq 0.05$, **$P \leq 0.01$.

Table 5b Menthol: effects of habituation for amplitudes (μV) and latencies (ms)

Parameter	Flow dilution	Trial no. 1–10	Trial no. 11–20
N1/P2 (A)**	1:2	5.26 (3.25)	7.31 (2.83)
P3–1 (A)*	1:10	6.27 (3.46)	4.64 (3.86)
P3–1 (A)**	1:2	6.84 (4.77)	3.91 (4.04)
P3–2 (A)**	1:10	4.87 (4.87)	2.73 (3.38)
P2 (L)*	1:10	619 (89)	657 (68)
P2 (L)**	none	634 (86)	651 (85)
P3–1 (L)**	1:5	890 (81)	951 (88)
P3–2 (L)**	1:10	1074 (105)	1117 (91)
P3–2 (L)*	1:5	1126 (135)	1164 (97)
P3–2 (L)*	none	1080 (117)	1113 (118)

A = amplitude, L = latency (related to the activation of the current switch), means (standard deviations, ±) for the main effect 'trial position': †$P \leq 0.10$, *$P \leq 0.05$, **$P \leq 0.01$.

Effects of attention

Except for the P3–2 amplitude in response to the lowest concentration of linalool, all amplitudes of the whole CSERP evoked by linalool were larger when the odors had to be actively attended to. Although this effect was significant only for the P3–1 amplitude in response to the highest concentration [$F(1,9) = 4.99$, $P = 0.05$], it was found in response to all odor concentrations. The latencies of the four CSERP components did not vary systematically with the amount of attention, because the direction of the attention effect changed with the different concentrations of linalool.

In response to menthol there was no effect of attention on the amplitudes of the early components (N1, P2), however, the amplitudes of the late positive components (P3–1, P3–2) were systematically enlarged when the odor had to be attended to actively. This effect was found for all odor concentrations and was significant for the P3–2 amplitude when the highest odor concentration was presented [$F(1,9) = 7.73$, $P = 0.02$]. Whereas the latencies of the CSERP components did not vary with the amount of attention when the olfactory system was stimulated with linalool, all latencies but one were shorter in the active attention condition when the trigeminal system was stimulated. The only exception was the P2 latency which was shorter during passive attention in response to the second lowest menthol concentration.

The effects of attention on the CSERP are presented in Table 6, and in Figure 7 the grand averages separated for the active and passive attention condition are shown.

Discussion

Regarding the literature on CSERPs it has been questioned whether the dependence of the CSERP on the odor concentration is a valid effect. The documented influence of concentration might have been due to effects of trigeminal stimulation or to effects of evaluative processes. In the present study we examined the CSERPs in response to olfactory (linalool) and trigeminal (menthol) chemosensory stimuli and secondly, varied the amount of attention.

Summarizing the results, it was found that an increase in olfactory stimulus concentration leads to faster early stimulus processing (reduced latency of the N1 component). However, the amplitudes of the CSERP did not vary with the concentration of the olfactory stimulant. By contrast, the amplitudes of the early (N1/P2) and late (P3–1) components of the CSERP were enlarged when higher concentrations of the trigeminal stimulus were used. Even though this effect was less pronounced for the latencies of the CSERP, the latencies of the N1, P3–1 and P3–2 components were shortest in response to the highest stimulus concentration. Both odors had a similar scalp distribution and evoked the largest amplitudes at parietal scalp areas. However, the parietal dominance of the early component complex N1/P2 was more pronounced for the olfactory stimulus. Moreover, we found that the pleasantness of both odors decreased with higher stimulus concentration and that the use of the verbal descriptors for the odors changed with odor concentration: the higher the

Table 6a Linalool: effects of attention for amplitudes (μV) and latencies (ms), means and standard deviations (±)

Parameter	Flow dilution							
	1:10		1:5		1:2		None	
	Active	Passive	Active	Passive	Active	Passive	Active	Passive
N1/P2 (A)	7.29 (4.48)	4.04 (2.61)	5.36 (2.84)	4.19 (2.54)	5.27 (3.32)	4.91 (3.86)	5.59 (2.24)	3.69 (2.21)
P3–1 (A)	5.92 (1.98)	5.17 (5.74)	5.54 (3.25)	4.48 (2.96)	7.12 (5.07)	4.14 (6.83)	7.22 (4.17)*	3.18 (3.31)
P3–2 (A)	2.61 (3.63)	4.13 (2.58)	3.75 (2.46)	3.64 (2.95)	5.49 (3.41)	2.97 (6.01)	4.74 (4.91)	2.80 (4.13)
N1 (L)	466 (21)	495 (43)	448 (25)	483 (69)	488 (34)	433 (86)	444 (66)	441 (42)
P2 (L)	654 (69)	670 (68)	670 (87)	672 (89)	710 (83)	651 (83)	629 (76)	625 (74)
P3–1 (L)	830 (62)	956 (116)	926 (83)	906 (145)	942 (39)	936 (85)	864 (49)	889 (135)
P3–2 (L)	1142 (106)	1217 (184)	1184 (59)	1165 (197)	1224 (53)	1194 (128)	1109 (106)	1161 (133)

A = amplitudes, L = latencies (related to the activation of the current switch), main effect 'attention': $*P \leq 0.05$.

Table 6b Menthol: effects of attention for amplitudes (μV) and latencies (ms), means and standard deviations (±)

Parameter	Flow dilution							
	1:10		1:5		1:2		None	
	Active	Passive	Active	Passive	Active	Passive	Active	Passive
N1/P2 (A)	4.15 (1.97)	3.42 (2.35)	3.80 (1.10)	4.15 (2.32)	5.53 (3.76)	5.43 (1.69)	4.44 (2.61)	6.52 (2.69)
P3–1 (A)	6.27 (3.74)	3.62 (3.96)	6 06 (1.99)	5.26 (2.33)	6.63 (4.35)	5.19 (4 19)	8.41 (2.55)	6.53 (4.72)
P3–2 (A)	6.22 (3.37)	2.98 (3.29)	3.97 (2.74)	3.68 (2.95)	4.27 (2.88)	3.22 (3.68)	7.32 (2.91)*	2.85 (3.52)
N1 (L)	462 (45)	498 (78)	458 (38)	467 (95)	470 (86)	515 (56)	437 (83)	477 (67)
P2 (L)	625 (41)	649 (94)	668 (45)	638 (79)	616 (101)	689 (60)	624 (73)	654 (80)
P3–1 (L)	865 (37)	876 (105)	885 (54)	940 (72)	916 (33)	923 (101)	851 (59)	855 (94)
P3–2 (L)	1028 (42)	1142 (146)	1104 (79)	1180 (126)	1202 (59)	1230 (120)	1043 (110)	1113 (138)

A = amplitudes, L = latencies (related to the activation of the current switch), main effect 'attention': $*P \leq 0.05$.

concentration of linalool, the higher was the degree of agreement between the subjects. The inter-rater agreement also increased with the concentration of menthol (until the second highest concentration). The concentration-dependent activation of the trigeminal nerve was indicated by the observation that more subjects described menthol as pungent at higher stimulus concentrations. However, the odor intensity was not estimated correctly by most subjects. Analyses of effects of habituation within the trial sets revealed no consistent change of the components across time. It is therefore concluded that the odors were perceived as distinct single stimuli and not as a series of trials. The amplitude of the late positive components was strongly affected by the amount of attention, this effect was independent of the kind of odor and concentration step. Finally, it has been shown by the application of odorless control air that the CSERPs are not due to somatosensory artifacts.

Referring to acoustic stimuli, it has repeatedly been demonstrated that the amplitude of the preattentive early N1 component as well as of the so-called vertex potential (N1/P2) increases with higher stimulus concentrations (review by Näätänen and Picton, 1987). In ERP research the basic assumption has been made that the amplitude of a component depends on the amount of neuronal generators which trigger this electrical brain response (Coles and Rugg, 1995). The perception of a highly concentrated stimulus might therefore result in the activation of more neuronal cell assemblies than the perception of a less concentrated stimulus. Since Kobal and Hummel (1991) demonstrated a clear dependence of the amplitude and latency of the CSERP on different CO_2 concentrations, similar mechanisms are probably responsible for the enlargement of the N1/P2 amplitude evoked by trigeminal stimuli. It has been shown by magnetoencephalographic recordings that stimulation with CO_2 leads to an activation of neurons

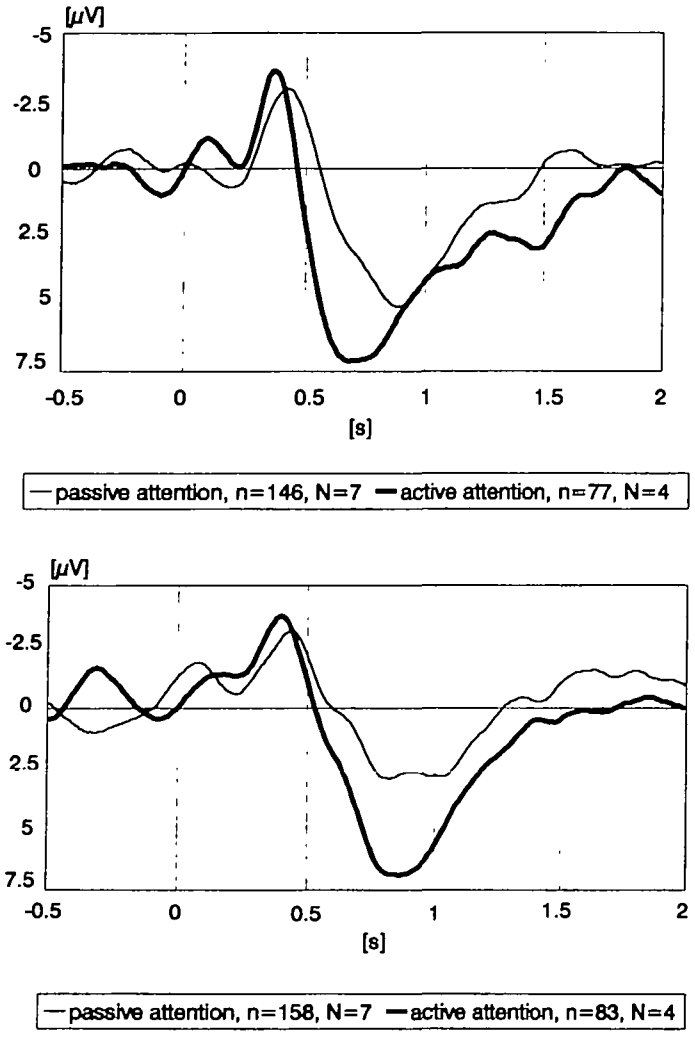

Figure 7 Grand averages showing the effects of attention for linalool (top) and menthol (bottom). The CSERPs are recorded from Pz in response to the lowest concentration. At time point 0 the odor is supposed to reach the nasal mucosa.

within and near to the secondary (SII) somatosensory cortex (Huttunen *et al.*, 1986). In our study we could parallel these results by the observation that higher menthol concentrations result in a stronger neuronal response and therefore in larger amplitudes of the early components (N1, P2). The classification of menthol as a strong trigeminal stimulus (Doty, 1995) is in line with our observation that anosmic subjects responded with distinct CSERPs to the stimulation with menthol (Leplow *et al.*, 1994, see also Figure 1). Moreover, the subjective sensations of coolness and pungency support the evidence that menthol activated the trigeminal nerve. An increase in menthol concentration also resulted in larger amplitudes of the more endogenous P3–1 component. This effect can be explained by the negative valence of the higher stimulus concentrations (see Johnston *et al.*, 1986).

According to the studies with anosmic subjects (Leplow *et al.*, 1994), the linalool concentrations used in this experiment were supposed to activate only the I. cranial nerve. Moreover, the subjects did not report trigeminal sensations when linalool was presented. The scalp distribution of the olfactory N1/P2 complex was slightly larger at parietal scalp areas than the trigeminal evoked N1/P2: this result is similar to the findings of Hummel and Kobal (1992) and Kobal *et al.* (1992) who reported that the N1/P2 amplitude is larger at parietal electrode positions after olfactory stimulation and larger at central recording positions after trigeminal stimulation. However, the results of the two working groups are difficult to compare, because we consider the P2 component found by Kobal and co-workers to be similar to our late positive complex (Pause *et al.*, 1996b). Referring to the N1 component (which might be comparable) an odor (olfactory/trigeminal) by site interaction was only reported once (Livermore *et al.*, 1992) and negative results were obtained in another study (Hummel and Kobal, 1992).

The amplitudes of the CSERP were not affected by different concentrations of linalool. However, increased concentrations led to a faster stimulus processing (N1 latency). As the CSERPs did not habituate within the trial sets (ISI = 50 s), all odors were perceived as single stimuli and not within a train of stimuli. Thus the possibility of carry-over effects between the trial sets, which were separated by 10 min breaks, can be excluded. Moreover, carry-over effects due to habituation would have caused longer latencies and smaller amplitudes during the course of the experiment. However, as we applied the odor concentrations in an ascending series the effects of shorter latencies (linalool) and larger amplitudes (menthol) with higher odor concentrations can not be caused by sequence artifacts.

Our results are in agreement with the effects of another olfactory stimulus (H_2S) on the CSERP (Thiele and Kobal, 1984). Thiele and Kobal randomly applied the different odor concentrations and could also only find an effect of odor concentration on the latencies of the CSERP. Considering olfactory perception, it therefore has to be questioned if an enhanced stimulus concentration is correlated with an increased neural activation. Alternatively, it should be discussed whether different odor concentrations are mainly perceived as quality differences and thereby activate different neuronal generators. From subjective rating studies it is known that odor quality changes with concentration and that different concentrations of the same

odor may be perceived as qualitatively different odors (Gross-Isseroff and Lancet, 1988). In our study the perceived quality of linalool also changed slightly with the different concentrations: the lowest concentration was perceived as predominately fruity and lemon-like. Most subjects described the second lowest concentration as fragrant and the second highest concentration as aromatic. The highest concentration of linalool was described as floral, fragrant and lemon-like. Moreover, we found that more subjects used the same descriptors when the concentration was increased. Therefore the ascribed odor quality seems to change from more odor independent internal categories at lower concentrations to more odor-dependent external categories with higher concentrations. Similar to the findings of the intensity–quality relations concerning the odor perception within one subject, the quality of odors changes with the sensitivity across subjects (Stevens and O'Connell, 1991, O'Connell *et al.*, 1994). The observation that quality perception systematically changes with the specific sensitivity for an odor led Stevens and O'Connell (1991, p. 57) to the assumption that 'most odor molecules interact with more than one perceptual channel (receptor process) and that any individual alteration in the relative specificity or deletion in the number of such receptor processes could alter the pattern of interaction and thus should give rise to alterations in the quality or intensity of the resulting odor perception'.

Moreover, the most salient feature of odors seems to be their valence (Ehrlichman and Bastone, 1992) rather than their intensity. Valence ratings change more rapidly with odor concentration than intensity ratings (Moskowitz *et al.*, 1976), indicating that varying odor concentrations can be judged more differentially using their hedonics than by describing their intensities. In the present study there was a strong tendency ($P = 0.07$) for higher linalool concentrations to be perceived as less pleasant. However, the intensity ratings did not predict the real odor concentration. It is in line with these considerations that subjects can remember odor quality much better than odor concentration (Barker and Weaver, 1983, Engen *et al.*, 1991). Whereas the forgetting curve for odors is obviously flatter than for acoustic or visual stimuli (Engen, 1982) and single-trial learning suffices to store the odor quality in long-term memory, the memory for odor intensity has already faded after 3 s (Engen *et al.*, 1991).

The assumption that concentration differences are perceived as quality differences is supported by the findings of Firestein and Werblin (1989) who measured membrane currents in vertebrate olfactory receptor neurons. They demonstrated that olfactory receptor neurons only respond to a very narrow concentration range of a given odor. Similar predictions for odor intensity coding arise from extracellular recordings from lobster olfactory receptor cells (Johnson *et al.*, 1987). The results revealed that different odor concentrations evoked different patterns of activity across the sensory receptors. Meredith (1986) demonstrated that also the neurons of the mammalian olfactory bulb respond with different patterns to different odor concentrations: those cells which are activated by more than one odor concentration show usually a non-monotonic intensity–response function.

Besides these considerations about quality–intensity interactions, the results of the present study reveal that higher odor concentrations lead to a faster neuronal response of the brain. A concentration-dependent latency for the activation of the ionic current in olfactory receptor cells has been described by Firestein and Zufall (1993), and Getchell *et al.* (1984) summarized that the time required for odorant uptake and degradation in the olfactory epithelium is dependent on stimulus concentration and quality. Shortened response latencies for higher odor concentrations have also been found for neurons of the salamander olfactory bulb (Cinelli *et al.*, 1995). The importance of temporal aspects in odor quality coding was underlined by Kauer (1991) who reported the response characteristics of the olfactory bulb to different odors. Recently, Laing (1994) pointed out that odors in mixtures are probably identified by their temporal characteristics.

Regarding these considerations it is concluded that quality coding within the olfactory system is more important than quantity coding: unlike other sensory systems the olfactory system is highly specified in detecting a large number of qualitatively different odors (cf. Buck and Axel, 1991). Odor quality can be stored in long-term memory for the whole of one's life and the odor's valence, which is the main feature for odor processing, is decisive for behavioral approach or withdrawal. It is also obvious from the CSERP data that the subjective stimulus significance counts for the strongest neuronal brain activity in odor processing. The small exogenous components N1 and P2 are followed by a large late positive complex (P3). This P3 component does not vary with stimulus features but is sensitive to the stimulus meaning, subjective probability and to the amount of attention.

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