

## Attentional Modulation of Central Odor Processing

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### Abstract

Two studies were conducted to investigate the influence of attention on the components of the chemosensory event-related potential (CSERP). In the first study the odors linalool and eugenol were delivered to six male subjects, in the second study three male and two female subjects were presented with their own body odor (axillary hair) and the body odor of a same sex donor. In both studies the odors were presented in an oddball paradigm under ignore and attend conditions via a constant-flow olfactometer. In the ignore condition attention was diverted from the odors with a distractor task, while in the attend condition the subjects were asked to respond to the infrequently occurring odor. In both studies the allocation of attention led to a decrease in the latency of the early components (N1, P2, N2) and to an increase in the amplitude of the late positivities. The modulation of the early components suggests that attentional gating in olfaction might already be effective at an early processing level.

### Introduction

In the last fifteen years the recording of chemosensory event-related potentials (CSERP) has become established as an objective method in the assessment of cortical odor processing. Due to its high temporal resolution, this measure allows a differentiated view of the various steps involved in odor perception and evaluation. For the auditory, visual and somatosensory modality different components which reflect specific information processes have been identified within the ERP. These components can be characterized as more exogenous or more endogenous: exogenous components (e.g. N1) indicate initial stimulus perception and are in general determined by physical stimulus features such as intensity (Näätänen and Picton, 1987), whereas endogenous components (e.g. P3) reflect more complex processes such as stimulus recognition and evaluation, and vary with stimulus significance and attentional investment (Pritchard, 1981; Donchin and Coles, 1988).

Investigation into the CSERP components has focused mainly on the influence of external mediators such as odor intensity (Kobal and Hummel, 1991; Prah and Benignus, 1992; Pause *et al.*, 1997) and stimulus quality, especially the differentiation between olfactory and trigeminal chemoreception (e.g. Kobal and Hummel, 1988; Kobal *et al.*, 1992; Livermore *et al.*, 1992; Pause *et al.*, 1997).

However, experimental task demands and the psychological state of the subject must be taken into account when evaluating and interpreting changes in the amplitude and latency of these components, as the parameters of the

CSERP may be distinctly altered if task demands require the subject to evaluate certain classes of stimuli.

Pause *et al.* (1996), for example, presented different concentrations of citral within an active oddball paradigm. The subjects were instructed to attend to the odors and to respond to an infrequently occurring 'target odor' (high concentration citral). Pause *et al.* observed an enhanced late positivity, a P3, following or overlapping the P2 in response to stimuli that were processed as subjectively important: correctly identified targets (hits) and misidentified standard stimuli (false alarms). They could further differentiate two subcomponents of the P3: an early positivity (P3-1) that habituated over the course of the session and a later positivity (P3-2) that did not. Both components were most prominent at the parietal recording site. Lorig *et al.* (1993) also found a parietally dominant P3-like positivity in response to different concentrations of *n*-butanol within a signal-detection paradigm. Subjects were instructed to indicate the detection of an odor with a motor response.

Besides task demands, it is important to identify which general cognitive, emotional and attentional parameters influence the waveform of the CSERP and whether changes in odor-evoked responses are actually modality specific. For example, Schemper *et al.* (1981) showed that a deteriorating ability to apply cognitive labels to odorants contributed largely to an observed decline in the identification performance of elderly subjects.

The influence of attention on the CSERP waveform has only once been systematically examined. Pause *et al.* (1997)

found that the amplitude of both the N1 and P3 was enhanced when the subjects were instructed to press a button every time they perceived an odor compared with a condition where subjects were asked to simply relax during odor presentation. However, no study has so far focused on automatic processing of olfactory stimuli. The aim of the present studies was therefore to investigate, with the aid of CSERPs, how the processing of olfactory stimuli is affected by the allocation of attention and whether attentional effects are modulated by the complexity and significance of the stimulus material.

A classic paradigm for the investigation of attention in ERP research (Squires *et al.*, 1975; Näätänen, 1990) involves the presentation of two classes of stimuli, frequent and infrequent stimuli, under 'ignore' and 'attend' conditions. In the ignore condition the subjects are generally asked to ignore the stimuli and are, in most cases, also instructed to focus on a specified 'distractor task'. Under attend conditions subjects are required to discriminate frequent and infrequent stimuli, e.g. by showing a motor reaction in response to the infrequent stimulus.

Both experiments described in this paper consisted of an ignore and an attend condition conducted on separate days. In the first experiment subjects were presented with artificial odorants whereas in the second study body odor, a complex, biologically significant mixture, was used as the stimulus material.

## Experiment 1

### Methods

#### Subjects

Seven healthy male subjects (aged 20–25 years) took part in the first experiment. Before the first session the subjects' sensitivity for linalool and eugenol was determined using a forced-choice, staircase procedure (14 dilutions in half-decimal logarithmic steps) for each odorant. For one subject the thresholds for linalool and eugenol differed by six dilution steps. He was excluded from further participation. None of the remaining six subjects was impaired in his olfactory acuity due to allergies, chronic medication or nasal surgery. Three persons described themselves as sinistrals, three as right-handed. All subjects gave informed consent.

#### Stimuli and stimulus presentation

In the first experiment eugenol (99%, Aldrich, Steinheim, Germany; 1.35 ppm) and linalool [(±), 97%, Aldrich; 11.22 ppm], dissolved in 1,2-propanediol (99%, Merck, Darmstadt, Germany; 1:50 v:v for both odors), were used as odorants. The odors were presented within a warmed (34°C at the nasal outlet) and humidified (80%) constantly flowing airstream to the left nostril of the subject non-synchronously to breathing. In the olfactometer the odorless interval current and the carrier current for the odorized air were simultaneously activated (method according to

Kobal and Hummel, 1991). A computer-controlled solenoid valve initiated which current was removed through a vacuum. This method guarantees that the presentation of the odor is not preceded or overlapped by somatosensory sensations due to e.g. flow fluctuations. It also provides a rapid rise-time which is critical for the interpretability and comparability of the CSERP's time characteristics. The flow rate of the interval current (98 ml/s) equaled the sum of the carrier current (92 ml/s) and the odorous air flow (6 ml/s). The presentation of the odor was initiated through a computer-controlled solenoid valve, 75 ms after activation the stimuli reached the nasal outlet. Stimulus duration was 200 ms.

The subjects were instructed to breathe through their mouth and to disconnect the nasal and oral cavity by closing their soft palate (technique of velopharyngeal closure). During the EEG recording they received feedback on their breathing via an oscilloscope.

#### Design

In the first two sessions (ignore condition) the subjects were instructed to ignore the odors and concentrate on an auditory distractor task (counting the target-word 'you' in slow English rock songs). One of the odors appeared frequently ( $P = 0.8$ ), the other infrequently ( $P = 0.2$ ). The subjects attended two sessions as each odor served once as the standard stimulus and once as the deviant stimulus. The two sessions were in general conducted 8 days apart. In the following two sessions (attend condition) the subjects were instructed to attend to the odors and respond to the infrequent odor by lifting their index finger. Subjects were allowed to practice discriminating both odors before EEG recording started. All sessions consisted of three series in which the odors were presented in 10 blocks of five. As the interstimulus interval (ISI; 8 s) within the blocks was comparably short, a time interval of 60 s was interspersed between the blocks to decrease habituation. The experimental procedure was identical for all conditions except for the initial threshold test in the first session.

The ignore sessions always preceded the attend sessions to keep subjects naive about the number, quality and probability of the different odors used in the experiments. The experimental procedure and demands in the attend condition could have facilitated an elaborate representation of the odors, e.g. the use of verbal labels, making it harder for subjects to withdraw their attention from the odors in a subsequent ignore session.

#### EEG recording and data analysis

According to the 10–20 system, the EEG was recorded from Fz, Cz and Pz, and referenced to linked mastoids. Oz served as the ground. The electrooculogram (EOG) was monitored with three electrode pairs according to Elbert *et al.* (1985) in reference to linked earlobes. The electrodes (Ag/AgCl) were attached to the cleaned skin (Omniprep, Weaver, USA) with

EC2-TM paste (Grass, USA). Electrode impedance was usually  $<5$  kOhm.

The EEG data were recorded for 6 s with one second baseline prior to the stimulus onset. All signals were A–D converted with a 12-bit resolution and digitized at 125 Hz per channel. The EEG and EOG were amplified using a 0.016 Hz (–3 dB) highpass filter and a 30 Hz (–3 dB) lowpass filter. All trials showing eye movement or blink artifacts exceeding 100  $\mu$ V in the first 2 s after stimulus onset were excluded from the further analysis. The remaining trials were corrected using a multiple regression model (Elbert *et al.*, 1985) with the three EOG channels as predictors.

EEG data were averaged separately for electrode position, odor category (standard versus deviant), odor quality (linalool versus eugenol) and attention (ignore versus attend). The averaged potentials of each subject were then screened for maximum negative and positive peaks within previously defined latency ranges: N1 (350–550 ms), P2 (500–700 ms), N2 (600–800 ms), P3-1 (700–900 ms) and P3-2 (800–1200 ms). The amplitudes were measured against the averaged prestimulus baseline.

The data were submitted to a four-way analysis of variance (ANOVA) for repeated measurements (program no. 34; Fillbrandt, Kiel, Germany): attention (ignore, attend)  $\times$  odor quality (eugenol standard–linalool deviant, linalool standard–eugenol deviant)  $\times$  odor category (standard, deviant)  $\times$  electrode position (Fz, Cz, Pz). The ANOVA was based on a randomized block factorial design for within-subject comparisons (Kirk, 1968). In the present paper only the results concerning the influence of attention are reported and discussed (for further details see Schott *et al.*, 1994).

The significance level for all comparisons was  $P < 0.05$ . Degrees of freedom were corrected by  $\epsilon$  according to Huynh and Feldt (1976). Single comparisons were calculated using *t*-tests.

## Results

The N2 amplitude was more negative under ignore conditions [ $F(1,115) = 21.08$ ,  $P < 0.001$ ,  $\epsilon = -0.245$ ], whereas the P3-1 amplitude was significantly larger in the attend condition [ $F(1,115) = 55.81$ ,  $P < 0.001$ ,  $\epsilon = -0.225$ ] and for deviant odors [ $F(1,115) = 13.84$ ,  $P < 0.01$ ,  $\epsilon = -0.225$ ]. However, the interaction attention  $\times$  odor category [ $F(1,115) = 14.52$ ,  $P = 0.001$ ,  $\epsilon = -0.225$ ] indicated that the attended deviant stimuli alone accounted for this effect [standard/attended:  $t(3) = -5.33$ , standard/ignored:  $t(3) = 7.91$ , deviant/ignored:  $t(3) = 7.98$ ]. The comparison also revealed that attended standards elicited a more pronounced P3-1 than ignored standards and deviants [standard/ignored:  $t(3) = 2.59$ , deviant/ignored:  $t(3) = 2.65$ ]. The attended odors also elicited a larger P3-2 amplitude than ignored stimuli [ $F(1,115) = 30.89$ ,  $P < 0.001$ ,  $\epsilon = -0.268$ ]. Figure 1a compares the mean amplitudes of all components under ignore and attend conditions.

All components showed shorter latencies in the attend condition: N1 [ $F(1,115) = 8.10$ ,  $P < 0.05$ ,  $\epsilon = -0.299$ ], P2 [ $F(1,115) = 20.23$ ,  $P = 0.001$ ,  $\epsilon = -0.263$ ], N2 [ $F(1,115) = 60.83$ ,  $P < 0.001$ ,  $\epsilon = -0.244$ ], P3-1 [ $F(1,115) = 52.94$ ,  $P < 0.001$ ,  $\epsilon = -0.277$ ] and P3-2 [ $F(1,115) = 116.96$ ,  $P < 0.001$ ,  $\epsilon = -0.247$ ] (see Figure 1b). Figure 2a–d shows the grand averages for standard and deviant stimuli in both conditions separated for odor quality.

## Discussion

The results of the first experiment show that only the late positivities (P3-1, P3-2) were enhanced by the allocation of attention whereas the amplitudes of the earlier components (N1, P2) were not affected. The difference in the N2 amplitude between the attend and the ignore condition is difficult to interpret. From the mean amplitudes it seems most likely that the strong late positivities already overlap the time window of the N2 and therefore cause an attenuation of the N2 amplitude in the attend condition. Deviant stimuli only elicited a significantly larger P3-1 and P3-2 than the standards when the subjects were instructed to attend to and discriminate the odors.

Studies from other modalities (e.g. Donchin and Coles, 1988) have also found that the P3 does not occur or is attenuated when attention is directed towards another channel. When stimuli are associated with a task the subject is required to thoroughly evaluate the incoming stimuli. In the case of the present oddball paradigm the subject needs to filter out the behaviorally relevant stimuli (targets) from a row of irrelevant background odors and decide whether or not to respond to the stimulus. However, as the attended standards also elicited a larger P3 than unattended standards and deviants, part of the increase in the olfactory P3 amplitude can be interpreted as a genuine attention effect.

Although the amount of neuronal activity did not obviously change for the early components, the processing speed, visible in the latencies, was reduced for all components in the attend condition, probably allowing a more efficient transduction of olfactory signals to cortical structures when actively attending to the odors.

## Experiment 2

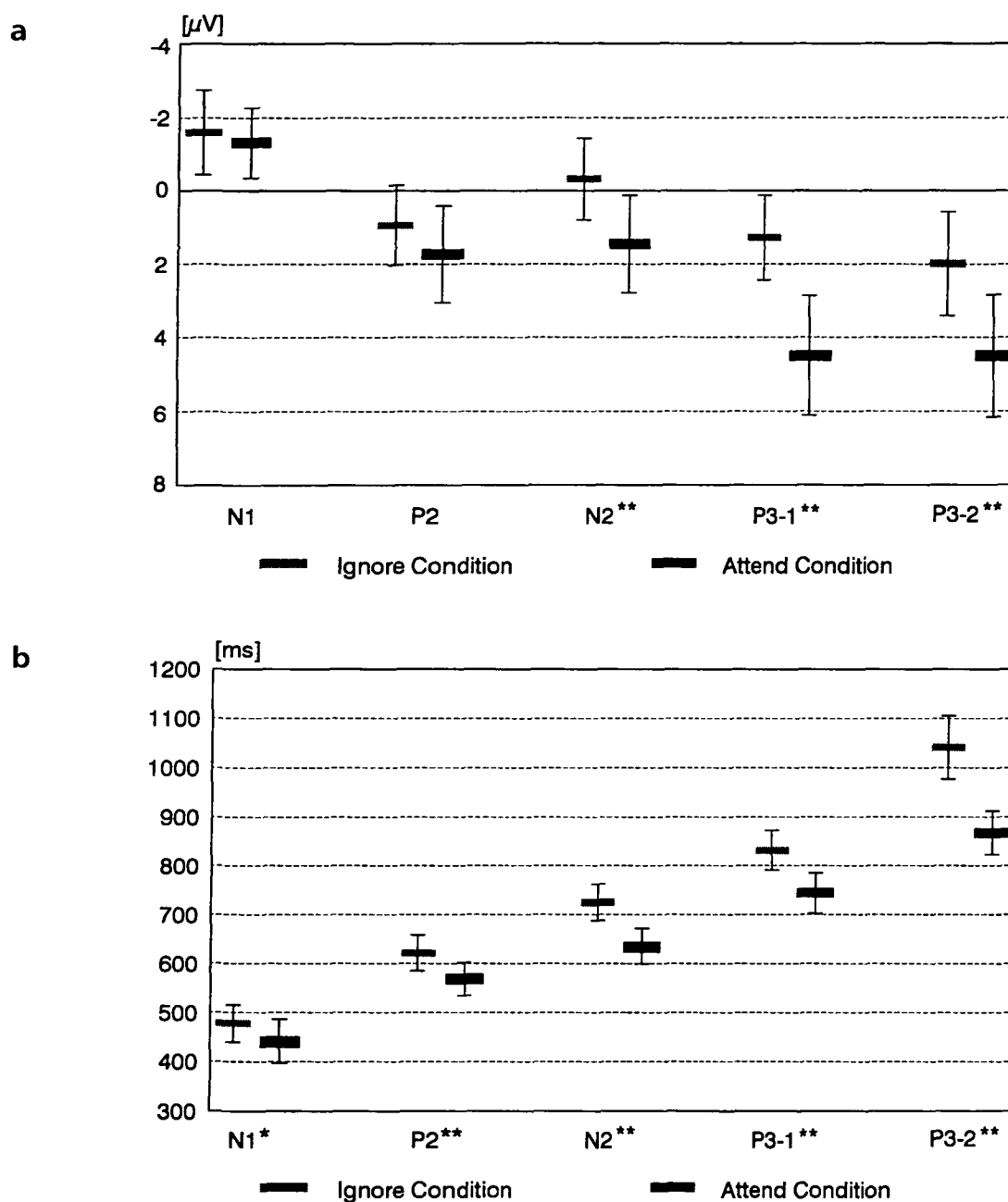
### Methods

#### Subjects

Three men and two women participated in the second experiment (aged 20–27 years). Four of the subjects were dextrals, one was sinistral. No subject suffered from any metabolic disease or any disease of the respiratory system. All subjects gave informed consent. Five further subjects (two female) were recruited for the donation of axillary hair.

#### Stimuli and stimulus presentation

Axillary hair from the perceiving subject and from a donor

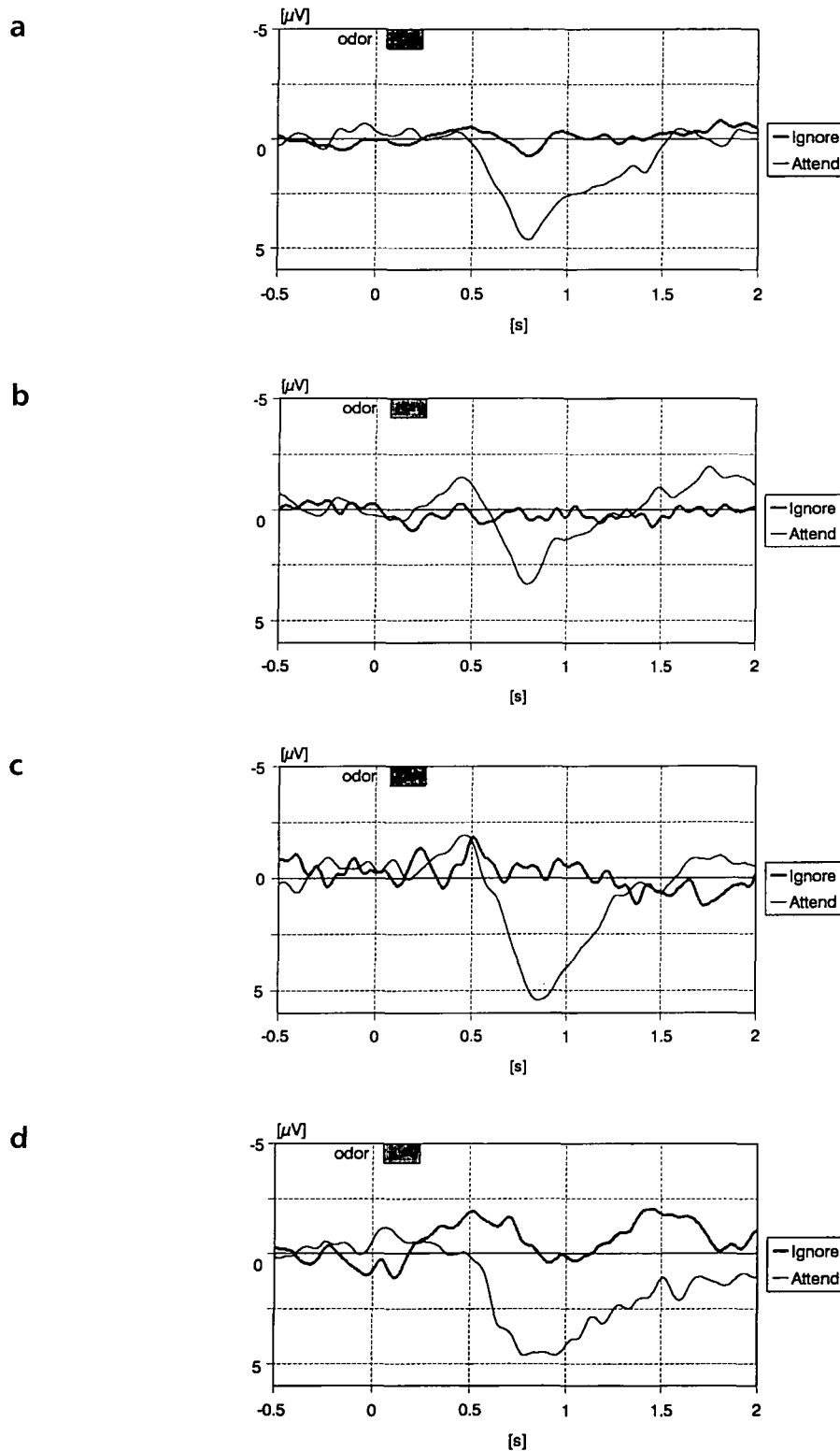


**Figure 1** (a) The mean amplitudes and standard deviations of all components (N1, P2, N2, P3-1, P3-2) of the ignore and the attend condition of Experiment 1 for all subjects ( $n = 6$ ); \* $P < 0.05$ ; \*\* $P < 0.01$ . The amplitudes are averaged across odor category (standard/deviant), odor quality (eugenol/linalool) and electrode position (Fz, Cz, Pz). (b) The mean latencies and standard deviations of all components (N1, P2, N2, P3-1, P3-2) of the ignore and the attend condition of Experiment 1 for all subjects ( $n = 6$ ); \* $P < 0.05$ ; \*\* $P < 0.01$ . The latencies are averaged across odor category (standard/deviant), odor quality (eugenol/linalool) and electrode position (Fz, Cz, Pz).

of the same sex were used as the olfactory stimuli in the second experiment. On the day before the donation the subjects were asked not to use soap or deodorant and to refrain from eating garlic, onions and asparagus, as well as from consuming alcoholic beverages. The axillary hair was either directly employed on the day of donation or was stored at  $-20^{\circ}\text{C}$ . The amount of axillary hair used in the

olfactometer varied between 20 and 70 mg between sessions but was always held constant within one session.

The odors were presented via a computer-controlled constant flow olfactometer non-synchronously to breathing (Burghart, Wedel, Germany; 45 ms delay between the activation of the solenoid valve and the arrival at the nasal outlet). Due to a new location of the olfactometer within the



**Figure 2** (a) Grand average (standards/eugenol) across six subjects: ignore condition versus attend condition, recorded from Pz. [The grand average of the attend condition contains correctly identified standards (correct rejections) and misidentified standards (false alarms).] (b) Grand average (standards/linalool) across six subjects: ignore condition versus attend condition, recorded from Pz. [The grand average of the attend condition contains correctly identified standards (correct rejections) and misidentified standards (false alarms).] (c) Grand average (deviants/eugenol) across six subjects: ignore condition versus attend condition, recorded from Pz. [The grand average of the attend condition contains correctly identified deviants (hits) and misidentified deviants (misses).] (d) Grand average (deviants/linalool) across six subjects: ignore condition versus attend condition, recorded from Pz. [The grand average of the attend condition contains correctly identified deviants (hits) and misidentified deviants (misses).]



laboratory, the odors were delivered to the right nostril of the subject in the second experiment. The odorous air (30 ml/s) was added to a carrier current (70 ml/s) so that the flow rate of both currents (100 ml/s) was equal to the amount of clean room air presented during the ISI. The temperature of all currents was held constant at 37°C and the humidity was always >80%. The subjects could not perceive the switch between clean room air and odorous air (flow fluctuation 4–5 ml/s). Pilot sessions had shown that a stimulus duration of 200 ms, as in the first experiment, could not guarantee a sufficiently intense perception of the body odor. As the odor could not be intensified by using a larger amount of axillary hair, the stimulus duration was increased to 600 ms in the second experiment. This change in odor presentation was not likely to endanger the comparability of experiments 1 and 2 as according to findings of Kobal (1981) the amplitude and latency of the CSERP are influenced by the characteristics of the stimulus onset rather than by the stimulus duration.

### Design

In the second experiment the subjects only attended two sessions. The ignore session was again always conducted before the attend session. In each session the subjects were confronted with four series of 60 trials. The trials were presented in six blocks of 10, with an interstimulus interval of 8 s and an interblock interval of 60 s. The probability of the standard odor was again 80%, and that of the deviant odor was correspondingly 20%. In contrast to the first experiment, the deviant odor was changed within one session. Thus two series were conducted using the subject's own body odor as the standard stimulus and two with the body odor of another donor as the standard stimulus. The sequence of the series was counterbalanced within a session but not between subjects.

In the ignore condition the subjects were again instructed to ignore the odors and focus on an auditory distractor task. All subjects were asked to count words containing a specified letter (K, B, W, L) within a German fairy tale. Counting words with a specified letter within musical pieces had proved to be too difficult in a previous test with one subject. In the attend condition they were again asked to attend to the odors and respond to the deviant odor. As the deviant was changed throughout the session, subjects were always given an opportunity to practice the distinction of both odors before the new series started.

### EEG recording and data analysis

Scalp and facial electrodes were placed as described for the first experiment. The EEG data were recorded for 6 s with one second baseline prior to the stimulus onset. All signals were A–D converted with a 12-bit resolution and digitized at 128 Hz per channel. The EEG and EOG were again amplified within a (–3 dB) passband extending from 0.016 to 30 Hz.

The statistical comparisons were conducted with a four-

way analysis of variance (ANOVA) for repeated measurements (program no. 34; Fillbrandt, Kiel, Germany) as in the first experiment: attention (ignore, attend) × odor quality (self standard/non-self deviant, non-self standard/self deviant) × odor category (standard, deviant) × electrode position (Fz, Cz, Pz), with a significance level of  $P < 0.05$ .

### Results

As in the first experiment the N2 amplitude was more negative in the ignore condition [ $F(1,92) = 7.09$ ,  $P < 0.05$ ,  $\epsilon = -0.371$ ]. The P3-1 was again sensitive to attention and showed a markedly larger amplitude in the attend condition [ $F(1,92) = 19.88$ ,  $P < 0.01$ ;  $\epsilon = -0.364$ ]. The P3-2 amplitude, however, was only slightly increased when the odors were attended to [ $F(1,92) = 4.19$ ,  $P < 0.1$ ;  $\epsilon = -0.381$ ] (see Figure 3a). Regardless of the attentional investment deviant stimuli always elicited larger positivities than standard stimuli: P2 [ $F(1,92) = 11.71$ ,  $P < 0.01$ ;  $\epsilon = -0.353$ ], P3-1 [ $F(1,92) = 11.65$ ,  $P < 0.01$ ;  $\epsilon = -0.364$ ] and P3-2 [ $F(1,92) = 8.98$ ,  $P < 0.05$ ;  $\epsilon = -0.381$ ].

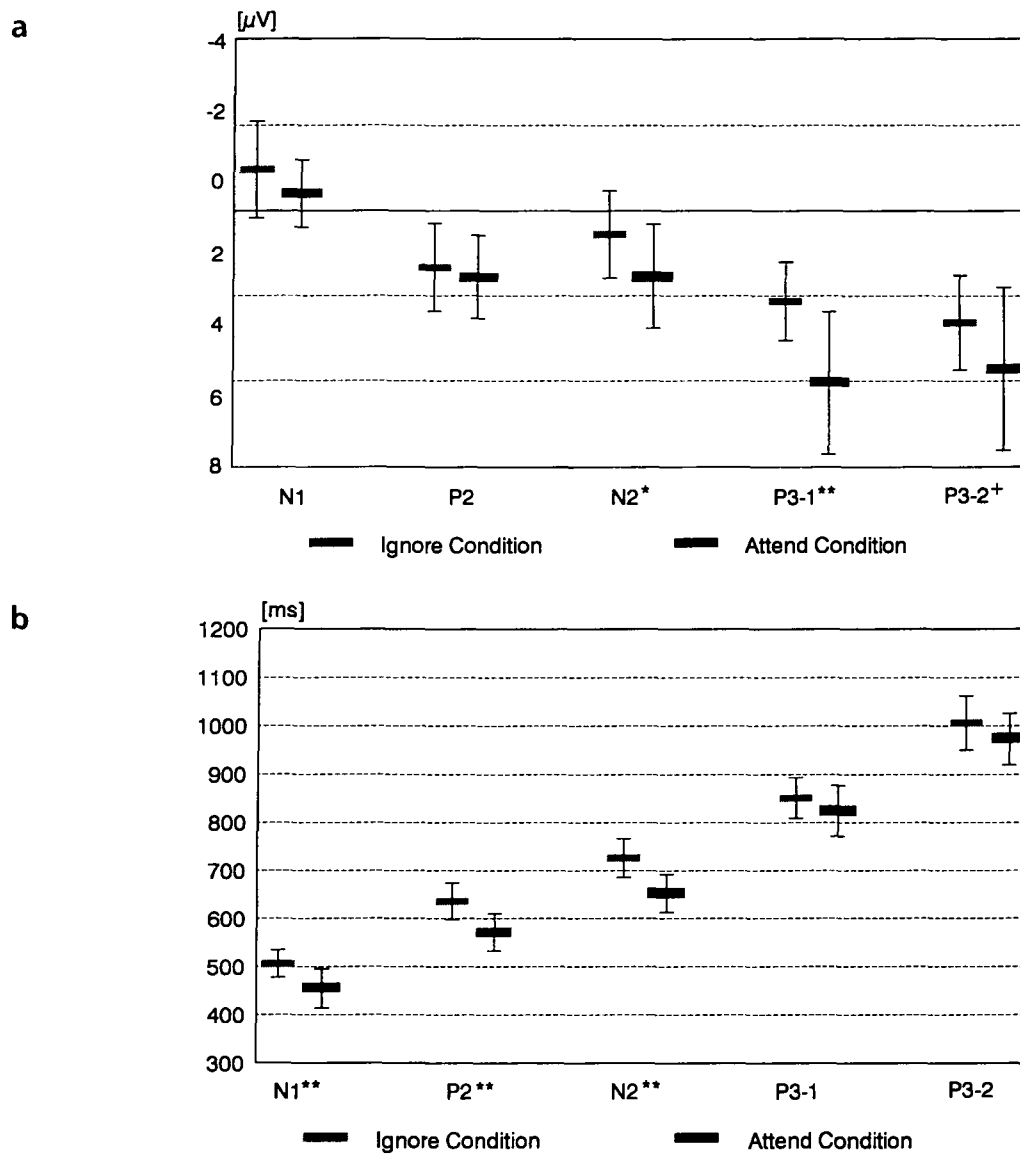
In this study only the earlier components showed shorter latencies in the attend condition: N1 [ $F(1,92) = 15.58$ ,  $P < 0.01$ ;  $\epsilon = -0.380$ ], P2 [ $F(1,92) = 19.03$ ,  $P < 0.01$ ;  $\epsilon = -0.371$ ] and N2 [ $F(1,92) = 24.32$ ,  $P < 0.01$ ;  $\epsilon = -0.378$ ]. The latencies of the P3-1 and P3-2 did not differ between conditions. Figure 3b compares the mean latencies obtained under ignore and attend conditions. The grand averages in response to standard and deviant odors of both conditions are shown in Figure 4a–d.

### Discussion

In the second experiment a larger amplitude could clearly be observed for the P3-1 but only tentatively for the P3-2 under attend conditions. The latencies of the earlier components (N1, P2, N2) were again significantly reduced when the subjects attended to the odors. The late positivities, however, did not show faster latencies. In contrast to the first experiment, the deviant body odors elicited larger positivities, including the P2, in both conditions. As the P3 has been found to be sensitive to the emotional content of a stimulus (Naumann *et al.*, 1992), this result could indicate that, in contrast to the artificial odors of the first experiment, the deviant body odors were perceived and processed as significant in spite of the instruction to ignore the odors. The increase in the P2 amplitude in response to deviant stimuli, however, is not in line with the results of the first experiment or with previous findings in the CSERP literature (Pause *et al.*, 1996). We therefore assume that the separation of the P2 and the P3-1 component was not completely successful in the second experiment.

### General discussion

Both experiments show that attention differentially modulates the parameters of the CSERP: under the attend

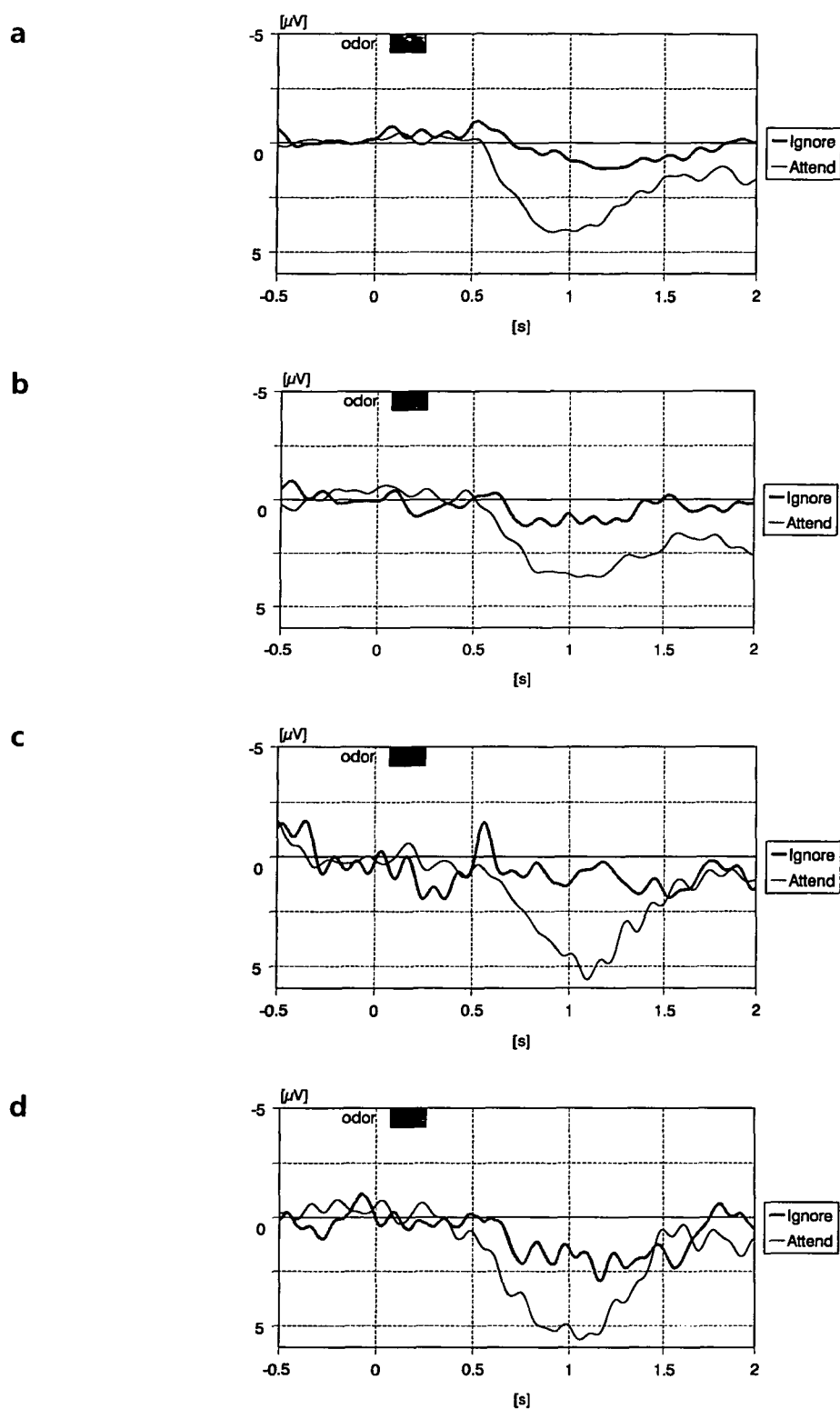


**Figure 3** (a) The mean amplitudes and standard deviations of all components (N1, P2, N2, P3-1, P3-2) of the ignore and the attend condition of Experiment 2 for all subjects ( $n = 5$ );  $^+P < 0.1$ ;  $*P < 0.05$ ;  $^{**}P < 0.01$ . The amplitudes are averaged across odor category (standard/deviant), odor quality (own body odor/different body odor) and electrode position (Fz, Cz, Pz). (b) The mean latencies and standard deviations of all components (N1, P2, N2, P3-1, P3-2) of the ignore and the attend condition of Experiment 2 for all subjects ( $n = 5$ );  $^+P < 0.1$ ;  $*P < 0.05$ ;  $^{**}P < 0.01$ . The latencies are averaged across odor category (standard/deviant), odor quality (own body odor/different body odor) and electrode position (Fz, Cz, Pz).

condition the earlier components (N1, P2, N2) show significantly faster latencies, whereas the most prominent modulation of the late positivities is an increase in amplitude when the odors are attended to.

In visuo-spatial attention the P1, N1, P2 and N2 components have been found to be sensitive to the allocation of attention. However, the impact of visuo-spatial attention is only visible in an increase in the amplitude, but not the latency, of the early components. The allocation of attention is therefore considered to provide a sensory gain in the attended channel. 'The effect of attention is manifest as an amplitude modulation of these peaks without any

changes in their latencies, polarities, and waveshapes. Such a result is consistent with a mechanism of sensory gating, since it implies that the principal effect of attention on the neural generators of these sensory evoked component is simply to increase or decrease their level of activation' (Mangun and Hillyard, 1990). It is very interesting that for odors it is not the amount of sensory gain (amplitude) but the speed of sensory processing (latency) that appears to be enhanced by attention. This implies a high share of temporal coding within olfactory stimulus processing, which has already been suggested for the encoding of odor intensity and quality (Laing *et al.*, 1994; Wehr and Laurent,



**Figure 4** (a) Grand average (standards/different body odor) across five subjects: ignore condition versus attend condition, recorded from Pz. [The grand average of the attend condition contains correctly identified standards (correct rejections) and misidentified standards (false alarms).] (b) Grand average (standards/own body odor) across five subjects: ignore condition versus attend condition, recorded from Pz. [The grand average of the attend condition contains correctly identified standards (correct rejections) and misidentified standards (false alarms).] (c) Grand average (deviants/different body odor) across five subjects: ignore condition versus attend condition, recorded from Pz. [The grand average of the attend condition contains correctly identified deviants (hits) and misidentified deviants (misses).] (d) Grand average (deviants/own body odor) across five subjects: ignore condition versus attend condition, recorded from Pz. [The grand average of the attend condition contains correctly identified deviants (hits) and misidentified deviants (misses).]



1996; Pause *et al.*, 1997). Mangun and Hillyard (1990) further state that components sensitive to attention provide a cue to the time point within the first processing of a stimulus at which attentional modulation takes place. Näätänen (1992) specifies that attentional modulation of the more exogenous components such as the P1 or N1 suggests that neuronal transmission is already influenced before the 'initial stimulus representation'. Our results indicate that the first, more exogenous components of the CSERP seem to vary with attentional investment, thus it is conceivable that attentional modulation takes place at relay stations before the cortical representation, probably at the level of the piriform cortex or maybe even at bulbar level. Imaging techniques could help identify the central structures responsible for the amplification of olfactory input.

The modulation of exogenous components, however, has been mainly observed for visuo-spatial attention. Selective attention towards stimulus orientation, stimulus size and color, however, results in an endogenous negative displacement overlapping the first negativity (Näätänen, 1992). For the auditory modality it has also been found that a larger N1 amplitude in response to attended tones is actually caused by a superimposed endogenous negative wave. This so-called processing negativity (PN) supposedly represents a comparative process between an attentional trace and the incoming stimuli (Näätänen, 1982; Alho, 1992). In contrast to the previously described gain theory of attention, the existence of an attention-sensitive endogenous component could indicate that attention does not enhance the initial processing of a stimulus but leads to 'separate matching processes between the sensory input and the attentional trace' (Alho, 1992, p. 248). The results from the auditory and visual modality emphasize that careful separation of components within the ERP is necessary to adequately address how psychological states, such as attention, influence stimulus processing. However, the findings of the second experiment show that a clear identification and differentiation of smaller components, such as the P2, within the CSERP cannot always be unambiguously achieved.

The present results also suggest that attentional and task demands should be well controlled in studies employing CSERPs as a dependent variable. Although most laboratories already employ tasks that help the subject to fix his or her attention on the odors (e.g. counting the odors, discriminating odors), special care should be taken in studies with subjects whose ability to direct attention or engage sustained attention towards the odors may be affected. This might be the case for older populations, psychiatric patients and also children. Possible solutions might be to control for attentional deficits and/or to adjust the stimulus presentation, e.g. by choosing long ISIs (Morgan *et al.*, 1997), to keep attentional demands similar for patients and controls, or to include an auditory control condition. Otherwise results that suggest smaller amplitudes in patient populations will yield very little specificity to

what process is altered and whether the altered process is actually related to olfactory processing. Careful evaluation is required to determine whether decreases in amplitude actually reflect decreases in sensory ability especially when this interpretation is not supported by the behavioral data.

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## References

- Alho, K. (1992) *Selective attention in auditory processing as reflected by event-related brain potentials*. *Psychophysiology*, 29, 247–263.
- Donchin, E. and Coles, M.G.H. (1988) *Is the P300 component a manifestation of context updating?* *Behav. Brain Sci.*, 11, 357–427.
- Elbert, T., Lutzenberger, W., Rockstroh, B. and Birbaumer, N. (1985) *Removal of ocular artifacts from the EEG—a biophysical approach*. *Electroenceph. Clin. Neurophysiol.*, 60, 455–463.
- Huynh, H. and Feldt, L.S. (1976) *Estimation of the box correction for degrees of freedom from sample data in randomized block and split-plot design*. *J. Educ. Stat.*, 1, 69–82.
- Kirk, R.E. (1968) *Experimental Design: Procedures for the Behavioral Sciences*. Brooks/Cole, Belmont, CA.
- Kobal, G. (1981). *Elektrophysiologische Untersuchungen des menschlichen Geruchssinns*. Thieme Verlag, Stuttgart.
- Kobal, G. and Hummel, C. (1988) *Cerebral chemosensory evoked potentials elicited by chemical stimulation of the human olfactory and respiratory nasal mucosa*. *Electroenceph. Clin. Neurophysiol.*, 71, 241–250.
- Kobal, G. and Hummel, T. (1991) *Human electro-olfactograms and brain responses to olfactory stimulation*. In Laing, D.G., Doty, R.L. and Breipohl, W. (eds), *The Human Sense of Smell*. Springer, Berlin, pp. 199–215.
- Kobal, G., Hummel, T. and Van Toller, S. (1992) *Differences in human chemosensory potentials to olfactory and somatosensory chemical stimuli presented to left and right nostrils*. *Chem. Senses*, 17, 233–244.
- Laing, D.G., Eddy, A., Francis, G.W. and Stephens, L. (1994) *Evidence for the temporal processing of odor mixtures in humans*. *Brain Res.*, 651, 317–328.
- Livermore, A., Hummel, T. and Kobal, G. (1992) *Chemosensory event-related potentials in the investigation of interactions between the olfactory and the somatosensory (trigeminal) systems*. *Electroenceph. Clin. Neurophysiol.*, 83, 201–210.
- Lorig, T.S., Sapp, A.C., Campbell, J. and Cain, W.S. (1993) *Event-related potentials to odor stimuli*. *Bull. Psychon. Soc.*, 31, 131–134.
- Mangun, G.R. and Hillyard, S.A. (1990) *Electrophysiological studies of visual selective attention in humans*. In Scheibel, A.B. and Wechsler, A.F. (eds), *Neurobiology of Higher Cognitive Function*. The Guilford Press, New York, pp. 271–295.

- Morgan, C.D., Covington, J.W., Geisler, M.W., Polich, J. and Murphy, C. (1997) *Olfactory event-related potentials: older males demonstrate the greatest deficits*. *Electroenceph. Clin. Neurophysiol.*, 104, 351–358.
- Näätänen, R. (1982) *Processing negativity: an evoked potential reflection of selective attention*. *Psychol. Bull.*, 92, 605–640.
- Näätänen, R. (1990) *The role of attention in auditory information processing as revealed by event-related potentials and other brain measures of cognitive function*. *Behav. Brain Sci.*, 13, 201–288.
- Näätänen, R. (1992) *Attention and Brain Function*. Hillsdale, NJ, Lawrence Erlbaum.
- Näätänen, R. and Picton, T. (1987) *The N1 wave of the human electric and magnetic response to sound: a review and an analysis of the component structure*. *Psychophysiology*, 24, 375–425.
- Naumann, E., Bartussek, D., Dietrich, O. and Laufer, M.E. (1992) *Assessing cognitive and affective information processing function of the brain by means of the late positive complex of the event-related potential*. *J. Psychophysiol.*, 6, 285–298.
- Pause, B.M., Sojka, B. and Ferstl, R. (1997) *Central processing of odor concentration is a temporal phenomenon as revealed by chemosensory event-related potentials (CSERP)*. *Chem. Senses*, 22, 9–26.
- Pause, B.M., Sojka, B., Krauel, K. and Ferstl, R. (1996) *The nature of the late positive complex within the olfactory event-related potential*. *Psychophysiology*, 33, 376–384.
- Prah, J.D. and Benignus, V.A. (1992) *Olfactory evoked responses to odorous stimuli of different intensities*. *Chem. Senses*, 17, 417–425.
- Pritchard, W.S. (1981) *The psychophysiology of the P300*. *Psychol. Bull.*, 89, 506–540.
- Schemper, T., Voss, S. and Cain, W.S. (1981) *Odor identification in young and elderly persons: sensory and cognitive limitations*. *J. Gerontol.*, 4, 446–452.
- Schott, P., Krauel, K., Pause, B., Sojka, B. and Ferstl, R. (1994) *The detection of olfactory deviance represented in the olfactory evoked potential*. In Apfelbach, R., Müller-Schwarze, D., Reutter, K. and Weiler, E. (eds), *Chemical Signals in Vertebrates VII*. Pergamon, New York, pp. 543–548.
- Squires, N.K., Squires, K.C. and Hillyard, S.A. (1975) *Two varieties of long-latency positive waves evoked by unpredictable auditory stimuli in man*. *Electroenceph. Clin. Neurophysiol.*, 38, 387–401.
- Wehr, M. and Laurent, G. (1996) *Odour encoding by temporal sequences of firing in oscillating neural assemblies*. *Nature*, 384, 162–166.

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