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The Effects of Hedonic Properties of Odors and Attentional Modulation on the Olfactory Event-Related Potentials

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Abstract The purpose of this study was to investigate the influence of the hedonic properties of odors and the attention of subjects on components of the olfactory event-related potentials (OERP). The subjects were seven healthy male students. Two odors (orange and eugenol) of different hedonic properties were presented to the subjects via a constant-flow olfactometer during an oddball paradigm under ignore and attend conditions, and the OERP were then established. The latencies of the OERP were not affected by the qualitatively different odors, whereas the amplitude of late positive component (P3) during the presentation of orange was significantly larger than that during the presentation of eugenol. On the other hand, the allocation of a subject's attention led to a decrease in the latency and to an increase in the amplitude of P3. Moreover, the amplitude of P3 increased significantly when the pleasant odor (orange) in the rare stimulus was presented under the attend condition. These results suggested that hedonic property, distribution of attention, and the interaction between these factors may influence the OERP components. *J Physiol Anthropol, 20 (1): 7-13, 2001* http://www.jstage.jst.go.jp/en/

Keywords: olfactory event-related potentials (OERP), odor, attention, hedonic property

Introduction

Event-related potential (ERP) has been established as a parameter to investigate cortical processing during auditory and visual tasks. The ERP reflecting the endogenous condition is elicited by a change in mental condition. In the experiment, the ERP could be measured as the cognitive potential during an "oddball" task. Recently, it was reported that olfactory stimuli also induced the reaction potentials on cognition (Kobal and Hummel, 1992a; Kobal et al., 1992b; Pause et al., 1996). Thus, measuring the olfactory event-related potentials (OERP) enables us to noninvasively evaluate the process (various steps) of odor perception in the cerebral cortex.

The late positive component (P3) of ERP especially depends on the endogenous condition. The effects of odor cognition on P3 have been studied by using various tasks (Lorig et al., 1993; Pause et al., 1996; Prah and Benignus, 1992). Lorig et al. (1993) found a parietally dominant P3-like positivity within the responses to different concentrations of n-butanol during a signal-detection paradigm. Furthermore, chemosensory event-related potential (CSERP) included components depending on the features of a stimulus (the 'exogenous' components N1 and P2) and components depending on stimulus evaluation (the 'endogenous' component P3) (Lorig et al., 1993). Pause et al. (1996) investigated the responses of ERP components to different concentrations of citral during 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). In the results, the amplitude and latency of the components on N1 and P2 were influenced by the concentration of an odor stimulus, whereas the change in those parameters on the P3 component depended on the subjective stimulus significance and stimulus probability (Pause et al., 1996). Taking these results together, we believed that the 'endogenous' component (P3) was an important index to use in investigating the complicated processing of such cognition and evaluation in response to odor stimulus. In a previous study, we investigated the relationship between EEG and the hedonic properties of odors. We found that increase in brain activity was observed mainly in the parietal and posterior temporal regions when subjects evaluated odors as comfortable, whereas significant brain activity was not observed when subjects evaluated odors as uncomfortable (Masago et al., 2000). Therefore, it is suggested that the subjective evaluation of an odor stimulus may influence brain activity. However, it was unclear whether the P3 reflecting the endogenous condition in the brain was affected by the differences in the subjective factor to the different odor qualities.

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As mentioned above, attention to the presentation of an odor (the task of counting the frequency of a target odor) influenced the components of the CSERP (Pause et al., 1996). In the attend condition to odor presentation (the task of reacting to a presented odor), the amplitudes on N1 and P3 were significantly greater than those of the relax condition (Pause et al. 1997). Prah and Benignus (1992) also reported that the amplitude of olfactory P3 increased according to the attention a subject paid to an odor (the odor presentation in a low probability or counting task of a target odor). Furthermore, the allocation of attention to different qualitative odors (linalool and eugenol) led to a decrease in the latency of the early components (N1, P2 and N2) and to an increase in the amplitude of the late positivity (P3) (Krauel et al., 1998). In these previous studies, however, the effect of the subjective factor to different qualitative odors was not sufficiently discussed. It was unclear whether or not the interaction between the qualitative differences of odors and the allocation of attention influenced the OERP components.

Therefore, the aim of the present study was to investigate the influence of odor hedonic properties and attention on components of OERP. To this end, we evaluated the OERP, especially the late positive component (P3) depending on the emotional responses to the stimuli, when the odors of different hedonic properties were presented during an oddball paradigm under ignore and attend conditions.

Methods

Subjects

Seven healthy male students (aged 21–23 years) took part in the experiment. Before the experiment, the subjects were evaluated as to whether or not they could detect the odors used in the experiment. All subjects could detect the two odors and were not impaired in their olfactory acuity due to allergies, chronic medication, or nasal surgery. All subjects described themselves as right-handed.

Stimulus presentation

In this experiment, orange oil (limonene 85%, Wako Pure Chemical Industries, Ltd.) and eugenol (95%, Wako Pure Chemical Industries, Ltd.) were used to represent different hedonic properties of odors. Prior to the experiment, subjects performed a subjective evaluation of hedonic scale of each odors (three point scale with disgusting at −1, neutral at 0 and pleasant at +1). An additional subjective evaluation of hedonic scale of each odors (five point scale with disgusting at −2, slightly disgusting at −1, neutral at 0, slightly pleasant at +1 and pleasant at +2) was conducted to confirm the reproducibility of the subjective perception of odor after a few days. In the olfactometer, an odor bottle (orange or eugenol) and a bottle for humidifying air were stored in warm water. The air stream with each odor, maintained in a steady condition (air temperature 35°C, relative humidity 80% at the nasal outlet), was delivered from the olfactometer to the left nostril of each subject via a Teflon tube. The ratio between the odors was balanced in such a way that each odor was equally perceivable in the mixture of odor and humidified air (to achieve this balance, twice as much humidified air was mixed with the orange odor as was mixed with the eugenol). This technique was developed by Kobal (Kobal, 1985; Kobal and Hummel, 1991a) and guarantees that the presentation of the odor is not preceded or overlapped by somatosensory sensations due to, for instance, flow fluctuations. The presentation of each odor was not synchronized with a subject's breathing pattern. The odors were achieved by mixing pulses of the stimulants in a constant air stream (total flow rate 140 ml/s). The stimulus duration was kept to 200 ms. Each odor (orange or eugenol) was replaced using a computer-controlled solenoid valve. The interstimulus interval (ISI) of odor stimulation was randomized between 15 and 25 seconds in order to avoid a subject's anticipating the timing of the next presentation of an odor. In the previous studies (Kobal, 1985; Kobal and Hummel, 1988; Kobal and Hummel, 1991a), in order to control the amount of odorous molecules reaching the nasal mucosa, the subjects were asked to close the connection between the nasal and the oral cavity with their soft palate. In this experiment, however, subjects were asked to breathe normally through the mouth to avoid focusing their attention on breathing through the nose.

All experiments were conducted in an acoustically shielded chamber at a constant ambient temperature of 26°C, relative humidity of 60% and illuminance of 20 lx. The subjects rested in a comfortable sitting position and closed their eyes throughout the experiment. White noise (50 to 70 dB SPL) was applied via earphone to mask the clicking sound of the stimulator switching odors.

The odors with different hedonic properties were presented during an oddball paradigm. One of the odors was presented frequently, while the other appeared rarely (frequent orange/rare eugenol or rare orange/frequent eugenol). The ratio of frequent to rare stimuli was set at 3:1. In the two sessions (ignore condition), the subjects were requested to ignore each odor and to count the number of target tones (350 or 700 Hz) within the white noise (an auditory distracter task). These target tones were presented asynchronously to odor presentations. On the other hand, in the other two sessions (attend condition), the subjects were instructed to ignore the same auditory tone and count the number of rare odor stimuli. The number of rare stimuli was adjusted 25 times in each session on average. The order

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of condition and odor presentation was counterbalanced for each subject.

EEG recording

According to the 10–20 system, the electroencephalogram (EEG) and the electrooculogram (EOG) were recorded from Fp1, Fp2, F3, F4, C3, C4, F7, F8, T3, T4, P3, P4, T5, T6, O1and O2, and referenced to linked earlobes. Electrode impedance was usually < 10 kOhm. The EEG data were recorded for 2500 ms with a 500 ms baseline prior to the stimulus onset. All signals were digitized at 400 Hz per channel. The EEG and EOG were amplified by using a 0.03 Hz highpass filter and a 30 Hz lowpass filter. All trails with eye movement or blink artifacts were excluded from the data and further analysis.

To calculate the OERP wave, EEG data were averaged separately for electrode position, odor category (frequent or rare), odor quality (orange or eugenol) and attention (ignore or attend). The averaged olfactory potentials of each subject were then screened for four peaks by determining their positive or negative maximum within a defined latency range. The peaks of the OERP were labeled N1, P2, N2, and P3. The following latency windows were chosen: 350–600 ms for the first negative peak (N1), 450–700 ms for the first positive peak (P2), 600-800 ms for the second negative peak (N2), and 700–1000 ms for the second positive peak (P3). Since the olfactory N1 and P2 components reflected similar processing stages (Pause et al., 1996), the amplitudes of N1 and P2 were defined as peak-to-peak amplitudes (N1/P2). In addition, the amplitudes of the N2 and P3 components were defined separately as peak-to-baseline amplitudes. The amplitudes were measured against the averaged prestimulus baseline (500 ms).

Statistical analysis

The data were subjected to a four-way analysis of variance (ANOVA) for repeated measurements: attention (ignore or attend) × odor quality (orange or eugenol) × odor category (frequent, rare) × electrode position (Fp1, Fp2, F3, F4, C3, C4, F7, F8, T3, T4, P3, P4, T5, T6, O1 and O2). One-way ANOVA and the post-hoc test were performed to compare data, when the interaction among the factors was detected. The significance level for all comparisons was $p<0.05$.

Results

Subjective evaluation

In the subjective evaluation before the experiment, eugenol was judged as unpleasant by six of the seven subjects and neutral by one subject. Orange was described as pleasant by four subjects and neutral by three subjects. Similarly, all subjects judged eugenol as unpleasant in the additional subjective evaluation. Orange was described as pleasant by four subjects, slightly pleasant by two subjects and neutral by one subject. Since no subjects evaluated orange as negative in both tests, eugenol was described as less pleasant than orange.

Odor category

The latencies in OERP did not differ between odor categories. The amplitudes of all components increased significantly in the rare odor stimulus: N1/P2 [$F(1, 6) = 423.86$, $p<0.0001$], N2 [$F(1, 6) = 45.44$, $p < 0.0001$], P3 [$F(1, 6) = 94.85$, $p < 0.0001$].

Effects of odor quality

The difference in odor quality did not influence the latencies of OERP components. Likewise, the N1/P2 amplitudes did not differ between odor qualities, whereas the N2 amplitude was significantly negative in the presentation of eugenol [$F(1, 6) = 11.19$, $p=0.0009$]. Furthermore, the P3 amplitude in the presentation of orange increased significantly compared with that of the presentation of eugenol [$F(1, 6) = 5.51$, $p=0.0194$]. Figure 1 shows OERP components separated by two factors (odor quality and odor category). These figures showed typical OERP of one subject because each wave of data exhibited a wide range of subject's variation. There was interaction between odor quality and odor category: N2 [$F(1, 6) = 14.70$, $p=0.0001$], P3 [$F(1, 6) = 11.67$, $p=0.0007$]. The N2 and P3 amplitudes in the rare odor stimulus were significantly greater in the presentation of orange than that of eugenol: N2 [$p<0.01$], P3 [$p<0.01$].

Effects of attention

The latencies in OERP components decreased significantly under the attend condition: N1 [$F(1, 6) = 74.12$, $p<0.0001$], P2 [$F(1, 6)=88.24$, $p<0.0001$], N2 [$F(1, 6) = 118.19$, $p<0.0001$], P3 [$F(1, 6) = 177.57$, $p<0.0001$] (Fig. 2a). The N2 amplitude was significantly negative under the ignore condition [$F(1, 6) = 25.81$, $p<0.0001$]. The P3 amplitude in the attend condition was significantly larger than that in the ignore condition: P3 [$F(1, 6) = 17.74$, $p<0.0001$] (Fig. 2b). There was interaction between attention and odor category on the amplitude of the OERP component. The effect of attention on the amplitude of the OERP component was seen only in the rare odor stimulus: N2 [$F(1, 6) = 23.39$, $p<0.0001$], P3 $F(1, 6) = 156.84$, $p<0.0001$].

The relationship between attention and odor quality

In the latencies of OERP, interaction between attention and odor quality was not detected. However, the interaction between attention and odor quality was observed in P3 amplitudes [$F(1, 6) = 6.18$, $p = 0.0133$]. The P3 amplitude in the presentation of orange was significantly larger than that in eugenol, when the rare

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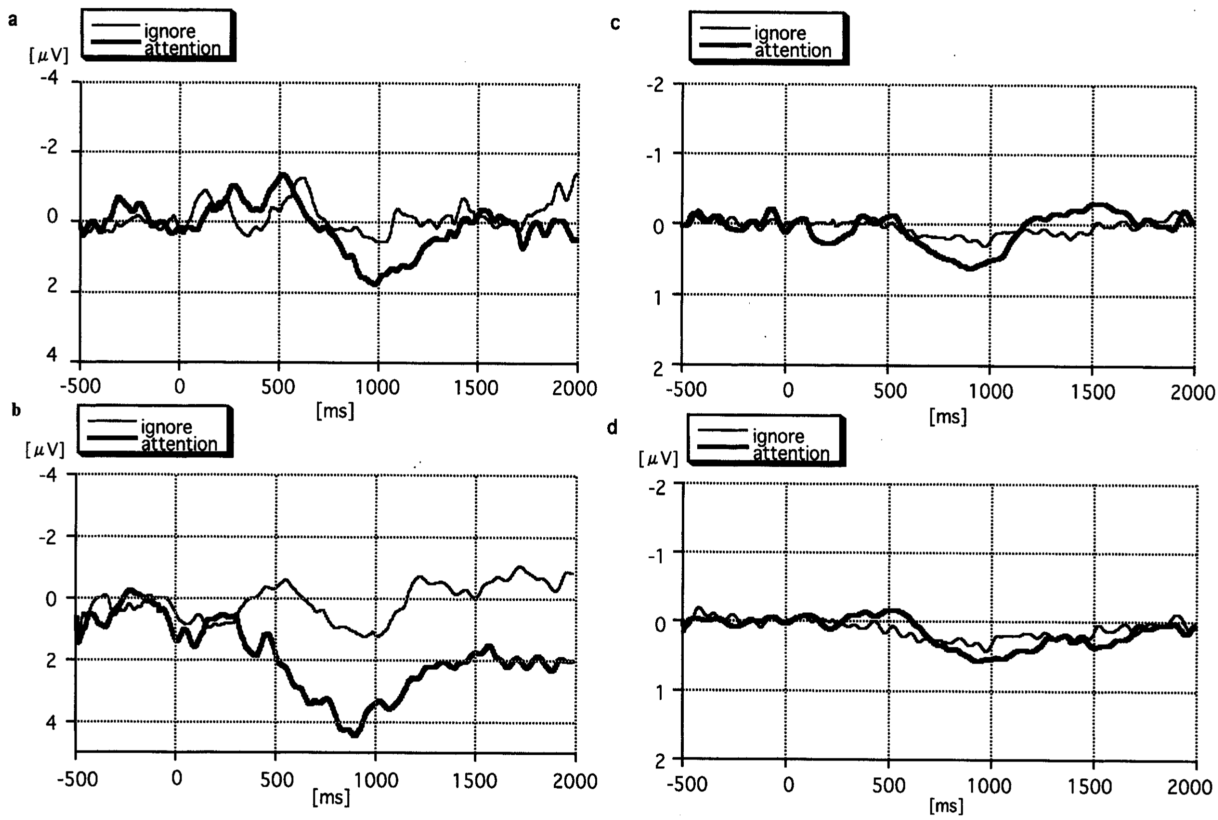

Fig. 1 (a) OERP from one subject: ignore condition versus attend condition, recorded from T4 (rare eugenol). (b) OERP from one subject: ignore condition versus attend condition, recorded from T4 (rare orange). (c) OERP from one subject: ignore condition versus attend condition, recorded from T4 (frequent eugenol). (d) OERP from one subject: ignore condition versus attend condition, recorded from T4 (frequent orange).

stimulus was presented under the attend condition ($p<0.01$: Fig. 3).

Electrode position

The latencies of OERP components did not differ between electrode positions. On the other hand, the amplitudes at several sites showed differences between electrode positions: N1/P2 [F (15, 96) = 2.07, $p=0.0106$], N2 [F (15, 96) = 5.05, $p<0.0001$], P3 [F (15, 96) = 2.34, $p=0.0033$]. The N1/P2 amplitude was larger at P3, P4: $p<0.05$ [P3>F7, F8, Fp1, O1, O2 and T3; P4 > O2 and T3]. In the rare odor stimulus, the N2 amplitude at P3 and P4 was significantly negative compared with that at the other sites ($p<0.05$). The P3 amplitude was larger at frontal (F3, F4 and F8) and temporal (T4) scalp areas: $p<0.05$ [F3>C4, O2, P3 and P4; F4>O2 and P4; F8>C3, C4, O1, O2, P3, P4, T3 and T6; T4>O2 and P4].

Discussion

The main findings of this study were: 1) the latencies of OERP components decreased significantly under the attend condition, whereas the difference in odor quality did not influence those latencies; 2) the amplitude of P3 in the presentation of orange was significantly larger than that in the presentation of eugenol; 3) moreover, the amplitude of P3 increased significantly when the pleasant odor (orange) in the rare stimulus was presented under the attend condition.

The shortening latency of OERP components shows a high share of temporal cording within olfactory stimulus processing on perception or cognition (Krauel et al., 1998). In the present study, allocation of attention to an odor decreased the latencies of OERP components. In other studies, the encoding of attention to an odor and odor intensity induced the shortening latency of OERP components (Laing et al., 1994; Krauel et al., 1998). These earlier results were consistent with the current findings. It was indicated that the allocation of attention to an odor stimulus might lead to the efficient transmission of olfactory signals to the cortex. On the other hand, since the changes in latencies were not observed according to the difference in odor quality (pleasant versus unpleasant) in this experiment, the odor quality may not affect the temporal factor on sensory processing.

The rare odor stimulus induced a significant increase in the P3 amplitude compared with the frequent stimulus (Prah and Benignus, 1992; Polich et al., 1994). In the present study, the amplitude of OERP components in the

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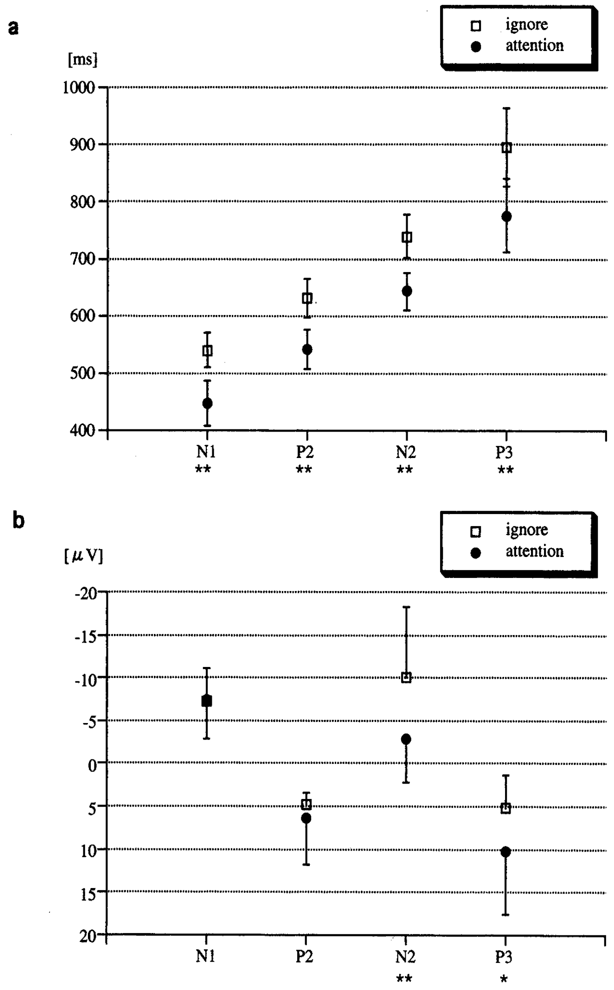

Fig. 2 (a) The average of latencies and standard deviations of all components (N1, P2, N2, P3) of the ignore and the attend condition for all subjects (n = 7). The latencies are averaged across odor category (frequent, rare), odor quality (eugenol, orange), and electrode position. (b) The average of amplitudes and standard deviations of all components (N1, P2, N2, P3) of the ignore and the attend conditions for all subjects (n = 7). The latencies are averaged across odor category (frequent, rare), odor quality (eugenol, orange), and electrode position; *: p < 0.01; **: p < 0.0001.

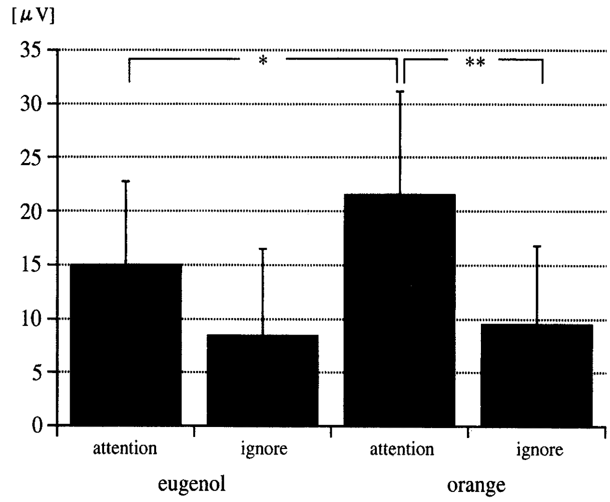

Fig. 3 The average of amplitudes and standard deviations of P3 components of the ignore and the attend conditions for all subjects (rare condition); *: p < 0.01; **: p < 0.0001.

rare odor stimulus was also significantly larger than that in the frequent stimulus. In general, the amplitude to the rare stimulus of an odor is larger than that to a frequent stimulus. Thus, it was considered that the protocol of odor presentation designed in this experiment is suitable for the investigation of OERP components.

The odor quality and the allocation of attention to odor showed no effect on the amplitude of the earlier components (N1/P2). On the other hand, the N2 amplitude in the attend condition of an odor was significantly negative compared to that in the ignore condition in this study. Krauel et al. (1998) suggested that N2 amplitude attenuated in the attend condition of an odor, because the strong late positivities (P3) overlapped the time window of the N2. In the present study, the N2 amplitude decreased in the attend condition, in contrast to the enhancement of P3 amplitude. Thus, the current results also supported their opinion that N2 amplitude was related to that of P3.

Odor hedonic property induced an increase in amplitude of the early component (N1/P2) alone, and there was no relationship between the P3 amplitude and hedonic evaluation (Kobal et al., 1991b). On the other hand, the P3 amplitude increased simultaneously with the increase in odor concentration (Pause et al., 1997). However, those authors described that this increase in amplitude was independent of the higher odor concentration, and supported the theory of Gross-Isseroff and Lancet (1988), in which different concentrations of the same odor may be perceived as qualitatively different odors. Thus, it was concluded that the increase in P3 amplitude was associated with the difference in quality evaluation (Pause et al., 1997). The discrepancy between these results may be due to the difference in odor hedonic property or in experimental design. In the present study, the P3 amplitude in the presentation of orange was significantly larger than that in the presentation of eugenol, and this difference, depending on the odors' hedonic properties, was seen remarkably for the rare odor stimulus. Interestingly, we found that EEG (alpha wave) during the presentation of different quantitative odors would change according to differences in subjective evaluations of odors (Masago et al., 2000). Taken together, these results suggested that the P3 amplitude might be influenced by odor quality.

The allocation of attention to odor induced increased P3 amplitude (Pause et al., 1997; Krauel et al., 1998). In the present study, the P3 amplitude in the attend condition also increased significantly independent of

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odor quality. In ignore and rare stimulus conditions, however, the P3 amplitude to the presentation of orange tended to increase more than that to the presentation of eugenol. These results led to the possibility that the effect of attention on P3 amplitude is much greater than that of odor quality.

The interaction between attention and odor quality was observed in P3 amplitudes in the present study. The P3 amplitude in the presentation of orange (pleasant) was significantly larger than that in eugenol (unpleasant) under attend and rare odor stimulus conditions. On the contrary, Kobal et al. (1991b) reported the presentation of hydrogen sulfide (unpleasant) produced a considerably larger amplitude of the late positive component (LPC). The discrepancy between our findings and Kobal's results may have several causes. One is that the difference in P3 amplitude between orange and eugenol may have been caused by the difference in odor concentration rather than odor quality. Pause et al. (1997) mentioned that the latencies of the earlier components were shortened by the increase in odor concentration. However, in this study the latencies of the early component did not differ between orange and eugenol. This indicates that the difference in odor concentration was unlikely to influence the difference in P3 amplitude between orange and eugenol. Another possible reason would be that the allocation of attention to odor might have changed with the difference in subjective evaluations of different odors. Kobal and Hummel (1992a) pointed out that the increase of LPC amplitude during the presentation of hydrogen sulfide (unpleasant) could be due to its unpleasant nature and to the possibility that hydrogen sulfide may command more attentive resources than the pleasant smell of vanillin. On the other hand, the P3 amplitude to the attention to low-concentration linalool (pleasant) increased, whereas that to the high-concentration linalool (unpleasant) decreased (Pause et al. 1997). Thus, more resources might be allocated to attend to odors of different subjective evaluations, independently of an odor's pleasantness. This suggests that the interaction between allocation of attention and a more attention-getting odor induced the increase in P3 amplitude. In the present study, accordingly, the pleasant orange may command more attentive resources than the unpleasant eugenol, so that the effects of the attention that the odor quality elicits may induce the difference in P3 amplitude under the attend condition.

In the present study, the largest amplitudes of all components appeared at the parietal or temporal scalp areas. The amplitudes of the olfactory P3 also were largest at the temporal scalp areas (Hummel et al., 1992; Kobal et al., 1992b). In addition, the alpha wave of EEG was attenuated at the parietal and posterior temporal regions (Masago et al., 2000). Based on these results on brain activity and scalp areas, these regions might relate to the processing of the complicated and integrative neuronal activities of odor perception.

In conclusion, we investigated the effects of the hedonic properties of odor and attention modulation on OERP components. The results suggested that hedonic property, allocation of attention to an odor, and interaction between odor quality and attention may influence the late positive component (P3) of the OERP.

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