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Enhancement of theta band electroencephalogram activities during unmatched olfactory-taste stimulation

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Abstract

This study aimed to investigate how odor stimulation affects taste perception. Electroencephalogram

(EEG) signals were measured from the frontal region of the head in normal subjects, and frequency

analyses were performed. Each odor stimulation was delivered while the subject tasted chocolate, using

chocolate paste as the odorant for 'matched odor stimulation', and garlic paste for 'unmatched odor

stimulation'. Differences appeared in EEG signals. Comparing frequencies of EEGs under 'unmatched

odor stimulation' with those under 'matched odor stimulation' showed that the occupancy rate of the theta-frequency band under 'unmatched odor stimulation' was higher than that under 'matched odor stimulation'. Interestingly, a negative correlation existed between the occupancy rate of the theta-frequency band and the subjective feeling of chocolate sweetness. The present findings suggest that when we receive unmatched smell against the foods, subjective feelings are disturbed, and theta-band brain activity is increased while cross-checking the unmatched information.

Introduction

Taste and smell are fundamental ways of obtaining chemical information for humans. A feeling of deliciousness is produced by perception of these chemical senses. The molecules causing tastes and smells bind to gustatory and olfactory receptors expressed on the tongue and olfactory epithelium, respectively. The resulting chemical signals are first conveyed to the primary gustatory and olfactory cortices, then the information is processed at higher levels of the cortex (1-4). The gustatory and olfactory cortices are strongly connected with the limbic system, and these chemical senses are thus also strongly connected with emotion (5-6). The limbic system plays important roles in memory storage, retrieval, recognition and the production of various emotional feelings (2, 7-9). The perceived deliciousness of food may therefore be partly based on memory and emotion with regard to the food, formed by personal experience.

Many foods contain specific substances that produce their particular tastes and odors. Food odor can increase the taste intensity of food (10, 11), acting through cross-modal interactions (12, 13). We can recognize foods by referring to the combination of taste and smell (14). When the smell of a food differs from the smell that the food usually has, we may experience difficulty in recognizing the food. In such cases, the processing of chemical information might be disturbed. However, the precise mechanisms involved in such disturbance have remained unclear.

Chocolate is a familiar food, usually associated with feelings of pleasantness and increased positive mood. (15, 16). Chocolate can be easily identified by the combination of its smell and taste, so the present study focused on chocolate. The deliciousness of chocolate might be enhanced or attenuated, depending on the associated smells. The frequency of electroencephalogram (EEG) signals is related to underlying activities of the brain, and is used for investigating perceptual, cognitive and emotional functions (17-21). The present study adopted the method of Fast Fourier Transform (FFT) analysis, and investigated how changes in feelings of a taste correlate with brain activities when applying unmatched odor stimulation.

Materials and Methods

All procedures performed in studies involving human participants were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Declaration of Helsinki and its later amendments or comparable ethical standards. The institutional ethics committee at Tokushima University approved the present study (No. 2575-2). Informed consent was obtained from all individual participants included in the study.

Nine healthy participants with a mean (± standard deviation) age of 30.2 ± 12.3 years were included in experiments using chocolate as a tastant, and another nine healthy participants with a mean age of 33.3 ±

15.8 years were included in control experiments using no tastant. EEGs were recorded from the frontal

region of the scalp (Fp1, Fp2), using an Alphatec IV EEG recorder (Brain Function Research &

Development Center (BFRDC), Osaka, Japan). Frequency analyses of EEGs were performed with a

MinD Sensor V (BFRDC). During one session (60 s), data were collected every 1 s. The sampling rate

was 1024 Hz. EEG epochs with artifacts were automatically identified, and artifact-free EEG epochs were

adopted for frequency analysis.

Participants sat down in a body sonic chair (RFRESH1 Excellent, Tokyo, Japan), and listened to

consonant music for relaxation. Milk chocolate (Morinaga & Co., Tokyo, Japan) was used as a tastant.

Chocolate paste (Morinaga & Co., Tokyo, Japan) was used as an odorant for 'matched odor stimulation',

and garlic paste (House Food Corporation, Tokyo, Japan) was used as an odorant for 'unmatched odor

stimulation'. At the start of the session, the participant held a small piece of chocolate in the mouth, and

tasted it. For odor stimulation, the odorant was smeared onto cosmetic paper, and placed close to the nose.

EEGs were recorded for 60 s per session. After the session, the participant was asked to rate the

perception of chocolate sweetness, as the 'chocolate sweetness score' (0, no feeling of chocolate

sweetness; +5, extreme feeling of chocolate sweetness). As a reference for chocolate sweetness,

participants were asked to consider the sweetness of chocolate with no odor stimulation as a chocolate

sweetness score of 2.5. As a control experiment, odor stimulation with chocolate paste or garlic paste was

delivered in the same way mentioned above to participants without taste stimulation, and EEGs were

recorded for 60 s per session. As another control experiment, EEGs were recorded for 60 s per session while tasting chocolate without odor stimulation. When a small piece of chocolate is carried to the mouth, olfactory receptors detect the odor of the chocolate retronasally (22). All participants could distinguish the odors of milk chocolate (retronasal) and chocolate paste (orthonasal), when the odors are presented separately. However, the retronasal pathway provides a smaller olfactory input than the orthonasal pathway (23, 24). We therefore adopted cases using no odorants to represent the condition of no odor stimulation.

Individual frequencies were analyzed from 4 Hz to 23 Hz. The occupancy rate of each frequency was calculated as follows. The power of each frequency was divided by summed power for all frequencies, and the ratio was defined as the unit occupancy rate (%). Activity in each frequency was first assessed by the unit occupancy rate per second. Unit occupancy rates through one session (60 s) were then averaged, and we adopted those data for the 'occupancy rate' (%) in this study. Details of EEG recordings and data analysis have been described in a previous report (25).

Results

Data were collected from nine healthy participants in experiments using chocolate as a tastant. As a reference, all participants rated the chocolate sweetness score for tasting chocolate without odor stimulation as 2.5. Chocolate sweetness score with odor stimulation applied was then rated based around that reference. Subjective feelings of chocolate sweetness were compared between cases of 'unmatched odor stimulation' and 'matched odor stimulation'. In all participants, chocolate sweetness scores for 'matched odor stimulation' were higher than the reference score. Conversely, scores for 'unmatched odor stimulation' were lower than the reference score. Differences in chocolate sweetness scores between the two cases were significant (Origin8; OriginLab Co. USA; n=9; unmatched, 1.1 ± 0.49; matched, 3.9 ± 0.33 (mean ± S.D.); paired t-test, $P=4\times10^{-6}$; Fig. 1). Interestingly, in addition to decreased feelings of sweetness, participants showed a tendency to be unable to discern what the food was in cases of 'unmatched odor stimulation'.

Objective differences between 'unmatched odor stimulation' and 'matched odor stimulation' conditions were apparent in EEG signals collected from the nine healthy participants. Profiles of mean occupancy rates obtained from frequency analysis are shown in Figure 2A and 2B. Figure 2C shows profiles of the two conditions superimposed. The present study focused on theta, alpha and beta frequency bands. To assess the occupancy rate of the respective frequency bands, areas surrounded by the lines of occupancy rates and the frequency axis were calculated (Hz×%), and termed 'areal occupancy rate' (Fig. 2C). Mean areal occupancy rates of respective frequency bands under conditions of unmatched and

matched olfactory stimulations are shown in Figure 2D. To investigate which frequency bands of EEG reflected different patterns of olfactory stimulation, areal occupancy rates under the condition of 'unmatched odor stimulation' were subtracted from those under the condition of 'matched odor stimulation', and compared. Mean differences for theta, alpha and beta bands were 5.25 ± 4.48, -2.83 ± 2.49 and -3.49 ± 4.01 (mean ± S.D.), respectively. One-way analysis of variance (ANOVA) (Origin8; OriginLab Co. USA) was used to evaluate the statistical significance of 'areal difference values' in the three frequency bands mentioned above. Statistical differences in areal difference values were identified (F=15.1; P=5.7×10^{-5}). Scheffe's post-hoc test was then used to detect significant differences between areal difference values in respective frequency bands. These analyses revealed that differences in areal difference values between 'unmatched odor stimulation' and 'matched odor stimulation' conditions were significantly greater in the theta frequency band than in other frequency bands (alpha: F=10.4, P=5.5×10^{-4}; beta: F=12.2, P=2.2×10^{-4}). This suggests that unmatched olfactory stimulation enhances EEG activities in the theta frequency band.

Subjective differences (Fig. 1) and objective differences (Fig. 2) might be correlated. In other words, brain activities in the theta band might correlate with disturbance in taste perception, when 'unmatched odor stimulation' was applied. Correlations between chocolate sweetness score and areal occupancy rate in the theta, alpha and beta bands were therefore examined. In the theta frequency, a negative correlation was seen between chocolate sweetness score and areal occupancy rate (n=18, R^2=0.282, F=7.69, P=0.01;

Fig. 3A). In the same way, correlations between chocolate sweetness scores and areal occupancy rate in

the alpha frequency band were examined. In this situation, no correlation was identified between

chocolate sweetness score and areal occupancy rate (n=18; R^2=0.038, F=1.66, P=0.22; Fig. 3B). For the

beta frequency band, no correlation was evident between chocolate sweetness scores and areal occupancy

rate (n=18; R^2=0.12, F=3.34, P=0.09; Fig. 3C). These results suggest that when taste perception is

disturbed by unmatched olfactory stimulation, EEG activities in the theta frequency band were enhanced.

The possibility remains that the increases in theta band EEG activity during unmatched olfactory

stimulation are caused by the effect of garlic odorant stimulation itself. We therefore investigated

influences of odor stimulation on EEG frequency without taste stimulation. EEG signals were collected

from nine healthy participants. Profiles of mean occupancy rates obtained from frequency analysis in the

case of garlic and chocolate olfactory stimulation are shown in Figure 4A and 4B, respectively. In Figure

4C, profiles of the two conditions are superimposed. Figure 4D shows mean areal occupancy rate of the

respective frequency bands under conditions of garlic and chocolate olfactory stimulations. To investigate

whether patterns of EEG frequency bands between the two kinds of olfactory stimulation differ, areal

occupancy rates under the condition of 'garlic odor stimulation' were subtracted from those under the

condition of 'chocolate odor stimulation', and compared. Mean differences in theta, alpha and beta bands

were -0.92 ± 3.15, -0.73 ± 3.46 and -0.25 ± 2.60 (mean ± S.D.), respectively. One-way ANOVA (Origin8;

OriginLab Co. USA) was used to evaluate statistical significance of the 'areal difference values' in all

three frequency bands mentioned above. No significant differences in areal difference values were apparent among the three frequency bands (F=0.68; P=0.52). This shows that increases in theta band EEG activity in the case of unmatched olfactory stimulation were not attributable to the effect of garlic odorant stimulation itself.

Profiles of mean occupancy rates obtained from frequency analysis in the case of chocolate taste stimulation without odor stimulation are shown in Figure 5A. To investigate additional effects of smell on taste stimulation, mean areal occupancy rates of respective frequency bands under the condition of chocolate taste stimulation with and without odorant stimulation were compared (Fig. 5B, 5C). Areal occupancy rates under the condition of 'garlic-odor with chocolate-taste stimulation' were subtracted from those under the condition of 'chocolate taste stimulation'. Mean differences in theta, alpha and beta bands were 4.29 ± 4.80, -2.49 ± 3.13 and -2.74 ± 5.13 (mean ± S.D.), respectively. One-way ANOVA (Origin8) was used to evaluate the statistical significance of 'areal difference values' in all three frequency bands mentioned above. Significant differences were seen in areal difference values (F=7.25; P=0.003). Scheffe's post-hoc test was then used to detect significant differences between areal difference values in the respective frequency bands. These analyses revealed that differences in areal difference values between conditions of 'garlic-odor with chocolate-taste stimulation' and 'chocolate taste stimulation' were significantly greater in the theta frequency band than in other frequency bands (alpha: F=5.2, P=0.01; beta: F=5.6, P=0.01). This shows that an additional effect of garlic odor stimulation while

tasting chocolate was enhancement of theta-band EEG activities. Next, areal occupancy rates under the condition of 'chocolate-odor and chocolate-taste stimulation' were subtracted from those under the condition of 'chocolate taste stimulation'. Mean differences in theta, alpha and beta bands were -0.97 ± 3.35, 0.34 ± 2.75 and 0.74 ± 3.88 (mean $\pm$ S.D.), respectively. One-way ANOVA (Origin8) was used to evaluate the significance of 'areal difference values' in all three frequency bands mentioned above. No significant differences in areal difference values were evident among the three frequency bands ($F=0.64$; $P=0.54$). This shows that we could not find any additional effects of chocolate odor stimulation while tasting chocolate.

Discussion

Humans receive external information through various sensory receptors. The information is integrated during processes from perception to cognition, which involve emotion and memory (8, 26). Cognitive processes requires past experiences, and we can recognize objects when we have a stored experience of that object. One object contains various modes of information, and the specific combination of contained information is extremely important for recognition. When one mode of information does not match with the recollection of an object, recognizing that object may be difficult. During the cognitive process, the

brain tries to cross-check unmatched information against the object, which may induce different patterns of brain activity compared with cases in which all information matches with the object.

We used chocolate as a tastant, and chocolate paste and garlic paste as odorants in the present study. All participants rated chocolate sweetness high when the matched odor stimulation was applied (Fig. 1). Under this condition, feelings that the food in the mouth definitely represented chocolate were increased, supporting the notion that the smell helped in the recognition of chocolate. On the other hand, all participants rated chocolate sweetness as low when the unmatched odor was applied. In this case, feelings that the food in the mouth was chocolate were decreased, indicating that smell can disturb the recognition of chocolate. Although taste thresholds should be measured for more precise evaluation of taste perception, we used sweetness scores to allow easy understanding of subjective feelings of chocolate taste, including deliciousness.

By comparing occupancy rate profiles between conditions of unmatched and matched odor stimulation while tasting chocolate, a small bulge was identified in the frequency range from 4 Hz to 8 Hz that we recognized as the theta rhythm in the case of unmatched odor stimulation (Fig. 2A). Given the large areal difference values in the theta frequency band, compared with those in other frequency bands, the theta frequency band may play a role in information processing when we perceive smells that do not match the corresponding foods (Fig. 2). Since we had to consider the possibility that the small bulge in the theta frequency band was a garlic odor-evoked response, we investigated profiles of occupancy rates

in the case of only odor stimulation (Fig. 4). However, we could find neither a small bulge in the theta frequency band nor differences between garlic odor-evoked and chocolate odor-evoked responses in all frequency bands (Fig. 4D). The small bulge in the theta frequency band in the case of unmatched odor stimulation under chocolate tasting thus seems unlikely to have been caused by only odor stimulation.

Figure 5A shows profiles of occupancy rate in the case of only chocolate taste stimulation without odorant stimulation. Profiles were similar to the profiles in the case of matched odor stimulation while tasting chocolate. Figure 5C shows no variance among differences between conditions of only chocolate tasting and matched odor stimulation while tasting chocolate in the respective frequency bands. We thus could not find additional effects of matched odor stimulation compared to taste stimulation. A possible cause may be that the odor produced from chocolate itself in the oral cavity enters the nasal cavity, and olfactory neurons are stimulated retronasally (22). When retronasal odor stimulation is presented without orthnasal odor stimulation, retronasal olfaction might work more efficiently (27). Figure 5B shows a comparison of areal occupancy rates between chocolate tasting alone and unmatched odor stimulation while tasting chocolate in the respective frequency bands. The statistical results were similar to the results obtained from comparison between conditions of unmatched and matched odor stimulation while tasting chocolate (see Results and Fig. 2D). The similarity might be due to the very few additional effects of chocolate odor stimulation on EEG activities to chocolate taste stimulation, as mentioned above.

In recent years, frontal midline theta rhythm (Fm theta) in humans has been reported to reflect mental

concentration as well as meditative state (17, 19, 28-30). Human studies using EEG and magnetoencephalogram (MEG) analysis suggest that the origin of Fm theta activities when executing tasks or decision making that requires mental concentration or in a meditative state are interactions between the anterior cingulate cortex (ACC) and the medial prefrontal cortex (30-32). Indeed, the ACC along with the orbitofrontal cortex are regarded as areas where taste and olfactory information converge (33). Another candidate for sources of Fm theta activities is the hippocampus. Recent studies suggest that oscillatory synchrony between the hippocampus and medial prefrontal cortex play a crucial role in not only memory integration, but also retrieval of memories (34-36). The hippocampus and mPFC are able to retrieve, exchange, integrate, and re-encode multiple memories, and contribute to memory-based decision making (36, 37). An oscillatory coupling exists between the hippocampus and mPFC, and theta oscillation is required when the association memory is transferred from the hippocampus to the mPFC (38-40).

The present study shows that the theta band appeared while perceiving smells that did not match the food being tasted. In addition, in this case, subjective feeling of sweetness decreased, and participants tended to be unable to discern what the food was. The feeling of perturbance might induce concentration, resulting in generation of the theta rhythm activity. Indeed, error-related theta waves are observed in the medial prefrontal cortex (41). Although we cannot address sources of the theta rhythm, the present results suggest that theta-band brain activities emerge when cross-checking unmatched information.

Ethical approval: All procedures performed in studies involving human participants were in accordance

with the ethical standards of the institutional and/or national research committee and with the 1964

Helsinki declaration and its later amendments or comparable ethical standards.

Informed consent: Informed consent was obtained from all individual participants included in the study.

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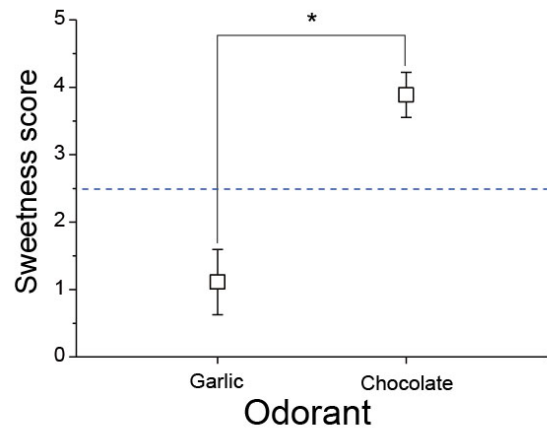
Figure legends

Fig 1: Comparison of chocolate sweetness scores. Subjective feelings of chocolate sweetness under conditions of unmatched (garlic) and matched (chocolate) odor stimulation while tasting chocolate. Sweetness scores were averaged and plotted (mean ± standard deviation). Note the significant difference between chocolate sweetness scores and chocolate recognition scores (*).
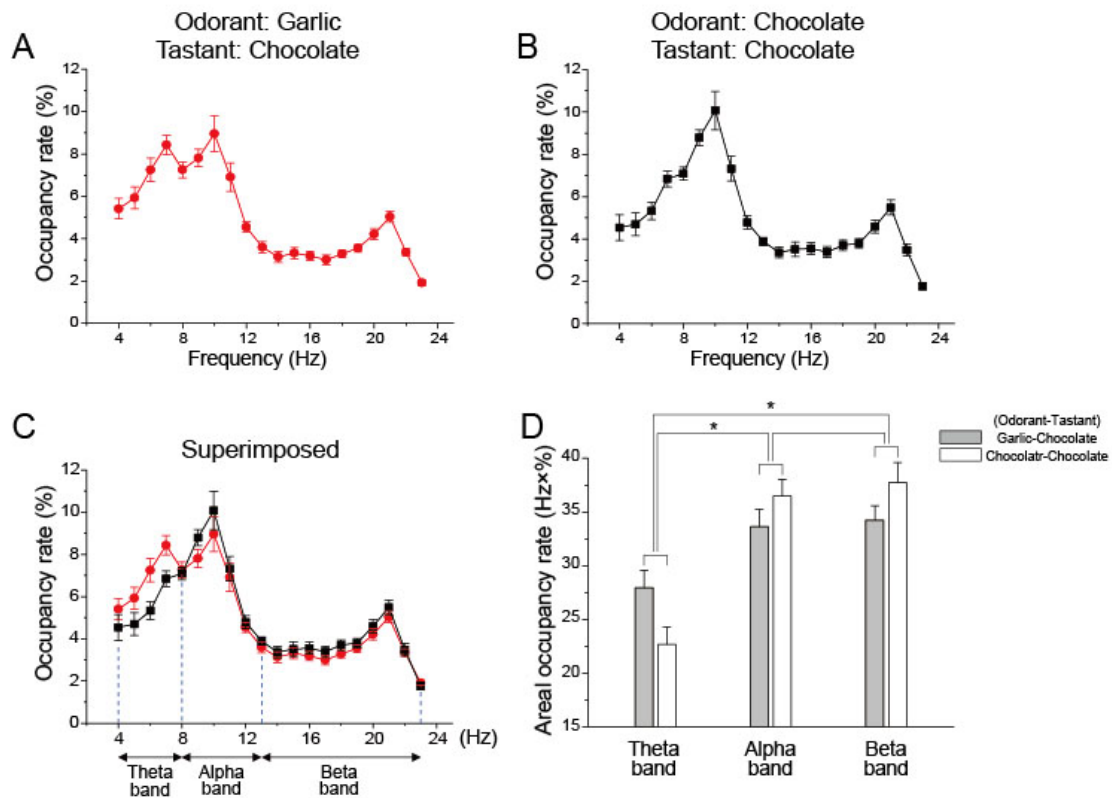
Fig 2: Comparison of EEG frequency activities obtained from unmatched and matched odor stimulation-evoked EEG responses under tasting chocolate. (A-C) Profiles of mean occupancy rates obtained by FFT analysis of EEG signals. Mean occupancy rate of respective frequency (4-23 Hz) under conditions of unmatched (garlic) odor stimulation (A) and matched (chocolate) odor stimulation (B) while tasting chocolate (mean ± standard error). (C) Profiles of mean occupancy rates for the two cases are superimposed, and the three frequency bands we focused on are shown. (D) Mean areal occupancy rates in the case of unmatched and matched odor stimulations are shown. Differences in areal occupancy rates between cases are compared among the three frequency bands. Note that the difference is significantly greater in the theta frequency band as compared to other frequency bands (*).
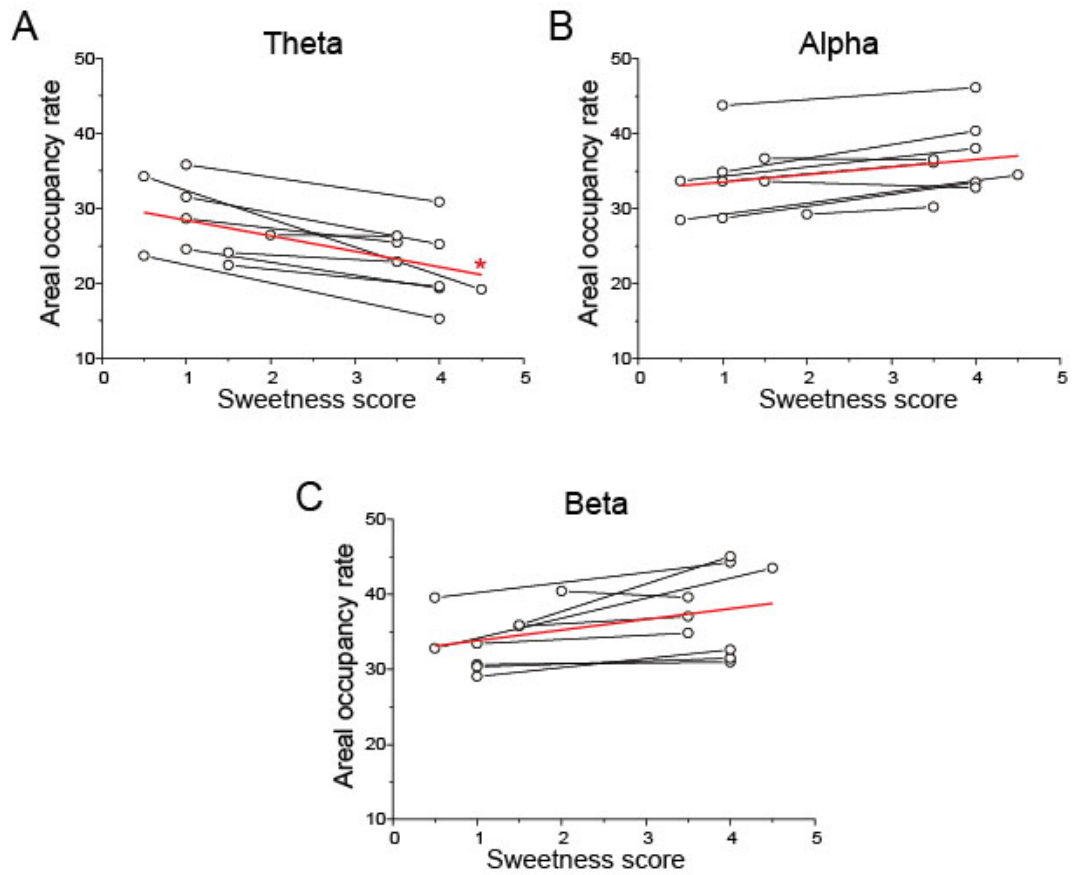
Fig 3: Relationships between individual subjective sweetness scores and areal occupancy rate in respective frequency bands. Each data point consists of the sweetness score and areal occupancy rate. A set of two points was obtained from the same participant in the case of unmatched and matched odor stimulation, and the set of two points was connected with a line. Data obtained from all participants are plotted together. Red lines shows linear fitting. Note that in the theta frequency band, sweetness scores correlate with areal occupancy rate (*).
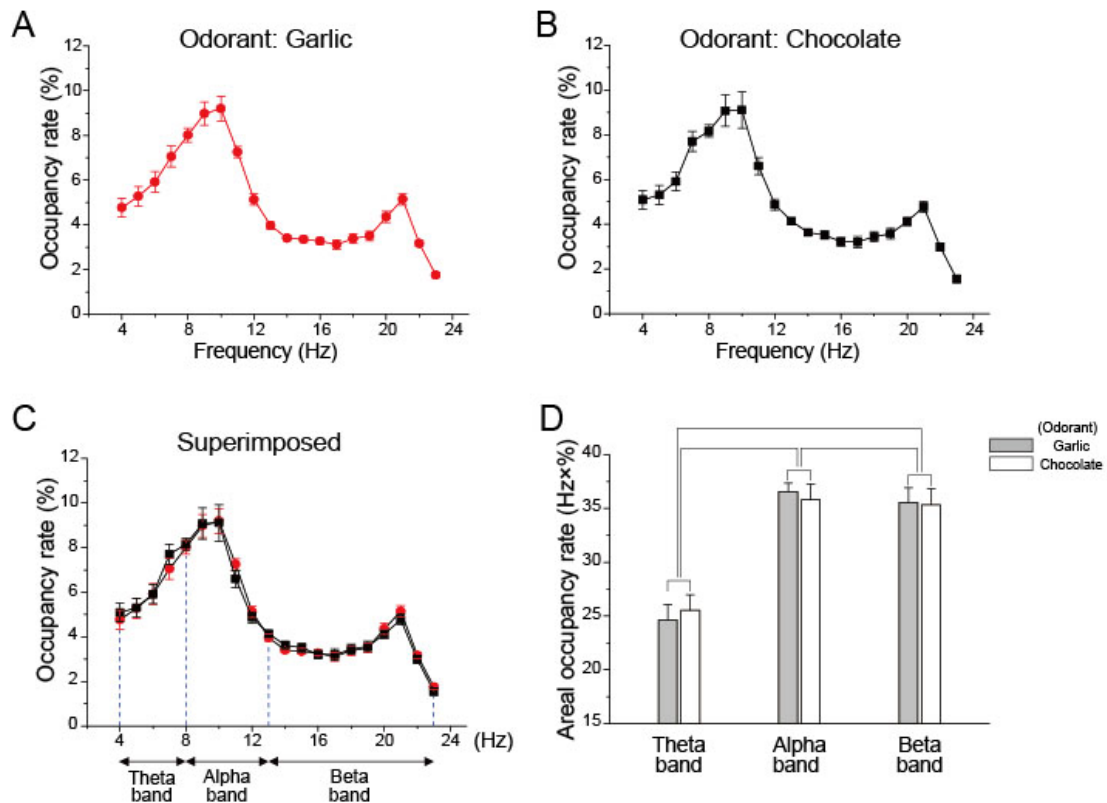
Fig 4: Comparison of EEG frequency activities obtained from garlic and chocolate odor stimulation-evoked EEG responses without taste stimulation. (A-C) Profiles of mean occupancy rates obtained by FFT analysis of EEG signals. Mean occupancy rate of respective frequency (4-23 Hz) under conditions of garlic odor stimulation (A) and chocolate odor stimulation (B) (mean ± standard error). (C) Profiles of mean occupancy rates of the two conditions are superimposed, showing the three frequency bands that we focused on. (D) Mean areal occupancy rates in the case of garlic and chocolate odor stimulation are shown. Differences in areal occupancy rates between the two cases are compared among the three frequency bands. Note that no significant differences in areal difference values are seen among the three frequency bands.
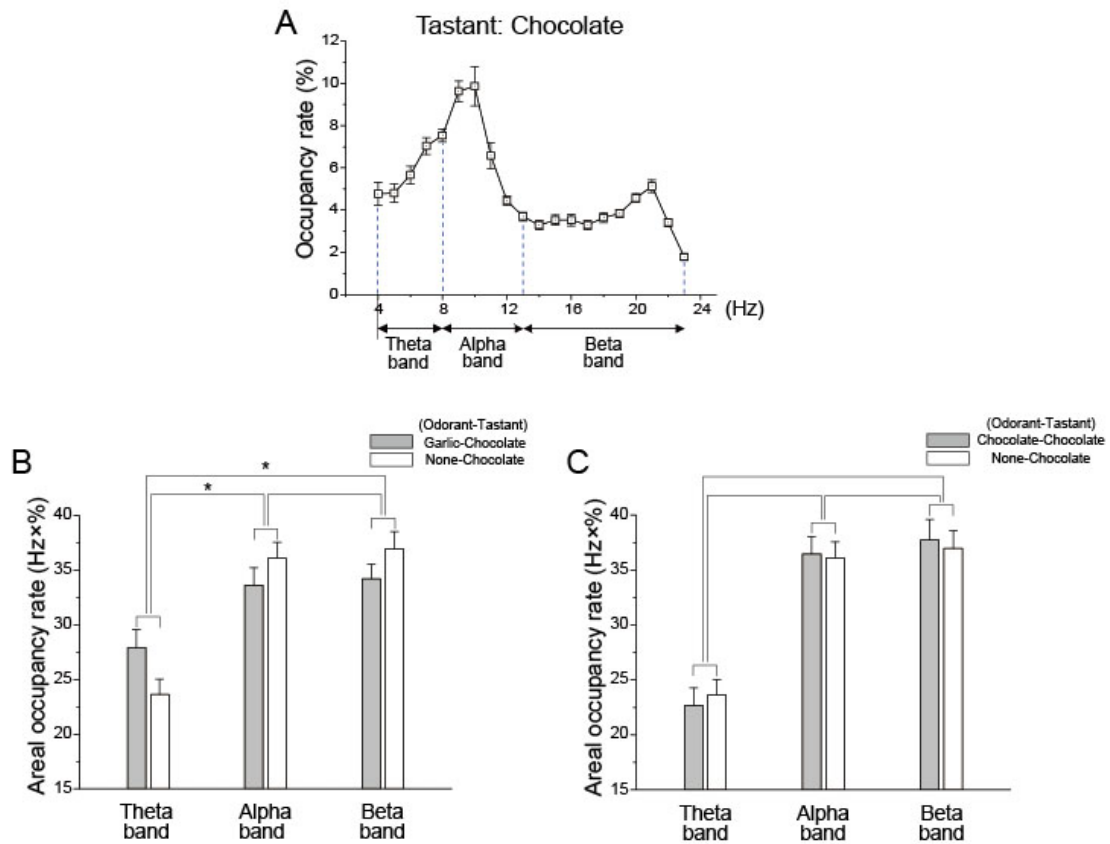
Fig 5: EEG frequency activities under chocolate taste stimulation, and comparison of mean areal occupancy rate of respective frequency band between cases of no odor and odor stimulation while tasting chocolate. (A) Mean occupancy rates for respective frequencies (4-23 Hz) in cases of no odor stimulation while tasting chocolate (mean ± standard error). (B) Mean areal occupancy rates in the case of garlic odor stimulation while tasting chocolate and in the case of no odor stimulation while tasting chocolate are shown. Differences in areal occupancy rates between the two cases are compared among the three frequency bands. Note that the difference is significantly greater in the theta frequency band as compared to other frequency bands (*). (C) Mean areal occupancy rates under conditions of chocolate odor stimulation while tasting chocolate and under conditions of no odor stimulation while tasting

chocolate are shown. Differences in areal occupancy rates between the two conditions are compared

among the three frequency bands. Note that no significant differences in areal difference values are seen

among the three frequency bands.