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Dried-Bonito Aroma Components Enhance Salivary Hemodynamic Responses to Broth Tastes Detected by Near-Infrared Spectroscopy

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ABSTRACT: To elucidate the effects of aroma from dried bonito (*katsuo-bushi*) on broth tastes caused by the central integration of flavor, optical imaging of salivary hemodynamic responses was conducted using near-infrared spectroscopy (NIRS). A reconstituted dried bonito flavored broth produced a significantly larger hemodynamic response than the odorless broth taste solutions for 5 of the 10 panelists, who felt that the combination of the aroma with the tastes was congruent. In the remaining 5 panelists who felt the combination incongruent, the flavored broth did not cause the enhancement of response. Moreover, when the odor-active smoky parts were removed from the flavoring, the reconstituted flavoring did not enhance the response in the former five panelists. These results indicate that NIRS offers a sensitive method to detect the effect of specific congruent aroma components from dried-bonito broth on the taste-related salivary hemodynamic responses, dependent on the perceptual experience of the combination of aromas and tastes.

KEYWORDS: *saliva secretion, NIRS, hemodynamic responses, flavor, aroma, broth, dried bonito*

INTRODUCTION

During food intake, flavor perception results from simultaneous activation of the gustatory, olfactory, and trigeminal sensation systems. Especially olfactory stimulation through the retronasal pathway greatly contributes to the flavor perception of foods.[1,2] The perception of specific flavors typically results from specific aromas. The perceived intensity of a taste is enhanced only if the aroma is perceptually similar to the taste.[3−5] The effective combinations of taste and aroma are shown to be congruent pairings, which presumably reflect the food consumption experience.[6] These findings suggest that the manner of integrating gustatory and olfactory signals of foods in the brain depends on one's previous experiences with taste and aroma pairings.[7]

Dried bonito (*katsuo-bushi*), which is made through processes such as boiling bonito (*Katsuwonus pelamis*) in water, repeated smoke-drying, trimming, and inoculation with molds, is an important ingredient in *dashi* (Japanese broth). The characteristic flavors of dried bonito are very popular with the Japanese population,[8] because dried-bonito broth has long been used to reinforce the flavor of foods in many Japanese cuisines. Some dimethylpyrazines with a roasted note and guaiacol and 4-methylguaiacol with a smoky note were considered to be the main compounds that contributed to the aroma of dried bonito.[9] Although the broth contains types of umami substances,[10] such as monosodium glutamate (MSG), inosine 5′-monophosphate (IMP), and *N*-lactoylguanosine 5′-monophosphate (*N*-lactoyl GMP), the aroma also contributes to its desirability, its enhancement, and the characteristics of the flavor. The flavor of the broth includes both enhanced saltiness and improved palatability[11] and probably results from the consumption experiences of Japanese people.

Multichannel near-infrared spectroscopy (NIRS) is a noninvasive optical technique that continuously monitors changes in the concentration of hemoglobin in the cerebral vessels.[12] Recently, Sato et al.[13] showed that NIRS can also be used to measure extracranial hemodynamic signals that accompany saliva secretion from the parotid gland in response to taste stimuli. The taste-induced hemodynamic signals are remarkably large and show a characteristic slow time course. Moreover, the recording of the hemodynamic signals with NIRS enabled us to test subjects in a normal, seated position with minimal restriction of movement during drinking. In the present study, we therefore used NIRS to record hemodynamic signals accompanying saliva secretion in response to the dried-bonito broth stimuli during the subjects' sensory evaluation of the broth quality and the effect of the aroma of dried bonito on taste. The subjects had been familiar with dried-bonito broth since childhood. We compared the responses to the broth solutions, which either included (flavored broth) or excluded (odorless broth) the dried-bonito aroma constituents. Using this method, we assessed how the presence of particular flavorings (specific congruent or incongruent aromas of dried-bonito) modified the salivary hemodynamic signals. We show that the salivary hemodynamic signals measured by the NIRS are a useful objective indicator for studying the central integration of aroma and taste signals of foods in natural settings.

MATERIALS AND METHODS

Subjects. Ten healthy panelists (three males and seven females with a mean age of 30.5 ± 4.6 years), all of whom were employees of the Technical Research Center of T. Hasegawa Co., Ltd., Kawasaki,

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Japan, participated in this study. All of the panelists were native Japanese who had been familiar with dried-bonito broth since childhood and were trained to recognize and quantify aromas with about 100 odorous chemicals and raw materials. All of the procedures and methods were in keeping with the politics and principles described in the Declaration of Helsinki. Written informed consent was obtained after a complete explanation of the study. To avoid any influence of environmental stress, each subject was seated comfortably in a room controlled for temperature, humidity, and brightness throughout the experiments.

Stimuli. The odorless broth and the flavored broth provided the basic stimuli set. The odorless broth consisted of the mixed amino acid−nucleotide solution and the same concentrations of amino acids, nucleotides, and sodium chloride (NaCl) as in a dried-bonito extract (Shimaya Co., Inc., Yamaguchi, Japan), a 1% solution, which is the concentration of the extract that is used for cooking (Table 1). It was

Table 1. Composition of the Odorless Broth (Percent of Weight)

	odorless broth		odorless broth
NaCl	0.03500	threonine	0.00077
IMP	0.01520	alanine	0.00183
GMP	0.00520	proline	0.00139
aspargine	0.00146	tyrosine	0.00068
glutamic acid	0.00569	valine	0.00079
serine	0.00087	methionine	0.00077
glycine	0.00111	isoleucine	0.00031
histidine	0.01237	leucine	0.00093
arginine	0.00282		

prepared using the following reagents: NaCl (Naruto Sangyo K.K., Tokushima, Japan); IMP, GMP, L-glutamic acid, L-threonine, L-tyrosine and L-leucine (Ajinomoto Co., Inc., Tokyo, Japan); L-serine, L-proline, L-histidine, L-arginine, L-valine, and L-isoleucine (Kyowa Hakko Chemical Co., Ltd., Tokyo, Japan); DL-alanine (Musashino Kagaku K.K., Saitama, Japan); DL-methionine (Hamari Chemicals Ltd., Osaka, Japan); L-asparagine−H_2O (Nippon Rika Co., Ltd., Tokyo, Japan); and glycine (Nippon Kayaku Co., Ltd., Tokyo, Japan), which were formulated by weight. The flavored broth consisted of the odorless broth plus dried-bonito aroma constituents. The flavoring contained odor-active and available volatile compounds based on an analysis of dried-bonito broth aroma constituents.[14−16] When the 10 ppm volatile compounds were added to the odorless broth, the subjects sensed a dried-bonito broth-like aroma when they drank the flavored broth. The reconstituted volatile compounds were separated into two parts. One was 5.6 ppm phenols part with a smoky note, which consisted of 2,6-dimethoxyphenol, phenol, 4-methylguaiacol, *m*-cresol, guaiacol, 2,6-dimethoxy-4-methylphenol, *o*-cresol, and 4-ethylguaiacol. The part was one of the major and the main aroma constituents for sensing the dried-bonito aroma. The other was the remaining parts of the flavoring. The latter aroma, nonsmoky aroma parts, in combination with the odorless broth, was used as an incongruent, nonsmoky flavored broth. Ten milliliters of the odorless or the flavored broth was given to each subject as a test sample using a disposable cup. The broth was heated to 60 °C. The stimuli and concentration were chosen on the basis of psychophysical tests performed on a panel of subjects. All of the stimuli were diluted and delivered in deionized water.

Attributes. To develop a vocabulary suitable for describing the aroma and taste integration of the broth solutions before the sensory evaluation, the panelists were presented with the odorless broth and a dried-bonito broth. They collaboratively discussed and reached a consensus on attributes to be used for their descriptive evaluations of the dried-bonito broth: three attributes to describe the complex flavor (thickness, consonance, and complexity) and two attributes for the taste and aroma intensity (umami intensity, aroma intensity) and overall palatability. A set of the odorless broth and the dried-bonito broth was presented to the panelists at the same time. The panelists were then requested to rate the perceived relative intensity of six attributes. The following labels were attached to the scale at equal distances (from left to right): for intensity, very weak, weak, somewhat weak, neither weak nor strong, somewhat strong, strong, very strong; for thickness, very thin, thin, somewhat thin, neither thin nor thick, somewhat thick and deep, thick and deep, very thick and deep; for consonance, very inconsonant, inconsonant, somewhat inconsonant, neither inconsonant nor consonant, somewhat consonant, consonant, and very consonant; for complexity, very simple, simple, somewhat simple, neither simple nor complex, somewhat complex, complex, very complex; for palatability, very unpalatable, unpalatable, somewhat unpalatable, neither unpalatable nor palatable, somewhat palatable, palatable, very palatable. The perceived relative intensity of the six attributes was scaled using a 14 cm long line with −3 for weak on the left and +3 for strong on the right side. Booths were set in the room, and each panelist was separately assigned to a booth to avoid influencing on another.

Experimental Procedure. Each panelist took part in one or two sessions. The single session was divided into parts (Figure 1A). The first was a test condition that consisted of a flavored broth stimulus (task) after a conditional odorless broth stimulus as a baseline task. The second part was a control condition that consisted of two identical odorless broth stimuli for baseline task and for task. The two-session procedure consisted of a congruent session, which used the reconstituted flavored broth and the odorless broth, and an incongruent session, which used the nonsmoky flavored broth and the odorless broth. Before each condition, the panelists performed a practice trial using the odorless broth as a known sample to gain familiarity with the tasting procedure in the sensory evaluation task as well as to gain intraoral familiarity with the broth. After confirmation of consensus on rating for the six attributes to be used for the evaluations of the odorless broth, each day's experiments started. At the beginning of each day, the session schedule was explained. After the optodes were placed on each subject's head, the subject was ready to begin the sensory evaluation task. Each condition consisted of sequential periods of a 60 s rest before the task, a 30 s task, and a 60 s rest after the task. At time 0, we asked the resting subject to start the task. The subject would then pick up the cup, drink the given sample solution, and place the cup back on the desk. The subject would finish swallowing by 5 s after starting and then concentrate on the sensory evaluation. After the 30 s task, the subject rested for 60 s. After each task, the subject completed a sensory evaluation questionnaire for the given sample. All of the samples were given to the subjects as unknown ones.

Optical Imaging. Optical imaging was conducted with the ETG-4000 Optical Topography System (Hitachi Medical Co., Tokyo, Japan) using a 3 × 11 optode set (16 photodetectors and 17 light emitters) with a total of 52 channels (Figure 2). Near-infrared laser diodes with two wavelengths (695 and 830 nm) were used as light emitters. Reflected lights were received by the detectors located 30 mm from the emitters. The optodes, which were mounted on a flexible cap, were carefully positioned on each subject's head such that the position was similar for all subjects. This configuration enabled us to detect signals simultaneously from the 52 channels that covered a 60 × 300 mm^2 frontal and temporal area of the head in both hemispheres and also completely covered the measurable areas for blood supply presumed to flow to the parotid gland.[13] Signals reflecting the relative changes to oxygenated hemoglobin concentration ([oxyHb]) and deoxygenated hemoglobin concentration ([deoxyHb]) were recorded from a starting baseline. The lowest center photodiode was located in the Fpz according to the international 10/20 system for electroencephalography (EEG) (Figure 2).

Data Analysis. The waveform of [Hb] changes in all 52 channels under the two conditions of tasks was calculated for each of the subjects. Because [oxyHb] correlates with saliva volumes,[13] we used the [oxyHb] changes as a measure of salivary hemodynamic signals. The mean [oxyHb] changes during the 30 s task for each channel were calculated for the subjects. To access the responses induced by the added aroma components, the responses to the flavored broth were

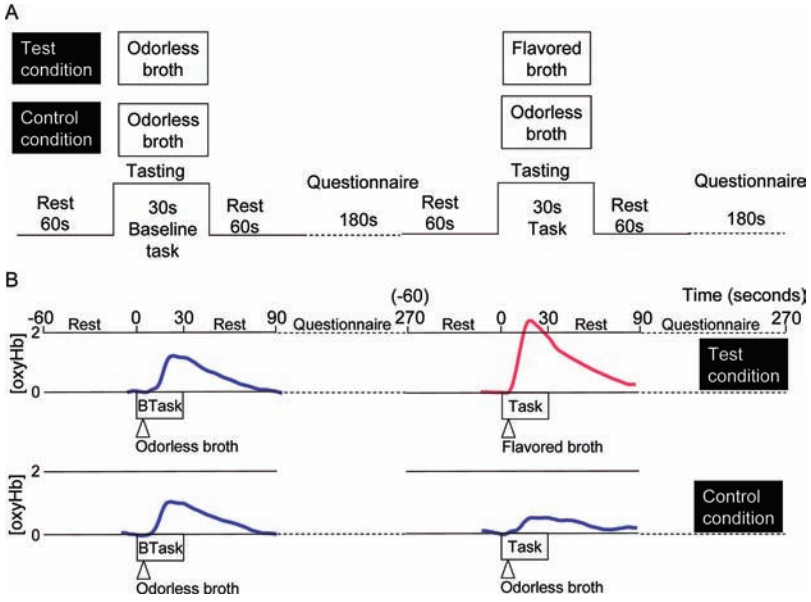

Figure 1. Experimental design and examples of a series of [oxyHb] responses. (A) Experimental design for one session for two days. The first session was a test condition that consisted of a flavored broth stimulus (task) after a conditional odorless broth stimulus as a baseline task. The second part was a control condition that consisted of two identical odorless broth stimuli for baseline task and for task. (B) Examples of a series of [oxyHb] responses recorded from a single position (channel 51) of a single subject. After a 60 s rest, the conditional odorless broth was given to the subject, and [oxyHb] response was recorded (blue trace) for the baseline task (BTask). After the 30 s task, the subject rested for 60 s and then engaged in a sensory evaluation questionnaire for the given sample for 180 s. The subject then started the task, and [oxyHb] response was recorded for the flavored broth in the test condition (red trace) and for the odorless broth in the control condition (blue trace).

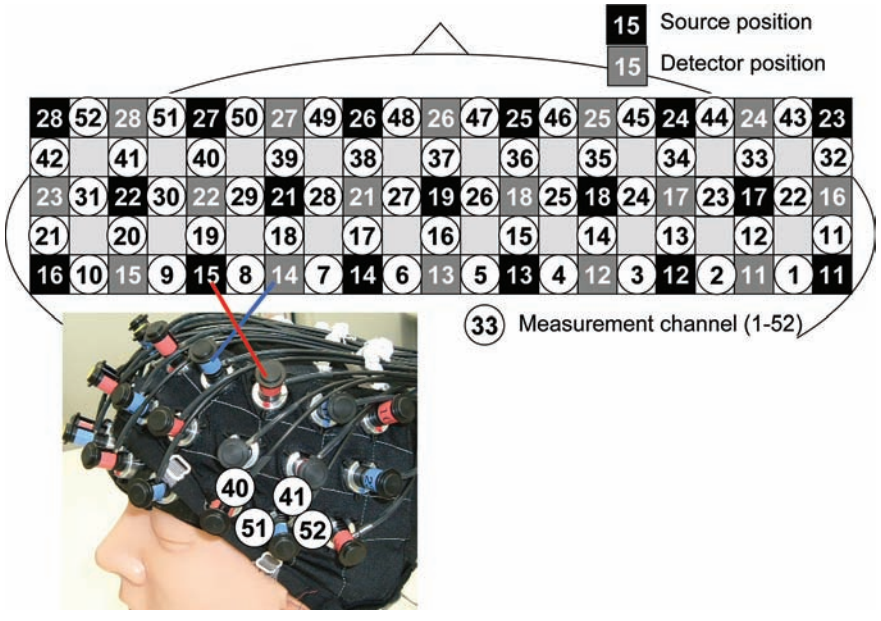

Figure 2. Schematic illustration of the multichannel array (52 channels, 3 × 11 grid) with location of photodetectors, light emitters (sources), and measurement points (channels). Channels 1−52 are depicted as white circles and located between photodetectors and light emitters, which are shown as black and gray squares, respectively.

compared to the baseline task (the conditional odorless broth stimulus) in the test condition and statistically analyzed relative to those from the repeated odorless broth stimuli in the control condition. The mean relative values of [oxyHb] during the 30 s task of some focused channels (channels 40, 41, 51, and 52 (left location) and channels 33, 34, 43, and 44 (right location)) were compared using repeated-measure analysis of variance (ANOVA) with the "stimulus" (test flavored condition and control odorless condition) and "probe location" (right and left) as the independent variables in each session. The statistical analyses were performed using SPSS (version 20.0J).

RESULTS AND DISCUSSION

Behavioral Data. Ten subjects were classified into two groups according to their answers on the sensory evaluation of the flavored broth. One group included five subjects who felt that the combination of the reconstituted aroma and the broth tastes was congruent (congruent group). The other included the remaining five subjects who did not observe such congruency (not-congruent group) (Figure 3A). Although the same flavored broth was given

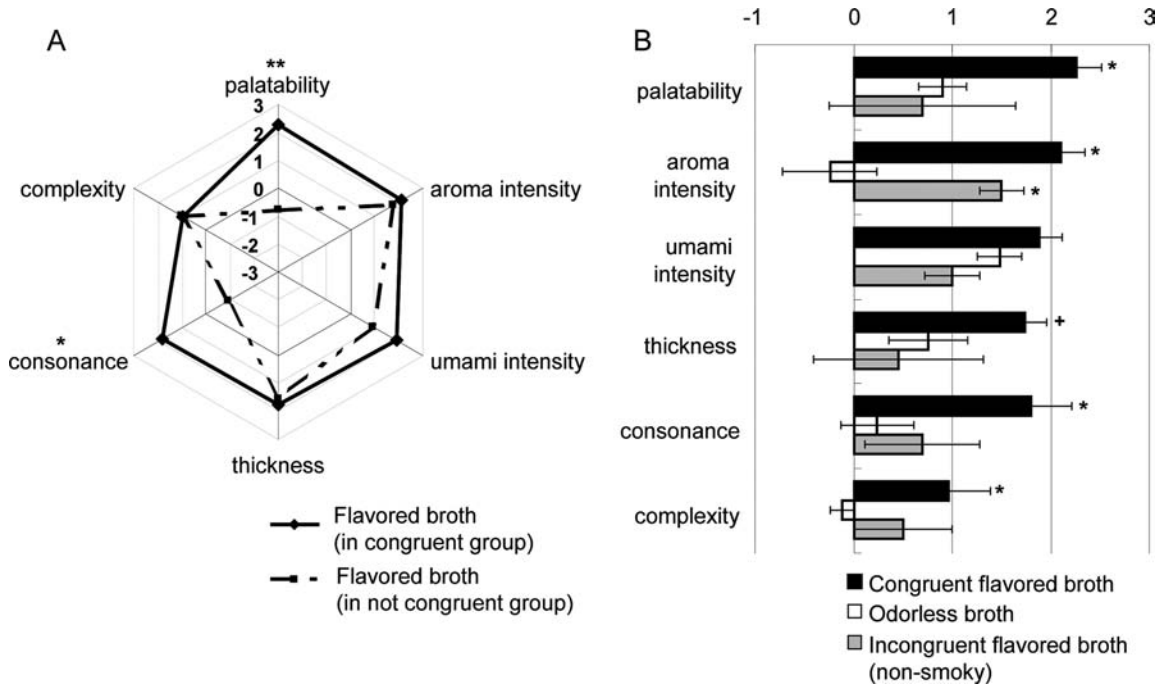

Figure 3. Subjects in the congruent group and not-congruent group show distinct sensory evaluation of the effect of adding dried-bonito aroma constituent on the broth taste. (A) A spider-web diagram represents the differences in mean scores of each descriptor of the flavored broth between groups (solid line, subjects of the congruent group; broken line, subjects of the not-congruent group) with the scale ranging from −3 to +3. The scores were compared with each other (**, $p < 0.01$; *, $p < 0.05$, Mann−Whitney's U test). (B) Mean scores ± SEM of each descriptor of the congruent flavored broth (black square) in the test condition were compared to those from the odorless broth (white square) in the paired control condition (*, $p < 0.05$; +, $p < 0.1$, Mann−Whitney's U test) in subjects of the congruent group in panel A. Those from the incongruent nonsmoky flavored broth (gray square) were compared to those from the paired odorless broth in the control condition (*, $p < 0.05$; +, $p < 0.1$, Mann−Whitney's U test).

to all 10 subjects, the congruent group responded with significantly higher rating for palatability and consonance of the flavored broth than the other group (Figure 3A). The congruent group completed another session using an incongruent, nonsmoky flavored broth as the flavored broth. A comparison of mean ratings revealed that the aroma intensities of both flavored broths (in the presence and absence of smoky aroma parts) were significantly greater than that of the odorless broth (Figure 3B), which suggests that the panelists sensed both the congruent dried-bonito-like aroma and the incongruent aroma well. On the other hand, the palatability, consonance, and complexity of the congruent flavored broth were significantly greater, and the thickness tended to be greater than those of the odorless broth, although no significant differences were found for these descriptors between those of the incongruent and the odorless broths (Figure 3B). Therefore, the congruent flavoring not only added dried-bonito-like aroma to the odorless broth but also enhanced the total flavor and improved palatability for subjects who perceived such congruency.

Optical Imaging of Salivary Hemodynamic Responses. The ten subjects displayed distinctive bilateral increases in [oxyHb] accompanied by decreases in [deoxyHb] in response to both the odorless and the flavored broth stimuli. An example of the hemodynamic responses to two odorless broth stimuli in the control condition is shown in the lower panel of Figure 1B. The upper panel of Figure 1B shows the response to the odorless broth stimulation followed by the response to flavored broth stimulation in the test condition. Figure 4 shows a grand average of the hemodynamic responses ([oxyHb], [deoxyHb]) to the flavored broth with the conditional responses to the odorless broth in the test condition for the five subjects in the congruent group. The largest and long-lasting [oxyHb] increases were found on the right temple region at channel 44 and on the left temple region at channel 51, with a peak latency at about 25 s and then a gradual return to the baseline. The patterns of such hemodynamics around channels 51 and 44 coincided with the reported salivary hemodynamic responses, which are speculated to be generated by the increased blood supply to the parotid gland.[13] We thus focused on responses around channels 51 and 44, and gave particular attention to [oxyHb] in channels 40, 41, 51, and 52 (left location) and channels 33, 34, 43, and 44 (right location).

To assess the effect of the added aroma, we addressed the question of whether the magnitudes of the responses differed in the presence and absence of the aroma constituents at these eight channels. The averaged values of the four channels in the left and right locations, respectively, for the mean relative [oxyHb] changes to the flavored broth when compared to the baseline task were compared to those from the repeated odorless broth stimuli in the control condition. For the statistical analysis, the mean relative values of [oxyHb] were compared using a 2 (stimulus: odorless and flavored broth) × 2 (probe location: right and left) ANOVA. This ANOVA showed a significant main effect of the flavor addition in the five subjects in the congruent group ($F(1,4) = 21.93$, $p = 0.009$). In striking contrast, no significant effect of the flavor addition was found in the not-congruent group (main effects of stimulus ($F(1,4) = 0.03$, $p = 0.87$) and probe location ($F(1,4) = 1.73$, $p = 0.26$)) (Figure 5).

The congruent dried-bonito aroma constituents clearly enhanced the responses to the odorless broth bilaterally for subjects who perceived congruency in the combination of

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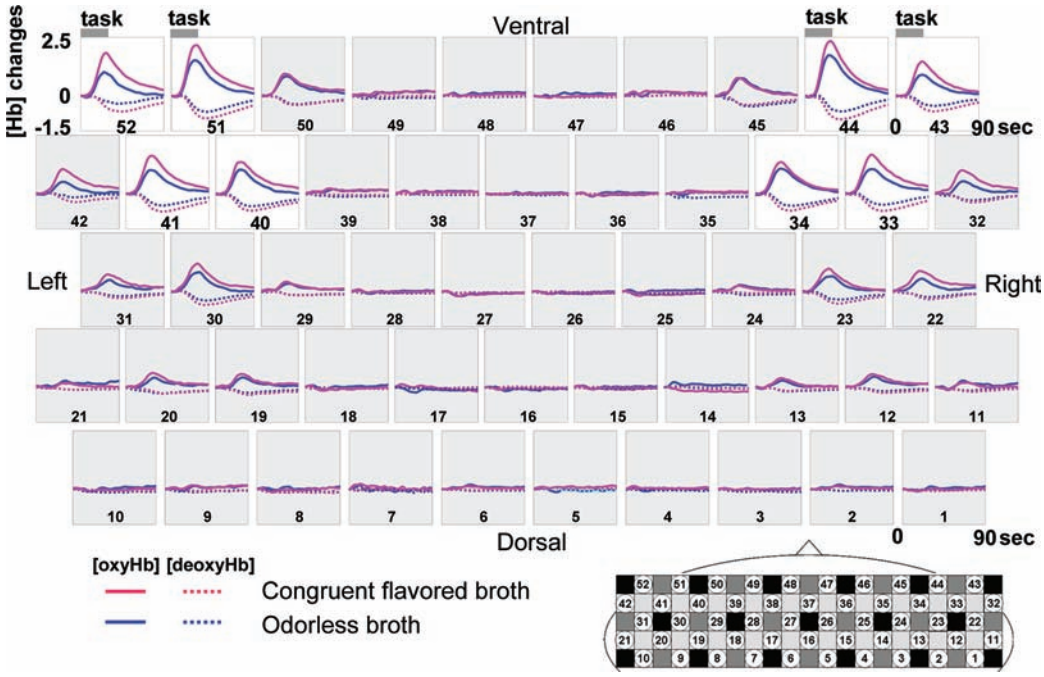

Figure 4. Grand averaged waveforms of oxygenated and deoxygenated hemoglobin concentration ([oxyHb] (solid lines) and [deoxyHb] (broken lines), respectively, for all channels plotted as [Hb] changes (mM·mm) versus time (s) in the test condition to the congruent flavored broth (red line) and to the conditional odorless broth during the baseline task (blue line), respectively. For each channel, the horizontal scale indicates seconds ranging from 0 to 90 and the vertical scale indicates mM·mm ranging from −1.5 to 2.5. The numbers superimposed on the forehead indicate the channel numbers. The task period from 0 to 30 s is marked above the channels.

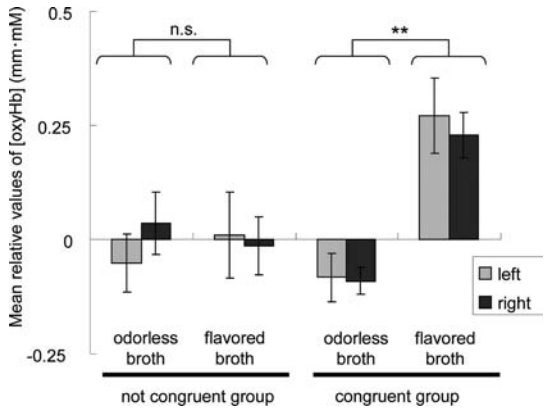

Figure 5. Subjects of the congruent group show significantly greater salivary hemodynamic responses to flavored broth than the odorless broth. Mean relative values ± SEM of [oxyHb] for the flavored broth and the odorless broth were compared to the baseline task in two groups (five panelists who felt the flavored broth was congruent (congruent group) and the remaining five who did not feel such congruency (not-congruent group): black bars, averages of mean relative values from four channels of right position; gray bars, those from left position). A 2 (stimulus: odorless and flavored broth) × 2 (probe location: right and left) ANOVA for the mean relative values of [oxyHb] in each group was conducted (**,$p < 0.01$; n.s. indicates not significant).

aroma and taste. Because the activation of salivary glands is under the control of central integration of olfactory and gustatory information of foods in the brain,[17−19] the salivary hemodynamic responses measured by the NIRS seem to be a useful indicator of the central evaluation of foods. Interestingly, the dried-bonito aroma constituents had little effect on the responses for subjects who did not observe such congruency. These results indicate an important correlation between the subjective sensory evaluation of the effect of dried-bonito aroma on broth taste and its objective evaluation by measuring the change in hemodynamic response accompanying saliva secretion. The present results suggest that the congruent aroma affected the neural representation of flavor, especially central taste and aroma integration, which may differ from person to person, resulting in enhanced or nonenhanced, taste-related hemodynamic responses, which could be accompanied by saliva secretion. These results raise the possibility that the recordings of salivary hemodynamic signals in each person using NIRS provide us a useful objective measurement of the influence of aroma on the taste of foods and drinks in general.

Congruent Aroma Affect Salivary Hemodynamic Responses. The flavored broth produced a greater increase in the salivary hemodynamic response than did the odorless broth in the congruent group. Then to assess whether the specific congruent aroma of dried bonito affected the responses, responses to the nonsmoky flavored broth were measured as an incongruent session in the same five subjects who showed the enhancement of salivary hemodynamic responses by the congruent aroma.

A comparison of the responses to the incongruent nonsmoky flavored broth with those to the odorless broth by a 2 (stimulus: odorless and nonsmoky flavored broth) × 2 (probe location: right and left) ANOVA revealed no significant effects of the incongruent flavor addition ($F(1,4) = 0.12$, $p = 0.75$) as well as probe location ($F(1,4) = 1.30$, $p = 0.32$) (Figure 6). Figure 7 shows the differences in salivary hemodynamic signals to the congruent and the incongruent flavored broths before subtraction of those at the baseline task. These results indicate that the specific congruent dried-bonito aroma significantly enhanced the salivary hemodynamic response to the odorless broth in the subjects who perceived a congruency of aroma/taste interaction, which was possibly due to their personal food consumption experiences.

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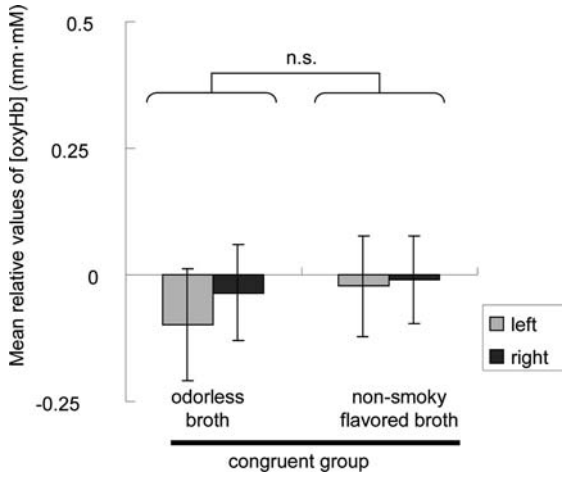

Figure 6. Mean relative values ± SEM of [oxyHb] for the nonsmoky incongruent flavored broth and the odorless broth compared to the baseline task in the congruent group who felt the reconstituted flavored broth was congruent in Figure 5 (black bars, averages of mean relative values from four channels of right position; shaded bars, those from left position). The ANOVA showed no significant effect adding nonsmoky incongruent flavor.

The present results also showed that when the smoky aroma, one of the important parts of the dried-bonito aroma, was removed from the flavoring, the reconstituted flavoring did not enhance the salivary hemodynamic response to the broth in the congruent group. This observation raises the possibility that the measurement of the salivary hemodynamic responses in the congruent group by NIRS can be used to identify particular aroma compounds that are responsible for the increased salivary hemodynamic response to taste stimuli of foods. In pursuing the application of this method in the identification of aroma compounds effective in enhancing the taste response, it would be necessary to consider that, in addition to aroma and taste, a number of component sensory modalities likely contribute to the detected salivary hemodynamic responses during the task, including water sensation and oral tactile and thermal sensations. Further studies would be necessary to determine the contribution of each sensory modality to the salivary hemodynamic responses.

Using NIRS, we measured salivary hemodynamic signals to the flavored broth while subjects sensorily evaluated the flavored broth under the natural setting. Large and long-lasting responses to the flavored and nonflavored broth stimulation were recorded during the sensory evaluation task bilaterally around the temple regions where the previous study showed hemodynamic responses to taste that accompany saliva secretion.[13] The majority of detected [oxyHb] responses using NIRS are thought to be generated by the increased blood supply to the parotid gland that accompanies the saliva secretion.[13] Although the hemodynamic responses of neocortical vessels might contribute to the detected [oxyHb] responses,[20−22] a functional MRI study indicates that the major responses originate extracranially and presumably from blood supply to the parotid grand.[13]

In addition, it would be necessary to the use precise methods for saliva collection to directly show the correspondence between the [Hb] response and parotid gland function. These methods include a putative method to measure the change in weight of tasted solution or a direct measurement method using a Lashley cup.[23] However, expelling the tasted sample, for example, is thought to induce an unnatural setting. In the present study, we thus focused on the differences in responses to the congruent and incongruent flavored broth stimuli when compared to the baseline task, with all tasks completed close together, per the norm in sensory evaluation. In addition, because taste stimuli affect salivation,[24−27] the base tastes of all of the stimuli were fixed to the same odorless broth throughout the experiments. Under our experimental condition, NIRS is thought to be sensitive enough to detect the differences in responses to the congruent and incongruent flavored broths, depending upon the degree of congruency that the subjects acquired from their previous experiences.

In summary, we have demonstrated that NIRS is a useful tool for detecting bilateral activation of salivary gland in response to flavored broth taste, which presumably correlates with the personal evaluation of the broth flavor. NIRS seems to be sensitive enough to detect the differences in quality of aroma in combination with tastes. These results indicate that the specific

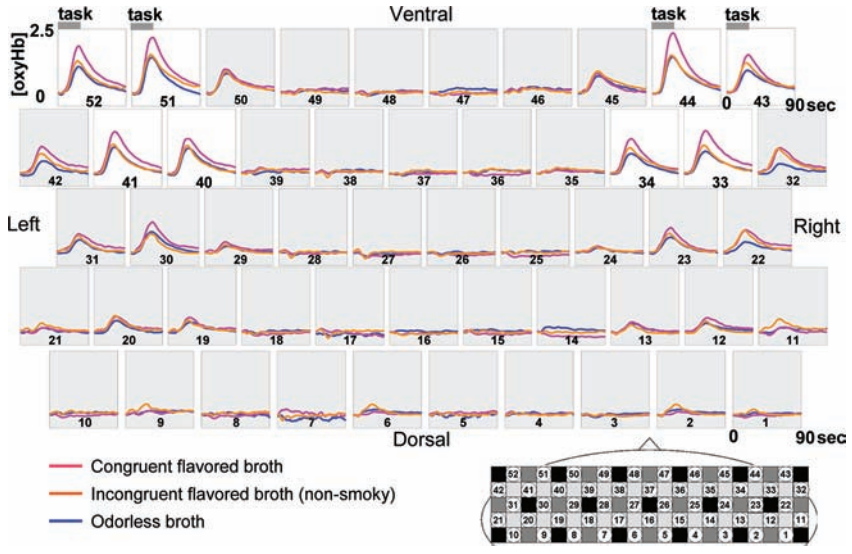

Figure 7. Distinct salivary hemodynamic responses to the congruent and the incongruent flavored broth in the congruent group. The red line indicates the grand average waveforms of [oxyHb] to the congruent flavored broth in the test condition shown in Figure 4, and the blue line indicates those to the odorless broth in the paired control condition. The orange line indicates those to the incongruent nonsmoky flavored broth in the incongruent session. For each channel, the vertical scale indicates mM·mm ranging from −0.5 to 2.5. Other descriptions are the same as in Figure 4.

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congruent mixtures of the reconstituted aroma components of dried-bonito broth enhance the taste-related hemodynamic responses, which could be accompanied by saliva secretion. The optical imaging of the responses provides a means to detect the influence of added aroma components on tastes, resulting in a means to detect the multisensory interaction of aroma and taste on the basis of the perceptual experience of the combination. It is still not clear how the brain functions in relation to the perception of flavor. However, the method of recording salivary hemodynamic responses to various foods with flavors by NIRS may help improve their perceptual quality.

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ABBREVIATIONS USED

NIRS, near-infrared spectroscopy; MSG, monosodium glutamate; IMP, inosine 5′-monophosphate; EEG, electroencephalography; [oxyHb], oxygenated hemoglobin concentration; [deoxyHb], deoxygenated hemoglobin concentration; ANOVA, analysis of variance; MRI, magnetic resonance imaging; SEM, standard error of the mean.

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