

## The Representation of the Human Oral Area in the Somatosensory Cortex: a Functional MRI Study

Jun J. Miyamoto<sup>1,2</sup>, Manabu Honda<sup>1,3</sup>, Daisuke N. Saito<sup>1</sup>, Tomohisa Okada<sup>1</sup>, Takashi Ono<sup>2</sup>, Kimie Ohyama<sup>2</sup> and Norihiro Sadato<sup>1,4,5</sup>

<sup>1</sup>Division of Cerebral Integration, National Institute for Physiological Sciences, Okazaki 444-8585, Japan, <sup>2</sup>Maxillofacial Orthognathics, Graduate School, Tokyo Medical and Dental University, Tokyo 113-8549, Japan, <sup>3</sup>SORST, Japan Science and Technology Agency, Kawaguchi 332-0012, Japan, <sup>4</sup>RISTEX, Japan Science and Technology Agency, Kawaguchi 332-0012, Japan and <sup>5</sup>Department of Functional Neuroimaging, Faculty of Medical Sciences, University of Fukui, Fukui, 910-1193, Japan

**The tactile sensation of the teeth is involved in various oral functions, such as mastication and speech. Using functional magnetic resonance imaging, we investigated the cortical sensory representation of the oral area, including the teeth. First, we identified the somatotopic representation of the lips, teeth and tongue in the postcentral gyrus (Gpoc). Tactile stimuli were applied to the lower lip, tongue and teeth. The foci activated by each stimulus were characterized by the center of gravity (COG) of activated areas. Secondly, we examined the rostro-caudal changes in the somatotopic organization in the Gpoc in terms of the overlap between each sensory representation. In the rostral portion of the Gpoc, the COG of the representation of teeth was located significantly superior to that of the tongue and inferior to that of the lip, consistent with the classical 'sensory homunculus' proposed by Penfield; however, this somatotopic representation became unclear in the middle and caudal portions of the Gpoc. The overlap between each representation in the middle and caudal portions of the Gpoc was significantly greater than that in the rostral portion of the Gpoc. These findings support the theory that the input from oral structures converges hierarchically across the primary somatosensory cortex.**

**Keywords:** fMRI, oral area, postcentral gyrus, somatosensory cortex, teeth representation

### Introduction

When one bites into a fresh apple, one can control the optimal force of the movement of the jaws and perceive its crispy texture through the sensory information arising from the teeth. Such information, especially from periodontal mechanoreceptors, is important in controlling biting behavior. Moreover, it provides feedback information during the initial contact with food in the chewing cycle and other manipulations involving the teeth; for example, while food is positioned and held prior to biting (Trulsson and Johansson, 1996). Periodontal afferents play an important role not only in the discrimination of interdental size or thickness (Morimoto, 1990; Jacobs and van Steenberghe, 1994) but also in the reflexes of the masticatory muscles, bite-force sensation (van Steenberghe, 1979; Linden, 1990) and oral stereognosis (Jacobs *et al.*, 1997). Although there are several human studies of peripheral tooth sensation (Trulsson *et al.*, 1992; Trulsson and Johansson, 1994, 1996, 2002), few have investigated tactile tooth sensation at the cortical level. Penfield and Rasmussen (1950) investigated human sensory somatotopy intraoperatively. In their study, the representation of the teeth, gingiva and jaws was located below that of the lips and above that of the tongue, and could not be subdivided. Since then, several non-invasive studies of human sensory somatotopy of oral structures have focused on

the postcentral gyrus (Yamashita *et al.*, 1999; Lotze *et al.*, 2000b; Nakahara *et al.*, 2004). In these studies, however, the representation of the teeth was not investigated. Human studies using functional neuroimaging are few and their results are inconsistent. Using magnetoencephalography (MEG) with electrical stimulation of the gingiva but not teeth, Nakahara *et al.* (2004) revealed that the dipole evoked by gingival stimulation was in the primary somatosensory cortex, located inferior to that of the lips and close to that of the tongue. Using functional magnetic resonance imaging (fMRI) and painless vibrotactile dental stimulation, Ettlin *et al.* (2004) found activation in bilateral insular cortex and the supplementary motor area; however, they found no activation in the primary somatosensory area. Hence, the representation of the teeth in the primary somatosensory cortex remains to be clarified.

Recently, a hierarchical structure of tactile information processing in the primary somatosensory cortex has been proposed (Iwamura, 1998). While the majority of neurons in area 3b have a receptive field confined to one finger, neurons with receptive fields covering multiple fingers increased towards the caudal portion of the postcentral gyrus (Iwamura *et al.*, 1980, 1983, 1993). This finding suggests that somatosensory information from different body parts can be integrated as they are conveyed caudally in the primary somatosensory cortex.

The purpose of the present study was to clarify the somatotopic organization of the oral area, including the teeth, in the primary somatosensory cortex in humans using fMRI. We studied the cortical organization along two orthogonal directions: ventro-dorsal (inferior-superior) and rostro-caudal. First, we characterized the somatotopic representation in the rostral portion of the postcentral gyrus (Gpoc) along the ventro-dorsal axis using the centers of gravity (COGs) of the activated areas induced by the tactile stimuli of teeth, lips and tongue. Secondly, we investigated how this somatotopic organization changes along the rostro-caudal axis in the Gpoc by locating the COGs and the overlap of activated areas of cortex. To address how this overlap changes, we classified the activated voxels in the Gpoc into two types: simple receptive field (SRF) voxels, which were activated by only one stimulus, and composite receptive field (CRF) voxels, which were activated by more than one stimulus. We then examined how the proportion of SRF and CRF voxels changed with caudal progression in the Gpoc.

### Materials and Methods

#### Subjects

Fourteen healthy volunteers (eight males and six females, mean age = 32.6 years, range 24–56 years) participated in this study. Thirteen

subjects were right-handed and one was left-handed according to the Edinburgh handedness inventory (Oldfield, 1971). None of the subjects had a history of neurological or psychiatric illness. The protocol was approved by the ethical committee of the National Institute for Physiological Sciences, Japan. Before the experiment, the subjects were informed in detail about the nature of the experiment, and gave their written informed consent for the study.

### Sensory Stimulation

Subjects were stimulated at three areas on the right side of the oral area: the lower lip, the tongue and the upper central incisor tooth. Tight, but comfortable, foam padding was placed around each subject's head to minimize any movement. The subjects wore a cheek retractor throughout the scanning period, so that the experimenter could stimulate the specific targeted intra-oral region without touching the surrounding structures.

For lower-lip stimulation, the tactile stimuli consisted of rubbing the lip using a stick with a piece of Velcro at its tip. The contact zone between the lip and the Velcro was ~5 mm wide. The lower lip was stimulated 1 cm to the right of the midline. The stick used for stimulation was fixed on a table that was set on both edges of the scanner bed to avoid it touching the subject's body. The stick was allowed to rotate around its long axis to minimize the possibility of touching the surrounding structures. The oscillating movement of the stick provided oscillating strokes of ~5 mm at the contact zone. The rotation was acoustically cued at a constant frequency of 1 Hz. Using the same settings, the anterior part of the tongue, 1 cm to the right of the midline, was stimulated. The right upper incisor tooth was also stimulated using the stick with a grooved rubber tip which held the tooth (Fig. 1). Oscillating movement of the stick provided torque force to the incisor at a constant frequency of 1 Hz.

Stimulation was provided by the same well-trained experimenter (J.J.M.) to minimize the variability of stimuli across the subjects. The subjects were instructed to remain still and to close their eyes in the scanner during the acquisition of functional scans. Before the experiment, each stimulus was tested in the scanner to confirm that the stimulation was clear and constant, and that the stick was touching only each target area specifically.

### Data Acquisition

The subjects underwent two scanning runs for each target area. Each run consisted of an alternating pattern of three stimulation and four rest periods, each of which was 20 s in duration. In each scanning run, 38 volumes were acquired using T2\*-weighted gradient echo-planar imaging (EPI) sequences using a 3.0 Tesla scanner (Allegra, Siemens, Erlangen, Germany). Each volume consisted of 32 oblique slices, each 3.0 mm in thickness without a gap, which were taken parallel to the



**Figure 1.** Device for tooth stimulation. The subject wore a cheek retractor. The stimulation device consisted of a stick with a grooved rubber at its tip that held the right central incisor. The stick was fixed on a table (not shown).

central sulcus so that the cortical representation of the oral area along the central sulcus could be observed in a single slice. The time interval between two successive acquisitions of the same slice was 4000 ms, with a flip angle (FA) of 90° and 52 ms of echo time. The field of view (FOV) was 192 mm and the in-plane matrix size was 128 × 128 pixels. For anatomical reference, T1-weighted magnetization-prepared rapid-gradient echo (MPRAGE) images (TR = 1460 ms, TE = 4.38 ms, FA = 8°, FOV = 192 mm, matrix size = 256 × 256 pixels, slice thickness = 3 mm) for each subject with the identical location parameters of EPI. In addition, high-resolution 3D T1-weighted MPRAGE (TR = 2500 ms, TE = 4.38 ms, FA = 8°, FOV = 230 mm, matrix size = 256 × 256 pixels, slice thickness = 1 mm) images were obtained for each subject.

### Data Analysis

The first three volumes of each scanning run of functional images were discarded due to unsteady magnetization, and the remaining 35 volumes per run (210 volumes per subject) were used for the analysis. The data were analyzed using statistical parametric mapping (SPM99; Wellcome Department of Cognitive Neurology, London, UK) (Friston *et al.*, 1994, 1995a,b) implemented in Matlab (Mathworks, Sherborn, MA).

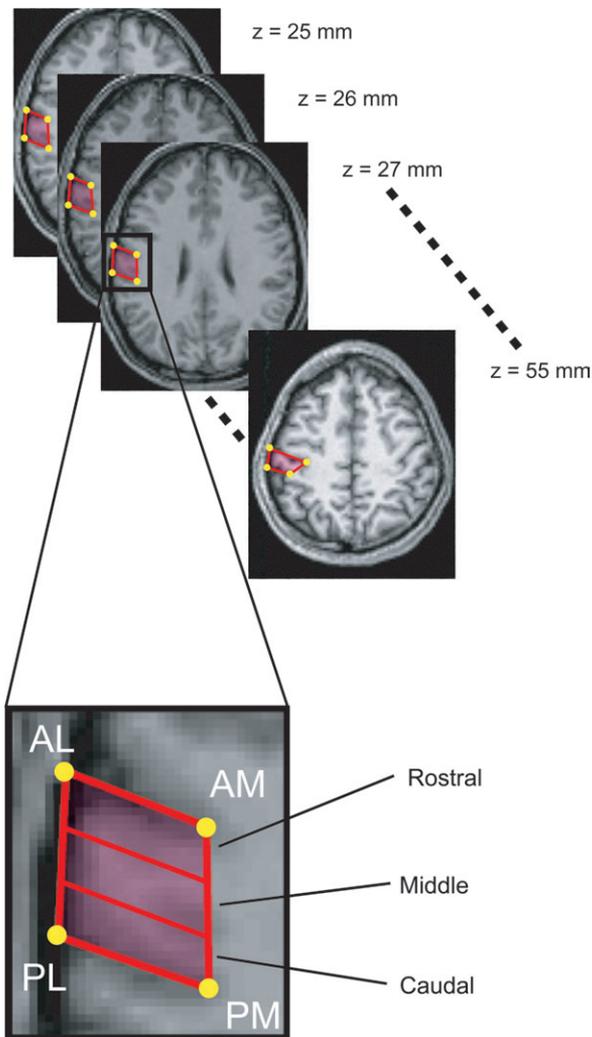
Head motion was corrected with the SPM99 realignment program (Friston *et al.*, 1995a). Following realignment, the high-resolution 3D T1-weighted MRI scans were coregistered to the functional images with reference to the anatomical T1-weighted MRI with the identical location parameters of the functional images. This is because EPIs are T2\*-weighted images with lower resolution, and hence are difficult to coregister with high-resolution 3D T1-weighted images directly. The parameters for affine and nonlinear transformation into a template of T1-weighted images already fitted to standard stereotaxic space (MNI template) (Evans *et al.*, 1994) were estimated with the coregistered high-resolution 3D T1-weighted images by the least-square means (Friston *et al.*, 1995a,b). The parameters were applied to the functional images. No spatial smoothing was applied because the analysis was performed primarily on a single-subject basis. A general linear model was used to identify voxels with stimulus-related signal changes. The stimulation period was modeled using a boxcar function convolved with a hemodynamic response function, and significant correlations between the observed response and the modeled response were estimated, yielding *t*-value maps.

### Region of Interest (ROI) Definition

The ROI of the oral representation was defined in the GPoC contralateral to the stimulated side. The ROI was defined in each axial slice of the normalized high-resolution anatomical image of each individual, which were 1 mm thick (Fig. 2).

First, the superior and inferior margins were defined in the axial slices as  $z = +25$  mm and  $+55$  mm, respectively. The superior margin corresponds to the anatomically defined motor hand areas identified by the anatomical landmark of the inverted-omega sign (Yousry *et al.*, 1997; Ferretti *et al.*, 2003). The motor hand area was used to locate the sensory hand area, which is immediately caudal to it (Jasper *et al.*, 1960; Stohr and Goldring, 1969; Broughton *et al.*, 1981; Allison *et al.*, 1989; Woolsey *et al.*, 1979; Ibanez *et al.*, 1995). Here we assume that the representation of the oral area of the primary somatosensory cortex is located inferior to that of the hand (Penfield and Rasmussen, 1950). The inferior margin ( $z = +25$  mm) was set based on previous studies to exclude activity in the second somatosensory cortex (Ruben *et al.*, 2001; Ferretti *et al.*, 2003). Individual analysis confirmed segregated activation clusters dorsal and ventral to the arbitrary border, corresponding to S1 and S2 respectively.

Secondly, the central and postcentral sulci were identified on the high-resolution anatomical images using standard procedures (Steinmetz *et al.*, 1990) for every slice between  $z = 25$  and 55 mm. Finally, the quadrilateral ROI including the GPoC was defined as follows. The antero-medial and postero-medial vertices of the ROI were defined as the fundus of the central and the postcentral sulci, respectively. The antero-lateral and postero-lateral vertices were defined as the points of intersection of the extension of the two sulci with the tangent to the arc drawn by the lateral margin of the GPoC. The quadrilateral ROI in each axial slice was defined as the enclosed region made by connecting these four points. Moreover, to delineate the changes in somatotopic organization from



**Figure 2.** Region of interest (ROI) defined at the postcentral gyrus. The axial slices from  $z = +25$  to  $+55$  mm of the anatomically normalized high-resolution T1-weighted image of one subject are displayed in the upper row. The lower row shows the quadrilateral ROI on one slice. The ROI in each axial slice was defined as an enclosed region made by connecting four vertices: the antero-medial (AM), postero-medial (PM), antero-lateral (AL) and postero-lateral (PL). Moreover, the ROI was divided into three sub-ROIs (rostral, middle and caudal). The lateral and medial sides of the quadrilateral were trisected, and the points marking 1/3 and 2/3 were connected to define three sub-ROIs.

the rostral to the caudal portion of the GPoC, the ROI was divided into three sub-ROIs (rostral, middle and caudal); the lateral and medial sides of the quadrilateral were trisected, dividing the region into thirds. Note that the voxels that lay outside the quadrilateral ROI were excluded from the analysis automatically by a masking procedure implemented in SPM99. The activated voxels in each stimulus condition within each sub-ROI were defined using SPM99, with a threshold of  $P < 0.05$  without correction for multiple comparisons.

#### Evaluation of the Location of the Sensory Representation

Using the  $t$ -values of all the significantly activated voxels in each sub-ROI, the Talairach's coordinates of the COGs (Lotze *et al.*, 2000a,b) were calculated to evaluate the location of the somatotopic representation of each stimulated site (Table 1). The evaluation of the location was performed in terms of the  $z$  coordinates of the COGs. The location of the COGs was subjected to a repeated-measures analysis of variance (RM-ANOVA), with the two within-subject factors of stimulated site (tongue, tooth and lip) and sub-ROIs (rostral, middle and caudal). Moreover, a separate RM-ANOVA was performed in each sub-ROI with

**Table 1**

The averaged coordinates of the centers of gravity of the cortical activations

Sub-region of interest	Stimulation	Averaged Talairach's coordinates, mm (SE)		
		$x$	$y$	$z$
Rostral	Lip	-55.5 (0.68)	-11.3 (0.63)	41.7 (0.51)
	Tooth	-55.8 (0.69)	-11.0 (0.60)	40.4 (0.59)
	Tongue	-57.1 (0.52)	-9.8 (0.65)	38.5 (0.74)
Middle	Lip	-58.3 (0.62)	-16.0 (0.68)	39.4 (0.65)
	Tooth	-57.6 (0.77)	-16.1 (0.68)	39.4 (0.36)
	Tongue	-58.1 (0.73)	-15.4 (0.86)	38.2 (0.53)
Caudal	Lip	-58.0 (0.50)	-21.2 (0.91)	39.1 (0.53)
	Tooth	-56.7 (0.50)	-22.2 (0.89)	40.8 (0.52)
	Tongue	-57.9 (0.49)	-21.1 (0.85)	39.1 (0.57)

stimulated site (tongue, tooth and lip) as the within-subject factor. In addition, our analysis was based on the hypothesis proposed by Penfield and Rasmussen (1950) that the representation of the teeth is located significantly superior to that of the tongue and inferior to that of the lip. Linear contrasts were used to compare the COGs of the tongue and lip representations against the representation of the tooth.

#### Evaluation of the Overlap of Sensory Representations

To evaluate the overlap of the cortical activations elicited by the three stimulated oral areas, SRF and CRF voxels were defined as the voxels activated by only one stimulus condition and by two or three stimulus conditions, respectively.

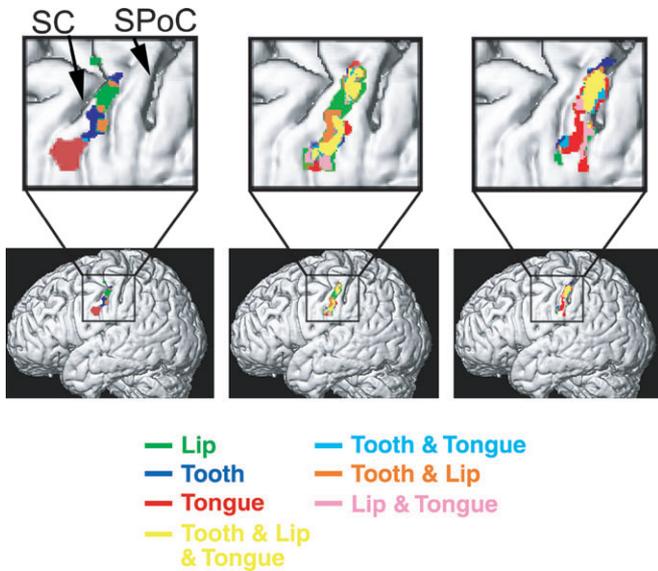
The proportion of the number of the CRF voxels to the number of total voxels activated by at least one stimulus condition was calculated in each sub-ROI and subjected to an RM-ANOVA with sub-ROI (rostral, middle and caudal) as the within-subject factor. Pairwise comparisons using linear contrasts were also performed to contrast rostral versus middle, and middle versus caudal. This was based on the idea that neurons in the GPoC with multiple receptive fields increased with a caudal progression, as shown in a previous animal study (Iwamura, 1998). In addition, to investigate whether this tendency was observed consistently for each different representation, we calculated separately the proportion of the number of CRF voxels activated by a particular stimulus condition to the number of total voxels activated by this particular stimulus condition; this was then subjected to an RM-ANOVA with two within-subject factors [sub-ROIs (rostral, middle and caudal) and stimulus site (tongue, tooth and lip)]. Pairwise comparisons using linear contrasts were also performed between the rostral and middle, and the middle and caudal, sub-regions.

#### Results

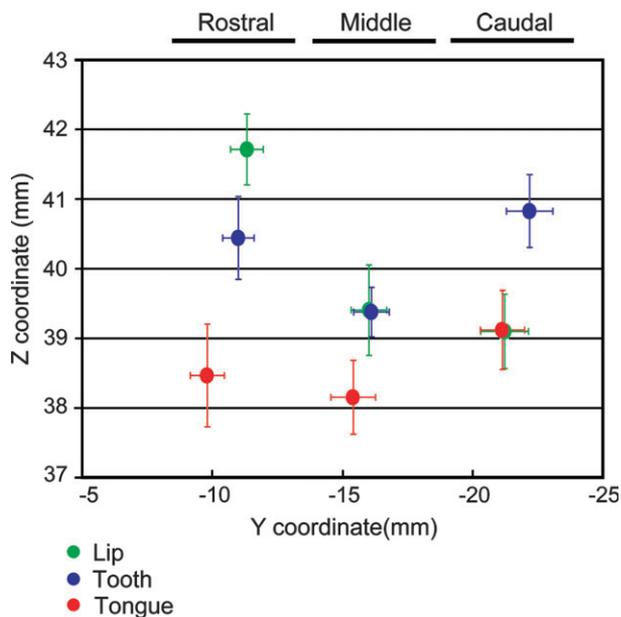
Typical individual data are shown in Figure 3. The activated foci during tooth stimulation were located between those for the tongue and lip, and were separated in the rostral portion of the GPoC, whereas they merged together in the caudal portion.

#### Location of Sensory Representation

In the rostral portion of the GPoC, the COG of the tooth representation was located between those for the lip and tongue, consistent with the 'sensory homunculus' (Penfield and Rasmussen, 1950). In the middle and caudal regions, however, this arrangement of COGs was less clear (Fig. 4). The RM-ANOVA for the entire data set of COG locations revealed significant main effects of stimulus site [ $F(2,26) = 4.796$ ,  $P = 0.017$ ] and sub-ROIs [ $F(2,26) = 12.885$ ,  $P < 0.001$ ], and their interaction [ $F(2,26) = 7.059$ ,  $P < 0.001$ ]. Separate RM-ANOVAs in each sub-ROI revealed significant main effects of stimulus site in the rostral [ $F(2,26) = 14.449$ ,  $P < 0.001$ ], middle [ $F(2,26) = 5.099$ ,  $P = 0.014$ ] and caudal [ $F(2,26) = 6.654$ ,  $P = 0.005$ ] regions. In the rostral portion of the GPoC, the comparison of the tongue and lip locations compared with the tooth location using the



**Figure 3.** The cortical representations in a typical subject. Activated foci induced by the lip (green), tooth (blue) and tongue (red) stimuli were rendered on the surface of the high-resolution image for this subject. In the rostral portion near the central sulcus (left), the activated clusters were more distinct from each other than in the caudal region near the postcentral sulcus (right). This figure was produced by filtering the functional images using an isotropic Gaussian kernel of 4 mm (full width at half maximum) for display purposes. SC, central sulcus; SPoC, postcentral sulcus.



**Figure 4.** The averaged coordinates of the centers of gravity (COGs) of the cortical activations. The z coordinates in Talairach's space (Talairach and Tournoux, 1988) of the COGs of the foci activated by each stimulus were plotted against the corresponding y coordinates. Data represent the averaged COG coordinates  $\pm$  SE across the subjects. The plots represent the lip-, tooth- and tongue-stimulation conditions (shown in red, green and blue, respectively). The COG of the tooth was located significantly superior to that of the tongue and inferior to that of the lip in the rostral region. However, this arrangement was not observed in the middle and caudal portions.

linear contrasts revealed the location of the tongue was significantly inferior to that of the tooth [ $F(1,13) = 7.588, P = 0.016$ ] and the location of the lip was significantly superior to that of the tooth [ $F(1,13) = 5.742, P = 0.032$ ]. In the middle portion, the comparison using the linear contrasts revealed that

the COG of the tongue was located significantly inferior to that of the tooth [ $F(1,13) = 7.335, P = 0.018$ ] but was not different from that of the lip [ $F(1,13) = 0.003, P = 0.954$ ]. In the caudal portion, the COG of the tooth was significantly superior to that of the tongue [ $F(1,13) = 11.628, P = 0.005$ ] and lip [ $F(1,13) = 8.819, P = 0.011$ ].

### Overlap of the Sensory Representations

The proportion of the CRF voxels increased gradually in the rostral-to-caudal direction (Fig. 5). The RM-ANOVA revealed significant main effects of sub-ROIs [ $F(2,26) = 6.154, P = 0.006$ ], and the pairwise comparison using linear contrasts revealed a significant increase from the rostral to the middle portion [ $F(2,26) = 7.629, P = 0.016$ ], although no significant increase was observed from the middle to the caudal regions [ $F(2,26) = 1.733, P = 0.211$ ]. The proportion of CRF voxels in each stimulus condition also increased gradually in the rostral-to-caudal direction (Fig. 6): the RM-ANOVA revealed significant main effects of sub-ROIs [ $F(2,26) = 7.134, P = 0.003$ ], but neither a significant main effect of stimulus site nor an interaction between sub-ROIs and stimulus site. Pairwise comparisons using linear contrasts revealed a significant increase from the rostral to middle regions for the tooth [ $F(1,13) = 6.286, P = 0.026$ ], the lip [ $F(1,13) = 8.378, P = 0.013$ ] and the tongue [ $F(1,13) = 7.663, P = 0.016$ ] conditions. However, no significant increase was found from the middle to caudal regions for the tooth [ $F(1,13) = 0.652, P = 0.434$ ], the lip [ $F(1,13) = 1.858, P = 0.196$ ] and the tongue [ $F(1,13) = 1.344, P = 0.267$ ] conditions.

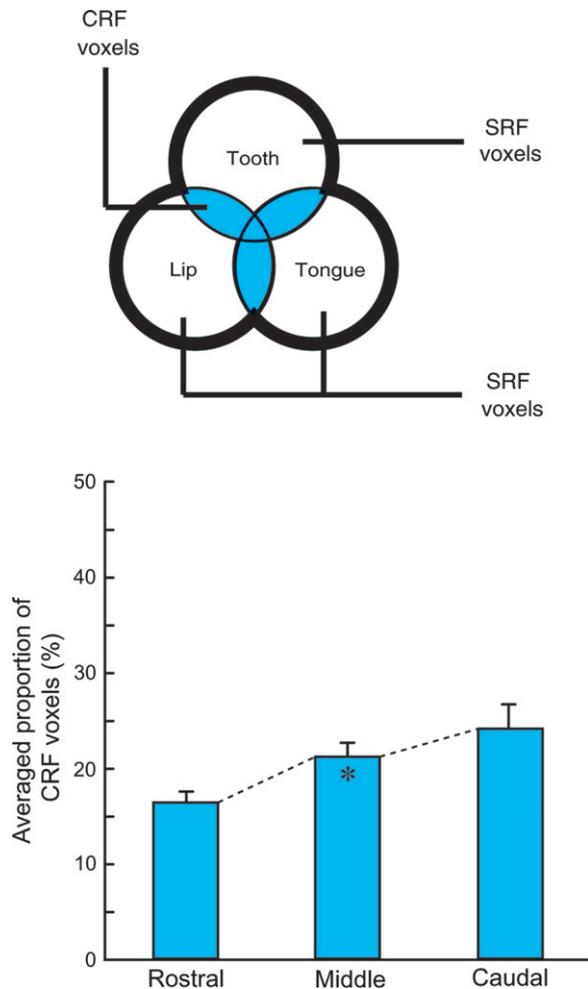
### Discussion

Using tactile stimulation to the oral regions, we showed that the cortical somatosensory representation of the tooth was located superior to that of the tongue and inferior to that of the lip in the rostral portion of the GPOC. This somatotopic organization was less clear in the middle and caudal portions of the GPOC. In addition, the proportion of CRF voxels increased in the rostral-to-caudal direction in all stimulus conditions, suggesting that the sensory representations of different oral regions showed more overlap in the middle and caudal regions than in the rostral portion of the GPOC.

### Somatotopic Representation

We used COGs to evaluate the somatotopic representations of the oral regions. COGs have previously been used for somatotopic mapping of the somatosensory or motor cortex, although the details of the experiments differed (Lotze *et al.*, 2000a,b; Hlustik *et al.*, 2001; Dechent and Frahm, 2003). This is partly because split representations, in which multiple regions were activated by one stimulus, were often observed in somatotopic mapping in non-human primates (Manger *et al.*, 1996). In the present study, we also observed split representations with multiple activated clusters induced by one stimulus (Fig. 3). COGs are useful in such cases to specify the location of the representation.

Brodmann's areas 3a, 3b, 1 and 2 correspond roughly to the fundus of the central sulcus, its posterior bank, the crown of the postcentral gyrus and the anterior bank of the postcentral sulcus, respectively (Geyer *et al.*, 1999, 2000; Grefkes *et al.*, 2001). Thus antero-posterior differences in somatotopic precision revealed by ROI analysis may be partly explained by the differences in underlying cytoarchitectonic structures.

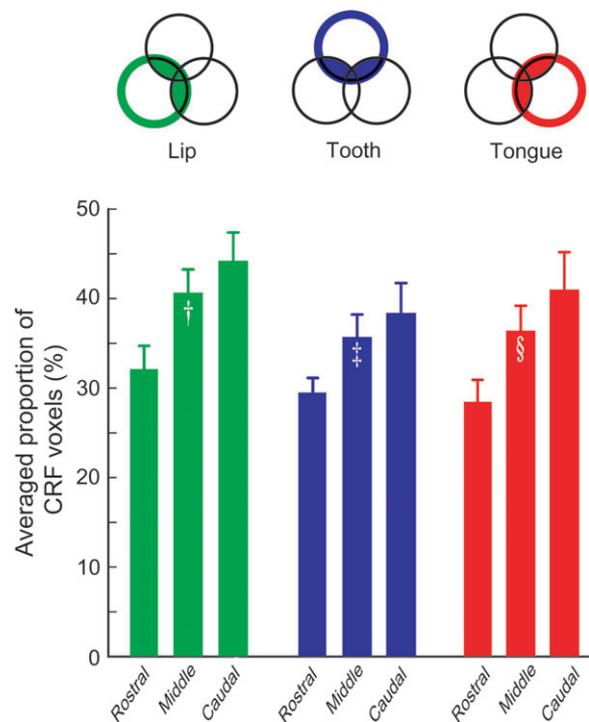


**Figure 5.** The proportion of the number of composite receptive field (CRF) voxels to the number of total voxels that were activated by at least one of three peripheral stimuli within each sub-region of interest (sub-ROI). The differences in the proportion of CRF voxels between the rostral versus middle and the middle versus caudal regions were calculated by pairwise comparisons using linear contrasts. \*A significant increase from the rostral-to-middle portion of the sub-ROI ( $P < 0.05$ ). The data represent averaged percentages of CRF voxels  $\pm$  SE.

The somatotopic organization of the teeth in the rostral portion of GPoC was similar to that reported in non-human primate studies in area 3b contralateral to the stimulated side (Manger *et al.*, 1996; Jain *et al.*, 2001). The present finding is concordant with the ‘sensory homunculus’ (Penfield and Rasmussen, 1950). In Penfield’s study, the subjects verbalized the subjective sensation induced by the electrical stimulation of the cortical surface. By contrast, in the present study, the subjects were given tactile stimuli peripherally and the brain responses were identified objectively using functional images. Although these two studies adopted different approaches, the converging results indicate that the sensory representation of the oral area in the primary somatosensory cortex is organized such that the tongue, teeth and lips are located in the ventral-to-dorsal direction.

#### The Overlap of the Cortical Activations

We found that the proportion of CRF voxels increased in the middle and the caudal regions compared with the rostral portion of the GPoC. These results are consistent with previous



**Figure 6.** The proportion of the number of composite receptive field (CRF) voxels in a particular stimulus condition to the number of total voxels activated by the same stimulus within each sub-region of interest (sub-ROI). The differences in the proportion of CRF voxels between the rostral versus middle, and the middle versus caudal, regions were calculated by pairwise comparisons using linear contrasts. Significant increase from the rostral to the middle portions of the sub-ROI <sup>†</sup>in the lip condition ( $P < 0.05$ ), <sup>‡</sup>in the tooth condition and <sup>§</sup>in the tongue condition, respectively. The data represent the averaged percentages of the CRF voxels  $\pm$  SE.

non-human primate studies regarding the sensory representation of the digits (Iwamura *et al.*, 1980, 1983, 1993) and the oral area (Toda and Taoka, 2001, 2002, 2004). In humans, a non-invasive study of finger representation suggests that a greater number of adjacent activated foci showed greater overlap in areas 1 and 2 than in area 3b, and there was a partial reversal of digit order (Kurth *et al.*, 2000). The present study indicates a similar organization for the representation of oral areas in the primary sensory cortex.

Because of this representational change, a hierarchical scheme for sensory information processing has been proposed such that the somatosensory information from different parts of the body are integrated as they are conveyed from the primary sensory-receiving stage to the more associative stage. For example, areas 3a and 3b receive dense projections from the thalamus and connect to areas 1 and 2 in the GPoC, while areas 1 and 2 receive far fewer projections directly from the thalamus than does area 3 (Jones and Powell, 1970; Jones, 1975; Jones and Burton, 1976). In addition, the latency of the neuronal responses to vibration stimuli was longer in area 2 than in areas 3 or 1 (Lebedev and Nelson, 1996). These results, and those of other human studies (Urbano *et al.*, 1997; Eskenasy and Clarke, 2000), suggest that the larger part of sensory information is conveyed serially via cortico-cortical connections between these areas.

The caudal portion of the GPoC might play an important role in integrating sensory information from various areas and sending it to other cortical regions. Anatomically, area 2 projects to the primary motor cortex (Burton and Sinclair,

1996). Functionally, inactivation of the digit region of area 2 is known to impair hand behavior (Hikosaka *et al.*, 1985), whereas inactivation of area 3b and area 1 did not. Mastication and articulation require multiple oral structures to work cooperatively and mastication is significantly affected by the loss of function of a single oral structure (Trullsson and Johansson, 1996). Hence, we suggest that the rostral-to-caudal progression of the overlap of sensory representations might indicate converging input from oral structures, including the teeth. This hierarchical representation might aid the complex coordinated control of the oral structures.

## Conclusion

To investigate the cortical organization of sensory information processing in humans of the oral region, including the teeth, we used fMRI to observe the activations induced in the primary somatosensory cortex following tactile stimulation of the lip, the incisor tooth and the tongue. The tooth representation, as expressed by the COGs, was located superior to that of the tongue and inferior to that of the lip in the rostral portion of the GPOc. The somatotopic organization of the oral structures was less distinct and showed more overlap in the caudal portion of the GPOc. These results might indicate a hierarchical organization of sensory information processing in the GPOc.

## Notes

This study was supported by Grant-in Aid for Scientific Research S#17100003 (N.S.) from the Japan Society for the Promotion of Science and by a Grant-in Aid for Scientific Research 018#17021045 (N.S.) from the Ministry of Education, Culture, Sports, Science and Technology of the Japanese Government.

Address correspondence to Norihiro Sadato, Division of Cerebral Integration, National Institute for Physiological Sciences, 38 Nishigonaka, Myodaiji, Okazaki 444-8585, Japan. Email: sadato@nips.ac.jp.

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