
Morphological Analyses of the Human Tongue Musculature for Three-Dimensional Modeling

Hironori Takemoto*
Laboratory of Physical
Anthropology
Graduate School of Science
Kyoto University
Kyoto, Japan

Skilled movements of the tongue in speech articulation reflect complex formation of the tongue musculature, although its description in the anatomical literature is rather limited for developing a realistic computational model of the tongue. This study presents detailed descriptions of the muscular structure of the human tongue based on macroscopic and microscopic observations and provides three-dimensional schemata of the tongue musculature. Histologic examination revealed that the tongue consists of five strata, stacked along the courses of the fibers of the genioglossus muscle in proximal-distal directions. This stratum structure exists in the entire tongue tissue, indicating that the lingual musculature can be divided into the inner and outer regions. The former consisted of the "stem" and "core," and the latter of the "cover" and "fringe." In gross dissection, the tongue was cut into wedge-like blocks along the course of the genioglossus muscle to examine muscle fiber arrangement. Using this approach, it was determined that serial repetitions of "structural units" composed the inner musculature of the tongue. Each unit consisted of a pair of thin muscle fiber laminae; one was composed of the genioglossus and vertical muscles, and the other of the transverse muscle. In the apex, the laminae lacked the fibers of the genioglossus. These findings have been incorporated in three-dimensional schemata of the tongue musculature.

KEY WORDS: human tongue muscle, lingual morphology, 3-D model, muscle-fiber lamina, speech production

The tongue, a unique motor organ in the human body, is composed almost entirely of muscle and contains no skeleton. Some of the tongue muscles arise externally from rigid structures, whereas others originate and terminate within the tongue proper. Activities of these muscles result in subtle movements of muscular structure and produce large deformations of the tongue's soft tissues. This property of tissue deformation is often referred to as a muscular hydrostat (Smith & Kier, 1989), indicating its resemblance to the elephant's trunk and the squid's tentacles. The muscular hydrostat in the tongue could be caused by its extremely complex musculature, though this cannot be stated with assurance because complete and precise anatomical descriptions are lacking.

An understanding of the complex organization of the human tongue musculature is a critical requirement for modeling the speech production mechanism. A few physiologically oriented models of the tongue have been proposed to simulate its three-dimensional deformation. These models aim to establish a computational simulation of speech production

*Currently affiliated with the Information Science Division of Advanced Telecommunication Research Institute International, Kyoto, Japan

processes (e.g., Wilhelms-Tricarico, 1995) or to synthesize naturally sounding speech by taking into account physiological processes (e.g., Dang & Honda, 1998). However, these models are based on a small body of anatomical data and may not sufficiently represent the actual structure of the tongue. Comprehensive studies of the tongue muscles are needed to realize anatomically plausible computational models of the tongue as a human speech organ.

Descriptions of gross anatomy of the tongue muscles are available in the literature. According to Barnwell (1976), there is general agreement among the lingual anatomists with regard to the apparent origin, course, and termination of each muscle. The tongue muscles are divided into extrinsic and intrinsic muscles according to their origins. The extrinsic muscles arise from the external organs and are inserted into the tongue, whereas the intrinsic muscles have both their origins and terminations within the tongue. The tongue can be segmented into a few parts based on the tissue constituents, and the manner of the segmentation can be described as a stratum. The mucous membrane is the superficial integumental stratum. The region below the mucous membrane, where the fibers of different muscles are intermingled, is called "the substance of the tongue" (Abd-El-Malek, 1939, p. 206). Inferior to the substance of the tongue there is only the genioglossus muscle. Furthermore, the substance of the tongue may be divided into a few layers or strata. Abd-El-Malek (1939) described a superficial stratum of the superior longitudinal muscle in the substance. Below this, Miyawaki (1973) observed a thick stratum of the transverse muscle. Some of the previous descriptions of the transverse and vertical muscles indicate that the arrangement of the fibers that compose the central part of the tongue has a certain regularity (e.g., Abd-El-Malek, 1939; Miyawaki, 1973; Sicher & DuBrul, 1988). Barnwell (1976), who reviewed Salter's work (Salter, 1852), quoted that "vertical and transverse fibers interdigitated and entirely occupied the center of the tongue, excluding the longitudinal fibers" (p. 36). The arrangement pattern of the transverse and vertical muscle fibers was called "interdigitation" (e.g., Abd-El-Malek, 1939, p. 206; Miyawaki, 1973, p. 27), "deccusating" (e.g., Abd-El-Malek, 1939, p. 205; Miyawaki, 1973, p. 28), or "interlacing" (Sicher & DuBrul, 1988, p. 172). These descriptions mean that the vertically running fibers and transversely running fibers intersect one another in an ordered manner in the central part of the tongue. Miyawaki's drawings (1973) lead us to observe such a rule, although it is not explicitly described in the text. It can be assumed that the unit of interdigitation is a sheet of muscle fibers, which will be called *lamina* in this study. Abd-El-Malek (1939) described the transverse muscle as "a series of lamellae" (p. 204), and Miyawaki's drawings (1973) suggest that the transverse muscle and the genioglossus or vertical

muscle lie one after the other along the long axis of the tongue. However, no previous reports have explicitly described the manner of "interdigitation."

The purpose of this study is threefold:

1. To describe the morphological features of each stratum in the tongue, which is composed of different muscles
2. To pinpoint where the interdigitation of muscle fibers takes place and how it is arranged
3. To build three-dimensional schemata of the lingual musculature based on the above examinations

Nomenclature

The following terms were used to describe regions of the tongue and their pertinent anatomical relationships (refer also to Figure 1).

Mucosal surface: the mucous membrane of the tongue from the apex to the radix

Substance of the tongue: the main part of the tongue, except the mucosal surface and the part where only the extrinsic muscles are observed

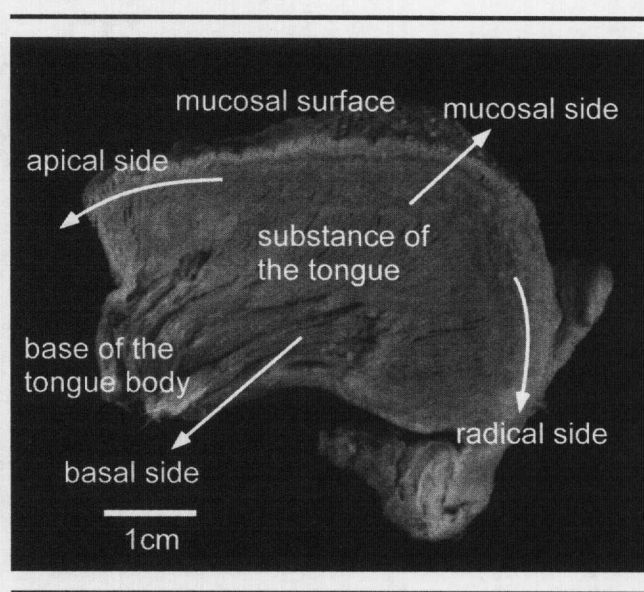
Base of the tongue: the proximal part of the genioglossus muscle

Mucosal side: the distal side of the genioglossus muscle

Basal side: the proximal side of the genioglossus muscle

Apical side: side to the tongue tip along the mucosal surface

Figure 1. Definitions of terms used in this study for naming parts and orientations of the tongue.



Radical side: side to the tongue root along the mucosal surface

Materials and Methods

Specimens

One hemisected tongue from an 85-year-old Japanese female was used for the histologic study of the layered structure of the tongue. Three specimens were used for detailed dissections to describe the relationship between intrinsic and extrinsic muscles in the body of the tongue. These specimens consisted of a right hemisected tongue of a 46-year-old male, a right hemisected tongue from a 90-year-old male, and left hemisected tongue from a 52-year-old male.

Histologic Study

One hemisected tongue was used for the histologic study of the full thickness of the tongue (i.e., mucosal surface to the base of the tongue). The specimen was cut into six wedge-shaped blocks along the lines that radiate from the base of the tongue to the mucosal surface (Figure 2). Each block was sectioned with a cryostat into 20 μm thick slices at an interval of 1 mm from the mucosal surface to the base of the tongue, approximately parallel to the surface of the tongue. The first slice was chosen at 1mm from the mucosal surface. The last one was determined at the point where the slice consists of the fibers of the genioglossus (GG) alone. All

the sections obtained from slicing were stained by the H & E procedure. The 20 μm thick transparent preparations were observed under a microscope.

Gross Dissection Studies

Systematic microdissection was undertaken to describe the extent and spatial relationships of muscles within the tongue. Specifically, this dissection was done to answer several questions about the detail of the substance of the tongue. These were (a) the anatomical relationship among the superior longitudinal muscle (SL), inferior longitudinal muscle (IL), styloglossus muscle (SG), and palatoglossus muscle (PG); (b) the insertion of the hyoglossus muscle (HG); and (c) the lamina pattern formed by the transverse muscle (T), GG, and the vertical muscle (V). Each of the three specimens was used to solve one of these anatomical questions. In one specimen (46-year-old male), the mucous membrane and submucosal layer was removed to expose the underlying muscles. The longitudinally running muscles were thus observed. In the second specimen (90-year-old male), muscle fibers of HG were traced within the substance of the tongue. The third specimen (52-year-old male) was dissected to observe the course and relation of T, GG, and V, which were located in the central part of the substance of the tongue. The examination was performed in the following steps. First, four wedge-shaped blocks were sectioned from the regions of the apex (the first block), tongue blade (the second block), palatal arch (the third block), and radix (the fourth block) in the same manner as was used in the histologic study. Second, the peripheral regions, which include the mucous membrane and the longitudinal fibers, were removed to isolate GG, V, and T in each block. Third, the fibers of the T, GG, and V were examined in each block to see whether they formed laminae. Fourth, the laminae were isolated by peeling them off under a binocular microscope. Finally, they were stained by the H & E procedure and observed under the binocular microscope. The attachments of the extrinsic muscles to rigid structures were examined before the samples were extracted from the oral cavity.

Three-Dimensional Reconstruction

Anatomical observations were schematically represented by a three-dimensional model, which was constructed computationally using a 3-D designing tool (Shade, Expression Tools, Inc.). Each tongue muscle was modeled into three-dimensional solid bodies, and they were arranged from the inside of the tongue to the outside to build the whole musculature of the tongue. Each muscle was modeled in the following way: First, a cross section of a muscle was drawn as a loop; second, the

Figure 2. Six blocks of the tongue separated roughly along fiber radiation of the genioglossus (GG). Lines on Block 4 indicate slice planes for histologic observation.

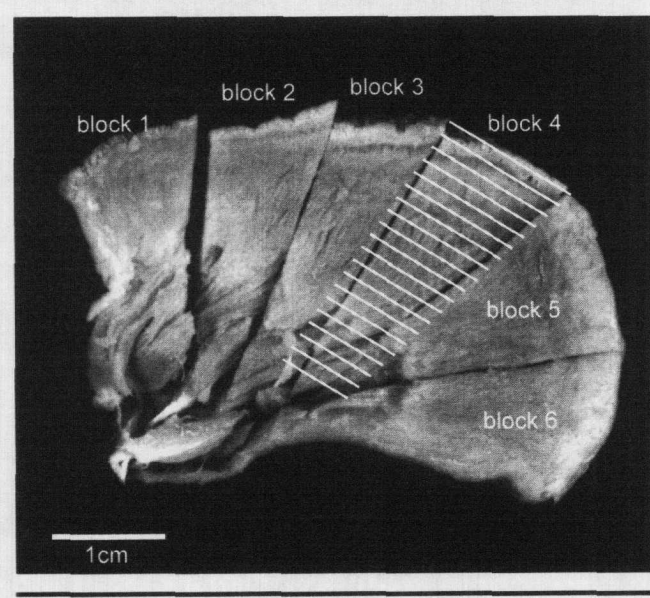


Table 1. Number of sections in each stratum of each block.

<i>Stratum I-IV</i>	Block 1	Block 2	Block 3	Block 4	Block 5	Block 6
<i>Stratum I</i>	1	1	1	1	2	3
<i>Stratum II</i>	2	4	9	10	4	4
<i>Stratum III</i>	8	8	10	10	12	9
<i>Stratum IV</i>	5	7	6	7	7	2
<i>Stratum V</i>	1	1	1	1	1	1

loop was extruded along the course of the muscle to form a three-dimensional object; third, the object's shape was adjusted according to the sketches and photographs; and finally, all of the objects were colored and texture-bitmapped to represent the course of the fibers. The hyoid bone was modeled by the same method using an actual specimen.

Results

Histologic Structure of the Tongue

Results of the examination of histologic sections of the tongue revealed a distinct layered relationship. Five distinct strata were observed in each of the blocks from the apex to root.

The extra-lingual fibers of HG and SG were found to insert into the lateral surface of the 4th, 5th, and 6th blocks. The thickness of each stratum in terms of the number of slices in each block is shown in Table 1. The morphology of each stratum is illustrated in Figure 3.

Stratum I: This was named the "mucosal stratum," because this section had no muscle fibers and it mainly consisted of the lingual papilla and the mucous epithelium (Figure 3[a]).

Stratum II: This was called the "SL stratum." In this stratum, longitudinal sections and cross sections of muscle fibers were observed. The former were the fibers of SL that passed postero-anteriorly, and the latter were the fibers of GG and V that coursed toward the lamina propria of the dorsum (Figure 3[b]).

Stratum III: This was described as the "T stratum," which exhibited the most complicated structure and formed a good part of the tongue. Longitudinal sections of fibers of T that ran medio-laterally were seen in the medial side. Toward the lateral lamina propria, the fiber sections became gradually short and round. Their cross sections appeared at the lateral border. The cross sections of fibers of GG and V were closely bounded side-by-side. These fibers were sandwiched between the fibers of T. The fibers of T and the fibers of GG and V lay one after the other in a regular manner (Figure 3[c]). The observation of the series of preparations belonging to the third layer showed evidence that the fibers of T, GG, and V formed a repetitive set of thin laminae and

that they "interdigitated" with each other in a lamina-by-lamina manner. Immediately medial to the lamina propria in the lateral border, the longitudinal sections

Figure 3. Sections of Block 3 in each stratum. 20 µm thick slices are made in parallel to mucosal surface and stained by Hematoxylin and Eosin. (a) *Stratum I*, (b) *Stratum II*, (c) *Stratum III*, (d) *Stratum IV*, and (e) *Stratum V*.

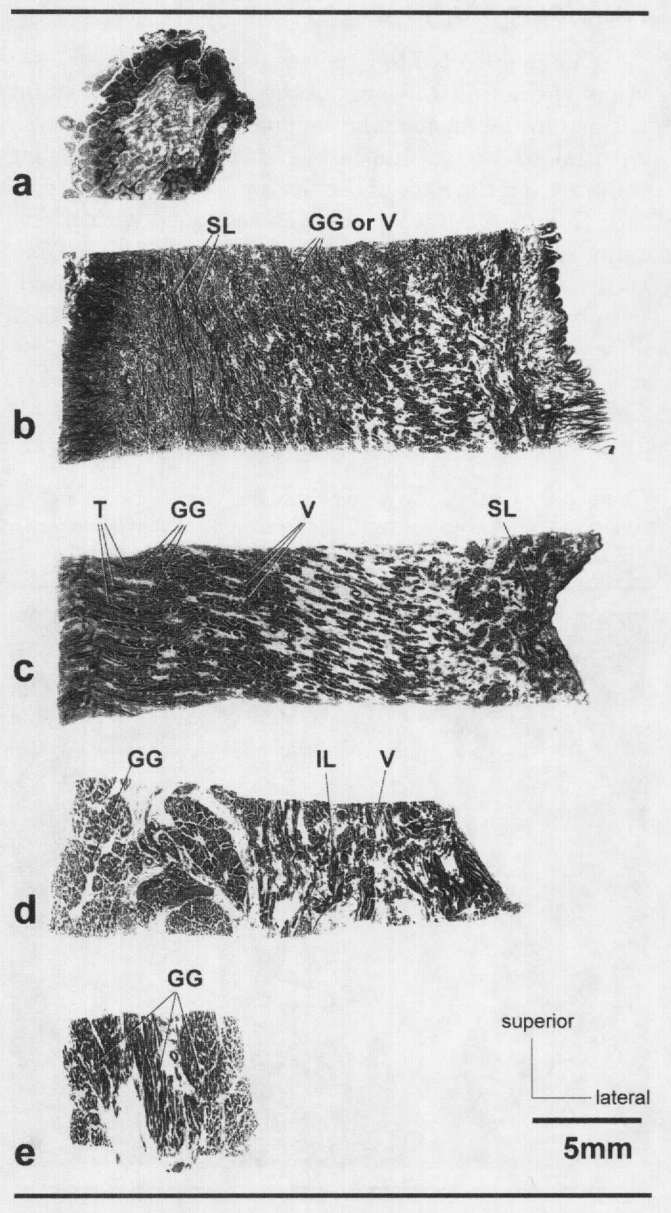
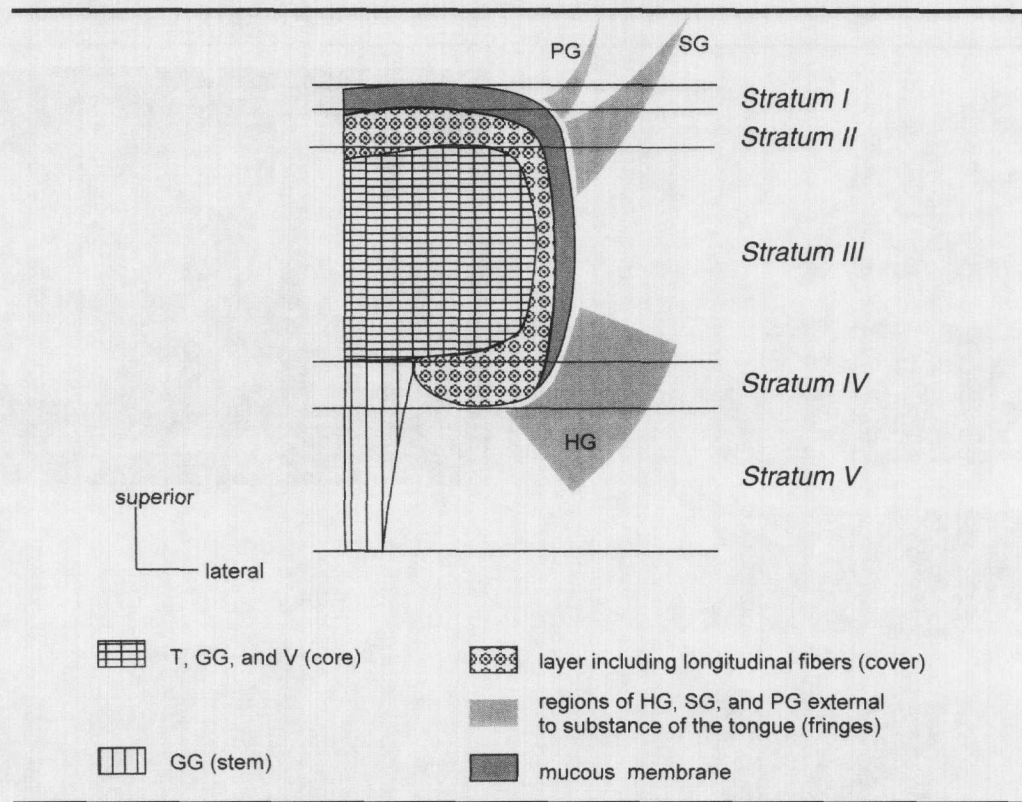


Figure 4. Schematic representation of the tongue's stratum structure. The layer including longitudinal fibers is composed of the superior longitudinal muscle (SL) at the top; the styloglossus (SG), palatoglossus (PG), and hyoglossus (HG) in the middle; and inferior longitudinal muscle (IL) at the bottom. GG: genioglossus, V: vertical muscle, and T: transverse muscle.



of the fibers ran antero-posteriorly. In the superior mucosal side, the fibers were of SL, whereas in the basal side they included other longitudinal fibers of the extrinsic muscles, such as SG and HG.

Stratum IV: This was labeled the "IL stratum." In this stratum, the cross sections of the fibers of GG were seen medially, and the longitudinal sections of the fibers of IL and cross sections of V were seen laterally (Figure 3[d]).

Stratum IV: This was categorized as the "GG stratum." In this stratum, only the cross sections of the radiating fibers of GG were found (Figure 3[e]).

According to the above findings, the basic structure of each block can be schematized as shown in Figure 4. The structural pattern was consistent across the six blocks (see also Figure 5, which shows *Stratum III* in every block), though the proportion of stratum thickness or the shape of the stratum differed from block to block.

Figure 4 shows that the tongue tissue was divided into four regions. The first was the most basal part, that is, *Stratum V*, which contained only the fibers of GG. The second was the medial part of *Stratum III*, which included T, GG, and V. The third was the part that included the longitudinal fibers in the substance of the

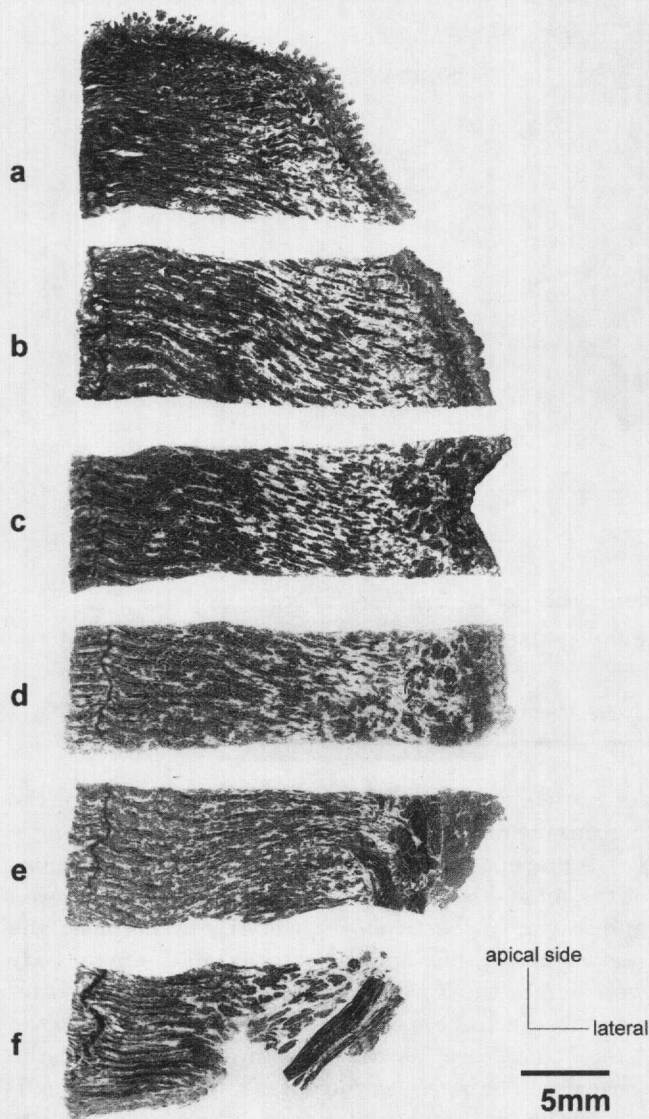
tongue, which covered the second part. The last was the mucous membrane, which overlaid the first three parts. In the present study, the first, second, and third regions of the tongue body were defined as the "stem," "core," and "cover," respectively (Figure 4). Furthermore, the regions of HG, SG, and PG external to the main body were named the "fringes" that projected from the posterior substance of the tongue (Figure 4). We grouped the "stem" and "core" as the inner musculature and the "cover" and "fringes" as the outer musculature. The fibers of the inner musculature course perpendicularly to the radical-apical direction, whereas the fibers of the outer musculature run in parallel.

Inter- and Intramuscular Relationships in the Tongue

SL, IL, and Lingual Portion of SG and PG

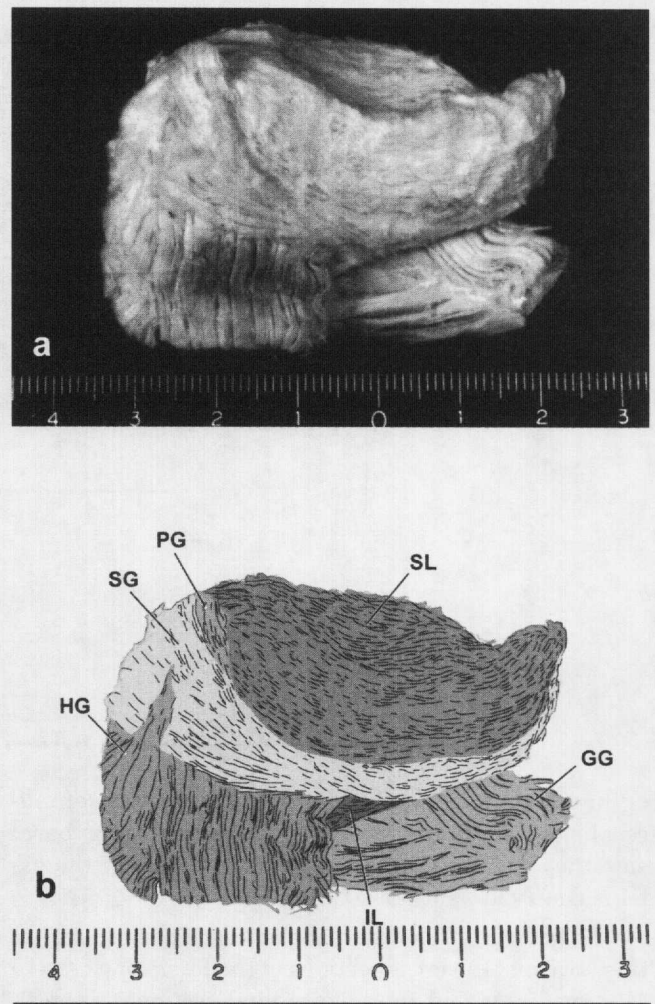
In Figure 6, the courses of SL, IL, and the lingual part of SG can be seen. SG reached the substance of the tongue at the level of the palatoglossal arch, and the fibers ran downward and forward on the lateral surface. The anterior fibers of SG ran forward, toward the apex

Figure 5. Sections of *Stratum III* from Block 1 to Block 6 shown in (a) to (f). All sections are 20 μm thick and stained by Hematoxylin and Eosin. Longitudinal sections of the transverse muscle (T) and cross sections of the genioglossus (GG) and vertical muscle (V) lie alternately from apex to radix (root).



on the inferior surface of the anterior free part of the tongue. PG reached the substance of the tongue just anterior to SG and merged with SG immediately. SL ran beneath *Stratum I* in the substance of the tongue from the radix to apex, and its lateral expansion was limited by SG. Near the palatoglossal arch, the fibers of SL coursed in the radix-apex direction although the fibers of SG ran infero-anteriorly, and thus these two muscles were distinguished from each other. It was difficult to separate the anterior fibers of these muscles because they coursed together to the apex. IL ran from the root to tip beneath the ventral surface of the tongue,

Figure 6. Dissection of specimen 1 (46-year-old male) to show longitudinal fibers of the substance of the tongue. (a) Photograph of lateral aspect of the tongue, and (b) its schema. GG: genioglossus, HG: hyoglossus, SG: styloglossus, PG: palatoglossus, SL: superior longitudinal muscle, and IL: inferior longitudinal muscle.



which could be identified near the anterior border of HG before entering into the substance of the tongue.

HG and Its Relationship to SG

In Figure 7, the course of the fibers of HG is shown in relation to SG. Most fibers of this muscle coursed upward and inward, passing under SG. Some of the fibers of both muscles interdigitated with each other. After intersecting SG, the fibers of HG slightly fan out beneath SL. The posterior fibers ran postero-medially after intersecting with SG.

GG, V, and T Muscles

The course and relationships of T, GG, and V are shown in Figure 8. In the second, third, and fourth blocks, both the fibers of T and the fibers of GG and V

Figure 7. Dissection of specimen 2 (90-year-old male) to show insertion of the hyoglossus (HG) into the substance of the tongue. (a) Photograph of lateral aspect of the tongue and (b) its schema. GG: genioglossus, SG: styloglossus, PG: palatoglossus, SL: superior longitudinal muscle, and IL: inferior longitudinal muscle.

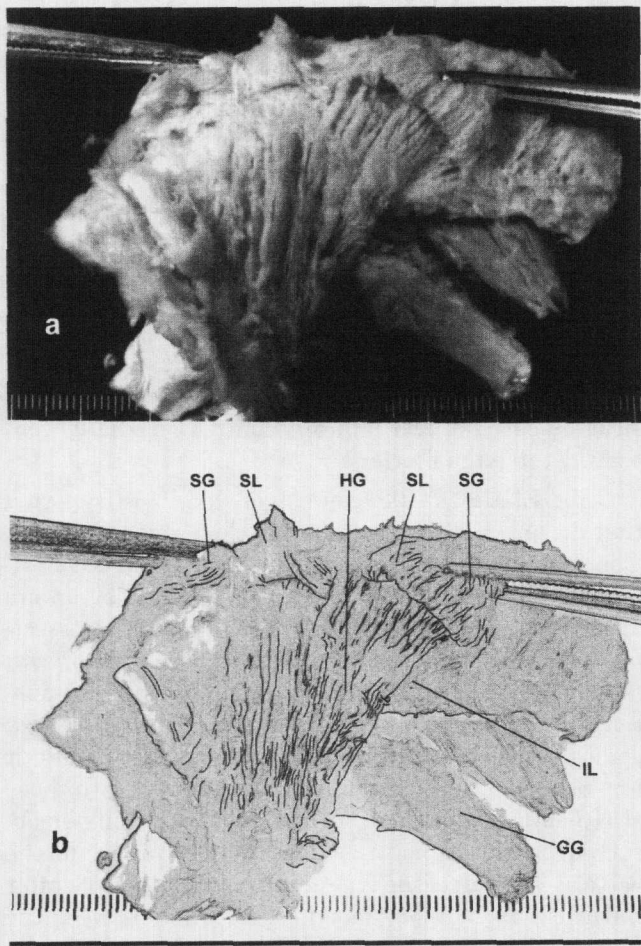
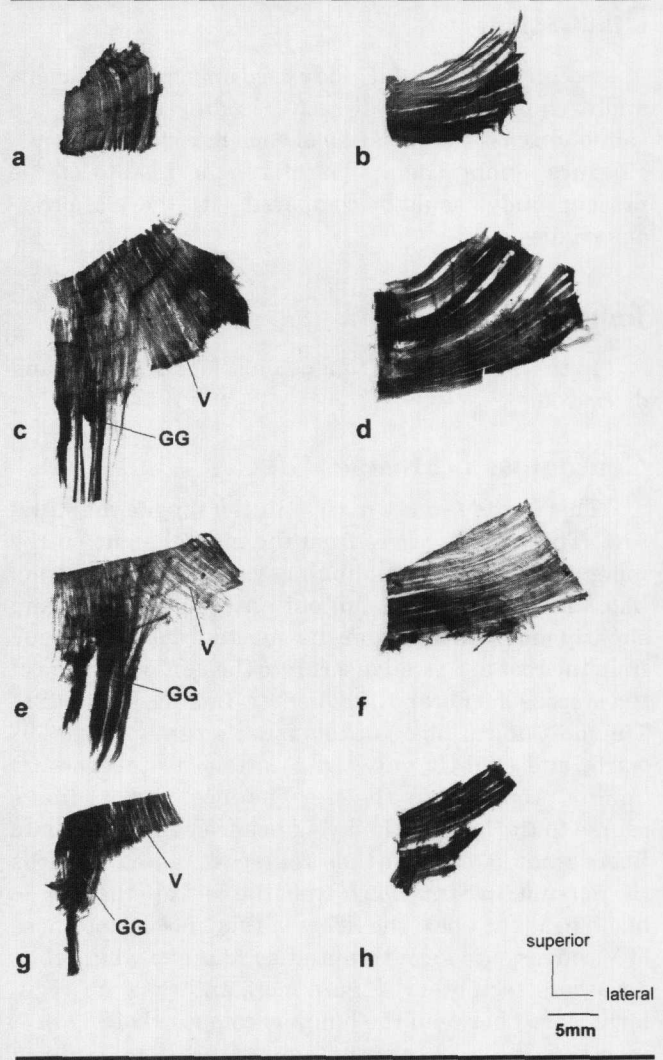


Figure 8. Dissection of specimen 3 (52-year-old male) to show fiber composition in laminae containing the genioglossus (GG) and vertical muscle (V), and transverse muscle (T) in apex, tongue blade, palatoglossal arch, and radix (root). (a) Lamina of V. (b) Lamina of T near apex. (c) Lamina of GG and V. (d) Lamina of T in the tongue blade. (e) Lamina of GG and V. (f) Lamina of T at level of the palatoglossal arch. (g) Lamina of GG and V. (h) Lamina of T near radix (root).



formed a set of thin laminae. The lamina of T was easily isolated by manual peeling from the lamina containing GG and V (Figure 8[b], 8[d], 8[f], and 8[h]). The fibers of GG were differentiated from those of V, but the fibers of these two muscles formed a unified lamina and they could not be separated (Figure 8[c], 8[e], and 8[g]). In the apex, where the fibers of GG were not observed, both V and T formed thin laminae respectively (Figure 8[a]). In the root, however, it was difficult to separate these laminae by manual peeling, because the irregular fibers were found more frequently than in the other blocks. In the large part of the tongue, the lamina of T and that of GG and V are regularly arranged one after another from the tongue blade to the dorsum near the root as shown in Figure 5. The number of the lamina repetitions was approximately one hundred.

The structure of the laminae and the arrangement rule revealed in the present study were summarized as follows:

1. The fibers of GG coursed from the base of the tongue to the dorsal mucosal surface, slightly fanning out laterally. The fibers of V arising from the ventrolateral submucosa inserted into the fiber radiation of GG. These two fibers together formed a thin lamina (Figure 8[c], 8[e], and 8[g]).
2. In the apical and radical sides of the lamina, the fibers of T coursed medio-laterally with a shallow arch and formed a thin lamina (Figure 8[b], 8[d], 8[f], and 8[h]).
3. These two laminae adhered together and repeated from the radix to apex (see also Figure 5). This regular

pattern was seen in the whole substance of the tongue, except for some irregularity found near vessels and nerves, especially in the radix. In the apex, where the fibers of GG did not reach, the lamina structure lacked the regular pattern by losing the component of GG (Figure 8[a]).

Discussion

Because the present study used only four specimens and each of them was dissected in different ways, we cannot discuss the variation of each muscle or the musculature among them. Therefore, the results of the present study should be compared with those of previous studies.

Tongue Muscles

In this section, each tongue muscle is described and discussed.

Genioglossus Muscle (GG)

This is the largest muscle in the tongue musculature. This muscle arises from the mental spine on the inner surface of the mandibular symphysis and a spine-like tendon. The fibers fan out antero-posteriorly and slightly medio-laterally in the substance of the tongue from the root to tip and insert into the lamina propria of the mucous membrane after penetrating the layer of SL. The most apical fibers of this muscle run upward, forward, and slightly outward to attach to the dorsum lamina propria near the tip. The most radical fibers course to the body of the hyoid bone. The intermediate fibers gradually change their courses to radiate towards the dorsum. In *Stratum III* from the radix to the tongue blade near the apex, the fibers of this muscle and those of V converge to form thin unified laminae where they decussate each other (Figure 8[c]), and they are regularly placed between the laminae composed of T.

No description of the laminae was found in the previous studies. A disagreement exists as to whether the most anterior fibers of this muscle actually reach the tip. Langdon, Klueber, and Barnwell (1978) concluded that "the anterior-most fibers...could be traced as far anteriorly as could the lingual septum, viz., to a point just short of the tip of the tongue" (p. 112). On the contrary, Doran and Bagget (1972) reported that "none of its fibers pass to the apex or tip of the tongue" (p. 409) in many mammals, including man. In the present study, it was observed that the apical region (up to about 8 mm from the apex) contained no fibers of this muscle in the third specimen (52-year-old male) as shown in Figure 8(a). Abd-El-Malek (1939) and Langdon et al. (1978)

reported that in the distal part of this muscle near the mucous membrane some of the medial fibers decussate with those of the opposite side. In the present study, however, this observation could not be made because hemisected tongues were used.

Hyoglossus Muscle (HG)

This is a thin, quadrangular muscle in the lateral view. The anterior border of this muscle is longer than the posterior. This muscle originates from the lateral part of the anterior surface of the body of the hyoid bone and from the whole length of the greater horn. Most fibers slightly radiate antero-dorsally, being inferior to SL, after they intersect with the fibers of SG. The posterior fibers run postero-medially after intersecting with SG and insert into the lamina propria of the dorsum of the tongue. The posterior part of this muscle exists on the lateral surface of the hypoglossal membrane which situates between HG laterally and GG medially, containing the lingual artery.

Abd-El-Malek (1939) and Miyawaki (1973) reported that the anterior fibers of this muscle course to the apex along the margin between SG superiorly and IL inferiorly. In the present study, the most anterior fibers were observed to course upward and forward, after intersecting with SG. Abd-El-Malek (1939) reported that "both the middle and posterior fibers...join the fibers of superior longitudinal muscle dorsally and transverse and genioglossus ventrally" (p. 207). In the present study, it was observed that the fibers of T connected with those of HG in the substance of the tongue. Cruveilheir observed "continuity between fibers of this muscle and the vertical fasciculi of the tongue" (Cruveilheir, 1853, after Barnwell, 1976, p. 35), but the connection between the fibers of V and those of HG was not observed in the present study.

Styloglossus Muscle (SG)

This muscle originates from the anterior and lateral surfaces of the distal part of the styloid process and passes downward, inward, and forward to reach the lateral border of the tongue. After this muscle enters the substance of the tongue posterior to the palatoglossal arch, it becomes flattened to form a triangular sheet in the lateral view and separates into three segments. The posterior fibers run downward within the hypoglossal membrane and intersect with the fibers of HG. The middle fibers stretch medially to join the fibers of T after intersecting the fibers of HG in the region shared by HG medially and SG laterally. The anterior fibers run to the apex along the lateral margin of the tongue substance between the fibers of IL ventrally and the fibers of SL dorsally. Near the apex, the fibers become indistinguishable from the fibers of SL and IL.

Abd-El-Malek (1939) described the medial fibers, which end "by decussating superficially with the lateral surface of the hyoglossus muscle" (p. 207). Based on the microscopic dissection of 14 fetus tongues, Barnwell (1977) reported the fibers of this muscle "projected medially approximately half way to the midline, closely approaching the lateral borders of m. genioglossus before terminating in the connective tissue investment or becoming indistinguishable from the fibers of m transversus linguae" (p. 12). The present study supported the observation by Barnwell (1977). DuBrul (1976) revealed that the anterior fibers of the left and right join together at the midsagittal plane. In the present study, it was observed that, in the apex, the right and left fibers converge together in the midline.

Palatoglossus Muscle (PG)

This muscle is the smallest of all the extrinsic muscles. This muscle arises from the soft palate, runs downward within the palatoglossal arch, and reaches the substance of the tongue anterior to SG. Then, this muscle runs infero-anteriorly, but more obliquely than SG, and immediately merges with SG.

This muscle is sometimes categorized into the palatal muscle group (e.g., Kuehn & Azzam, 1978; Miyawaki, 1973) and sometimes into the tongue muscle group (e.g., Doménech-Ratto, 1977; Salter, 1852). The innervation of this muscle is still uncertain; Doménech-Ratto (1977) reported that no nerve fibers penetrated this muscle. Langdon, Klueber, and Barnwell (1979) performed detailed histologic dissection and reported that this muscle has three different pathways: medial fibers joining with T, anterior fibers terminating in the submucosa of the anterior half of the tongue, and inferior fibers to blend with fibers of SG. In the present study, only the inferior fibers were observed, because the fibers of this muscle were too scarce to be distinguished from those of other muscles.

Superior Longitudinal Muscle (SL)

This muscle exists immediately inferior to the lamina propria in the dorsum, extending from the radix to apex in the postero-anterior direction and from the top of the dorsum to the upper border of SG in the medio-lateral direction. In the middle and medial part, this muscle forms a thick stratum, but in the other peripheral part it becomes a thin sheet. Most fibers of this muscle run parallel in the postero-anterior direction. Near the root posterior to the terminal sulcus, however, the arrangement of the fibers is less ordered and dispersed than in the anterior. Near the apex, the fibers run slightly medially.

With respect to the origin and termination of this muscle, no consensus has been achieved. Barnwell,

Klueber, and Langdon (1978) reported that "a majority of investigators noted the superior longitudinal musculature arises from an intermittent origin on the lamina propria along the dorsum of the tongue" (Abd-El-Malek, 1939; Cruveilhier, 1844; Salter, 1852; Strong, 1956, after Barnwell, Klueber, et al., 1978, p. 5). Barnwell, Klueber, et al. (1978) mentioned that this muscle originates from near the terminal sulcus and terminates in the anterior third of the tongue. Miyawaki's drawings (1973) indicated that the fibers of this muscle are continuous from the root to tip. Although intermittent terminations were not evident in the present study, the fact that the thickness of this muscle is varied from part to part suggests that the fibers run discontinuously along the long axis of the tongue. Barnwell, Klueber, et al. (1978) reported that the fibers converge medially to attach to the medial septum near the apex, which was confirmed in the present study.

Inferior Longitudinal Muscle (IL)

This muscle arises from the surrounding area of GG medially and HG laterally near the root and runs forward along the lateral side of GG from the radix to apex. In the part anterior to the frontal border of HG, the fibers course to the apex between GG medially and SG laterally in the ventral part of the tongue. Near the apex of the tongue, the fibers of this muscle and SG appear to join together.

Abd-El-Malek (1939) reported three attachments of this muscle. The first is the medial attachment, which is in conjunction with the ventro-lateral fibers of GG. The second is the lateral attachment that is located on the body and root of the greater horn of the hyoid bone. The last is the minor attachment on the stylohyoid ligament between the lateral and medial attachments. In the present study, only the second attachment was observed. Barnwell, Langdon, and Klueber (1978) observed that this muscle could be divided into two parts, the anterior and posterior segments, that were not distinguished in the present study.

Vertical Muscle (V)

This muscle exists as a series of thin laminae in the substance of the tongue. The fibers of this muscle originate from the ventro-lateral submucosal and run superomedially to terminate at the lamina propria of the tongue dorsum. In the middle of its course, in *Stratum III*, the fibers of this muscle form unified laminae together with the fibers of GG. In most of the substance of the tongue, from near the apex to radix, the unified laminae of GG and V are sandwiched between the laminae of T. Near the apex, where the fibers of GG are not found, only the fibers of this muscle form thin laminae.

No previous studies referred to the lamina of this muscle. Miyawaki (1973) wrote that "this muscle is only

found in the superior half of the tongue" (p. 29) based on observation of the coronal sections. In the present study, however, the cross sections of the fibers of this muscle were observed in *Stratum IV* between the fibers of IL lateral to the lingual artery. Thus, contrary to Miyawaki (1973), the fibers were also seen in the ventral half of the tongue. Klueber, Langdon, and Barnwell (1979) reported that this muscle becomes sparse in the portion posterior to the foramen cecum. In the present study, however, the fibers of this muscle in the radical part were found to be as dense as in the more anterior parts.

Transverse Muscle (T)

This muscle is situated as a series of thin laminae in the substance of the tongue. The fibers of this muscle arise from the medial septum and course dorso-laterally to terminate at the lamina propria in the lateral border of the tongue. Most of the fibers are convex downward, and others are direct transversely and ventrally. The laminae of this muscle and that of GG and V are arranged one after another in an ordered manner from the radix to apex to make a bulky mass of the tongue.

The descriptions by former investigators are consistent with regard to the origin, course, and attachment of this muscle (Abd-El-Malek, 1939; Klueber et al., 1979; Miyawaki, 1973; Strong, 1956). As to the lamina structure, only Abd-El-Malek (1939) summarizes this muscle as "a series of lamella" (p. 204).

The Stratum Structure and Musculature of the Tongue

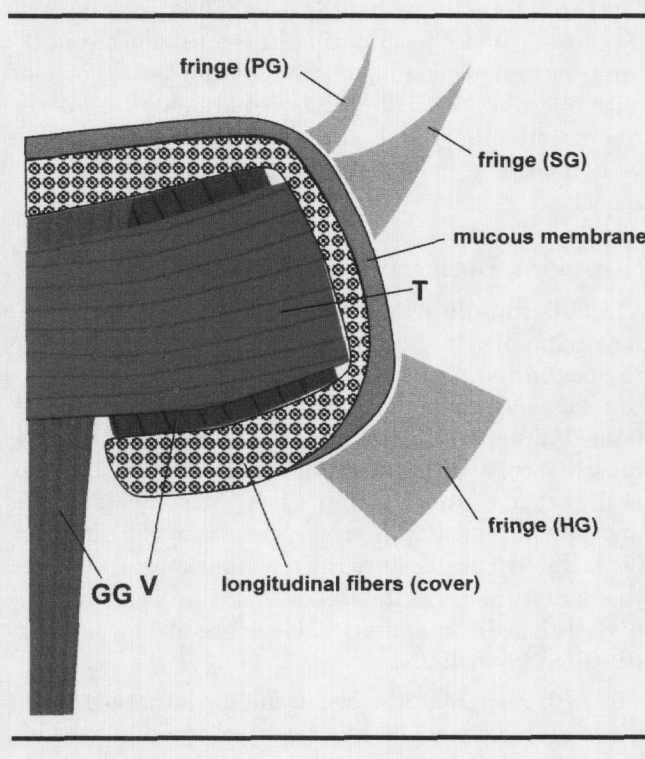
Although the origin, course, and termination of each tongue muscle has been extensively described (e.g., Abd-El-Malek, 1939; Barnwell, 1977; Barnwell, Klueber, et al., 1978; Barnwell, Langdon, et al., 1978; Klueber et al., 1979; Langdon et al., 1978; Langdon et al., 1979; Miyawaki, 1973), no study to date has addressed the details of the layered relationship among the muscles in the tongue. It appears that this relationship was appreciated by Gray (1974), where the anatomical feature of layering was applied (without much elaboration) to the description of the tongue from its mucosal surface to the base. Furthermore, a few studies have used the term stratum or layer to describe the geometry of certain tongue muscles. Abd-El-Malek (1939) described SL as "a thin sheet" in its peripheral part and noted "fibers of V decussate intimately with the strata of the transverse muscle" (p. 204). Miyawaki (1973) stated that "SL is a layer of muscle...just beneath the layer of submucous tissue" (p. 28) and "T forms a fairly thick stratum beneath the whole extent of SL" (p. 28). They both agreed that T and V form a thick stratum together, constituting "a considerable part of the central mass of the tongue"

(Abd-El-Malek, 1939, p. 205) or "a main part of the dorsal half of the tongue" (Miyawaki, 1973, p. 28).

In the present study, the structure of the whole tongue tissue was explored in the five strata from the base of the tongue to the mucosal surface (see Figures 3 and 4). The tongue was sectioned into blocks along the course of the fibers of GG. The observation by this unique method successfully demonstrated that the strata from the base to the mucosal surface are seen in each block. Many previous studies adopted the standard three sections (i.e., the sagittal, coronal, and transverse sections) in spite of the fact that the tongue is a round body. Were the tongue sliced in the standard manner, it would be difficult to recognize the coherent stratum structure of the tongue. Therefore, the present method offers an appropriate approach to observe and describe the muscular arrangement of the whole tongue.

The major discovery in the present study was the lamina structure of the inner musculature of the tongue. This morphological characteristic has been only partially reported. Abd-El-Malek (1939) described the form of T as "a series of the lamellae" (p. 204), without mentioning the relation with the laminae of V and GG. The regular arrangement of muscle laminae has been shown only in photographs and drawings without descriptions (Klueber et al., 1979; Miyawaki, 1973).

Figure 9. Schematic drawing of structural unit of inner musculature of the tongue. Unit consists of the two laminae: one is combined lamina of the genioglossus (GG) and vertical muscle (V), and the other is lamina of transverse muscle (T).



The results of this study provided evidence that a pair of the lamina of GG and V and that of T was the "structural unit" of the inner musculature of the tongue. Figure 9 shows the structural unit formed by the muscle fiber laminae, from the same view as that of Figure 4.

Note that the typical lamina structure was observed in the "core" of the inner musculature, whereas in the "cover" the fibers of each lamina diverged and intersected other longitudinal fibers (SL, IL, HG, and SG) to terminate at the lamina propria of the mucous membrane.

Building Three-Dimensional Schemata of the Lingual Musculature

A three-dimensional model of the tongue was developed from dissection data in the present study. The model illustrated in Figure 10 resulted from integrating the findings of both histologic and dissection phases of the present study. The 3-D schemata represent the reconstruction process of the lingual musculature from its

inner musculature ("stem" and "core") to the outer musculature ("cover" and "fringes").

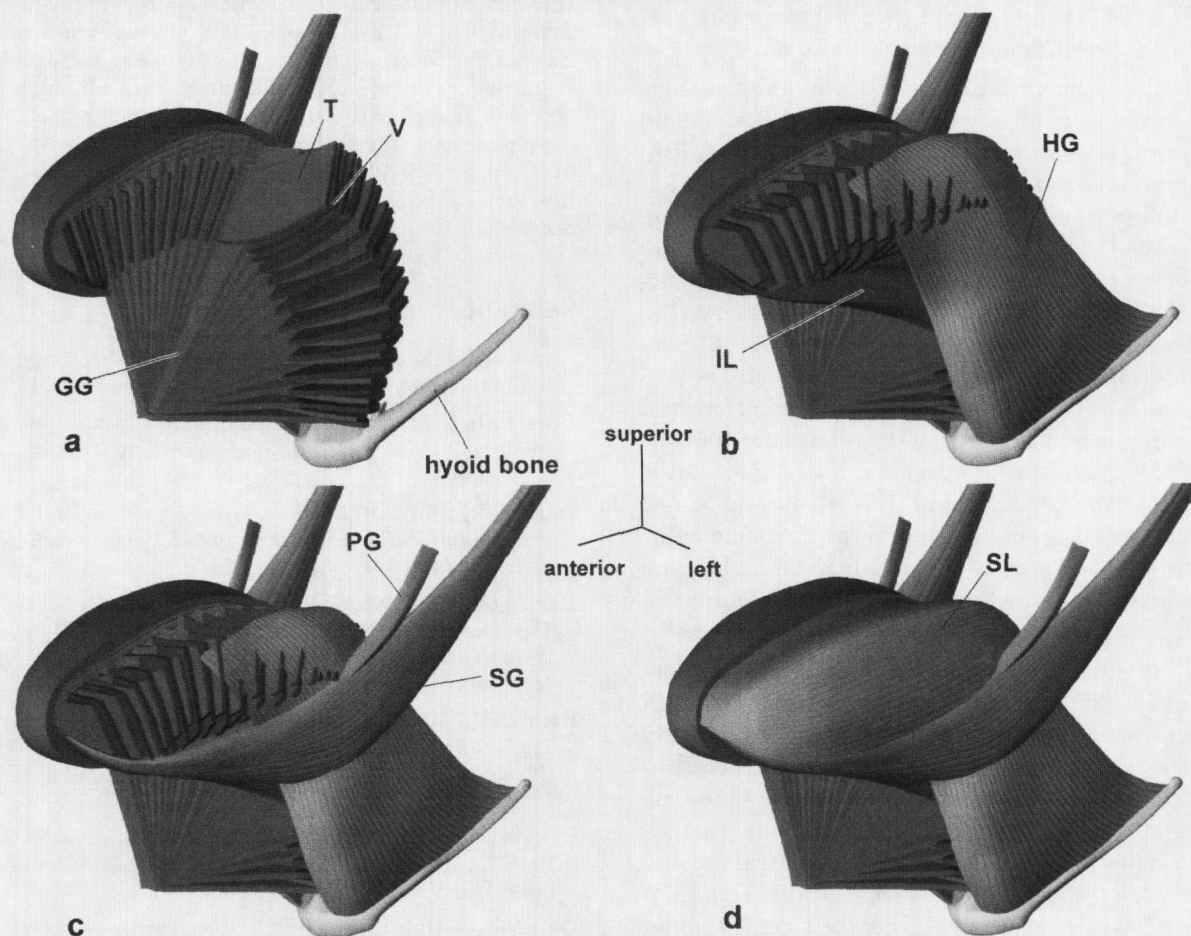
1. The "structural units" repeat one after another from the radix to apex, constructing the inner musculature of the tongue (Figure 10[a]).

2. HG originates from the hyoid bone and courses to the dorsal region of the inner musculature. IL arises between HG and the inner musculature and runs to the apex on the ventral surface of the inner musculature (Figure 10[b]).

3. SG and PG run forward, downward, and inward to reach the lateral border of HG and then course to the apex on the lateral surface of the inner musculature (Figure 10[c]).

4. SL, which arises from the back surface of the inner musculature, runs in the radix-apex direction on the superior surface of the inner musculature to form the "cover" together with IL and the lingual part of HG, SG, and PG (Figure 10[d]).

Figure 10. Three-dimensional schemata of the tongue musculature indicating geometrical arrangement of muscle fibers from inner (a) to outer (d) musculature. (a) Arrangement of structural units of inner musculature. (b) Inferior longitudinal muscle (IL) and hyoglossus (HG). (c) Styloglossus (SG) and palatoglossus (PG). (d) Superior longitudinal muscle (SL).



5. The mucous membrane wraps the "cover" as the integument (right half of the tongue in all schemata in Figure 10).

The following two notions should be addressed here regarding the simplifications in the 3-D schemata. First, this model contains only 24 schematic "structural units" in the inner musculature of each half, whereas the actual tongue possesses a much larger number of "structural units" (i.e., about 100 "structural units" were found in the histologic preparations), and many of them are often not as clearly demarcated as represented in the schemata. Second, the "cover" is shown as a smooth sheath in the model and appears to include its fibers only, whereas in reality the fibers of the inner musculature penetrate the cover to terminate in the lamina propria of the dorso-lateral mucous membrane.

Contributions to Computational Physiological Models of the Tongue

In this section, we discuss the potential biomechanical properties of the tongue based on the present study as a guide to construct computational physiological models of the tongue that are driven by muscle contraction parameters (e.g., Dang & Honda, 1998; Wilhelms-Tricarico, 1995). These issues are considered in terms of the "core," "cover," and "structural units."

Musculature similar to that of the human tongue is found in animal motor organs. Smith and Kier (1989) reported that elephant trunks and squid tentacles consist of three types of muscle fibers running in the following (different) directions: "perpendicular to the long axis," "parallel to the long axis," and "wrapped helically or obliquely around the long axis." In those organs, according to their report, the perpendicular fibers exist in the central part, whereas the other two types of fibers are situated in the peripheral part. Although the human tongue is not as long as the elephant trunk or squid tentacles and it bends in the middle length of the dorsum, according to the course against the long axis, it is assumed that the "structural units" ("stem" and "core") of the human tongue correspond to the "perpendicular fibers" in the elephant trunk or squid tentacles, the "cover" corresponds to the "parallel fibers," and the "fringes" correspond to the "helical or oblique fibers."

From the above point of view, movements and deformations of the human tongue can be clearly understood. Contractions of the "structural units" ("stem" and "core") deform the tongue in the direction perpendicular to the dorsum of the tongue or elongate the tongue along the long axis, consequently moving and protruding the tongue forward. Asymmetrical contractions of the "cover" bend the tongue in various directions. Contractions of one of the "fringes" twist the tongue around the long axis. The fact that the "cover" and "fringes" are

located in the periphery of the tongue indicates an advantage of tongue deformation because, as Smith and Kier (1989) pointed out, "this location provides greater leverage for bending than a more central location near the axis of the organ" (p. 33). In short, the inner musculature has the function of protruding and elongating the tongue forward, whereas the outer musculature controls the movements of the tongue tip.

The present study revealed that the tongue has a highly organized structure. The newly obtained knowledge on this structure should facilitate better understanding of the tongue musculature and realistic computational simulation of tongue movements or deformation in speech articulation and deglutition.

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Contact author: Hironori Takemoto, PhD, Information Science Division, Advanced Telecommunication Research Institute International, 2-2-2 Hikaridai, Seika-cho, Soraku-gun, Kyoto 619-0288, Japan.
Email: takemoto@isd.atr.co.jp