

## Descent of the hyoid in chimpanzees: evolution of face flattening and speech

Takeshi Nishimura<sup>a,\*</sup>, Akichika Mikami<sup>b</sup>, Juri Suzuki<sup>b</sup>, Tetsuro Matsuzawa<sup>b</sup>

<sup>a</sup> *Laboratory of Physical Anthropology, Department of Zoology, Graduate School of Science, Kyoto University, Kitashirakawa Oiwake-cho, Sakyo, Kyoto 606-8502, Japan*

<sup>b</sup> *Primate Research Institute, Kyoto University, Inuyama, Aichi 484-8506, Japan*

Received 1 September 2005; accepted 27 March 2006

### Abstract

The human supralaryngeal vocal tract develops to form a unique two-tube configuration with equally long horizontal and vertical cavities. This anatomy contributes greatly to the morphological foundations of human speech. It is believed to depend on the reduced growth of the palate and on the developmental descent of the larynx relative to the palate. Anatomically, the descent of the larynx is accomplished through both the descent of the laryngeal skeleton relative to the hyoid and the descent of the hyoid relative to the palate. We have studied the development of three living chimpanzees using magnetic resonance imaging. Our previous study showed that, as in humans, chimpanzees show rapid laryngeal descent, with changes in the relative proportion of the vocal tract during early infancy. However, this is not accompanied by the descent of the hyoid relative to the palate, although it is achieved with the descent of the laryngeal skeleton relative to the hyoid. Here, we show that subsequently the chimpanzee hyoid also descends to maintain the rapid descent of the larynx, similarly to humans. We argue that the descent of the larynx probably evolved in a common ancestor of extant hominoids, originally to confer an advantage via a function unrelated to speech. Thus, the descent of the larynx per se is not unique to humans, and facial flattening was probably the major factor that paved the way for speech in the human lineage.

© 2006 Elsevier Ltd. All rights reserved.

*Keywords:* Descent of the larynx; Vocal tract; *Pan troglodytes*; MRI; Longitudinal study

### Introduction

The evolution of human speech has attracted much interest to better understand the evolution of language. Human speech has the distinct feature that humans can regularly utter several phonemes—including vowels and consonants—sequentially and rapidly in a short, single exhalation. It must be noted that speech per se is not the same as language and does not necessarily reflect the high intelligence of humans. However, this sophisticated feature of speech allows humans to turn much information that is encoded by language in the brain

into sounds and to communicate it to others rapidly and efficiently (P. Lieberman, 1984). Therefore, even if language and speech arose independently in the human lineage, an understanding of the evolution of speech would shed light on the evolution of language with which we are endowed today.

Theories of speech physiology and acoustics demonstrate that humans have a unique anatomy of the supralaryngeal vocal tract (SVT) that underlies its sophisticated manipulation in the production of speech. Humans and nonhuman mammals basically make use of the same machinery for speech and vocalization: the lungs generate sound power, the vocal folds in the larynx comprise the sound sources, and the SVT resonates the sources to generate voiced sounds with some bands of the formant frequencies, e.g., vowels in speech (Fant, 1960; P. Lieberman and Blumstein, 1988; Titze, 1994; Stevens, 1998; Fitch and Hauser, 2003; Riede et al., 2005). The

\* Corresponding author.

*E-mail addresses:* [nishimur@anthro.zool.kyoto-u.ac.jp](mailto:nishimur@anthro.zool.kyoto-u.ac.jp) (T. Nishimura), [mikami@pri.kyoto-u.ac.jp](mailto:mikami@pri.kyoto-u.ac.jp) (A. Mikami), [suzuki@pri.kyoto-u.ac.jp](mailto:suzuki@pri.kyoto-u.ac.jp) (J. Suzuki), [matsuzaw@pri.kyoto-u.ac.jp](mailto:matsuzaw@pri.kyoto-u.ac.jp) (T. Matsuzawa).

distribution pattern of the formants defines the different kinds of vowels that form the platform for vocal communication. These are determined by the resonance properties of the SVT and these properties in turn are dictated by the volumetric topology of the tract, which can be estimated from a function of the sequential cross-sectional area along the tract. The SVT in most mammals, including humans, is principally composed of two cavities: the horizontal oral and vertical pharyngeal cavities designated here the SVT<sub>H</sub> and SVT<sub>V</sub>, respectively. In nonhuman mammals, the SVT<sub>V</sub> is much shorter than the SVT<sub>H</sub> (Negus, 1949; P. Lieberman, 1984; Laitman and Reidenberg, 1993; Dyce et al., 1996). Their epiglottis, which is attached to the thyroid cartilage of the laryngeal skeleton, maintains contact with the velum and prevents the SVT<sub>V</sub> from facing the movable tongue. The tongue is also long in the horizontal direction, fitting this configuration. Although this anatomy allows the oral cavity to function as a single resonator, it prevents the pharyngeal cavity from contributing much in that capacity (P.H. Lieberman et al., 1969; P. Lieberman, 1984; Fitch, 2000a; Fitch and Hauser, 2003). Thus, nonhuman mammals have physical constraints to any rapid sequential modification of the cross-sectional areas of the SVT. In contrast, adult humans have an equally long SVT<sub>H</sub> and SVT<sub>V</sub>. Their epiglottis is separated from the velum, and this produces a long oropharyngeal region facing the dorsal surface of the tongue, rostral to the laryngopharyngeal region that faces the epiglottis (P. Lieberman, 1984; Crelin, 1987; Zemlin, 1988; Titze, 1994). The vertical dimension of the tongue is almost equal to the horizontal dimension to fit this configuration, and the internal musculature of the tongue makes the surface highly mobile (Takemoto, 2001). In anatomical terms, these features allow the shapes of the SVT<sub>H</sub> and SVT<sub>V</sub> to be sequentially and rapidly modified by tongue movements, semi-independently of each other (P.H. Lieberman et al., 1969; P. Lieberman, 1984; Fitch, 2000a; Fitch and Hauser, 2003). Thus, humans are capable of extensive modification of the resonant properties of the SVT, which in turn modify the laryngeal sounds, forming the complex sequential phonemes of speech in a single, short exhalation.

In newborn humans, the larynx is positioned close to the palate so there is little vertical pharyngeal space (Negus, 1949; P. Lieberman, 1984; Crelin, 1987; D.E. Lieberman et al., 2001). However, the major descent of the larynx causes the epiglottis to descend relative to the velum (Negus, 1949; Roche and Barkla, 1965; Sasaki et al., 1977; Crelin, 1987; Westhorpe, 1987; Fitch and Giedd, 1999; Vorperian et al., 1999, 2005). This establishes a long oropharyngeal space, rostral to the laryngopharyngeal region in the SVT<sub>V</sub>. Thus, the SVT<sub>V</sub> lengthens rapidly compared with the SVT<sub>H</sub>, and can function as a resonance tube of equivalent volume (P. Lieberman, 1984; Crelin, 1987; Titze, 1994; Fitch, 2000a).

The laryngeal skeleton is suspended from the hyoid apparatus, and the hyoid is in turn suspended from the mandible and cranial base by muscles and ligaments (Zemlin, 1988). Anatomically, two processes accomplish the descent of the larynx: the descent of the laryngeal skeleton relative to the hyoid, and the descent of the hyoid relative to the palate. This process has

been evaluated with detailed measurements on humans from X-ray photographs (D.E. Lieberman and McCarthy, 1999; D.E. Lieberman et al., 2001) and magnetic resonance imaging (MRI; Fitch and Giedd, 1999; Vorperian et al., 1999, 2005). We have studied the development of three living chimpanzees using MRI. Our previous study compared the growth of the SVT in chimpanzees and humans during the first two years of life, and showed that—as in humans—chimpanzees show rapid laryngeal descent, with changes in the relative proportion of the SVT<sub>H</sub> and SVT<sub>V</sub> (Nishimura et al., 2003). Another MRI study (Nishimura, 2005), using a cross-sectional ontogenetic series of embalmed specimens, confirmed this developmental change during early infancy. However, that study also showed that the larynx is lowered only slightly and the horizontal oral cavity grows largely during the juvenile period, causing the proportion of the SVT in chimpanzees to differ from that in humans. Unfortunately, embalming artifacts precluded the study of developmental changes in the position of the hyoid and epiglottis relative to the palate. Therefore, the descent of the chimpanzee larynx is considered to depend primarily on the descent of the laryngeal skeleton relative to the hyoid, but not on the descent of the hyoid *per se* (Nishimura et al., 2003; Nishimura, 2005). Thus, the human 1:1 proportion of the SVT<sub>H</sub> to SVT<sub>V</sub> is still believed to depend on the greater proportional descent of the hyoid during the evolution of the human lineage (Negus, 1949; P. Lieberman, 1984; Crelin, 1987; Flügel and Rohen, 1991; Houghton, 1993; Laitman and Reidenberg, 1993; Nishimura, 2003, 2005; Nishimura et al., 2003). In fact, the term “descent” of the larynx or hyoid often implies the proportional changes of SVT toward such a configuration (here we use the terms “descent” and “descent” without any such implication). Here, we used MRI to evaluate the developmental changes in SVT anatomy in three living chimpanzees aged between two-and-a-half and five years, and we use the results to discuss the evolution of the descent of the larynx.

## Methods

### *MRI procedures*

We have studied the development of three living chimpanzees, named Ayumu (male), Cleo (female), and Pal (female), using MRI. They were born in 2000 and were reared by the biological mothers in the Primate Research Institute (PRI), Kyoto University, Japan (Matsuzawa, 2003). The care and use of the subjects conformed to the guidelines of the PRI (1986, 2002). The chimpanzees were scanned at scheduled intervals from four months to five years of age (Appendix 1). Here, we evaluate the measurements made from two-and-a-half to five years. The scans for Ayumu at four and six months of age were excluded from the analyses in our previous study (Nishimura et al., 2003) because the images were slightly obscured by motion artifacts.

The MRI examination protocol used here was essentially the same as described in a previous study (Nishimura et al., 2003) and was approved by the Ethics Panel of the PRI

(2002). Sagittal tomographic images of the growing chimpanzee head and neck were taken with a General Electrics Signa Profile MRI scanner (0.2 Tesla) at the PRI, using the extremity or head receiving-coil. The subjects were anesthetized intramuscularly with 3.5 mg ketamine hydrochloride (Sankyo Co., Ltd., Tokyo, Japan) and 0.035 mg medetomidine hydrochloride (Meiji Seika Kaisha Ltd., Tokyo, Japan) per kilogram of body weight. After four years of age, they were sedated orally using 3.75 mg of droperidol (in 1.5 ml) before being anesthetized. They were placed supine with their heads fixed to the custom acrylic plastic pad within the coil with belts, so they were always placed in the same posture for scanning. The mid-sagittal plane of the head was adjusted to the laser lights of the MR scanner. This procedure inevitably bends the neck slightly at the level inferior to the vocal folds (Fig. 1). All imaging sequences were sagittal spin echo series with time-to-echo durations ranging from 17 to 32 ms, time-to-repeat durations of 600 ms, fields of view ranging from 18 to 28 cm with 2.7 mm or 3.0 mm slice thicknesses, and 0.8 mm or 0.5 mm gaps between slices using an acquisition matrix of  $192 \times 192$  with two excitations. These parameters were chosen generally based on subject size (Appendix 1). The matrix of all MR images was  $256 \times 256$  pixels, and image resolutions ranged from  $0.70 \times 0.70$  to  $1.09 \times 1.09$  mm/pixel (Appendix 1).

### Measurements

MR images were transferred from the scanner to a personal computer, using Vox-Base Transmit software (J-Mac System, Sapporo, Japan). The images were converted from DICOM to TIFF format, using Intage software (KGT, Tokyo, Japan). These images were evaluated using Adobe PhotoShop CS software (Adobe Systems, San Jose, CA, USA) to record measurement points and standard planes. Measurement points and standard planes on the mid-sagittal plane included the following anatomical landmarks: anterior nasal spine (ANS); anterior tubercle of the atlas (ATA); endoprosthion (EPr); hyoid bone (HB); posterior nasal spine (PNS); posterior oropharyngeal wall (POW); palatal plane (PP); posterior pharyngeal wall line (PPW); and vocal fold (VF). These definitions (Table 1) are those defined for chimpanzees by Nishimura (2005) and are roughly equivalent to those used for radiographic studies of humans (D.E. Lieberman et al., 2001). The present study used two additional points: epiglottis (EG) and velum (VL). These definitions (given in Table 1) were those used for chimpanzees by Nishimura et al. (2003).

The coordinate values of the measurement points for linear dimensions were measured three times from MR images,

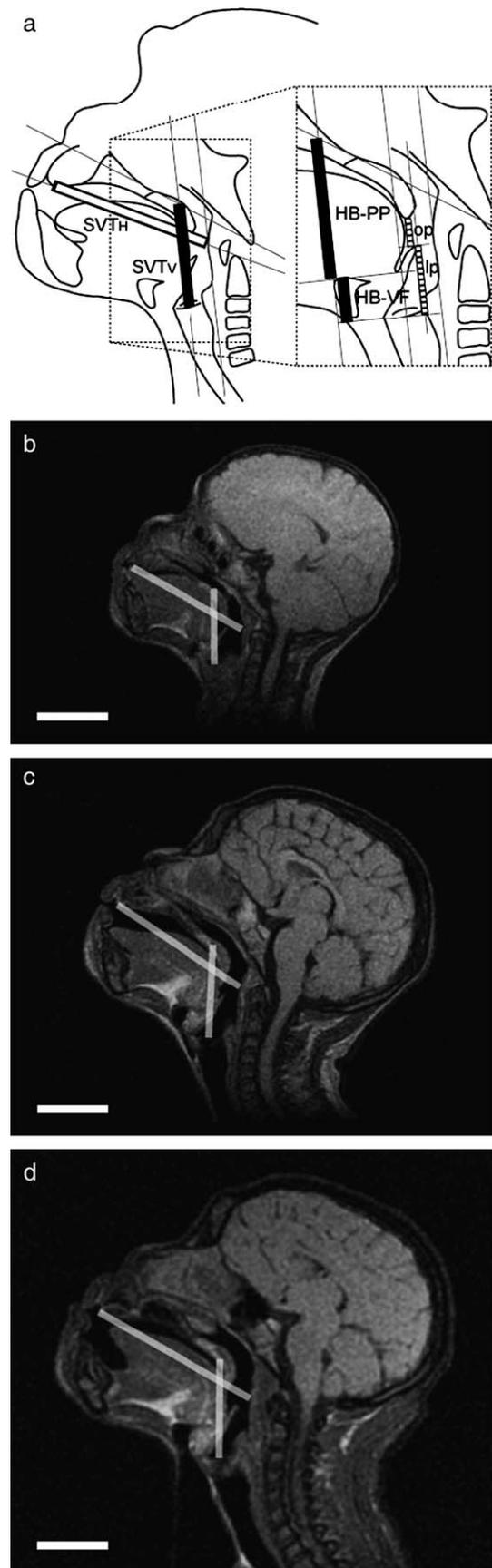


Fig. 1. Growth of the SVT in chimpanzees. a, Left, mid-sagittal diagram of  $SVT_H$  (outlined) and  $SVT_V$  (filled) lengths. Right, diagram of the distances from the hyoid to the vocal folds (HB–VF) and to the palate (HB–PP); the oropharyngeal (op) and laryngopharyngeal (lp) dimensions. See Methods for definitions of the dimensions. b–d, Mid-sagittal magnetic resonance images of a female chimpanzee (Pal) at: b, four months of age; c, two years of age; and d, four years of age. Scale bar = 3.0 cm.

Table 1  
Definitions of the measurement points and standard planes used

Landmarks and planes	Abbr.	Definition
Anterior nasal spine	ANS	The most anterior inferior point of the piriform aperture of the nose, which is roughly equivalent to the most anterior root point of the nasal septum <sup>1</sup>
Anterior tubercle of the atlas	ATA	The superior–inferior midpoint of the anterior tubercle of the atlas <sup>2</sup>
Epiglottis	EG	The most superior point of the epiglottis
Endoprosthion	EPr	The most anterior inferior point of the lingual surface of the alveolar premaxilla
Posterior nasal spine	PNS	The most posterior point of the maxillary body at the level of the nasal floor at the junction of the hard and soft palates
Posterior margin of the oral cavity	POC	Plane from PNS to EPr–POW, parallel to the posterior pharyngeal wall (PPW)
Posterior oropharyngeal wall	POW	Point on the posterior pharyngeal wall opposite the anterior tubercle of the atlas along the plane from EPr to ATA
Palatal plane	PP	The line from the ANS to PNS
Posterior pharyngeal wall	PPW	The most posterior straight line of the pharyngeal wall from the level of the velum to the laryngeal orifice
Vocal folds	VF	The anterior–posterior midpoint of the vocal folds
Velum	VL	The most posterior inferior point of the palatine velum, excluding the uvula

All landmarks and planes were defined on the mid-sagittal plane of the MR images.

<sup>1</sup> This definition is the same as that for chimpanzees used by Nishimura (2005) and Nishimura et al. (2003), but is different from that used by D.E. Lieberman et al. (2001) in the narrow sense because no true anterior nasal spine is found in chimpanzees.

<sup>2</sup> This definition is the same as that used for chimpanzees by Nishimura (2005) and Nishimura et al. (2003), but is different from that used for the human ATA (D.E. Lieberman et al., 2001). The human ATA is defined as the most anterior and superior point of the anterior tubercle of the atlas that projects on the sagittal plane in radiographs. This point was identified only obscurely on mid-sagittal MR images of chimpanzee subjects, so the chimpanzee ATA was here redefined as being roughly equivalent to the human ATA.

using ImageJ software (W. Rasband, National Institute of Mental Health, Bethesda, MD, USA). If the values did not agree, they were remeasured. Measurements included: SVT<sub>H</sub> length, along the EPr–ATA line from the EPr to the POW; SVT<sub>V</sub> length, parallel to the PPW from the VF to the PP; the distances from the hyoid to the palatal plane and to the vocal folds (HB–PP and HB–VF, respectively), parallel to the PPW from the HB to the PP and to the level of VF (see the keys to Fig. 1a). These definitions of dimensions are those used for chimpanzees by Nishimura (2005) and are similar to those used for humans by D.E. Lieberman et al. (2001). Although there are some inconsistencies in the abbreviations of measurement points and standard planes, the dimensions are the same as those used previously (Nishimura et al., 2003; Nishimura, 2005). The present study also examined the lengths of the oropharyngeal (op) and laryngopharyngeal (lp) parts of the vertical pharyngeal cavity, parallel to the PPW from the EG to the levels of the VL and VF, respectively (see the key to Fig. 1a). These dimensions are the same as those used by Nishimura et al. (2003).

#### Comparing growth phases between chimpanzees and humans

The measurements were recorded for the chimpanzees at ages ranging from four months to five years (Nishimura et al., 2003; present study). Those for humans by D.E. Lieberman et al. (2001) were taken from one month to thirteen years and nine months of age. The developmental patterns were compared in terms of the developmental ages of both species after their chronological ages were adjusted to correspond to dental eruption stages, which reflect analogous growth phases in both species. In this study, three growth stages, “early

infancy”, “late infancy”, and the “juvenile period”, were defined as the dental stage from birth to before the eruption of the deciduous dentition, the stage from the eruption of the deciduous dentition to before the eruption of the first molars, and the stage after the eruption of the first molars and before the eruption of the second molars, respectively. Based on studies of dental eruption ages in captive living chimpanzees (Conroy and Mahoney, 1991; Kuykendall et al., 1992) and European-derived humans (Hurme, 1949; Lysell et al., 1962; Smith and Garn, 1987; Smith, 1991), the chronological ages of the chimpanzees and humans were adjusted to correspond to dental stages. In chimpanzees, “early infancy” is defined here as the period from birth to one year of age, “late infancy” as the period from one to three years of age, and the “juvenile” stage as the period from three to seven years of age. In humans, “early infancy” is defined as the period from birth to two-and-a-half years of age, “late infancy” as the period from two-and-a-half to six years of age, and the “juvenile” stage as the period from six to twelve years of age (Fig. 2). Thus, the developmental patterns were examined here up to five years of age in chimpanzees and compared with those published for up to nine years of age in humans (Fig. 2).

#### Results

The scan for Ayumu at 52 months of age showed that, at the time of scanning, the tongue was contracted anterosuperiorly, probably causing additional elevation of the hyoid and larynx (Fig. 3; Appendix 2). Although this indicates the dynamic anatomy of the chimpanzee vocal tract (discussed below), the scan was excluded from the analyses of the developmental changes in resting anatomy of the SVT.

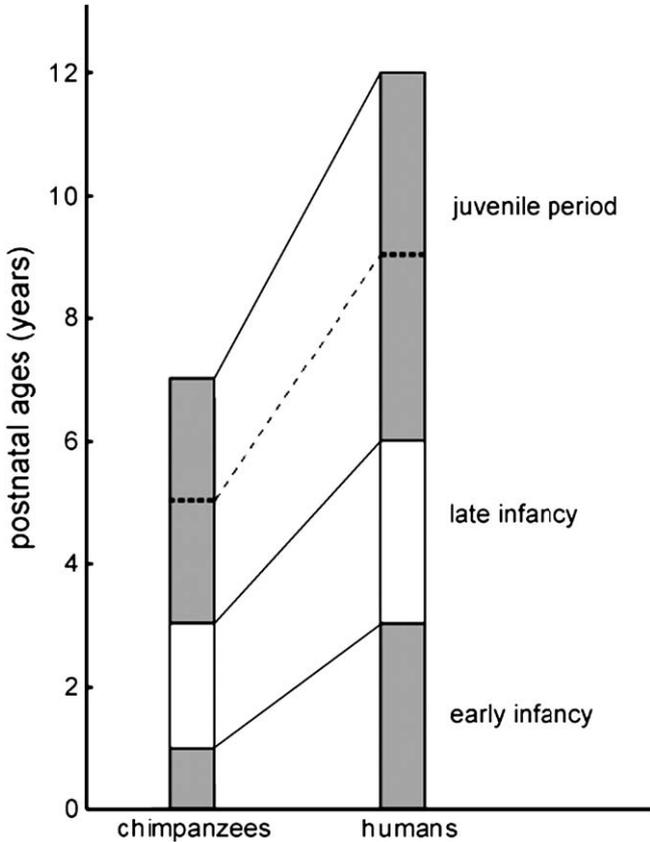


Fig. 2. Analogous growth phases in chimpanzees and humans. The chronological ages of the species are expressed in terms of dental stages, based on the dental eruption ages. Here, we compare the SVT development of both species until the growth phase indicated by the dotted line.

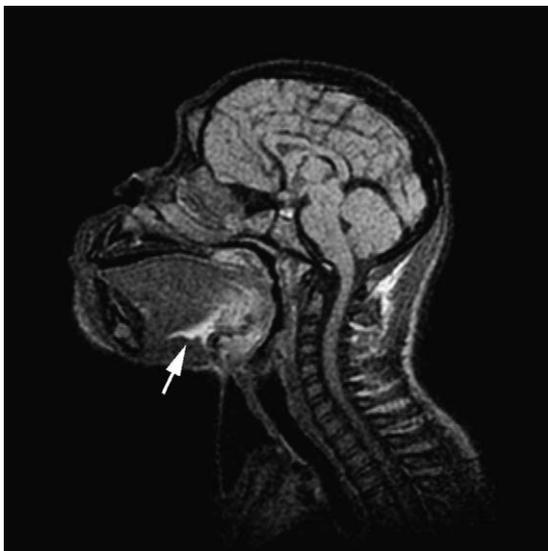


Fig. 3. MRI scan of Ayumu at 52 months of age. When capturing the image the tongue was contracted and the hyoid was pulled antero-superiorly. This is shown by the deformed connective tissue between the *genioglossus* and *geniohyoideus* muscles (arrow; white tissue on the image), compared with the images of Figure 1.

In chimpanzees, the  $SVT_V$  increases more than the  $SVT_H$  during early infancy (Nishimura et al., 2003), but thereafter the  $SVT_H$  shows greater growth relative to that of the  $SVT_V$  (Fig. 1). This is reflected in the age-related changes in the ratio of the  $SVT_H$  to  $SVT_V$  lengths shown in Figure 4a and Appendix 2. Although the absolute values are greater in chimpanzees than in humans, the ratio decreases in chimpanzees—as in humans—during early infancy (Nishimura et al., 2003). After late infancy, it consistently decreases to reach the adult ratio of 1:1 by nine years of age in humans (D.E. Lieberman et al., 2001), whereas in chimpanzees the direction of change in the ratio reverses, and it increases to reach the ratio of 2.10 at five years of age. Figure 4b and Appendix 2 show

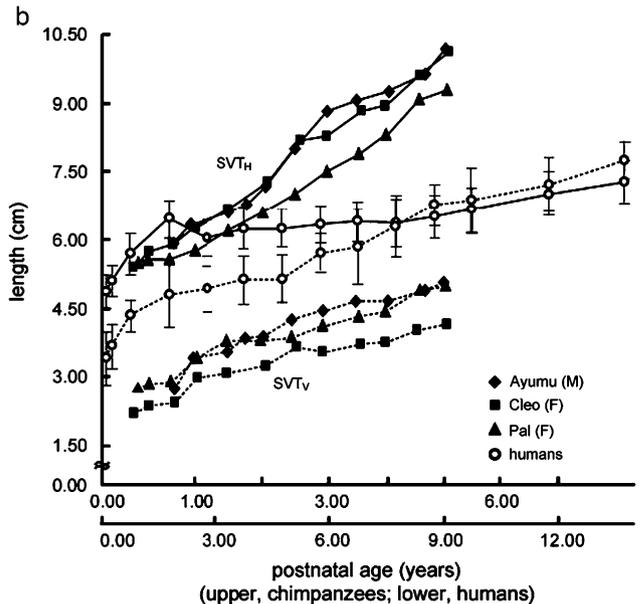
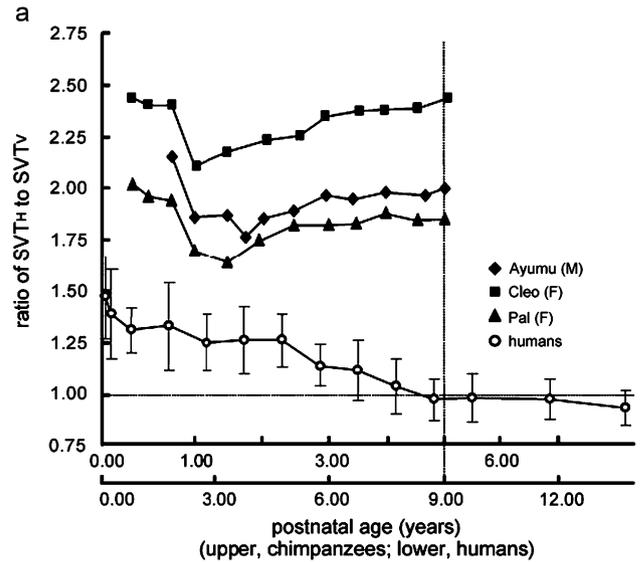


Fig. 4. Growth of the SVT in the three chimpanzees: Ayumu (male, diamonds), Cleo (female, squares), and Pal (female, triangles). Measurements on humans (pooled sexes, open circles) are from D.E. Lieberman et al. (2001), with permission. a, Age-related changes in the ratio of  $SVT_H$  to  $SVT_V$  lengths. b, Growth of the  $SVT_H$  (continuous line) and the  $SVT_V$  lengths (dotted line).

the growth changes in SVT<sub>V</sub> and SVT<sub>H</sub> lengths measured by MRI in living chimpanzees. During early infancy, the growth patterns of these dimensions in chimpanzees are similar to those in humans, although the absolute values of the SVT<sub>V</sub> are smaller in chimpanzees than in humans (Nishimura et al., 2003). Thereafter, the SVT<sub>H</sub> in humans grows much more slowly (D.E. Lieberman et al., 2001), whereas in chimpanzees it continues to increase greatly and reaches 9.8 cm at five years. In contrast, even after late infancy, the growth pattern of the SVT<sub>V</sub> in chimpanzees is similar to that in humans; the chimpanzee SVT<sub>V</sub> grew consistently to 4.7 cm at five years of age. Thus, the different changes in the proportions of the SVT between chimpanzees and humans after late infancy do not involve the growth of the SVT<sub>V</sub>, and result from the greater growth of the chimpanzee SVT<sub>H</sub>.

As for the growth of the SVT<sub>V</sub>, the laryngeal skeleton of chimpanzees descends rapidly relative to the hyoid in early infancy, but the hyoid descends only slightly relative to the palate in that period (Nishimura et al., 2003). Thereafter, the laryngeal skeleton continues to descend gradually, but the hyoid descends rapidly. This finding is demonstrated in Figure 5 and Appendix 2. The distance from the hyoid to the vocal fold (HB–VF) increases rapidly to 1.1 cm by the first year of age, whereas the distance from the hyoid to the palate (HB–PP) shows only a negligible change in the first year of life (Nishimura et al., 2003). After late infancy, the HB–VF measure continues to increase to 2.2 cm at five years of age, but the HB–PP increases steeply from 2.9 cm to 5.4 cm at that age. A growth-related change in the descent of the laryngeal skeleton relative to the hyoid, similar to that of chimpanzees, is also observed in humans. Although the human hyoid descends relative to the palate even in early infancy, it continues to descend and this descent is more rapid than the descent of the laryngeal skeleton relative to the hyoid after late infancy (D.E. Lieberman et al., 2001). During that period, the epiglottis continues to descend gradually from the velum in chimpanzees, as in humans, to lengthen the oropharyngeal part rostral to the laryngopharyngeal parts (Fig. 5c, Appendix 2). Thus, after late infancy in chimpanzees, the major descent of the larynx is also accounted for by the descent of the hyoid, as in humans, and it causes elongation of an oropharyngeal part.

**Discussion**

This study provides no evidence for the idea that the rapid descent of the larynx or hyoid arose uniquely in the human lineage to allow the configuration of the equally long SVT<sub>H</sub> and SVT<sub>V</sub> to develop and thus permit the acquisition of speech in this lineage (Negus, 1949; P. Lieberman, 1984; Crelin, 1987; Houghton, 1993; Laitman and Reidenberg, 1993; Nishimura, 2003, 2005; Nishimura et al., 2003). Some gross anatomical studies using a cross-sectional ontogenetic series of embalmed chimpanzee specimens have suggested a developmental lowering in the position of the larynx or hyoid in chimpanzees (Kelemen, 1948; Avril, 1963; Jordan, 1971), but it was unclear whether this was analogous to the descent of the larynx in

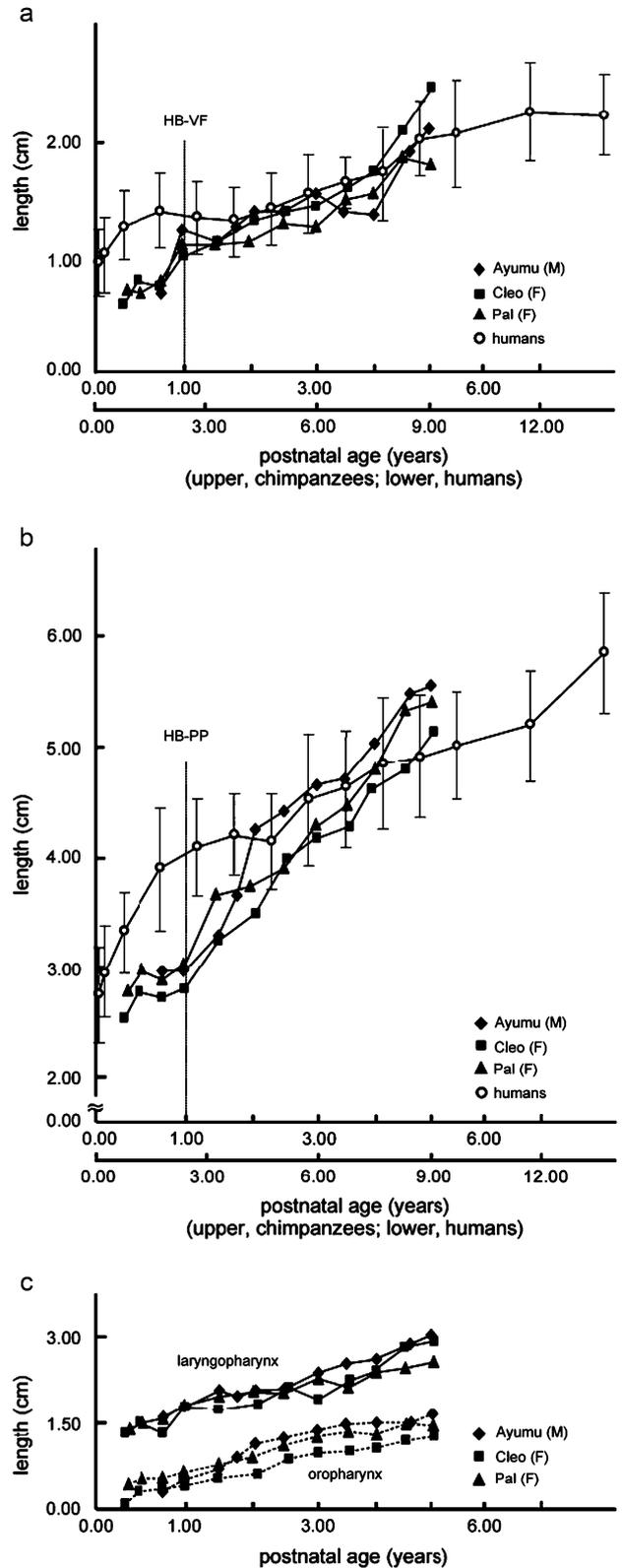


Fig. 5. Increases in the dimensions of the SVT<sub>V</sub>. a, Distance from the hyoid to the vocal folds (HB–VF). b, Distance from the hyoid to the palate (HB–PP). c, Growth of the laryngopharyngeal (lp, continuous line) and oropharyngeal (op, dotted line) parts of the vertical pharyngeal cavity. The symbols for individual subjects used in the present study and for humans taken from D.E. Lieberman et al. (2001) are as in Figure 4.

humans. Our previous study (Nishimura et al., 2003) confirmed that chimpanzees show a laryngeal descent with changes in the relative proportion of the  $SVT_H$  to  $SVT_V$  during early infancy, but this is not identical to the phenomenon in humans. Another MRI study using a cross-sectional ontogenetic series of embalmed chimpanzee specimens (Nishimura, 2005) showed relative changes in the  $SVT_H$  and  $SVT_V$  similar to those observed in the present study. However, the low resolution of the cross-sectional samples allowed the conclusion to be drawn that the adult configuration of the chimpanzee SVT results, at least partly, from a lesser descent of the larynx compared with that in humans, i.e., a lack of any major descent of the hyoid (Nishimura, 2005). Here, our longitudinal MRI study confirms that this descent of the hyoid is shared with chimpanzees, despite differences in the developmental trajectory of the SVT configuration between humans and chimpanzees.

However, there are slight differences in the timing and rate of the hyoid descent in humans and chimpanzees. Although this issue must be resolved in the future using a larger sample, it might be caused by the development of the laryngeal air sac in chimpanzees. Whereas humans have no sac, chimpanzees have a huge sac extending superiorly from the bilateral laryngeal ventricles, between the hyoid and thyroid cartilage bilaterally, and expanding anteriorly to the ventral region of the neck (Kelemen, 1948; Negus, 1949; Starck and Schneider, 1960; Avril, 1963; Hayama, 1970; Hewitt et al., 2002). This sac developed to reach the dorsal aspect of the body of the hyoid at four months of age for all three subjects in the present study (a small dark pouch on Fig. 1b; Nishimura et al., *in press*), and the associated anatomical changes might thereby contribute to elevate the hyoid in early infancy.

Regardless of these slight differences, the descent of the chimpanzee larynx and hyoid continues to lower the epiglottis from the velum and pulls the tongue down in the pharynx, elongating an oropharyngeal region facing the dorsal surface of the tongue. The chimpanzee epiglottis is believed to maintain contact with or to remain close to the velum even in adults, based on examinations using embalmed cadavers (Laitman and Heimbuch, 1982; P. Lieberman, 1984; Fitch, 2000a; Nishimura, 2005). However, MRI studies in living chimpanzees showed that the epiglottis loses contact with the velum in early infancy (Nishimura et al., 2003), as in humans (Sasaki et al., 1977), so that an oropharyngeal region is secured in the adult (Nishimura, 2006). Inevitably, the position of the epiglottis relative to the velum is affected by embalming artifacts (Nishimura, 2005) and varies actively in living animals (see Fig. 3; Fitch, 2000b). The latter suggests that the head posture at scanning (Nishimura et al., 2003; Nishimura, 2006; present study) might always lower or additionally elevate the epiglottis of the living subjects, although the present analysis carefully excluded any measurements in the nonresting subject (Ayumu at 52 months of age). However, in these studies, the neck of all the subjects was always bent slightly at the level below the vocal folds (Nishimura et al., 2003; Nishimura, 2006; present study). In addition, a varied head posture has little influence on the  $SVT_V$  dimension, which

reflects the position of the vocal folds relative to the palatal plane (Nishimura, 2005). This suggests that the position of the epiglottis, which is attached to the thyroid cartilage of the laryngeal skeleton, is also retained relative to the velum, regardless of the varied head posture. These facts suggest that varying head postures have limited influence on the over- or underestimation of oropharyngeal measures. This study showed the steady elongation of the oropharyngeal region, under the same conditions; unfortunately, there is no comparable information about the growth rates of the human oropharyngeal and laryngopharyngeal components. On the other hand, the human pharynx, defined as a linear dimension from VL to VF, increases from 2.63 cm at two to four years of age to 3.92 cm at nine to ten years of age, an increase of 49% (Fitch and Giedd, 1999). This increase is similar to the increases in sum of the oropharyngeal and laryngopharyngeal parts in the corresponding periods in chimpanzees: the sum of the two parts increases from 2.84 cm at two years of age to 4.30 cm at age five, an increase of 51% (Appendix 2). In humans, the pharyngeal dimension continues to increase to 5.64 cm in the adult (19 to 25 years of age), an increase of 114%. Despite little comparable information in living chimpanzees, an adult male subject at 23 years of age shows the sum of 5.58 cm, an increase of 96% (unpublished data, although the MR image is shown in Nishimura, 2006). Taking consideration of the secondary descent of the human larynx in the pubertal period (an additional elongation of the pharyngeal dimension; Fitch and Giedd, 1999), this indicates that the development of the pharyngeal dimension is similar in the two species. In addition, the timing in the loss of contact between the epiglottis and velum is similar approximately analogous in humans and chimpanzees: before 12 to 18 months in humans (Sasaki et al., 1977), and before 6 months in chimpanzees (Nishimura et al., 2003). This suggests that the development of the oropharyngeal dimension in chimpanzees is approximately analogous to that in humans. Although this issue must be resolved in the future using larger samples of humans and chimpanzees with varied head positions, it is probable that the major descent of the larynx, elongating an oropharyngeal region, was shared fully by the last common ancestor of chimpanzees and humans.

Uncertainty remains regarding the evolutionary path involving the major descent of the laryngeal skeleton and hyoid before the divergence of the human from the chimpanzee lineage. A study using computed tomography (CT) demonstrated a slight descent of the larynx and hyoid relative to the palate in macaques from birth to 24 years of age (Flügel and Rohen, 1991). The measurements reported by those authors cannot be directly compared with the studies of humans (D.E. Lieberman et al., 2001) and chimpanzees (Nishimura et al., 2003; Nishimura, 2005; present study) because of a discrepancy in the definitions. However, they suggest that an increase of the vertical dimension of the SVT in the first six months of macaques may be roughly similar to those in the corresponding periods of the other two species, although the measurements after six months of macaques must be excluded because of their

scarcity and irregularity. Based on the studies of dental eruption ages in macaques (Schultz, 1933; Iwamoto et al., 1984), the period from birth to six months of age corresponds to “early infancy” defined here for humans and chimpanzees. In macaques, the distance from the palate to the glottis increases from 1.2 cm on day one to 1.9 cm at six months of age, an increase of 58% (Flügel and Rohen, 1991). The SVT<sub>V</sub> in humans increases from 3.40 cm at one month to 4.92 cm at two years and nine months of age, an increase of 44% (D.E. Lieberman et al., 2001). In chimpanzees, it grows from 2.47 cm at four months to 3.26 cm at one year of age, an increase of 32% (Nishimura et al., 2003; see Appendix 2). Taking consideration of a lack of measurements in the periods earlier than one month for humans and four months for chimpanzees, these increases in the vertical dimension of the SVT in early infancy are similar in all three species. However, it must be noted that macaques have a laryngeal air sac opening above the anterior commissure of the glottis, extending superiorly to reach the dorsal aspect of the hyoid body and expanding inferiorly to the ventral region of the neck (Negus, 1949; Hayama, 1970; Hewitt et al., 2002). Although the development of this macaque air sac is still unclear, the developing sac might lower the laryngeal skeleton additionally relative to the hyoid in early infancy. In fact, although the descent of the larynx also continues after late infancy in macaques, CT scans show that the descent in macaques does not separate the epiglottis from the velum, producing no or little oropharyngeal space even in adults (Flügel and Rohen, 1991). Moreover, the laryngeal skeleton is separated from the hyoid and assured of mobility independent of the hyoid in hominoids, including humans, but this is in contrast to other anthropoids whose laryngeal skeletons are locked into the hyoid body and are tied tightly with or directly articulated with the greater horn of the hyoid, according to the comparative anatomy of adult cadaver specimens (Nishimura, 2003). Although this issue must be resolved in the future using larger samples and similar methods, these facts suggest that the descent of the larynx in macaques is not analogous to that seen in humans and chimpanzees. The major descent of the larynx may thus have evolved in two steps: the descent of the laryngeal skeleton relative to the hyoid in a common ancestor of all extant hominoids (Nishimura, 2003; Nishimura et al., 2003), and descent of the hyoid relative to the palate in a common ancestor of humans and chimpanzees. On the other hand, the descent of the laryngeal skeleton may have accompanied the descent of the hyoid. The hyoid provides the base of the tongue muscles and it is physically linked to the laryngeal skeleton, mandible, and cranial base through muscles, ligaments, and other soft tissues (Zemlin, 1988; Titze, 1994). The hyolaryngeal complex plays an important role in integrated functions of the pharynx and larynx, such as deglutition, breathing, and vocalization (Negus, 1949; P. Lieberman, 1984; Crelin, 1987; Zemlin, 1988; Hiiemae and Palmer, 1999). The complexity of the anatomy and the integrated nature of the vital functions of the hyolaryngeal complex raise the possibility that the major

descent of the laryngeal skeleton and hyoid may have arisen in a single shift to facilitate these integrated functions in a common ancestor of extant hominoids.

It is likely that the major descent of the larynx originally conferred advantages for functions unrelated to the sophisticated articulation of speech, because the faculty arose in the human lineage after its divergence from the chimpanzee lineage. This argument is also supported by the situation of a descended larynx in nonprimate mammals (Fitch, 2000b; Fitch and Reby, 2001; Weissengruber et al., 2002; Reby et al., 2005). Fitch and Reby (2001) showed that the position of the larynx in the males of some species of deer is similar to that in adult humans and that they lower the larynx to produce resonance at lower frequencies during the roaring of the rut season. This modification in vocalization possibly contributes to exaggeration of their perceived body size to increase the repulsive effects against other males (Reby et al., 2005). The ability to lower the hyolaryngeal complex is also found in the vocalizing of dogs, which have a resting anatomy with the epiglottis maintaining contact with the velum (Fitch, 2000b). That such dynamic lowering of the larynx exists in independent lineages clearly indicates the selective advantage or advantages of vocalization, independent of speech and language, and can account for the static low position of the larynx that was achieved with the developmental descent of the larynx in humans and chimpanzees. Such nonlinguistic advantage might be achieved by the secondary descent of the human larynx, which effects formant frequencies and probably underlies the vocal remodeling process during the puberty of human males (Fitch and Giedd, 1999). However, the integrated nature of the function of the hyolaryngeal complex makes it unlikely that any single selective advantage involving vocalization can account for the major descent and resulting low position of the larynx. The integration of deglutition and breathing suggests that an advantage in such physiology unrelated to vocalization may partly account for it (Nishimura, 2003). Such dynamic capabilities of the vocal tract and hyolaryngeal complex strongly indicate that critical evidence for this issue will be provided by evaluations of dynamic activities to perform a physiological function, not just by evaluations of the static anatomy of the SVT. Chimpanzees also show some dynamic activities, for example contraction of the tongue to pull up the hyoid (see Fig. 3) and retraction of the tongue to lower the hyolaryngeal complex (see Fig. 3 in Nishimura, 2005); unfortunately, there is no information about the relationships between such activities and physiological performances. Thus, such information in nonhuman primates and mammals will facilitate our understanding of the evolutionary pathway involving the major descent and static low position of the larynx against both phylogenetic and functional backgrounds.

Although this study suggested that the descent of the larynx and hyoid in chimpanzees is analogous to that in humans, but not to that in macaques, the adult configuration of the SVT in chimpanzees resembles that of macaques

rather more than humans (Nishimura, 2005, 2006). Here, the ratio of  $SVT_H$  and  $SVT_V$  lengths in chimpanzees is higher than that in humans already in infancy, and it increases after late infancy—in contrast to humans—to result in a distinct final SVT configuration. Such differences between humans and chimpanzees were probably established by the evolution of facial flattening—the reductions of facial prognathism and projection—in the human lineage, but not by that of laryngeal descent itself. Similar developments in the pharyngeal configuration strongly suggest that the  $SVT_V$  dimension in chimpanzees probably corresponds approximately to that in humans even at birth and later, despite smaller absolute values of the  $SVT_V$  length in chimpanzees than in humans. This is supported in particular by the similar timing of the loss of contact between the epiglottis and velum. In contrast, the MR images show that the face is already projected and prognathic in chimpanzee infants (Fig. 1b). These characteristic differences in facial shape between the two species partly arise in prenatal development (Enlow, 1990; Ackermann and Krovitz, 2002; Penin et al., 2002; Mitteroecker et al., 2004). These facts suggest that the  $SVT_H$  dimension in chimpanzees does not correspond to that in humans already at birth, although the absolute values of the  $SVT_H$  length per se are similar. If so, this difference is principally involved in causing the higher ratio of the  $SVT_H$  and  $SVT_V$  lengths during infancy in chimpanzees compared with humans. In addition, after late infancy, the disparity of the  $SVT_H$  growth trajectory contributes to differentiate further the SVT configuration in chimpanzees from that in humans. This fact supports the idea that the evolutionary attainment of a 1:1 proportion of the  $SVT_H$  and  $SVT_V$  required facial flattening rather than the additional descent of the larynx in the human lineage. Such reorganization of the facial architecture probably involved modifications to mandibular form. In anatomical terms, modification of the mandibular height affects the position of the hyoid (D.E. Lieberman et al., 2001), and therefore the facial flattening might have been accompanied by an additional descent of the hyoid. However, this does not mean that such facial flattening squeezed the tongue into the pharynx, which makes the larynx descend along the neck (Negus, 1949; Flügel and Rohen, 1991; Aiello, 1996, 1998; Mithen, 2005). The present study provides critical evidence for the idea that facial flattening merely produced a short, horizontal dimension for the tongue, fitting the  $SVT_H$  configuration in the human lineage, independently of the descent of the hyoid, which had already increased the vertical dimension. These reductions in facial prognathism and projection were long-term trends in primate and human evolution (Klein, 1989; Wood, 1992; Aiello and Dean, 1998; Fleagle, 1999; Wood and Collard, 1999; Trinkaus, 2003), and therefore it is unlikely that the selective advantage afforded by speech originally accounted for this rearrangement. Thus, facial flattening has probably evolved only secondarily, with anatomical consequences that facilitated the evolution of sophisticated spoken language in the human lineage.

## Conclusions

The major descent of the larynx and the reduced growth of the face essentially constitute the “ontogeny” of the morphological foundations of speech in humans (Negus, 1949; P. Lieberman, 1984; Crelin, 1987; Zemlin, 1988; Flügel and Rohen, 1991; Laitman and Reidenberg, 1993; Fitch and Giedd, 1999; D.E. Lieberman et al., 2001). However, this study does not support the “evolutionary” hypothesis that this descent occurred in the human lineage, and thereby produced the SVT configuration with an equally long  $SVT_H$  and  $SVT_V$ , leading to the origins of speech. The major descent of the larynx arose before the diversification of human and chimpanzee lineages, but it has not led to such a configuration of the SVT. Briefly, the term “descent” of the larynx has no implication for the proportional changes toward such an SVT configuration. The attainment of the SVT configuration unique to humans required facial flattening—modifications in the facial development to reduce the oral horizontal dimension—rather than additional laryngeal descent in the human lineage. These two separate developmental mechanisms probably arose independently during the evolution of nonhuman primates and humans, which were secondarily advantageous for speech in the latter. Therefore, it is unlikely that the faculty for speech evolved in humans through a single coordinated adaptive shift in all the relevant biological foundations. Instead, we propose the concept of a multiple-step evolution of the disparate elements in response to different selection pressures during the long period of primate evolution. This is also possibly the case for the evolution of the cognitive foundations of language (e.g., Matsuzawa, 2001). Rather than using one unique feature as evidence for the evolution of speech and language, a multidisciplinary approach should contribute greatly to our understanding of the evolution of the biological foundations of language.

## Acknowledgments

We are grateful to A. Kato, K. Kumazaki, N. Maeda, S. Goto, K. Matsubayashi, M. Tomonaga, M. Tanaka, Y. Hamada, and the staff of PRI for daily veterinary care for the three chimpanzees and/or support for the MRI examinations. We thank D.E. Lieberman and his colleagues for kindly permitting us to use the numerical data from D.E. Lieberman et al. (2001). Portions of this work were performed at PRI under 2004 and 2005 PRI Cooperative Research Programs (Grant 4-1 and 3-1 to T. N.). This work was supported by a Research Fellowship of the Japan Society for the Promotion of Science (JSPS) for Young Scientist (Grant 16000326 to T. N.), by Grants-in-Aid for the Biodiversity Research of the 21st Century Center of Excellence (Grant A14 to Kyoto University), and for Specially Promoted Research (Grants 12002009, 16002001 to T. M.) from the Ministry of Education, Culture, Sports, Sciences, and Technology of Japan, and by the JPSP Core-to-Core Program HOPE (Grant 15001 to T.M.).

### Appendix 1. Subjects used, their ages at the times of scans, and major parameters of scanning

Subjects	Age (months)	Pixel sizes <sup>1</sup> (mm/pixel)	FOV (mm)	Thickness (inter-slice gap) <sup>2</sup> (mm)	
Ayumu	4	0.74	190	2.7 (0.8)	
	6	0.70	180	3.0 (0.5)	
	9	0.74	190	2.7 (0.8)	
	12	0.70	180	3.0 (0.5)	
	18	0.70	180	3.0 (0.5)	
	22	0.90	230	2.7 (0.8)	
	25	0.86	220	3.0 (0.5)	
	30	0.98	250	3.0 (0.5)	
	36	1.09	280	3.0 (0.5)	
	42	0.98	250	3.0 (0.5)	
	48	0.98	250	3.0 (0.5)	
	52	0.98	250	3.0 (0.5)	
	54	0.98	250	2.7 (0.8)	
	60	0.98	250	3.0 (0.5)	
Cleo	4	0.70	180	3.0 (0.5)	
	6	0.70	180	3.0 (0.5)	
	9	0.70	180	3.0 (0.5)	
	12	0.74	190	2.7 (0.8)	
	18	0.70	180	3.0 (0.5)	
	25	0.86	220	3.0 (0.5)	
	31	0.98	250	3.0 (0.5)	
	36	0.98	250	3.0 (0.5)	
	43	0.98	250	3.0 (0.5)	
	48	0.98	250	3.0 (0.5)	
	54	0.98	250	3.0 (0.5)	
	60	0.98	250	3.0 (0.5)	
	Pal	4	0.70	180	3.0 (0.5)
		6	0.74	190	2.7 (0.8)
9		0.70	180	3.0 (0.5)	
12		0.70	180	3.0 (0.5)	
18		0.70	180	3.0 (0.5)	
24		0.86	220	3.0 (0.5)	
30		0.98	250	3.0 (0.5)	
36		0.98	250	3.0 (0.5)	
42		0.98	250	3.0 (0.5)	
48		0.98	250	3.0 (0.5)	
54		0.98	250	3.0 (0.5)	
60		0.98	250	3.0 (0.5)	

<sup>1</sup> The values varied irregularly during infancy, but had little influence on the accuracy in measurements (see Results).

<sup>2</sup> This means that the slice interval of all scans was 3.5 mm, regardless of differences in slice thickness and inter-slice gap.

### Appendix 2. Measurements of dimensions

Subjects	Age (months)	SVT <sub>H</sub>	SVT <sub>V</sub>	Oropharynx (op)	Laryngopharynx (lp)	HB–PP	HB–VF
Ayumu	9	5.93	2.75	0.29	1.60	3.00	0.70
	12	6.33	3.41	0.49	1.78	2.98	1.27
	18	6.59	3.53	0.67	2.07	3.39	1.14
	22	6.78	3.84	0.89	1.97	3.71	1.28
	25	7.17	3.87	1.12	2.05	4.30	1.41
	30	8.03	4.25	1.23	2.08	4.46	1.42
	36	8.80	4.47	1.35	2.38	4.68	1.58
	42	9.04	4.65	1.45	2.54	4.74	1.42
	48	9.25	4.67	1.48	2.61	5.06	1.38
	52	9.06	4.63	1.11	2.85	4.17	1.61
	54	9.63	4.90	1.48	2.86	5.50	1.95
	60	10.16	5.08	1.66	3.03	5.57	2.19

Subjects	Age (months)	SVT <sub>H</sub>	SVT <sub>V</sub>	Oropharynx (op)	Laryngopharynx (lp)	HB–PP	HB–VF	
Cleo	4	5.39	2.21	0.07	1.31	2.57	0.60	
	6	5.73	2.39	0.30	1.50	2.81	0.80	
	9	5.88	2.45	0.34	1.30	2.76	0.76	
	12	6.26	2.97	0.39	1.78	2.83	1.03	
	18	6.66	3.06	0.53	1.71	3.34	1.16	
	25	7.27	3.26	0.60	1.82	3.58	1.32	
	31	8.19	3.64	0.87	2.11	4.04	1.41	
	36	8.29	3.53	0.97	1.91	4.22	1.47	
	43	8.84	3.73	1.00	2.24	4.31	1.62	
	48	8.95	3.76	1.06	2.43	4.69	1.78	
	54	9.59	4.02	1.17	2.82	4.85	2.19	
	60	10.10	4.15	1.25	2.93	5.14	2.58	
	Pal	4	5.50	2.73	0.42	1.39	2.80	0.72
		6	5.58	2.85	0.52	1.48	2.99	0.70
9		5.56	2.87	0.53	1.57	2.91	0.82	
12		5.78	3.41	0.63	1.81	3.04	1.12	
18		6.22	3.80	0.75	1.97	3.73	1.13	
24		6.60	3.79	0.88	2.04	3.81	1.16	
30		7.01	3.85	1.10	2.01	3.97	1.31	
36		7.50	4.12	1.26	2.28	4.32	1.28	
42		7.88	4.31	1.33	2.11	4.50	1.52	
48		8.31	4.41	1.27	2.38	4.81	1.57	
54		9.04	4.90	1.47	2.46	5.29	1.92	
60		9.25	5.00	1.47	2.56	5.39	1.82	

### References

- Ackermann, R.R., Krovitz, G.E., 2002. Common patterns of facial ontogeny in the hominid lineage. *Anat. Rec.* 269, 142–147.
- Aiello, L.C., 1996. Terrestriality, bipedalism and the origin of language. In: Runciman, W.G., Smith, J.M., Dunbar, R.I.M. (Eds.), *Evolution of Social Behaviour Patterns in Primates and Man*. The British Academy, London, pp. 269–289.
- Aiello, L.C., 1998. The foundations of human language. In: Jablonski, N.G., Aiello, L.C. (Eds.), *The Origin and Diversification of Language*. California Academy of Sciences, San Francisco, pp. 21–34.
- Aiello, L., Dean, C., 1998. *An Introduction to Human Evolutionary Anatomy*. Academic Press, New York.
- Avril, C., 1963. Kehlkopf und Kehlsack des Schimpansen (*Pan troglodytes*). *Gegenbaurs. Morphol. Jahrb.* 105, 74–129.
- Conroy, G.C., Mahoney, C.J., 1991. Mixed longitudinal study of dental emergence in the chimpanzee, *Pan troglodytes* (Primates, Pongidae). *Am. J. Phys. Anthropol.* 86, 243–254.
- Crelin, E.S., 1987. *The Human Vocal Tract*. Vantage Press, New York.
- Dyce, K.M., Sack, W.O., Wensing, C.J.G., 1996. *Textbook of Veterinary Anatomy*, second ed. W.B. Saunders, Philadelphia.
- Enlow, D.H., 1990. *Facial Growth*, third ed. WH Saunders, Philadelphia.
- Fant, G., 1960. *Acoustic Theory of Speech Production*. Mouton, The Hague.
- Fitch, W.T., 2000a. The evolution of speech: a comparative review. *Trends Cogn. Sci.* 4, 258–267.
- Fitch, W.T., 2000b. The phonetic potential of nonhuman vocal tracts: comparative cineradiographic observations of vocalizing animals. *Phonetica* 57, 205–218.
- Fitch, W.T., Giedd, J., 1999. Morphology and development of the human vocal tract: a study using magnetic resonance imaging. *J. Acoust. Soc. Am.* 106, 1511–1522.
- Fitch, W.T., Hauser, M., 2003. Unpacking “Honesty”: vertebrate vocal production and the evolution of acoustic signals. In: Simmons, A.M., Popper, A.N., Fay, R.R. (Eds.), *Acoustic Communication*. Springer–Verlag, New York, pp. 65–137.
- Fitch, W.T., Reby, D., 2001. The descended larynx is not uniquely human. *Proc. R. Soc. Lond. B Biol. Sci.* 268, 1669–1675.

- Fleagle, J.G., 1999. Primate Adaptation and Evolution, second ed. Academic Press, New York.
- Flügel, C., Rohen, J.W., 1991. The craniofacial proportions and laryngeal position in monkeys and man of different ages. (A morphometric study based on CT-scans and radiographs). *Mech. Aging Dev.* 61, 65–83.
- Hayama, S., 1970. The *Saccus laryngis* in primates. *J. Anthropol. Soc. Nippon* 78, 274–298 (in Japanese with English abstract).
- Hewitt, G., MacLarnon, A., Jones, K.E., 2002. The functions of laryngeal air sac in primates: a new hypothesis. *Folia Primatol.* 73, 70–94.
- Hiiemae, K.M., Palmer, J.B., 1999. Food transport and bolus formation during complete feeding sequences on foods of different initial consistency. *Dysphagia* 14, 31–42.
- Houghton, P., 1993. Neandertal supralaryngeal vocal tract. *Am. J. Phys. Anthropol.* 90, 139–146.
- Hurme, V.O., 1949. Ranges of normalcy in the eruption of permanent teeth. *J. Dent. Child.* 16, 11–15.
- Iwamoto, M., Hamada, Y., Watanabe, T., 1984. Eruption of deciduous teeth in Japanese macaques (*Macaca fuscata*). *J. Anthropol. Soc. Nippon* 92, 273–279 (in Japanese with English abstract).
- Jordan, J., 1971. Studies on the structure of the organ of voice and vocalization in the chimpanzees, part 1. *Folia Morphol. (Warzs)* 30, 97–126 (in Polish).
- Kelemen, G., 1948. The anatomical basis of phonation in the chimpanzee. *J. Morphol.* 82, 229–256.
- Klein, R.G., 1989. *The Human Career*. The University of Chicago Press, Chicago.
- Kuykendall, K.L., Mahoney, C.J., Conroy, G.C., 1992. Probit and survival analysis of tooth emergency ages in a mixed-longitudinal sample of chimpanzees (*Pan troglodytes*). *Am. J. Phys. Anthropol.* 89, 379–399.
- Laitman, J.T., Heimbuch, R.C., 1982. The basicranium of Plio-Pleistocene hominids as an indicator of their upper respiratory systems. *Am. J. Phys. Anthropol.* 59, 323–343.
- Laitman, J.T., Reidenberg, J.S., 1993. Specialization of the human upper respiratory and upper digestive system as seen through comparative and developmental anatomy. *Dysphasia* 8, 318–325.
- Lieberman, D.E., McCarthy, R.C., 1999. The ontogeny of cranial base angulation in humans and chimpanzees and its implications for reconstructing pharyngeal dimensions. *J. Hum. Evol.* 36, 487–517.
- Lieberman, D.E., McCarthy, R.C., Hiiemae, K.M., Palmer, J.B., 2001. Ontogeny of postnatal hyoid and larynx descent in humans. *Arch. Oral Biol.* 46, 117–128.
- Lieberman, P., 1984. *The Biology and Evolution of Language*. Harvard University Press, Cambridge.
- Lieberman, P., Blumstein, S.E., 1988. *Speech Physiology, Speech Perception, and Acoustic Phonetics*. Harvard University Press, Cambridge.
- Lieberman, P.H., Klatt, D.H., Wilson, W.H., 1969. Vocal tract limitations on the vowel repertoires of rhesus monkey and other nonhuman primates. *Science* 164, 1185–1187.
- Lysell, L., Magnusson, B., Thilander, B., 1962. Time and order of eruption of the primary teeth: a longitudinal study. *Odontol. Revy* 13, 217–234.
- Primate Origins of Human Cognition and Behaviour. In: Matsuzawa, T. (Ed.). Springer, Tokyo.
- Matsuzawa, T., 2003. The Ai project: historical and ecological contexts. *Anim. Cogn.* 6, 199–211.
- Mithen, S., 2005. *The Singing Neanderthals: The Origins of Music, Language, Mind and Body*. Weidenfeld & Nicolson, London.
- Mitteroecker, P., Gunz, P., Bernhard, M., Schaefer, K., Bookstein, F.L., 2004. Comparison of cranial ontogenetic trajectories among great apes and humans. *J. Hum. Evol.* 46, 679–697.
- Negus, V.E., 1949. *The Comparative Anatomy and Physiology of the Larynx*. William Heinemann Medical Books, London.
- Nishimura, T., 2003. Comparative morphology of the hyo-laryngeal complex in anthropoids: two steps in the evolution of the descent of the larynx. *Primates* 44, 41–49.
- Nishimura, T., 2005. Developmental changes in the shape of the supralaryngeal vocal tract in chimpanzees. *Am. J. Phys. Anthropol.* 126, 193–204.
- Nishimura, T., 2006. Descent of the larynx in chimpanzees: mosaic and multiple-step evolution of the foundations for human speech. In: Matsuzawa, T., Tomonaga, M., Tanaka, M. (Eds.), *Cognitive Development in Chimpanzees*. Springer-Verlag, Tokyo, pp. 75–95.
- Nishimura, T., Mikami, A., Suzuki, J., Matsuzawa, T., 2003. Descent of the larynx in chimpanzee infants. *Proc. Natl Acad. Sci. U.S.A.* 100, 6930–6933.
- Nishimura, T., Mikami, A., Suzuki, J., Matsuzawa, T. Development of the laryngeal air sac in chimpanzees. *Int. J. Primatol.* 28, in press.
- Penin, X., Berge, C., Baylac, M., 2002. Ontogenetic study of the skull in modern humans and the common chimpanzees: neotenic hypothesis reconsidered with a tridimensional Procrustes analysis. *Am. J. Phys. Anthropol.* 118, 50–62.
- Primate Research Institute, Kyoto University, 1986. *Guide for the Care and Use of Laboratory Primates*. Primate Research Institute, Kyoto University, Inuyama, Japan.
- Primate Research Institute, Kyoto University, 2002. *Guide for the Care and Use of Laboratory Primates*, second ed. Primate Research Institute, Kyoto University, Inuyama, Japan.
- Reby, D., McComb, K., Cargnelutti, B., Darwin, C., Fitch, W.T., Clutton-Brock, T., 2005. Red deer stags use formants as assessment cues during intrasexual agonistic interactions. *Proc. R. Soc. Lond. B Biol. Sci.* 272, 941–947.
- Riede, T., Bronson, E., Hatzikirou, H., Zuberbühler, K., 2005. Vocal production mechanisms in a non-human primate: morphological data and a model. *J. Hum. Evol.* 48, 85–96.
- Roche, A.F., Barkla, D.H., 1965. The level of the larynx during childhood. *Ann. Otol. Rhinol. Laryngol.* 74, 645–654.
- Sasaki, C.T., Levine, P.A., Laitman, J.T., Crelin, E.S., 1977. Postnatal descent of the epiglottis in man: a preliminary report. *Arch. Otolaryngol.* 103, 169–171.
- Schultz, A.H., 1933. Growth and development. In: Hartman, C.G., Straus Jr. W.L. (Eds.), *The Anatomy of the Rhesus Monkey*. Williams & Wilkins Company, Baltimore, pp. 10–27.
- Smith, B.H., 1991. Standard of human tooth formation and dental age assessment. In: Kelley, M.A., Larsen, C.S. (Eds.), *Advances in Dental Anthropology*. Wiley-Liss, New York, pp. 143–168.
- Smith, B.H., Garn, S.M., 1987. Polymorphisms in eruption sequence of permanent teeth in American children. *Am. J. Phys. Anthropol.* 74, 289–303.
- Starck, D., Schneider, R., 1960. Respirationsorgane: A. larynx. In: Hofer, H., Schultz, A.H., Starck, D. (Eds.), *Primatologia*, vol. 3–2. Karger, Basel, pp. 423–587.
- Stevens, K.N., 1998. *Acoustic Phonetics*. MIT Press, Cambridge.
- Takemoto, H., 2001. Morphological analyses of the human tongue musculature for three-dimensional modeling. *J. Speech Lang. Hear. Res.* 44, 95–107.
- Titze, I.R., 1994. *Principles of Voice Production*. Prentice-Hall, Englewood Cliffs.
- Trinkaus, E., 2003. Neandertal faces were not long; modern human faces are short. *Proc. Natl Acad. Sci. U.S.A.* 100, 8142–8145.
- Vorperian, H.K., Kent, R.D., Gentry, L.R., Yandell, B.S., 1999. Magnetic resonance imaging procedures to study the concurrent anatomic development of vocal tract structures: preliminary results. *Int. J. Pediatr. Otorhinolaryngol.* 49, 197–206.
- Vorperian, H.K., Kent, R.D., Lindstrom, M.J., Kalina, C.M., Gentry, L.R., Yandell, B.S., 2005. Development of vocal tract length during early childhood: a magnetic resonance imaging study. *J. Acoust. Soc. Am.* 117, 338–350.
- Weissengruber, G.E., Forstenpointner, G., Peters, G., Kubber-Heiss, A., Fitch, W.T., 2002. Hyoid apparatus and pharynx in the lion (*Panthera leo*), jaguar (*Panthera onca*), tiger (*Panthera tigris*), cheetah (*Acinonyx jubatus*) and domestic cat (*Felis silvestris f. catus*). *J. Anat.* 201, 195–209.
- Westhorpe, R.N., 1987. The position of the larynx in children and its relationship to ease of intubation. *Anaesth. Intensive Care* 15, 384–388.
- Wood, B., 1992. Origin and evolution of the genus *Homo*. *Nature* 355, 783–790.
- Wood, B., Collard, M., 1999. The changing face of genus *Homo*. *Evol. Anthropol.* 8, 195–207.
- Zemlin, W.R., 1988. *Speech and Hearing Science: Anatomy and Physiology*, third ed. Prentice-Hall, Englewood Cliffs.