



Ontogeny of postnatal hyoid and larynx descent in humans

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Abstract

Postnatal descent of the hyoid and larynx relative to the palate and mandible, which occurs uniquely in humans, is an anatomical prerequisite for quantal speech. This study tested the hypothesis that spatial constraints related to deglutition impose greater restrictions on the rate and degree of hyo-laryngeal descent than do adaptations for vocalization. Ontogenetic data on changes in the size and shape of the pharynx, the vocal tract, and the spatial positions of the larynx, hyoid, mandible and hard palate relative to each other and to the oral cavity were obtained for 15 males and 13 females from a longitudinal series of lateral radiographs (the Denver Growth Study) taken between the ages of 1 month and 14 years. To establish growth patterns, nine linear dimensions of the pharynx and 15 different pharyngeal and vocal-tract proportions were regressed against percentage growth. The results demonstrate that certain aspects of vocal-tract shape change markedly during ontogeny, especially in the first postnatal year and during the adolescent growth spurt. The ratio of pharynx height to oral cavity length (which is important for speech) decreases significantly ($P < 0.001$) from 1.5 to 1.0 between birth and 6–8 years, after which it remains stable. In contrast, regression analyses indicated that superoinferior spatial relations between the positions of the vocal folds, the hyoid body, the mandible and the hard palate do not change significantly throughout the entire postnatal growth period ($P < 0.05$). Sexual dimorphism in pharyngeal shape and size before the age of 14 years is very limited. The results suggest that the descent of the hyoid and larynx relative to the mandible is constrained by muscle function related to deglutition, highlighting the different functional roles of the hyoid during speech and oral transport. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Hyoid; Larynx; Pharynx; Vocal tract; Deglutition; Vocalization; Ontogeny

1. Introduction

Although there have been several studies (summarized below) of hyoid position relative to the vertebral column, the mandible, and the cranial base, there is little understanding of how spatial relations between

these regions change during ontogeny. In addition, we believe, there have been no longitudinal quantitative studies of overall growth of the vocal tract during ontogeny.

Data on the ontogeny of hyo-laryngeal descent are needed for testing hypotheses about functional constraints on both speech and deglutition. The low position of the human larynx relative to the hard palate, in combination with flexure of the cranial base and a short face, sets up a uniquely structured supralaryngeal vocal

Abbreviations: SVT, supralaryngeal vocal tract.

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tract that functions as a dynamic “two-tube” with equally long horizontal (SVT_H, from the posterior pharyngeal wall to the lips) and vertical (SVT_V, from the vocal folds to the velum) portions (Fig. 1). According to the quantal theory of speech (Fant, 1960; Stevens, 1972; Baer et al., 1991; Lieberman et al., 1992), it is especially advantageous for the ratio of SVT_V to SVT_H to be 1.0. This ratio, in combination with the tongue’s ability to modify independently the cross-sectional areas of SVT_V and SVT_H by approx. tenfold, enables humans to produce a wide range of acoustically differentiable sounds regardless of vocal-tract length (Lieberman, 1984; Beckman et al., 1995). Hyo-laryngeal descent is also important for deglutition. During swallowing, the coordination of supra- and infrahyoid muscles is partly a function of the spatial relations between the hyoid, epiglottis, mandible and mouth (Miller, 1982; Bosma, 1992; Palmer et al., 1992, 1997; Gay et al., 1994). However, hyo-laryngeal descent may be disadvantageous in humans because the low position of their hyoid causes the epiglottis to lose the ability to form a seal with the soft palate, increasing the risk of aspirating food, and of developing dysphagia from poor intermuscular coordination during deglutition (Dodds, 1989; Bosma, 1992; Palmer et al., 1992; Laitman and Reidenberg, 1997).

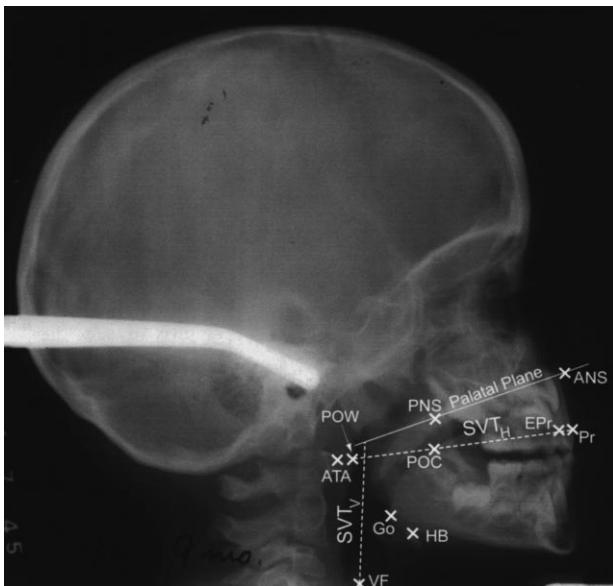


Fig. 1. Radiograph of a 4-year 9-month-old female (no. 106), showing landmarks and planes used in the analysis. See Table 1 for landmark definitions; also included are the horizontal and vertical dimensions of the supralaryngeal vocal tract SVT_H and SVT_V.

1.1. Hyoid and larynx position relative to the vertebral column, mandible and mouth

Accurate ontogenetic data on the size and shape of the pharynx are needed to test hypotheses about the dual roles of hyo-laryngeal descent in deglutition and vocalization. How and when the hyoid and larynx move inferiorly relative to the palate and jaw during ontogeny is poorly known, in part because the position of the hyoid and larynx relative to other structures can only be measured accurately in living individuals in comparable positions (e.g. upright, during quiet respiration and with closed jaws). During most of postnatal growth, the hyo-laryngeal complex descends relative to the face and cranial base but not relative to the vertebral column. At 23–25 weeks in utero, the fetal hyoid and larynx are high relative to the cervical vertebrae, with the larynx extending from the basioccipital to the level of C3 or C4 (Bosma, 1986; Magriples and Laitman, 1987). In the neonate, the hyoid lies opposite the junction between C2 and C3, just inferior to the mandible, and the larynx extends from approx. C3 to C4 (King, 1952; Laitman and Crelin, 1976; Senecail, 1979; Bosma, 1986).

The hyoid gradually descends relative to the skull until adulthood. By 2 years of age, the hyoid and larynx have attained their adult position relative to the cervical vertebrae, with the superior margin of the hyoid body opposite the junction between C3 and C4 (Carlsöö and Leijon, 1960; Roche and Barkla, 1965; Westhorpe, 1987). Some additional descent of the larynx occurs at puberty, resulting in a slight degree of sexual dimorphism, which is most probably a function of dimorphism in body size (Fitch and Giedd, 1999).

Numerous studies have found the position of the hyoid to be fairly conservative among adults relative to the vertebral column and skull. During quiet respiration, the greater horn of the hyoid body typically lies opposite the body of C3 or between the C3–C4 junction, with no significant differences in position between adult males and females (Bibby and Preston, 1981), and with either no or only slight differences in position among adults with various types of malocclusion or variations in craniofacial shape (Kumar et al., 1995; Athanasiou et al., 1991; Tallgren and Solow, 1987; Haralabakis et al., 1993). The resting position of the hyoid is usually normal in dysphagic individuals (Curtis, 1989), but failure to elevate the hyo-laryngeal complex properly during swallowing is a common cause of dysphagia, and may be associated with inadequate opening of the upper oesophageal sphincter as well as impaired protection of the airway during swallowing (Dodds et al., 1990).

1.2. Hyoid and larynx position relative to vocal-tract dimensions

Data are also needed on the ontogeny of hyo-laryngeal descent relative to the cranial base and mouth in order to document growth of the SVT, defined here as the portion of the pharynx which extends from the vocal folds to the front of the oral cavity. As noted above, the unique two-tube SVT in humans (Fig. 1) is characterized by equally long horizontal (SVT_H) and vertical (SVT_V) portions. Numerous factors, including the position and shape of the tongue, cheeks, lips, and mandible, influence the cross-sectional shapes of SVT_V and SVT_H , but to the best of our knowledge no longitudinal studies have directly measured SVT growth in humans. In a recent study, Fitch and Giedd (1999) used sagittal magnetic resonance images from 130 individuals aged 2.8 years and older to assess SVT growth, divided into several regions. They found significant increases in length in all portions of the SVT throughout childhood and puberty, but only the velar and pharyngeal portions of the SVT grew significantly during puberty and adulthood (14–25 years). Fitch and Giedd, however, used images produced with the individual in a supine position, and the sample was split into just three broad age categories (prepubertal, peripubertal and postpubertal).

1.3. Hypotheses to be tested

Our primary objective was to examine the ontogeny of hyoid and laryngeal descent and the growth of the vocal tract. A second objective was to test the hypothesis that spatial constraints related to deglutition impose greater restrictions on the rate and degree of hyo-laryngeal descent than those related to vocalization. Successful deglutition requires precise coordination of tongue, hyoid, epiglottis and oesophageal sphincter movements (Miller, 1982; Bosma, 1992; Thexton and Crompton, 1989). During a typical swallow, the suprahyoid muscles elevate and protrude the hyo-laryngeal complex, opening the upper oesophageal sphincter and pulling the larynx away from the path of the descending bolus. At the same time, the laryngeal sphincter constricts and the epiglottis flexes. As with other types of highly patterned reflexive actions, coordination of these movements is a function of the relative onset and duration of many muscle contractions and spatial relations between the mandible, tongue, hyoid, epiglottis and oesophageal sphincter. This study does not address patterns of muscle activity (see Miller, 1982; Hiiemae and Crompton, 1985; Palmer et al., 1992), but instead examines vertical distances between the larynx, hyoid, mandible and cranial base. As swallowing is primarily an involuntary, highly patterned reflex activity, muscular coordination among the components of the pharynx would

be expected to remain stable during ontogeny if the mandible, hyoid and larynx grow inferiorly at similar rates, thus maintaining consistent vertical spatial positions relative to each other. In contrast, if hyo-laryngeal descent is unconstrained by changes in suprahyoid muscle coordination related to deglutition, then there is no special reason for the hyoid, larynx and mandible to descend relative to the cranium at similar rates. Instead, the rate of hyo-laryngeal descent might be expected to equal that of anteroposterior facial growth to maintain the adaptive 1:1 ratio of SVT_H to SVT_V that characterizes the adult human vocal tract.

2. Materials and methods

2.1. Sample

Our sample was of 15 males and 13 females (Fig. 2) selected from the Denver Growth Study conducted by the Child Research Council, University of Colorado School of Medicine (McCammon, 1970). Those chosen were Caucasian Americans radiographed between 1931 and 1966 at a distance of 7.5 feet in lateral and frontal view at the age of 1, 3 and 9 months, and thereafter every 12 months until adulthood (Maresh and Washburn, 1938; Maresh, 1948). From the age of 1 year 9 months, the participants had been radiographed in a seated position with a radiographic cephalostat; young infants had been hand-held. All the sample exhibited Class I occlusions, and had substantially complete radiographic records. We used radiographs from each year up to 9 years 9 months, and thereafter from 11 years 9 months and 13 years 9 months, after which the larynx was often below the field of the radiograph. Pharyngeal dimensions were measured only in those who had been radiographed while apparently engaged in quiet respiration (e.g. not swallowing or vocalizing) and with their mandibles in resting (closed) position. The high quality of the radiographs allowed accurate identification of most cranial, mandibular and vertebral landmarks, the hyoid body, and many soft tissue structures including the epiglottis and, in most cases, the vocal folds and arytenoid cartilages of the larynx.

2.2. Measurements

Each radiograph was traced on translucent paper, recording the location of major landmarks, planes and dimensions of the cranial base, mandible, hyoid, larynx, and pharynx (defined in Table 1; illustrated in Fig. 1). All measurements were taken by one individual (RCM) using digital calipers accurate to 0.01 mm. One plane and three landmarks were chosen to represent major divisions of the pharynx that could be accurately determined in radiographs and bear some relation to the

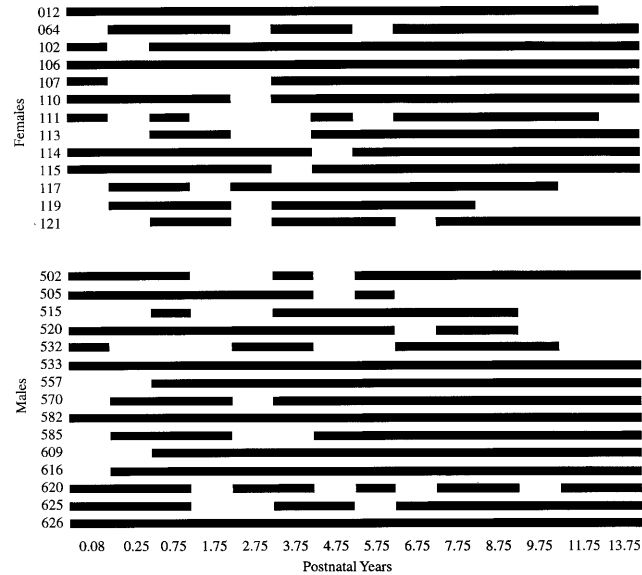


Fig. 2. Longitudinal sample used in the analysis; spaces indicate missing or poor-quality radiographs not used in analysis.

origins and insertions of the many muscles involved in hyo-laryngeal elevation and other pharyngeal functions related to deglutition and vocalization: (1) PP, the palatal plane, from the anterior to posterior nasal spines, which marks the roof of the mouth; (2) GO, the midline average of the most inferior and posterior positions on the mandible between the ramus and the body, which lies approximately at the same level as the inferior-most origin of the mylohyoid (Williams et al., 1995); (3) HB, the anterosuperior-most point on the hyoid body, which approximates to the level of insertion of many infra- and suprahyoid muscles; (4) VF, the anteroposterior midpoint at the level of the vocal folds, and thus the base of the SVT; the plane of VF also lies consistently below the base of the epiglottis. VF was only recorded in radiographs in which the “true” vocal folds of the glottis, which lie at the level of the arytenoid cartilages, were clearly distinct from the more superior vestibular, “false” vocal folds.

Six measurements of the vertical position of the hyoid and larynx relative to the hard palate and mandible were made parallel to the posterior wall of the pharynx: gonion to the palatal plane (GO–PP), the hyoid body to gonion (HB–GO), the hyoid body to the palatal plane (HB–PP), the vocal folds to gonion (VF–GO), the vocal folds to the hyoid body (VF–HB), and the vocal folds to the palatal plane (VF–PP). Three additional measures of SVT dimensions were made: maximum SVT_H length was measured from the lingual surface of the central incisors (EPr) to the posterior margin of the oropharyngeal wall opposite the anterior arch of the atlas (POW); the length of the oropharyngeal component of the SVT_H was measured along the

EPr–POW plane from POW to the posterior margin of the oral cavity (POC); the length of the oral portion of the SVT_H was measured along the EPr–POW plane from POC to Epr (thereby not including the lips). Maximum SVT_V height was measured parallel to the posterior pharyngeal wall from the level of the vocal folds (VF) to the palatal plane (ANS–PNS).

Variations in jaw position and cranial orientation relative to the vertebral column are a likely source of error among individuals younger than 1 year 9 months, who had been radiographed in hand-held position. Inspection of these radiographs, however, showed that care had been taken to hold the infants so that their heads were neither very flexed nor extended with respect to the atlanto-occipital joint. In addition, *F*-tests indicated that the SD of measures of pharyngeal dimensions were not significantly greater ($p > 0.05$) before than after 1 year 9 months of age, suggesting that this lack of postural control was not a major source of error.

2.3. Statistical analyses

All measurements were entered into Statview 4.5™ (Abacus Concepts, Berkeley, CA) for analysis. To test for possible effects of tracing and measurement error, measurements from five separate tracings of one radiograph (taken on different days) were compared. Absolute mean measurement error was 0.43 mm. A single-factor ANOVA indicated that replicate measurements from the same individual were not significantly different.

Means and SD were calculated for all measurements at each age for males, females and for both sexes combined. Single-factor ANOVA was used to compare values between age groups to determine the intervals at which changes in each measure were statistically significant at the $\alpha = 0.05$ level using Fisher's PLSD test (Sokal and Rohlf, 1995). Paired Student's *t*-tests were used to test whether males and females differed significantly at the $\alpha = 0.05$ level within each age group.

To test the hypothesis that spatial constraints related to deglutition have a greater influence on the rate and degree of hyoid and laryngeal descent than factors related to vocalization, comparisons were made of the vertical distances between the palatal plane, gonion, the hyoid body, and the vocal folds (see above). Shape (in this case, proportionality) was calculated using the 15 possible ratios between the six vertical dimensions these points comprise, and analysed ontogenetically using least-square regression analysis with percentage growth as the independent variable for both sexes. A slope that does not differ significantly from zero indicates no shape change over time. Post-hoc ANOVA (Scheffé's *F*-test) was used to test for significant differences between ratios at each age between male and female values. Parametric statistics were warranted because these ratios were normally distributed (as determined by a Lilliefors test).

3. Results

3.1. Ontogeny

Fig. 3 and Fig. 4 plot ontogenetic trajectories of the

vertical and horizontal components of the pharynx, respectively. Gonion, the hyoid and the larynx all descended gradually relative to the palatal plane and to each other throughout the postnatal growth period in a typical facial growth trajectory (Fig. 3). The most rapid changes occurred between 9 months and 2.75 years of age. By postnatal month 1, resting hyoid position averaged 1 cm below the mandibular margin with no significant changes detected until after 9 months of age [Fig. 3(B)]. A similar trajectory characterized the descent of the vocal folds below the gonion [Fig. 3(D)]. However, the hyoid descended relative to the palatal plane during the first 9 months [Fig. 3(A)], presumably because of rapid growth in the height of the mandibular ramus [Fig. 3(C)]. Although males had consistently lower hyoid bodies than females [Fig. 3(A)], the vocal folds lay consistently lower relative to the hyoid body in females than in males between 4.75 and 13.75 years [Fig. 3(E)]. Thus, total SVT_V did not differ significantly between males and females [Fig. 3(F)].

SVT_H growth (Fig. 4) differed in some important ways from SVT_V growth. The oropharyngeal component of SVT_H elongated by approx. 4 cm, reaching 95% of adult size by 1.75 years [Fig. 4(A)]. In contrast, the oral cavity had a facial growth trajectory, with growth spurts occurring before 2 years of age and during adolescence [Fig. 4(B)]. As a result, total SVT_H [Fig. 4(C)] followed a skeletal growth trajectory, with no apparent sexual dimorphism before 13.75 years of age. Fig. 4(D) summarizes changes in $SVT_H:SVT_V$ proportionality. Although the high position of the larynx in newborns made SVT_H roughly 50% longer initially than SVT_V , the hyoid and larynx descended relative to the

Table 1
Landmarks and planes used

Landmark	Abbr.	Definition
Anterior nasal spine	ANS	The most anterior point on the maxillary body at the level of the nasal floor, when projected on to the midsagittal plane
Anterior tubercle of atlas	ATA	Most anterior and superior point on the anterior tubercle of the atlas as projected on to the midsagittal plane
Endoprosthion	EPr	Midline point on the lingual surface of the central incisors, opposite the most anterior, inferior point on the alveolar surface of the premaxilla (Prosthion)
Gonion	GO	The point of maximum curvature of the posterior mandibular angle as projected on to the midsagittal plane
Hyoid body	HB	Most anterior and superior point on the hyoid body as projected on to the midsagittal plane
Posterior nasal spine	PNS	The most posterior point of the maxillary body at the level of the nasal floor at the articulation of the hard and soft palates
Posterior oropharyngeal wall	POW	Point on the posterior pharyngeal wall opposite the anterior tubercle of the atlas (as projected on to the midsagittal plane) along the plane from endoprosthion (EPr) to the anterior tubercle of the atlas (ATA)
Posterior margin of oral cavity	POC	Plane from PNS to EPr-POW, parallel to the posterior wall of the pharynx
Vocal folds	VF	Anterior-posterior midpoint of the vocal folds at level of the arytenoid cartilages

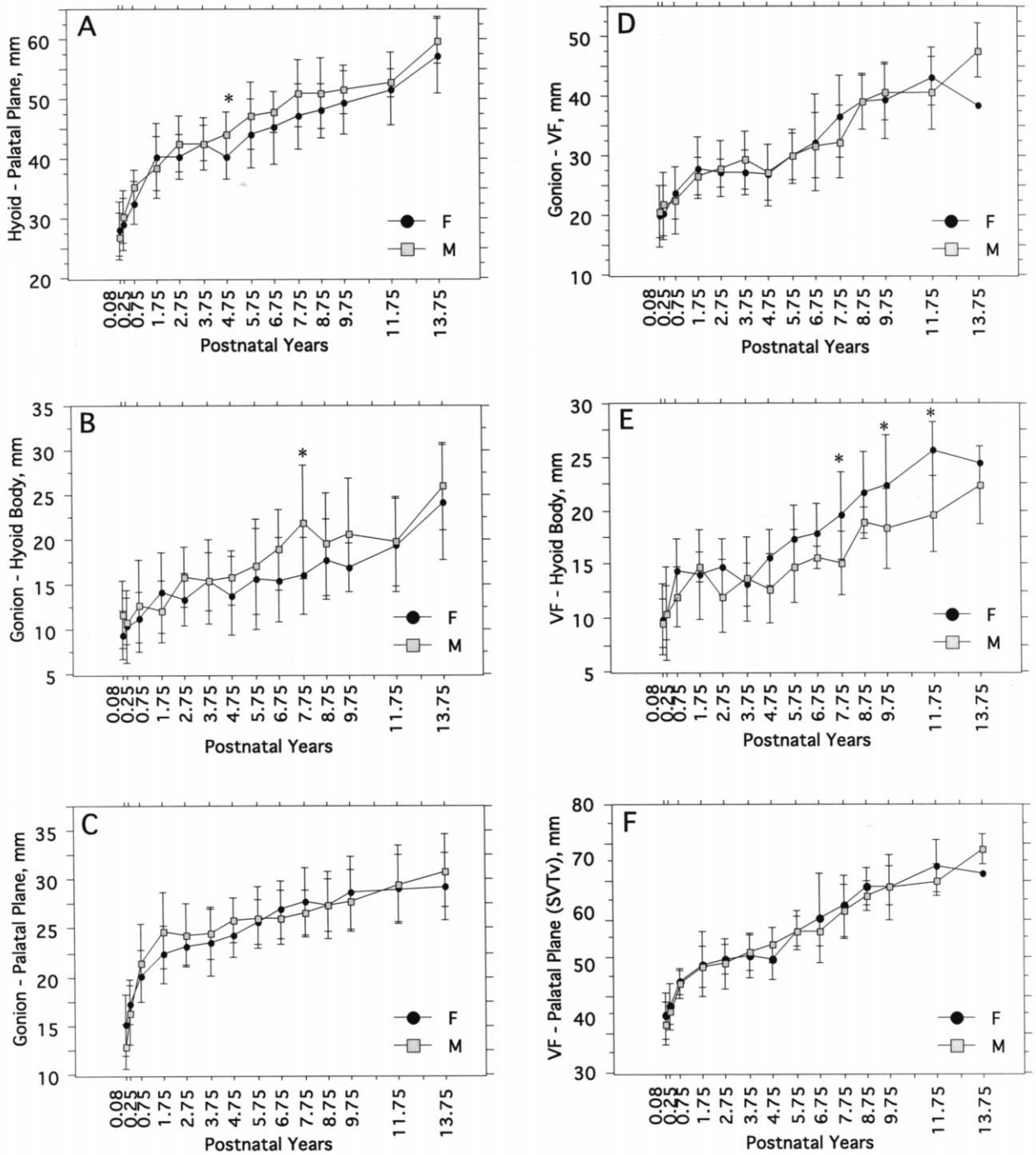


Fig. 3. Ontogenetic changes in six vertical dimensions of the pharynx between the vocal folds (VF), the hyoid body, gonion, and the palatal plane. Boxes indicate the mean for each sex; whiskers indicate 1 S.D. * indicates a degree of sexual dimorphism significant at $P < 0.05$.

palatal plane more rapidly than the oral cavity elongated. Both males and females attained an approx. 1:1 ratio of SVT_H/SVT_V between 6.75 years and 8.75 years,

with no subsequent significant deviation from this ratio before 13.75 years of age. The ratio of SVT_H/SVT_V dropped slightly below 1.0, possibly because lip length

was not measured as part of SVT_H . Consequently, proportional equality of SVT_H and SVT_V appeared to occur in two major ontogenetic shifts, one before 1 year of age, and the second between 4.75 and 7.75 years. No statistically significant sexual dimorphism in SVT_H/SVT_V was evident at any age analysed in this study.

3.2. Spatial relations

To test the hypothesis that spatial factors related to deglutition constrain the rate of hyo-laryngeal descent, we examined the pattern and extent to which the superior-inferior proportions of the pharynx change during ontogeny. Table 2 summarizes regression analyses between percentage postnatal age and the 15 possible ratios between the six vertical dimensions measured in this study (Fig. 5 illustrates three proportions, GO–PP/VF–PP, HB–PP/VF–PP, and GO–PP/HB–GO). Regression analyses showed that, with only a few exceptions, vertical proportions did not differ significantly from zero in either sex. In males and females, the slopes differed from zero only in shape ratios that included vocal-fold position relative to the hyoid body (with the exception of ratio 15 in males). In all these cases, slopes were only slightly different from 0.0, or had large confidence intervals. In addition, no signifi-

cant differences in slope were detected between sexes. In other words, the overall vertical proportions of the pharynx were restricted postnatally, while total SVT length doubled, and SVT_H/SVT_V changed from approx. 1.5 to 1.0.

4. Discussion

We demonstrate that growth in the vertical and horizontal portions of the pharynx occurs at different rates before 14 years of age. In particular, the relative vertical growth between the vocal folds, the hyoid, the base of the mandible and the hard palate maintains constant proportions between these regions, whereas the ratio of vertical to horizontal dimensions changes considerably. The SVT has two phases of growth in terms of proportionality: in phase I, before about 6–8 years of age, SVT_H/SVT_V ratios change by about 50%; in phase II, the ratios remain stable at approx. 1:1. These differences have several consequences. First, fully quantal speech, which is made possible by a 1:1 $SVT_H:SVT_V$ ratio, is not possible until about 6–8 years of age. However, as constant superior-inferior proportions are maintained between the larynx, the hyoid, the mandible and the hard palate, the pattern and timing of

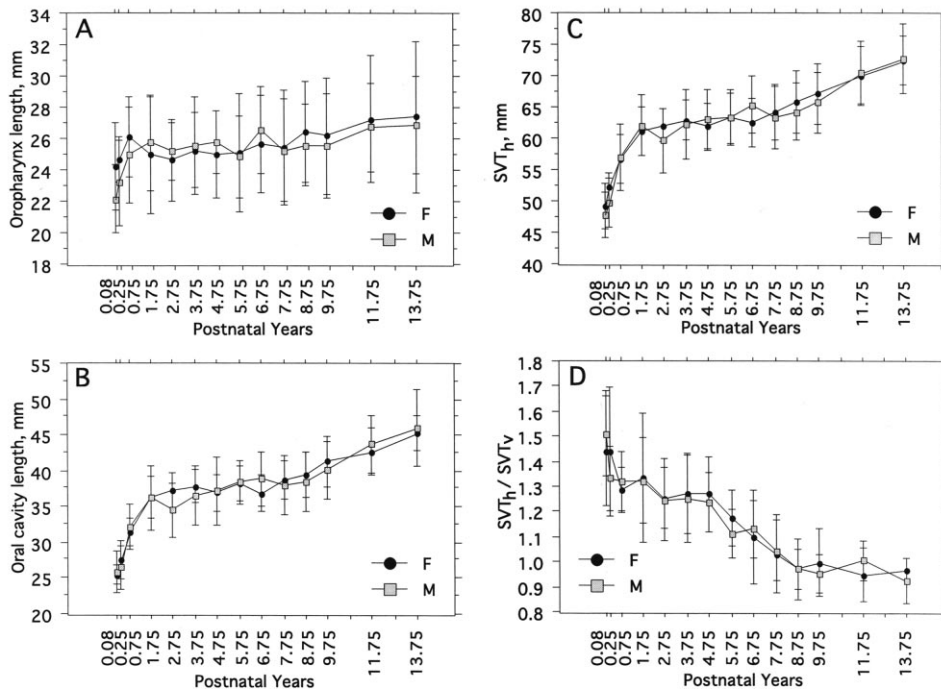


Fig. 4. Ontogenetic changes in horizontal dimensions of the pharynx (A–C), and the ratio of horizontal (SVT_H) and vertical (SVT_V) portions of vocal tract (D). Boxes indicate the mean for each sex; whiskers indicate 1 S.D. * indicates a degree of sexual dimorphism significant at $P < 0.05$.

Table 2
Least-square regression of vertical pharyngeal proportions vs percentage age

Shape ratio	Males			Females		
	Intercept	Slope	95% C.I. ^a	Intercept	Slope	95% C.I.
1. GO-PP/HB-PP	0.58	-0.04	±0.08	0.59	-0.03	±0.05
2. GO-PP/VF-PP	0.50	-0.09	±0.08	0.47	-0.05	±0.04
3. GO-PP/VF-GO	0.91	-0.20	±0.23	0.89	-0.11	±0.13
4. GO-PP/HB-GO	1.80	0.43	±0.47	1.88	-0.30	±0.25
5. GO-PP/VF-HB	1.87	0.35	±0.43	1.73	-0.47 ^b	±0.22
6. HB-GO/HB-PP	0.35	0.05	±0.06	0.33	0.04	±0.04
7. HB-GO/VF-PP	0.29	0.01	±0.06	0.27	-0.06	±0.05
8. HB-GO/VF-GO	0.53	0.00	±0.07	0.50	-0.01	±0.05
9. HB-GO/VF-HB	1.15	0.00	±0.29	0.99	-0.34 ^b	±0.20
10. VF-HB/HB-PP	0.32	0.04	±0.06	0.36	0.14 ^b	±0.07
11. VF-HB/VF-GO	0.05	0.06	±0.10	0.54	0.05	±0.07
12. VF-HB/VF-PP	0.26	0.02	±0.04	0.28	0.06	±0.04
13. HB-PP/VF-GO	1.70	-0.05 ^b	±0.03	1.56	-0.37 ^b	±0.13
14. HB-PP/VF-PP	0.84	-0.08 ^b	±0.04	0.81	-0.12 ^b	±0.05
15. VF-GO/VF-PP	0.51	0.09 ^b	±0.07	0.53	0.05	±0.04

^a C.I., confidence interval.

^b Slope significantly different from 0.0 ($P < 0.05$).

hyo-laryngeal muscle recruitment during deglutition can theoretically remain constant during ontogeny. This consistency contrasts with the SVT_H in the nasopharynx and oropharynx, where changes in spatial proportions affect the recruitment patterns of several muscles such as *m. levator veli palatini* (Bosma and Fletcher, 1962; Fletcher, 1973).

The hypothesis that pharyngeal growth maintains constant postnatal vertical proportions to provide stability in muscle recruitment patterns related to deglutition needs to be tested directly using electromyographic data on suprahyoid and infrahyoid muscle timing during deglutition from individuals of different ages. In addition, better-quality data are needed on pharyngeal growth in infants, and more data are needed on the relative position of these structures during the adolescent growth spurt after 13.75 years. A previous study using the same sample did find evidence for sexual dimorphism in the position of the hyoid relative to the palatal plane and mandible during puberty (Lieberman and McCarthy, 1999), which agrees with other studies (Bloch et al., 1990; Flügel and Rohen, 1991). Further data are therefore needed to investigate the position of the larynx in males and females during puberty to determine if the same spatial relations between the mandible, hyoid and larynx are maintained during this time. The issue of sexual dimorphism in the SVT is also important for acoustical analysis, as males are predicted to have longer vocal tracts and longer pharyngeal cavities than females, and as males tend to have larger bodies (Fitch, 1997).

This study therefore provides initial support for the hypothesis that growth of the pharynx is constrained by muscle function related to deglutition. Although the uniquely low position of the human hyoid and larynx relative to the mandible and cranium plays a crucial part in making human speech quantal, the rate of hyo-laryngeal descent appears to be constrained by the need to maintain functional equivalence among the hard tissue structures that interact with soft tissue structures involved in deglutition. These results highlight the different roles of the hyoid during speech and oral transport. As recently demonstrated by Hiiemae et al. (1999), the range of movement of the hyoid during speech in humans is considerably less than during the swallowing of various types of food. In particular, the adult hyoid is more protracted and has a considerably smaller range of superoinferior movement during speech than during swallowing and oral transport. This contrast presumably reflects the essential role of the suprahyoid muscles in elevating the hyo-laryngeal complex during the early portion of the pharyngeal swallow, and in then pulling the larynx out of the path of the descending bolus (Logemann et al., 1992). These actions, in concert with posterior thrusting of the tongue, aid in the posterior folding of the epiglottis. To prevent dysphagia, it is essential that the suprahyoid muscles effectively pull the hyo-laryngeal complex forward at the right time during deglutition, opening the upper oesophageal sphincter (Cook et al., 1989; Kahrilas, 1997). Lack of coordination of the suprahyoid muscles with the tongue, the pharyngeal constrictor

tors, and other hyo-laryngeal muscles may result either in poor protection of the airway with aspiration of food though the larynx, or in retention of food in the pharynx after swallowing (Dodds et al., 1990).

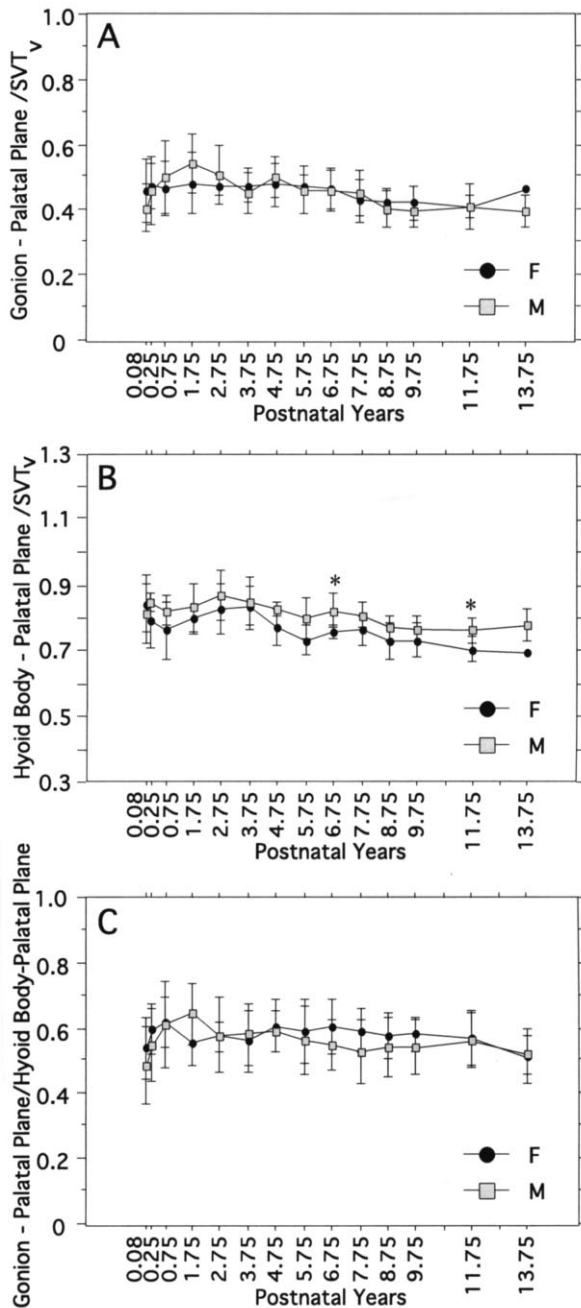


Fig. 5. Ontogenetic changes in three vertical proportions of the pharynx (from Table 2) between the hyoid body, gonion, and the palatal plane. Slopes do not differ significantly from 0.0 for males or females. Boxes indicate the mean for each sex; whiskers indicate 1 S.D. * indicates a degree of sexual dimorphism significant at $P < 0.05$.

The consistency of the vertical proportions of the pharynx in contrast to the changes in SVT_H relative to SVT_V during growth also helps to explain several aspects of speech development. Several studies indicate that the rate of speech perception error declines after 6–8 years of age (Buhr, 1980; Lieberman, 1980), the time when the SVT_H/SVT_V ratio reaches approx. 1.0 in the sample studied here, although this phenomenon may also be attributed in part to improved integration during this period between oral motor reflexes and complex motor skills (Smith et al., 1991; Wood and Smith, 1991). While it would clearly be advantageous for humans to achieve a SVT_H/SVT_V ratio of 1.0 earlier in growth, this would require a pattern of growth that would fail to maintain superoinferior proportionality among the components of the pharynx, thereby potentially compromising functional equivalence. Interestingly, the pharynx in non-human primates also appears to be constrained to maintain constant proportions during growth. Flügel and Rohen (1991) show that the monkey hyoid maintains a consistent rate of descent relative to the larynx when both dimensions are measured relative to the palatal plane. In *Macaca mulatta*, the hyoid descends 13–16 mm between postnatal week 2 and 6 years, and the larynx descends 14–17 mm during the same period. In *M. fascicularis*, the hyoid descends 7–19 mm between birth and 9 years, and the larynx descends 8–20 mm during the same period. More data, however, are needed to test more adequately the hypothesis that vertical spatial relations are maintained during growth in non-human primates and other mammals.

One interesting question raised by these results is why the human larynx descends postnatally rather than maintaining a constant, low position relative to the base of the mandible that would permit both quantal speech and proper deglutition. In other words, if a low hyo-laryngeal complex confers an advantage for speech production, why does it not arise in utero? One answer may concern the functional transition in respiration at birth. There is no need to separate the oral and respiratory tracts in the fetus, as the fetal lung contains amniotic fluid. However, at the moment of birth, the infant must immediately make the critical transition to breathing. Maintaining a high, intranarial larynx, which compartmentalizes the oral and respiratory pathways, may be a necessary condition for successful transition to spontaneous ventilation. The additional burden of constantly having to prevent aspiration of saliva, milk, and other substances into the trachea may also be too great a burden for an infant's incompletely developed neuromuscular system (Bamford et al., 1992).

Cranial size probably imposes additional constraints on the prenatal development of the hyo-laryngeal com-

plex. As noted above, the hyoid bone and larynx must descend in concert with enlargement of the superior–inferior dimension of the oral cavity and mandible. This coordination not only maintains a constant geometrical relation between the hyoid bone, the suprahyoid muscles, the tongue, and their attachments, but also links hyo-laryngeal descent to the eruption of the deciduous dentition. If eruption of the dentition and enlargement of the lower face were to occur prenatally, they would make vaginal delivery impossible, because the birth canal cannot accommodate a larger infant head. Alternatively, if the hyo-laryngeal complex was to descend prenatally, without a concomitant change in oral and mandibular dimensions, then the tongue would be enormous relative to the pharynx, increasing the risk of airway obstruction. Indeed, obstructive sleep apnoea is commonly caused by failure to maintain the patency of the upper respiratory tract (Kahn et al., 1994; Hoeve et al., 1999). These factors suggest that hyo-laryngeal descent must occur postnatally, and must be coordinated with enlargement of the mouth and mandible, as well as with eruption of the deciduous dentition.

Finally, although deglutition appears to constrain the rate of hyo-laryngeal descent, it is important to note that the hyo-laryngeal complex could also descend at other rates that would maintain constant (albeit different) vertical proportions between the hyoid, the base of the mandible and the hard palate. While the acoustical consequences of the unique $1.0 \text{ SVT}_H/\text{SVT}_V$ ratio in humans suggest that the trajectory of the human hyo-laryngeal is an adaptation for speech, other unique aspects of cranial shape may also influence the degree and rate of hyo-laryngeal descent (see Laitman and Crelin, 1976; Laitman et al., 1978). The angle between the posterior cranial base and the back of the midface uniquely flexes in humans, coincident with flexion between the anterior and posterior axes of the internal cranial base (reviewed in Lieberman and McCarthy, 1999). Whether or not flexion of the cranial base is an adaptation for bipedalism and/or encephalization in hominids, it is probably the primary reason why the oropharynx does not elongate appreciably during human ontogeny [Fig. 4(A)]. In contrast, the cranial base in non-human primates does extend markedly and thus significantly lengthens the nasopharynx and the underlying portions of the oropharynx throughout facial growth (Moore and Lavelle, 1974; Dmoch, 1976). Other unique human craniofacial characteristics that may be related to hyo-laryngeal descent and the unique configuration of the human pharynx include increased superoinferior growth of the nasomaxillary complex; a shortened face (including palate) that is retracted underneath the neurocranium (Weidenreich, 1941; Negus, 1949; Lieberman, 1998); and an upright cervical column that attaches to the centre of the cranium. The extent to which these features contribute to descent of the hyo-la-

ryngeal complex is still conjectural and requires further study.

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