Int J Primatol (2007) 28:483–492
DOI 10.1007/s10764-007-9127-7

Development of the Laryngeal Air Sac in Chimpanzees

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Received: 30 August 2005 / Accepted: 27 February 2006 /
Published online: 2 May 2007

Abstract Though many nonhuman primates possess a laryngeal sac, the great apes are unique in their great size. Though an enlarged sac probably arose in their common ancestor, its functional adaptations remain a matter of debate. Its development in extant great apes is likely to provide valuable information to clarify the issue. We used magnetic resonance imaging to examine the development of the laryngeal sac in 3 living chimpanzees, age 4 mo–5 yr, and identified 2 distinct growth phases of the sac. A gradual growth of the sac in early infancy results in a configuration so that it occupies the ventral region of the neck; many adult non-hominoid primates having a sac show the configuration. The subsequent rapid expansion of the sac in late infancy causes the final configuration in chimpanzees, wherein the sac expands into the pectoral, clavicular, and axillary regions. The latter phase possibly arose at latest in the last common ancestor of extant great apes and contributed to the evolution of the enlarged sac, despite the later evolutionary diversification in adult sac anatomy and growth. As many studies have advocated, the enlarged sac probably plays a role in vocalization in adults. However, physiological modifications in the laryngeal region during infancy are likely to provide valuable information to evaluate the functional adaptations of the enlarged sac in the great apes.

Keywords magnetic resonance imaging · *Pan troglodytes* · ventricular sac · vocalization

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Introduction

Many species of nonhuman primates have a laryngeal air sac, an accessory mucosal membrane pouch growing out from the laryngeal region (Hayama 1970; Hewitt *et al*. 2002; Negus 1949; Starck and Schneider 1960). There are 5 forms among nonhuman primates, based on the anatomy of the opening to the laryngeal region (Hayama 1970). Though there are controversies regarding the distributions of forms of air sacs among primates (Hewitt *et al*. 2002), all great apes and siamang definitely share 1 type: a ventricular sac that extends ventrally from bilateral laryngeal ventricles to fuse in front (Hayama 1970; Hewitt *et al*. 2002; Negus 1949; Starck and Schneider 1960). By contrast, other gibbons and humans have bilateral laryngeal ventricles, but no true laryngeal sac (Fitch 2000; Hayama 1970, 1996; Hewitt *et al*. 2002; Némai and Kelemen 1933; Negus 1949; Starck and Schneider 1960). The great apes are unique in having an enlarged sac extending into the pectoral and axillary regions (Avril 1963; Brandes 1932; Hayama 1970; Hewitt *et al*. 2002; Kleinschmidt 1938; Negus 1949; Raven 1950; Starck and Schneider 1960), though many other primates have a smaller sac, at the largest extending to the ventral region of the neck (Hayama 1970; Hewitt *et al*. 2002; Negus 1949; Starck and Schneider 1960).

In chimpanzees, the bilateral sacs fuse with each other in front of the region between the hyoid bone and the thyroid cartilage (Avril 1963). The fused sac expands superiorly to form an unpaired recess at the dorsal aspect of the hyoid body (hereafter, the hyoidal recess). Inferiorly, it forms a long unpaired recess along the ventral aspect of the laryngeal cartilages and trachea to reach the sternum (hereafter, suprasternal recess). From here, the sac expands further to form an unpaired recess at the ventral aspect of the pectoral region (hereafter, presternal recess) and bifurcates to form bilateral recesses extending into the infraaxillary regions (hereafter, axillary recesses).

The exact functions and evolutionary adaptations of the enlarged sac in the great apes remain matters of debate (Fitch and Hauser 2003; Hewitt *et al*. 2002;). The enlarged sac likely arose at the latest in the last common ancestor of the extant great apes, an evolutionary step that possibly involved changes in the rate or timing of existing developmental processes or novel growth processes (Gould 1977; McKinney and McNamara 1991; Rice 2000). Therefore, the changes in physiology that accompany distinct developmental events contributing to the formation of the enlarged sac in extant subjects are likely to shed light on its original functions. Unfortunately, there is little information on the growth of the laryngeal air sacs in great apes (Table I; Avril 1963; Brandes 1932; Huber 1931; Kleinschmidt 1938). We used magnetic resonance imaging (MRI) to examine the growth of the laryngeal air sac in 3 living chimpanzees age 4 mo–5 yr.

Methods

We studied 3 chimpanzees: Ayumu (male), Cleo (female), and Pal (female). They were born in 2000, and the biological mothers reared them in the Primate Research Institute, Kyoto University (PRI; Matsuzawa 2003). We took sagittal tomographic images of their necks at PRI via a General Electrics Signa Profile MRI scanner (.2 Tesla), at scheduled intervals from 4 mo to 5 yr of age (Table II). The MRI protocol and experimental procedure in this study are per Nishimura *et al*. (2003, 2006). We anesthetized the subjects intramuscularly with a mixed solution containing 3.5 mg of ketamine hydrochloride (Sankyo, Tokyo) and .035 mg of medetomidine hydrochloride (Meiji Seika Kaisha, Tokyo) per kg of body mass, but we sedated subjects>4 yr orally with 3.75 mg of droperidol (in 1.5 ml) before anesthetization. We scanned them, placing them supine with their heads fixed to the coil with belts. All imaging sequences are sagittal spin echo series with fields of view of 18–28 cm, with 2.7 mm or 3 mm slice thicknesses and .8 mm or .5 mm gaps between slices (Table II). The matrix of all MR images is 256×256 pixels, and image resolutions ranged from .7×.7 to 1.09×1.09 mm/pixel. Care and use of the subjects adhered to the guidelines of the PRI (1986, 2002), and the Ethics Panel of the PRI approved the MRI examination protocol.

We measured the linear dimensions of the laryngeal air sac on MR images transferred to a personal computer via ImageJ software (W. Rasband, National Institutes of Mental Health, Bethesda, MD; http://rsb.info.nih.gov/ij/). Standard planes on the midsagittal plane were as follows: VLT, ventral line of the trachea; ACG, the level of the anterior commissure of the glottis; SSt, superiormost level of the sternum. Definitions and illustrations are in Table III and Fig. 1, respectively. The measurements included L_H, the length of the hyoidal recess, parallel to VLT from the superiormost to the inferiormost points of a growing sac before it reached the ACG, or its length to the ACG after the sac had already grown below it; L_S, the

Table I Morphological studies on the laryngeal sir sac in great apes

Species	Studies	Sex	n[a]	Developmental stages (sample size)[b]
Pongo pygnaeus	Brandes (1932)	Male	14	Adult (10), adolescence (1), juvenile (1), neonate (1), 5 yr (1)
		Female	6	Adult (4), adolescence (1), juvenile (1)
		?	1	2 mo (1)
	Avril (1960)	Female	1	10 yr (1)
	Hayama (1970)	Male	2	Adolescence (2)
		Female	3	Adult (1), adolescence (2)
Gorilla gorilla	Kleinschmidt (1938)	Male	1	10 yr (1)
	Raven (1950)	Male	1	Adult (1)
	Hayama (1970)	Male	1	Adult (1), adolescence (1)
		Female	1	Adult (1), adolescence (1)
Pan troglodytes	Avril (1963)	Male	3	Infant (1), juvenile (1), 15 yr (1)
		Female	4	Fetus (1), infant (1), 6 yr (1), 9 yr (1)
		?	3	Juvenile (1), probably infant (2)
	Hayama (1970)	Male	1	Adolescence (1)
		Female	3	Adult (1), adolescence (2)
	present study	Male	1	4 mo–5 yr[c] (1)
		Female	2	4 mo–5 yr[c] (2)

2?=unknown

[a] Total sample size for each study.

[b] Developmental stages of the subjects and sample size at each stage. If known, chronological age of each subject at the time of study.

[c] We examined the subjects longitudinally, as in Table II.

Table II Ages of the subjects at the times of scans, parameters of MRI scanning, and measurements of dimensions

Subjects	Age (mo)	Pixel sizes[a] (mm/pixel)	FOV (mm)	Thickness (inter-slice gap)[b] (mm)	L_H (mm)	L_S (mm)
Ayumu	4	.74	190	2.7 (.8)	8.29	absent
	6	.70	180	3.0 (.5)	9.90	.49
	9	.74	190	2.7 (.8)	12.34	1.48
	12	.70	180	3.0 (.5)	15.34	2.33
	18	.70	180	3.0 (.5)	15.85	3.12
	22	.90	230	2.7 (.8)	15.74	4.36
	25	.86	220	3.0 (.5)	17.58	3.04
	30	.98	250	3.0 (.5)	18.48	8.15
	36	1.09	280	3.0 (.5)	21.42	14.32
	42	.98	250	3.0 (.5)	2.89	54.22[d]
	48	.98	250	3.0 (.5)	21.50	53.55[d]
	52	.98	250	3.0 (.5)	19.30	53.82[d]
	54	.98	250	2.7 (.8)	26.77	—
	60	.98	250	3.0 (.5)	28.05	—
Cleo	4	.70	180	3.0 (.5)	7.04	1.12
	6	.70	180	3.0 (.5)	1.25	.43
	9	.70	180	3.0 (.5)	8.58	1.37
	12	.74	190	2.7 (.8)	1.36	2.18
	18	.70	180	3.0 (.5)	1.86	1.96
	25	.86	220	3.0 (.5)	14.37	9.86
	31	.98	250	3.0 (.5)	18.50	38.84[d]
	36	.98	250	3.0 (.5)	18.71	39.90[d]
	43	.98	250	3.0 (.5)	21.33	—
	48	.98	250	3.0 (.5)	25.87	54.71[d]
	54	.98	250	3.0 (.5)	27.86	—
	60	.98	250	3.0 (.5)	29.69	—
Pal	4	.70	180	3.0 (.5)	9.21	absent
	6	.74	190	2.7 (.8)	1.44	.23
	9	.70	180	3.0 (.5)	8.44	2.88
	12	.70	180	3.0 (.5)	11.45	6.99
	18	.70	180	3.0 (.5)	13.78	9.67
	24	.86	220	3.0 (.5)	16.16	42.03[c]
	30	.98	250	3.0 (.5)	15.32	—
	36	.98	250	3.0 (.5)	18.97	48.82[d]
	42	.98	250	3.0 (.5)	17.84	5.82[d]
	48	.98	250	3.0 (.5)	22.23	—
	54	.98	250	3.0 (.5)	22.00	61.63[d]
	60	.98	250	3.0 (.5)	25.48	—

L_H=length of the hyoidal recess of the laryngeal sac; L_S=length of suprasternal recess of the laryngeal sac; absent=the suprasternal recess had not developed; —=no measurements because the landmarks were outside the image field.

[a] The values varied irregularly during infancy, but had little influence on the accuracy of measurements.

[b] This means that the slice interval of all scans was 3.5 mm, regardless of differences in slice thickness and interslice gap.

[c] The sac almost reached the superior edge.

[d] The sac had already expanded beyond the superior edge of the sternum.

length of the suprasternal recess, parallel to VLT, from the ACG to the inferiormost point of the growing sac before it reached the SSt, or the length to the SSt after the sac grew beyond that level (Fig. 1).

Table III Definitions for the standard planes used

Landmarks and planes	Abbr.	Definition
Level of the anterior commissure of the glottis	ACG	The line perpendicular to the VLT from the anterior commissure of the glottis at the base of the epiglottis
Superiormost level of the sternum	SSt	The line perpendicular to the VLT and tangential to superior surface of the sternum
Ventral line of the trachea	VLT	The most ventral straight line of the trachea

Results

We obtained good MR images showing the longitudinal growth in the laryngeal air sac for each subject (Fig. 2), though for Ayumu at 4 and 6 mo, the images are slightly obscure because of motion artifacts. Nevertheless, all the images were adequate for the evaluation of anatomical development (Table II; Fig. 3).

We identified a small pouch at the dorsal aspect of the body of the hyoid at 4 mo for all 3 subjects (Figs. 2a, 3). The sac expanded superiorly in the dorsal area of the hyoidal body and inferiorly to the level of the anterior commissure of the glottis by 6 mo at the latest, for all subjects (Fig. 3). The air sac continued to expand superiorly to occupy the entire dorsal area of the hyoidal body in the first year of life (Figs. 2b, 3). It gradually expanded inferiorly to sit along the ventral aspect of the laryngeal cartilages in early infancy, despite variations in growth rates (Figs. 2b, 3).

In all subjects, in late infancy the sac grew rapidly below the ventral aspect of the trachea to reach and extend beyond the superior edge of the sternum (Figs. 2c, 3): after 1.5 yrs for female Pal, after 2.5 yr for female Cleo, and after 3.5 yr for male Ayumu (Figs. 2c, 3). The supra-and presternal recesses of the sac then widened greatly (Fig. 2d). We did not evaluate further expansions of the sac into the pectoral, clavicular, or axillary regions, which we did not image.

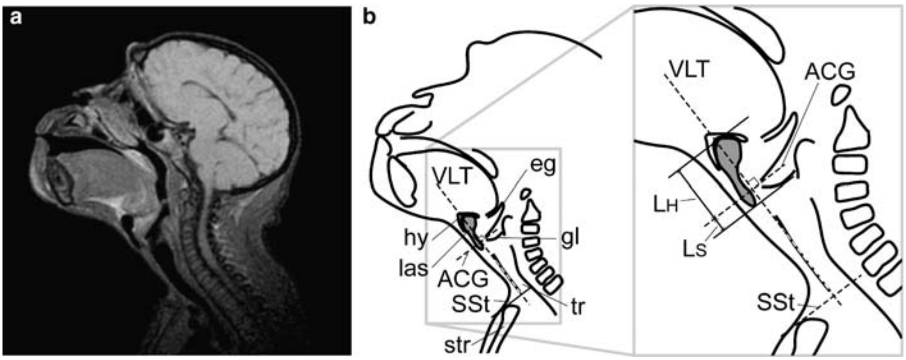

Fig. 1 Diagram of measurements of the laryngeal air sac. (**a**) Magnetic resonance (MR) image. (**b**) Lengths of the hyoidal recess (L_H) and the suprasternal recess (L_S) of the laryngeal sir sac (las). ACG= level of the anterior commissure of the glottis; SSt=superior-most level of the sternum; VLT=ventral line of the trachea (see also definitions in Table III); eg=epiglottis; gl=glottis; hy=hyoid bone; str=sternum; tr=trachea.

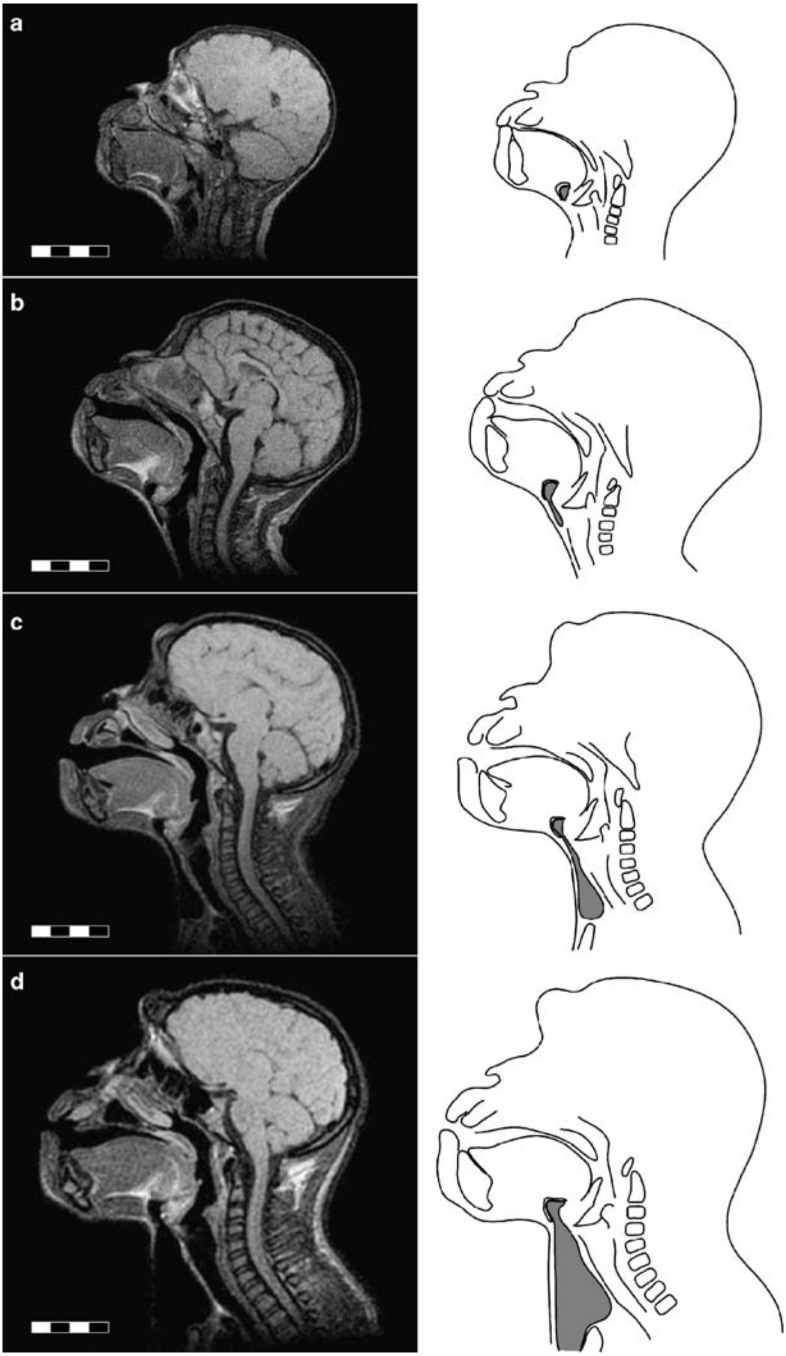

Fig. 2 MR images of the laryngeal air sac for the same female chimpanzee (Pal). (a) At 4 mo, a small pouch had formed in the dorsal area of the hyoid bone. (b) At 18 mo, the sac occupied the entire area dorsal to the hyoid bone and inferior to the ventral aspect of the laryngeal cartilages. (c) At 24 mo, the sac had expanded to reach the sternum. (d) At 48 mo, the sac had expanded inferiorly into the ventral aspect of the pectoral regions and had widened at the level of the trachea. Scale in cm.

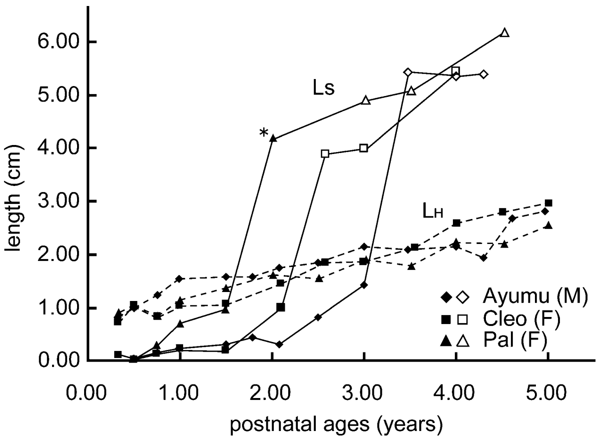

Fig. 3 Growth of the laryngeal sac in 3 chimpanzees: Ayumu (male, diamonds); Cleo (female, triangles), and Pal (female, squares). L_H=length of the hyoidal recess; L_S=length of the suprasternal recess of the sac. We could not measure L_S at some points because the landmarks were out of the image. Open symbols mean that the sac had already expanded beyond the superior edge of the sternum. The sac reached almost the superior edge of the sternoid at 2 yr of in Pal (*; Fig. 2c). In early infancy, the laryngeal sac grows gradually to form the configuration that most adult primate species having a sac show. After late infancy, the sac expands rapidly in the great apes. See also the definitions in Methods.

Discussion

MRI showed 2 distinct phases in the growth of the laryngeal air sac in chimpanzees. In early infancy, the laryngeal sac grows gradually to expand superiorly to the dorsal area of the body of the hyoid and then to extend inferiorly along the ventral aspect of the laryngeal cartilages. Many nonhominoid primates show such a configuration, despite differences in the forms of the sac. Despite controversies regarding the distributions of each type, depending on species, they have a subhyoid sac extending from a ventral midsagittal opening just above the glottis, an infraglottal sac forming from a ventral midsagittal opening between the thyroid and cricoid cartilages, a dorsal sac from a dorsal infraglottal opening between the cricoid cartilage and the first tracheal ring, or they may show bilateral supraventricular sacs arising from bilateral fissures above the ventricles (Hayama 1970; Hewitt *et al*. 2002; Negus 1949; Starck and Schneider 1960). The sac expands within the laryngeal in most species, and at its largest, it expands within the neck (Geist 1965; Hayama 1970; Hewitt *et al*. 2002; Hill and Booth 1957; Negus 1949; Starck and Schneider 1960; Tucker and Tucker 1975). By contrast, from late infancy, the chimpanzees showed a rapid expansion of the sac along the trachea and beyond the neck, despite the slight differences in the timing between subjects. Though we did not evaluate it, the growth phase possibly continues quite early in development to form a sac expanding into the pectoral, clavicular, and axillary regions. Siamang (*Synphalangus syndactylus*) have a ventricular sac, as in great apes, and their sac expands in part to reach the sternum (Hayama 1970; Marler and Tenaza 1977). A ventricular sac may therefore have an advantage over the other forms in enlargement of the laryngeal sac. However, siamang probably do not share the rapid growth phase, so their sac shows no large expansion. Thus, the rapid growth phase in late infancy is likely a derived phase that contributes principally to the formation of the enlarged sac in chimpanzees.

We found that the rapid growth phase of the laryngeal sac started in the 2 female subjects earlier than in the male, but it remains unclear whether this depends on the sexual dimorphism of the sac. In all great apes and siamang, both males and females have a similar configuration of the sac (Hayama 1970). However, all great apes probably show sexual dimorphism in the volume of the sac, which in turn depends on sexual dimorphism in body size. They also show sex-related differences in behavior patterns involving the laryngeal sac; e.g., inflation of the sac for resonance of thoracic percussion during drumming in male gorillas, and for size exaggeration displays in male orangutans (Marler and Tenaza, 1977; Tuttle 1986). Such differences might depend on sexual dimorphism in volume, but there is little information on the issue. Future studies using large longitudinal samples are necessary to determine whether sexual differences in developmental patterns might contribute to adult sexual dimorphism in sac volumes.

The sacs reached the dorsal region of the hyoidal body by 4 mo in all subjects, but we could not evaluate the time of fusion of the bilateral growing sacs. Avril (1963), using 6 chimpanzee cadavers ranging from the fetal to the subadult stage (Table I), found that the unilateral sac expands greatly and that another sac extends ventrally to fuse with it in the late juvenile period, suggesting that a unilateral sac would have expanded rapidly in late infancy in the subjects examined here. If this is true, fusion of the bilateral sacs by itself can have no influence on the rapid expansion of a sac in chimpanzees. However, the fusion in juvenile or adult periods may modify the functions of a unilateral large sac that has already expanded.

There is little information on the growth patterns of the large sac for other great apes (Table I). Adult gorillas have a configuration of the sac that is almost the same as that in chimpanzees (Avril 1963; Kleinschmidt 1938; Raven 1950). By contrast, orangutans have a different configuration, in which bilateral sacs extend inferiorly from the ventricles to the neck region and fuse in the pectoral region (Avril 1963; Brandes 1932; Huber 1931). However, in orangutans the unilateral sac expands greatly, and another sac expands inferiorly to fuse with it in the late juvenile period, as with chimpanzees (Brandes 1932; Huber 1931). Thus, though there are slight differences in the sac configuration, all the great apes possibly share a rapid expansion of the unilateral sac in late infancy.

The functions of the laryngeal sac in primates are still a matter of debate. Suggested functions include storage of expired air to increase oxygen uptake (Negus 1949) or reduction of the hyperventilation caused by a long sequence of repetitive loud calls (Hewitt *et al*. 2002), generating another sound source in the laryngeal ventricles (Brandes 1932; Huber 1931; Fitch and Hauser 2003; Kelemen 1948), resonating the laryngeal voice source to help produce loud and long calls (Gautier 1971; Fitch and Hauser 2003; Marler and Tenaza 1977; Napier and Napier 1985; Schön 1971; Schön Ybarra 1995), or buffering against the pressure induced by intensive expiratory airflow following air trapping during 3-dimensional arboreal locomotion (Hayama 1970; 1996). These functions excluding the first and last are relevant to vocalization. Though current analysis techniques and acoustic theory need to address such hypotheses (Lieberman 2006; Riede *et al*. 2006), vocal behavior patterns in great apes have attracted particular attention to the major functions of the enlarged sac in adults (Brandes 1932; Fitch and Hauser 2003; Hewitt *et al*. 2002; Huber 1931; Kelemen 1948; Marler and Tenaza 1977). However, an enlarged sac may not necessarily have evolved to be advantageous for an aspect of vocalization. Though the mature sac probably serves some of the aforementioned functions in adults, separate functions could have arisen-or disappeared-with each developmental event of the sac; e.g., gradual growth in early infancy, rapid expansion in late infancy, or fusion of the bilateral sacs in the late juvenile period. Thus, we suggest that, among the phases, physiological changes accompanying the rapid expansion of the sac in late infancy are likely to shed light on the original functional adaptations of the enlarged sac in the common ancestor of the extant great apes.

Despite differences in effect, the functions principally depend on some physiological modifications in the laryngeal region, including activities of related musculature and manipulation of the airflow. Unfortunately, few studies have evaluated growth-related changes in physiology in the laryngeal region in chimpanzees, probably because of technical limitations. Such studies on infants, not on juveniles and adults, promise to provide valuable insight into the original functional adaptations of the enlarged sac in the great apes and its apparent evolutionary loss in humans.

Acknowledgments We thank A. Kato, K. Kumazaki, N. Maeda, S. Goto, C. Hashimoto, and K. Matsubayashi, M. Tomonaga, M. Tanaka, Y. Hamada, and other staff of Primate Research Institute, Kyoto University (PRI) for permission for or help with the MRI examinations of 3 chimpanzee infants. We performed portions of this work at PRI under PRI Cooperative Research Programs (grant 4–1, 3–1 to T. Nishimura). A Research Fellowship of the Japan Society for the Promotion of Science (JSPS) for Young Scientist (grant 16000326 to T. N.), JSPS Core-to-Core program HOPE (grant 15001 to PRI), and Grants-in-Aid for Specially Promoted Research (grants 1200200916002001 to T. M.) and for the Biodiversity Research of the 21st Century Center of Excellence (grant A14 to Kyoto University) from the Ministry of Education, Culture, Sports, Sciences, and Technology of Japan provided financial support for the work.

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