The Evolution of Human Speech: The Role of Enhanced Breathing Control

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ABSTRACT   Many cognitive and physical features must have undergone change for the evolution of fully modern human language. One neglected aspect is the evolution of increased breathing control.

Evidence presented herein shows that modern humans and Neanderthals have an expanded thoracic vertebral canal compared with australopithecines and *Homo ergaster,* who had canals of the same relative size as extant nonhuman primates. Based on previously published analyses, these results demonstrate that there was an increase in thoracic innervation during human evolution. Possible explanations for this increase include postural control for bipedalism, increased difficulty of parturition, respiration for endurance running, an aquatic phase, and choking avoidance. These can all be ruled out, either because of their evolutionary timing, or because they are insufficiently demanding neurologically. The remaining possible functional cause is increased control of breathing for speech.

The main muscles involved in the fine control of human speech breathing are the intercostals and a set of abdominal muscles which are all thoracically innervated. Modifications to quiet breathing are essential for modern human speech, enabling the production of long phrases on single expirations punctuated with quick inspirations at meaningful linguistic breaks. Other linguistically important features affected by variation in subglottal air pressure include emphasis of particular sound units, and control of pitch and intonation. Subtle, complex muscle movements, integrated with cognitive factors, are involved. The vocalizations of nonhuman primates involve markedly less respiratory control.

Without sophisticated breath control, early hominids would only have been capable of short, unmodulated utterances, like those of extant nonhuman primates. Fine respiratory control, a necessary component for fully modern language, evolved sometime between 1.6 Mya and 100,000 ya. Am J Phys Anthropol 109:341–363, 1999.   © 1999 Wiley-Liss, Inc.

There has been considerable recent debate over the timing and factors involved in the evolution of human language, including its physical production, i.e., speech. Many types of evidence have been called into play, including brain size and form (e.g., Falk, 1980; Holloway, 1983; Tobias, 1987; Aiello and Dunbar, 1993), comparative language development (e.g., Savage-Rumbaugh et al., 1993), linguistic analysis (e.g., Bickerton, 1990; Pinker and Bloom, 1990; Wilkins and Wakefield, 1995), archaeological evidence of

tool production and cultural developments (e.g., Noble and Davidson, 1991; Schick and Toth, 1993), and skeletal features such as basicranial flexion (e.g., Lieberman and Crelin, 1971; Laitman, 1985), hyoid structure (e.g., Arensburg et al., 1990), and the size of the hypoglossal canal (Kay et al., 1998).

Some researchers support the theory that human language may have begun to evolve very early in human evolution, in the australopithecines (Holloway, 1983), whereas others support a somewhat later start in early *Homo* or *Homo erectus* (Falk, 1980; Aiello and Dunbar, 1993). However, even if some aspects of human language did appear as long ago as 2–4 million years ago, it may initially have been a very limited ability. Full human language may then have evolved gradually over a long period of time, although other researchers believe it largely emerged very recently in a sudden burst of development at the time of the cultural explosion of the Upper Palaeolithic, 40,000 years or so ago (e.g., Isaac, 1976; Noble and Davidson, 1991). There are also differences of opinion about the forerunners of full human language. It may have evolved from the vocalizations of our primate ancestors (e.g., Steklis and Raleigh, 1979; Steklis, 1985; Bradshaw, 1988; Dunbar, 1993; Hauser et al., 1993; Fitch and Hauser, 1995), or it may have had a more independent origin, such as gestural communication (e.g., Hewes, 1973, 1992; Calvin, 1992; Armstrong et al., 1994). Some form of simple protolanguage, without the syntactical complexities of full human language, may have developed first (Bickerton, 1990). However, whatever the evolutionary route and timing of the evolution of modern human language, a range of cognitive and physical features must have undergone change from the nonhuman primate condition, and these are unlikely all to have evolved at the same time. And, although some changes may have enhanced language abilities to a much greater extent than others, individual component changes could very well have provided adaptational advantage.

One apparently necessary feature for the production of fully modern human speech that has more or less been ignored in the language debate is the fine control of breathing, and hence of the subglottic air pressure that fuels sound production and effects some of its intricate variations. On the basis of work on the thoracic vertebral canal of the fossil hominid, KNM-WT 15000, it was previously suggested that this fine control was not present in *Homo ergaster* (or early *Homo erectus*) (MacLarnon, 1993; Walker, 1993). Here, variation in the size of the thoracic vertebral canal is investigated throughout the hominid fossil record, and the suggestion that the evolution of fully modern human speech required the development of finer breathing control is explored.

METHODS

Thoracic vertebral canal data

Measurements. The dimensions of the thoracic vertebral canal analyzed here are based on two measurements of the canal taken on each thoracic vertebra of the sample specimens. These measurements are: the narrowest height (dorso-ventral diameter) of the vertebral canal through each vertebra (vertebral measurement no. 10; Martin, 1928), and the narrowest width (transverse diameter) of the vertebral canal through each vertebra (vertebral measurement no. 11; Martin, 1928). From these two measurements, the narrowest cross-sectional area of the vertebral canal through each vertebra was calculated using the ellipse formula (area = $\Pi/4 \times$ height $\times$ width). This formula produces a reasonable approximation of the actual cross-sectional area of the vertebral canal (MacLarnon, 1987), though removal of the constant $\Pi/4$ would make no difference to any of the conclusions reached here.

The thoracic vertebral canal has fairly constant dimensions along its total length in modern primates (MacLarnon, 1987, 1993), but for ease of comparison the smallest measurements from the region for each specimen were used. These are the minimum dimensions of the canal between the cervical and lumbar enlargements, where the spinal cord and its bony encasement swell to provide innervation for the fore- and hindlimbs. The minimum cross-sectional area is the smallest area through an individual vertebra. As the minimum canal height and width do not necessarily occur in the same verte-

bra, the minimum cross-sectional area may be larger than would be calculated by combining the two individual linear measurements in the ellipse formula.

Sample. Measurements of the dimensions of the vertebral canal through the thoracic vertebrae of adult specimens of extant primate species collected for two previous studies (MacLarnon, 1987, 1993) are used here. The original sample (MacLarnon, 1987) comprised 44 specimens from 37 nonhuman species (5 apes, 10 Old World monkeys, 9 New World monkeys, 6 lorises, and 7 lemurs), and this sample was used to calculate baseline scaling relationships (n = 40, treating males and females of the same species separately). In the second study (MacLarnon, 1993), additional ape specimens were measured giving a total of 2 gibbons, 2 orangutans, 4 chimpanzees, and 4 gorillas. Seven adult humans from the Spitalfields' collection at the Natural History Museum, London, were measured (canal height and width), and published data for humans were taken from Haworth and Keillor (1962) (canal width) and Hinck et al. (1966) (canal width). Species and sex averages are presented in Table 1.

Measurements of the vertebral canal were also taken for all available thoracic vertebrae for a series of fossil hominids: *Australopithecus afarensis* (AL 288-1, cast), *A. africanus* (Sts 14, Stw 431), *Homo ergaster* (or early *H. erectus*) (KNM-WT 15000; MacLarnon, 1993), Neanderthals (La Chapelle, Shanidar 2 and Shanidar 3 (Trinkaus, personal communication); Kebara 2), and early modern *Homo sapiens* (Skhul 4). This fossil hominid sample comprises most of the known fossil hominids with sufficiently complete vertebral columns for the necessary measurements to be taken. For some of these specimens, the thoracic vertebral column is complete enough to be sure that the minimum heights and widths measured on the available thoracic vertebrae and calculated minimum cross-sectional areas are good estimates of the actual minima for the region. For other specimens, the minimum measurements taken could be a little larger than the actual minima (see Table 2).

Body weights. Body weights of the actual specimens were used in analyses for some of the extant primate species. Remaining body weights for these species were taken from a large collection based on numerous published and unpublished sources, using data from wild-caught specimens wherever possible (Martin and MacLarnon, unpublished data) (see Table 1).

Body weight estimates for the appropriate sex of the sample fossil hominid species were taken from published sources, as indicated in Table 2. Adult body weight estimates were used for the juvenile specimen KNM-WT 15000. Analyses based on modern human skeletons of known age indicate that thoracic vertebral canal dimensions in *Homo sapiens* reach adult size by 10 years, or about halfway through the growth period, and that they only increase by about 20% between first fusion at 2 years and adulthood (MacLarnon, 1993). The thoracic canal dimensions of KNM-WT 15000, which is estimated to have been at an equivalent stage of development to an 11-year-old human (Smith, 1993), can therefore be treated as adult, assuming that the growth pattern of the vertebral canal in *Homo ergaster* (or early *Homo erectus*) was similar to that of modern humans (MacLarnon, 1993).

Statistics. Best-fit lines were calculated for bivariate plots as principal major axes. Although debate continues over the most appropriate line-fitting technique for describing allometric relationships (e.g., Martin and Barbour, 1988; Pagel and Harvey, 1988; Aiello, 1992), where correlation coefficients are high there is very little difference between the results of the major methods (Aiello, 1992).

RESULTS

Figures 1–3, parts a, are log-log plots of each of the three minimum thoracic canal dimensions vs. body weight for the whole extant primate sample, plus the fossil hominids. Figures 1–3, parts b, are enlarged versions of the upper right portions of these plots. The lines drawn in describe the relationships between each of the canal dimensions and body weight for the extant primates less humans. The statistics for the

TABLE 1. *Minimum thoracic canal dimensions and body weights for extant primate species*

Species	Sex	Body weight (g)	n for canal measurements	Minimum thoracic vertebral canal measurements (ranges)		
				Height (mm)	Width (mm)	csa (mm²)
Original sample						
Nycticebus coucang	m	725	1	2.70	3.92	8.38
Perodicticus potto	f	935	1	3.72	4.77	14.10
Arctocebus calab-arensis	f	212.4	1	2.20	3.36	6.39
Euoticus elegantulus	m	291	1	2.28	2.65	5.09
Galago alleni	f	262	1	2.31	2.79	5.35
Otolemur crassicau-datus	m	1,165	1	2.91	3.79	9.11
Otolemur crassicau-datus	u	1,204	1	3.03	3.26	7.99
Microcebus murinus	u	66.5	1	1.58	2.10	2.89
Lemur catta	m	2,350	1	4.41	4.89	17.44
Eulemur fulvus	u	2,201	1	4.19	4.72	15.53
Varecia variegatus	u	3,100	1	4.91	5.29	20.82
Daubentonia madagas-cariensis	u	2,800	1	3.76	5.11	15.77
Indri indri	f	6,250	1	6.42	6.86	38.58
Propithecus diadema	u	6,500	1	5.70	6.00	27.80
Callithrix pencillata	f	287	1	2.40	2.76	5.35
Saguinus oedipus	m	325	1	2.32	3.05	5.56
Cebus apella	u	2,741	1	4.18	5.46	18.26
Saimiri sciureus	m	805	1	2.91	4.15	9.94
Aotus trivirgatus	f	1,200	1	3.19	3.91	10.04
Cacajao rubicundus	m	3,750	1	4.25	6.27	21.43
Lagothrix lagotricha	m	8,160	1	4.37	6.49	23.68
Ateles paniscus	u	8,804	1	5.51	6.98	31.63
Alouatta seniculus	f	5,807	1	4.51	5.92	21.48
Colobus satanas	m	10,683	1	5.83	6.97	33.01
Trachypithecus obscurus	f	6,360	1	5.75	6.69	33.75
Cercopithecus aethiops	m	4,878	1	5.63	7.85	35.41
Cercopithecus mitis	f	4,280	3	5.13 (5.17–5.39)	6.61	28.82
Cercopithecus mitis	m	7,374	3	5.22 (5.00–5.40)	7.44	32.59
Papio anubis	m	21,920	1	7.43	12.59	76.04
Papio cynocephalus	m	21,728	1	7.90	11.79	76.32
Cercocebus atys	f	7,800	1	5.90	7.82	38.47
Macaca fascicularis	f	3,614	1	4.76	6.63	26.24
Macaca fuscata	f	9,100	1	5.94	8.15	38.40
Hylobates concolor	f	5,749	1	5.40	7.13	30.24
Hylobates hoolock	u	6,700	1	6.34	6.32	32.42
Miopithecus talapoin	m	1,460	1	4.07	5.46	18.00
Pongo pygmaeus	m	73,388	1	9.33	13.28	103.68
Pan troglodytes	f	34,135	1	10.46	12.12	108.99
Gorilla gorilla	f	82,500	1	15.39	13.69	167.17
Gorilla gorilla	m	152,600	1	18.15	15.26	229.37
Complete ape sample						
Hylobates concolor	f	5,749	1	5.40	7.13	30.24
Hylobates hoolock	u	6,700	1	6.34	6.32	32.42
Pongo pygmaeus	m	73,388	2	10.72 (10.46–12.10)	11.99 (10.70–13.28)	107.49 (108.99–111.29)
Pan troglodytes	f	34,135	2	9.93 (9.40–10.46)	10.96 (9.80–12.12)	92.60 (76.20–108.99)
Pan troglodytes	m	34,135	2	9.05 (8.80–9.30)	12.30 (12.00–12.60)	88.45 (87.78–89.11)
Gorilla gorilla	f	82,500	2	13.35 (11.30–15.39)	13.35 (13.00–13.69)	141.27 (115.37–167.17)
Gorilla gorilla	m	152,599	2	15.48 (12.80–18.15)	15.73 (15.26–16.20)	196.62 (163.87–229.37)
Human data						
Spitalfields (MacLarnon, 1993)	f & m	60,000	7	14.4 (12.3–16.5)	15.9 (13.9–17.9)	207.3 (159.4–263.6)
Americans (Haworth and Keillor, 1962)	f & m	60,000	100		17.60	
White Americans (Hinck et al., 1966)	f & m	60,000	121		17.4 (13.9–20.8)	

csa, cross-sectional area; u, unknown.

TABLE 2. Minimum thoracic canal dimensions and body weight estimates used for fossil hominid sample

| Specimens | Species | Minimum dimensions of the thoracic vertebral canal (vertebra no.) | | | Body weight estimates (kg) | References for body weight estimates |
		Height (mm)	Width (mm)	Cross-sectional area (mm²)		
Al 288-1 (cast)	*Australopithecus afarensis*	12.3 (T8)[2]	10.2 (T6 and T8)[2]	98.5 (T8)[2]	29.3 (female)	McHenry (1992)
Sts 14	*Australopithecus africanus*	9.4 (T9)	9.6 (T9)	70.9 (T9)	30.2 (female)	McHenry (1992)
Stw 431	*Australopithecus africanus*	10.7 (T10)	11.5 (T10)	96.6 (T10)	40.8 (male)	McHenry (1992)
KNM-WT 15000	*Homo ergaster*	10.5 (T1)	11.9 (T10)	123.4 (T10)	68[1] (this specimen)	Ruff and Walker (1993)
Kebara 2	*Homo neander-thalensis*	12.8 (T6)	16.1 (T3)	211.2 (T6)	76	Ruff et al. (1997)
La Chappelle	*Homo neander-thalensis*	13.5 (T1)	17.3 (T8)	253.0 (T6)	76	Ruff et al. (1997)
Shanidar 2	*Homo neander-thalensis*		15.3 (T3)		76	Ruff et al. (1997)
Shanidar 3	*Homo neander-thalensis*	12.5 (T6)	17.0 (T7 and T10)	173.6 (T7)	76	Ruff et al. (1997)
Skhul 4	*Homo sapiens*	15.8 (T11)[2]	18.0 (T11)[2]	223.4 (T11)[2]	66.6	Ruff et al. (1997)

[1] KNM-WT 15000 is juvenile, estimated to be at an equivalent stage of development to an 11-year-old modern human (Smith, 1993). Assuming that the growth pattern of the vertebral canal in *Homo ergaster* was similar to that of modern humans, it would have reached adult dimensions by this developmental stage (MacLarnon, 1993). Therefore, the adult body weight estimate for KNM-WT 15000 by Ruff and Walker (1993) is used to compare relative canal dimensions.
[2] Specimens not complete enough to be certain that measurements are of thoracic minima.

best-fit lines describing the scaling of the minimum thoracic canal dimensions to body weight are presented in Table 3. In each case, these were calculated for three samples: the original sample of extant primates less humans; the original sample of extant primates less hominoids; and the complete sample of apes, including more recently collected data (see Table 1).

The samples of nonhominoids and apes were used to test whether these two groups form separate grades for the scaling of any of the three canal dimensions. In all three cases, the scaling statistics were very similar for the two groups (see Table 3). In addition, the equations for lines of the average slope values for the two groups, passing through their combined mean values for x and y, were calculated, for each of the three canal dimensions. Residuals for each species from these lines were calculated. In all three cases, the results of t-tests to compare the residuals of the two groups of species showed that they were insignificantly different (canal height, t = 0.012; canal width, t = 0.859; canal cross-sectional area (csa), t = 0.469; df = 39, $p > 0.05$ in all cases). These results show that nonhominoids and apes do not form separate grades for the scaling of any of the minimum thoracic canal dimensions.

From the statistics presented in Table 3 and from Figures 1–3, parts a, it can be seen that the minimum thoracic canal dimensions are all highly correlated with body weight across the nonhuman primates (r values = 0.97–0.98). In Figures 1–3, parts b, the relative positions of the fossil hominids can be seen more clearly.

In Figure 1, most of the fossil hominids fall within the narrow range of deviation of extant primates from the best-fit line. However, the earlier hominids, the australopithecines and *Homo ergaster,* mostly fall at the lower end of this range. Early modern humans and modern humans fall right at the upper edge of the modern nonhuman range of deviation from the line, as does *Australopithecus afarensis,* although in this last case, the thoracic canal height plotted is not definitely the minimum for the thoracic region (see Table 2). However, overall there is no clear evidence of any difference between the relative minimum thoracic canal heights of any of the hominids and the nonhuman primates, nor of major change in the relative canal height during human evolution.

In Figure 2, the australopithecines and *Homo ergaster* all fall close to or below the best-fit line, within the lower end of the range of deviation of the nonhuman pri-
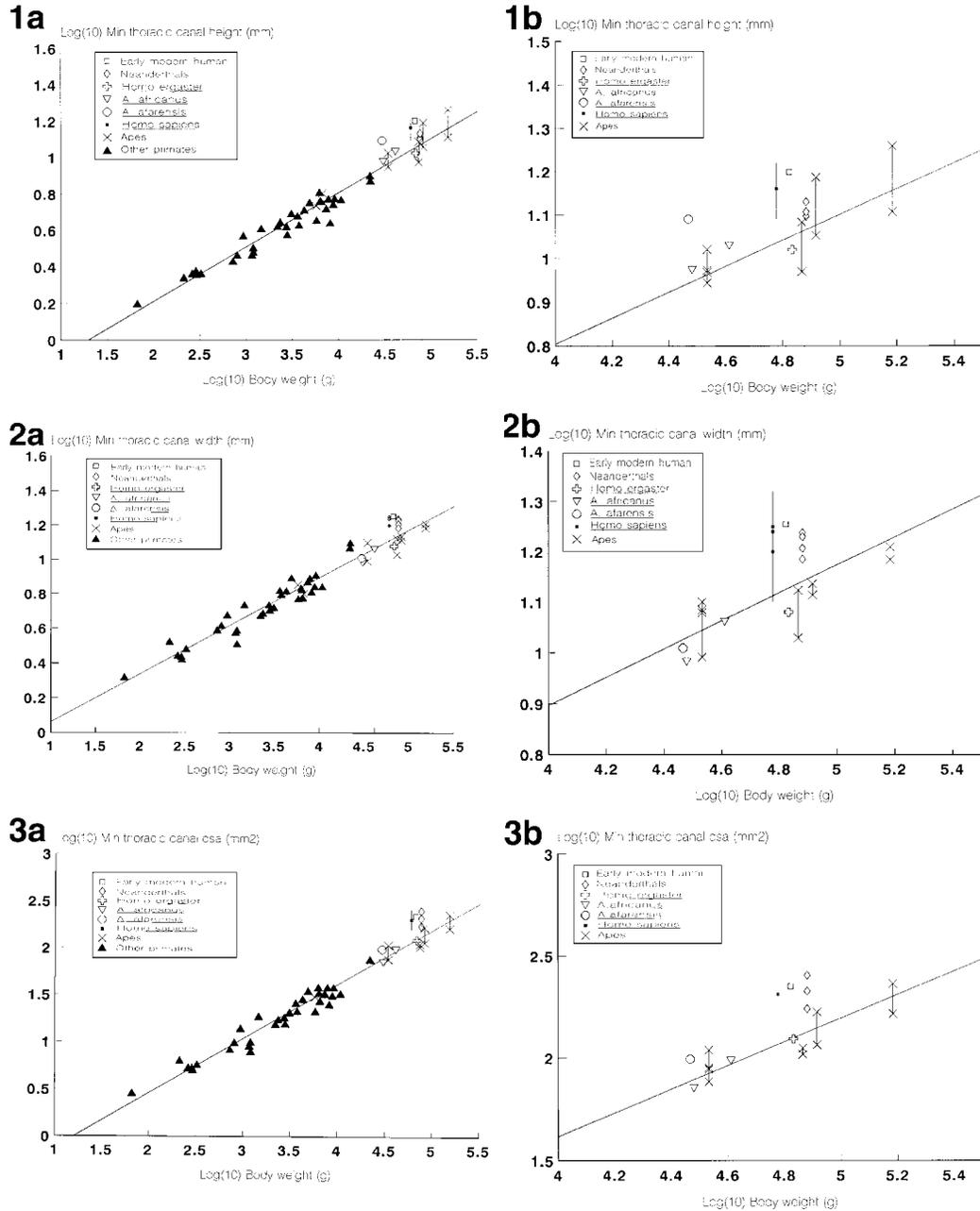
Figs. 1–3. Log-log plots of minimum thoracic canal dimensions (1—height; 2—width; 3—cross-sectional area) vs. body weight for extant primates and fossil hominids. The best-fit lines drawn in are the principal major axes for the original extant sample less humans (see Table 1). Parts **b** are enlarged versions of the upper right hand portions of parts **a.** For ape species, the range of measurements for each sex is shown in parts a, and all specimens in parts b. For extant humans, sample means and the maximum ranges of two standard deviations on either side of these are shown.

TABLE 3. *Statistics for log-log scaling equations relating minimum thoracic canal dimensions to body weight (g)*

y variable	Sample	n	Slope	95% confidence limits on slope	Intercept	r
Minimum thoracic canal height (mm)	Extant primates less humans	40	0.30	0.27–0.32	−0.38	0.97
	Extant primates less hominoids	34	0.27	0.25–0.30	−0.30	0.97
	Apes	7	0.30	0.23–0.36	−0.36	0.98
Minimum thoracic canal width (mm)	Extant primates less humans	40	0.28	0.25–0.39	−0.22	0.97
	Extant primates less hominoids	34	0.28	0.25–0.32	−0.23	0.95
	Apes	7	0.26	0.19–0.33	−0.15	0.97
Minimum thoracic canal cross-sectional area (mm²)	Extant primates less humans	40	0.58	0.54–0.62	−0.70	0.98
	Extant primates less hominoids	34	0.56	0.51–0.61	−0.63	0.97
	Apes	7	0.56	0.49–0.64	−0.63	0.99

mates. However, most of the Neanderthal, the early modern human (Skhul 4), and the 3 contemporary modern human sample means all fall above the extant nonhuman primate range. In general, however, the recent hominids have larger relative minimum thoracic canal widths than the other hominids and nonhuman primates. There is just some slight overlap of the Neanderthal and chimpanzee ranges of deviation from the best-fit line.

Figure 3 shows a very similar picture to the plots in Figure 2. All of the australopithecines and *Homo ergaster* have relative minimum thoracic canal cross-sectional areas within the lower end of the range of extant nonhuman primates. The Neanderthals and early and contemporary modern humans all have larger relative thoracic canal cross-sectional areas than all the nonhuman primates. This last result clearly depends on the body weight estimates for the fossils. The body weight estimates for the Neanderthals and early modern human would have to be as high as 109 and 118 kg, respectively, for their relative thoracic canal cross-sectional areas to be equal to that of the nonhuman primate with the largest relative canal area (a chimpanzee specimen). These would be extremely high estimates, and it therefore seems clear that the two fossil species do indeed have relatively larger thoracic canals than extant nonhuman primates.

DISCUSSION

The results presented here demonstrate that the thoracic vertebral canal of early fossil hominids was of similar relative size to that of extant nonhuman primates, and substantially smaller than that of modern humans. This has been shown for the two australopithecine species for which the relevant material is available, and for *Homo ergaster*. However, the Neanderthals had a thoracic vertebral canal of similar relative dimensions to modern humans, including early modern humans from Israel.

Vertebral canal dimensions, particularly of the middle and upper vertebral column, are quite well-correlated with those of the spinal cord contained within the canal in modern primates, and therefore canal dimensions can be interpreted in terms of the size of the spinal cord (MacLarnon, 1995). Evidence from the relative sizes of the major spinal cord tissues of extant primates indicates that it is only the grey matter of the modern human thoracic spinal cord that has expanded beyond the typical relative size for the order (MacLarnon, 1993). This demonstrates that it is local innervation in the thoracic region that has increased in humans, as the bulk of white matter containing nerve fibers passing through the thoracic region, to and from the hindlimbs, is of expected relative dimensions for a primate (MacLarnon, 1993). Measurements of the spinal nerves themselves were not collected, but presumably these are also larger in the thoracic region of humans, matching the increase in the volume of nerve cell bodies in the grey matter, and so further accounting for the increase in the girth of the vertebral canal in that area. This evidence indicates that thoracic innervation in earlier fossil hominids, australopithecines and *Homo ergaster,* was similar to that of extant nonhuman primates, but that Neanderthals and early modern humans had expanded tho-

racic innervation similar to that in extant humans.

Possible explanations for increased innervation by the thoracic spinal nerves

The thoracic spinal nerves innervate the muscles of the wall of the thorax (intercostal and subcostal muscles, transversus thoracis), the skin overlying this region, and the longitudinal muscles of the thoracic vertebral column (erector spinae, transversospinalis). They also supply muscles of the anterior abdominal wall (external and internal oblique muscles, transversus abdominis, rectus abdominis), but make little contribution to the innervation of the posterior abdominal muscles. Fibers from the first, or first and second, thoracic spinal nerves pass to the brachial plexus and contribute to the innervation of the arms, but the upper limbs are largely innervated by cervical spinal nerves. The diaphragm, which lies between the thoracic and abdominal cavities, is also almost entirely cervically innervated. This reflects the fact that it originates more cranially and migrates caudally during development (Romanes, 1984).

The thoracic and abdominal muscles that are the major targets of innervation from the thoracic spinal nerves have three or four main functions in humans. They are involved in the maintenance of upright posture and control of the trunk during movement, they are sometimes involved in expulsion such as coughing or defecating, and they are involved in the control of breathing. An increase in thoracic innervation is therefore presumably associated with one or more of these activities. Flexion, extension, and rotation of the trunk are actively controlled by trunk muscles, including the abdominal muscles and the longitudinal muscles of the spine, many of which are thoracically innervated. Bipedal locomotion necessitates good control of the upright trunk, in order to prevent its inefficient flailing about during locomotion, and for the initiation of forward motion from standstill (Lovejoy, 1988). More particularly, it has been proposed that the origin of bipedalism was related to the evolution of accurate throwing (Fifer, 1987), which involves arching of the back and twisting at the waist

followed by rapid release (Fifer, 1987) as important components of the well-coordinated, sequential movements needed to hit a distant target, such as prey (Calvin, 1982, 1992). Whether efficient bipedalism evolved for this particular reason, or primarily for locomotion, its development might have required an increase in the neural control of truncal movements, including thoracic neural control.

However, as the Nariokotome boy demonstrates, *Homo ergaster* was fully bipedal and had a flexible waist. There are very few differences between its postcranial skeleton and those of modern humans except that it was more robust (Ruff and Walker, 1993; Walker, 1993). Hence, any increase in the control of the trunk necessary for fully developed bipedalism would have taken place prior to the evolution of *Homo ergaster,* and yet this species had thoracic innervation similar to that of modern nonhuman primates, and not the increased innervation of modern humans. Therefore, the evolution of bipedalism does not explain the evolution of increased thoracic innervation (Walker, 1993; Walker and Shipman, 1996).

When expulsion for activities such as coughing, vomiting, defecation, and parturition is forceful, abdominal-muscles are contracted to increase intraabdominal pressure, and expiratory intercostal muscles may be contracted against a closed glottis, so increasing intrathoracic pressure (Romanes, 1984). For most of these activities there is no reason to think that their control might have increased during human evolution. However, human parturition is among the most difficult of any primate species, whereas in great apes giving birth is relatively straightforward (Rosenberg, 1992). The human difficulty results from the large size of the neonatal head in relation to the size of the birth canal through the pelvis, and the comparative shapes of the head and canal. Calculations based on pelvic size and shape, known adult brain size, and the relationship between neonatal and adult brain size in primates demonstrate that birth would probably have been no more difficult in australopithecines than in apes, though the mechanism may have altered (Rosenberg, 1992). Evidence from other early hominid species is

scarce, but it seems probable that the first species in which the neonatal head would have squeezed through the birth canal was *Homo ergaster* (or early *Homo erectus*), in which fast brain growth must have continued after birth in order to attain adult brain size (Begun and Walker, 1993). Greater muscular force might therefore have been required for birth in *Homo ergaster* compared with typical primates and earlier hominids. This could have involved more powerful contractions from abdominal and expiratory intercostal muscles, but the primary muscle involved is the uterine muscle, which is mainly sympathetically innervated. Because of this, and the fact that there is no evidence of increased innervation of abdominal and expiratory intercostal muscles until after *Homo ergaster,* increasingly difficult birth is apparently not the functional reason for increased thoracic innervation during human evolution.

The one remaining function of the muscles innervated by the thoracic spinal nerves is the control of breathing. Three functional changes, or suggested functional changes, during human evolution could have required an increase in the neural control of breathing. Firstly, as Carrier (1984) pointed out, the evolution of upright posture enabled the decoupling of the rhythm of breathing from a one-to-one relationship with the locomotor cycle, as the forelimbs no longer transmitted strong forces associated with weight transference and propulsion through the thoracic cage. This, Carrier (1984) went on to say, would have enabled bipeds to run more efficiently at more variable speeds than quadrupeds, being capable of matching breathing rates to oxygen requirements across a wide range of running speeds. Hence, they could have hunted prey to the point of exhaustion by chasing them at speeds inefficient for the less flexible quadrupeds, for whom a particular speed (for each gait pattern) is optimal.

Once again, however, the timing of this possible evolutionary change is not correlated with the post-*ergaster* (or early *H. erectus*) evolution of increased thoracic innervation, as early *Homo* or *Homo erectus* are proposed as the first endurance runners (Carrier, 1984; Trinkaus, 1984). It also seems improbable that the ability to vary the rate of rhythmical breathing according to variable oxygen requirements would need a gross increase in the innervation of the muscles involved, especially as this ability must to some extent be present in other species. Nevertheless, the changes highlighted by Carrier (1984) in the transmission of locomotor forces may have been important preadaptations for the later evolution of greater control of breathing for other purposes.

Secondly, if early human evolution went through an aquatic phase as some have suggested (Hardy, 1960; Morgan, 1972, 1982; Verhaegen, 1995), swimming and diving to gather food resources may have been facilitated by increased breath control (Morgan, 1982) enabling, for example, rapid inspirations followed by long slow expirations, rather than the usual more evenly divided breathing cycle. More detailed investigation, though, suggests that the human ability for greater breath control is not particularly well-suited to swimming and diving, and therefore probably did not evolve as an aquatic adaptation (Patrick, 1991). In any case, the aquatic phase is proposed to have taken place earlier than any of the known human fossil remains, or at least earlier than *A. afarensis* (i.e., >3.7 Mya) (Morgan, 1991). Therefore, the evolutionary increase in thoracic innervation identified here, which took place more recently than 1.6 Mya, cannot have been an aquatic adaptation.

The third possible functional reason for the evolution of increased breathing control is that it was necessary for the evolution of modern human speech. This could have been a secondary change necessitated by other developments. The human larynx is set lower in the throat than that of other primate species (Negus, 1949; Lieberman, 1968). The extended pharynx above the human larynx is manipulated for the production of various phonetic components as air is expired. The repositioning of the vocal apparatus may increase the likelihood of choking as the result of food entering the trachea rather than the esophagus (Laitman, 1985). This potential danger is combated in all mammals by interrupting respiration while swallowing (McFarland et al., 1994; McFarland

and Lund, 1995), but the suggested increased need for antichoking muscular action in humans may have required some increase in breathing control. However, it does not seem likely that this would have been sufficiently complex and variable to require gross neural development.

Much more likely, it is aspects of speech itself that required a significant increase in the innervation of breathing muscles, for, as Campbell (1968) stated, "the subtlety of control required of the intercostal muscles during (human) speech makes demands of the same order as those that are made on the small muscles of the hand." Evidence to support this statement is discussed below. It comes from two main sources: studies of human speech production itself, and comparisons of the production of human speech and the vocalizations of nonhuman primates.

Evidence that modifications to quiet breathing are important in human speech

Work by respiratory physiologists has demonstrated the importance of modifications to quiet breathing patterns for the production of the long, punctuated, and modulated utterances typical of human speech (e.g., Draper et al., 1959; Taylor, 1960; Ladefoged, 1968; Mead et al., 1968; Sears and Newsom Davis, 1968; Bouhuys, 1974; Campbell, 1968, 1974; Proctor, 1974; Hoit et al., 1988; Hixon and Weismer, 1995). Respiratory muscles control the subglottal air pressure (i.e., below the larynx) that fuels voice production in the upper respiratory tract. Most human speech takes place on expirations alone, interspersed with rapid inspirations, in a pattern very different from the more evenly divided breathing cycles of quiet breathing. Subglottal air pressure is also maintained and regulated throughout expirations of varying lengths. Respiratory muscles are active in preventing the general fading of sound volume that would result from the uncontrolled elastic recoil and gravitational deflation of the lungs and rib cage. They also enable sound production to continue beyond the point at which the normal minimum lung volume in quiet breathing is reached. Together, these complex aspects of breathing control enable adult humans to speak fluently in long sentences, without disruptive pauses for inspirations, and with the necessary quick inspiratory pauses placed at meaningful linguistic boundaries (Lieberman and Lieberman, 1973; Lieberman, 1984).

Control of subglottal pressure is also important to several other features which vary in human speech, including its intensity or loudness, the emphasis of particular syllables or phonemes, and pitch and intonation patterns (Ladefoged, 1968; Proctor, 1974; Hoit et al., 1990a; Stathopoulos and Sapienza, 1993). Changes in the length and shape of higher vocal tract structures, particularly the larynx, also affect these aspects of speech, and the relative importance of respiratory and laryngeal control can vary between individuals (Ladefoged, 1968; Stathopoulos and Sapienza, 1993). Evidence, however, suggests that respiratory control is the more important in modifying loudness and emphasis, both in speech (Lieberman, 1984; Hoit et al., 1990a; Stathopoulos and Sapienza, 1993) and in singing (Sundberg et al., 1993). In addition, although most phoneme production is controlled in the upper respiratory tract, for some languages there is also evidence that the production of certain consonants is differentiated by differences in subglottal pressures (Ladefoged, 1968).

At both the larger scale of breath cycles, and the finer scale of detailed features within phrases and words, therefore, subglottal pressure must be well-controlled for the production of human speech. Even at the larger scale this is quite complex. The recoil properties of the lungs and rib cage are different at different volumes, and so the production of a particular subglottal pressure requires different patterns of muscle activity according to the lung volume (e.g., Mead et al., 1968). Added to this is the finer control needed for subtle variation in emphasis, pitch, and intonation, and again, at any given lung volume, different respiratory muscle actions are needed to produce particular changes in air pressure, and different linguistic requirements may be superimposed on each other, e.g., falling pitch at the end of some phrases and emphasis of a particular syllable (Ladefoged, 1968). Differ-

ent languages make different demands, but all require subtle control of subglottal air pressure to convey their meaning (Lieberman, 1984).

The relatively few studies of voice disorders resulting from disruption of breathing control also confirm the importance of breath control in fluent human speech. Patients with cervical cord damage from C4/5 to C7/8 and consequent impairment of thoracic and abdominal muscle function suffer from an associated constellation of speech problems. These include the inability to produce other than short phrases, reduced loudness, and reduced contrasts in terms of stress or monotonal speech, as well as slow and therefore longer inspirations (Hixon and Putnam, 1983; Hoit et al., 1990a).

The subglottal pressure required to produce the specific air flow rate needed for a particular intensity or pitch of speech sound also changes with variation in the resistance of the upper respiratory tract. Changes in the shape of the larynx, pharynx, and mouth are the main causes of the production of different phonemes. Vibration of the vocal folds in the larynx causes the production of sound from the outflow of air from the lungs. Changes in the shape of the pharynx and mouth filter the frequency profile of this sound, or cause it to be released in uneven bursts. These variations are perceived by the listener as the different phonemes of human speech. All these changes to the shape of the upper respiratory tract alter its resistance to air flow. Therefore, the subglottal pressure needed to produce the specific air flow rate required for a particular pitch or intensity of speech varies according to the often rapidly changing sequence of phonemes produced. Subtle feedback mechanisms between the upper respiratory tract and the respiratory muscles are no doubt involved (e.g., Gould and Okamura, 1974). The flexibility and power of these systems is demonstrated by the ability of patients with injury to the upper respiratory tract to compensate by varying subglottal pressure outside the normal range in order to produce intelligible speech (e.g., Anthony, 1980).

The neural control of subglottal pressure during human speech must also involve cognitive factors, and hence feedback be-

tween the brain and spinal cord. At the finer level, variation in emphasis, pitch, and intonation, which involve respiratory control, can alter the meaning conveyed by phonemes, words, and phrases (Ladefoged, 1968). There is also evidence that at the grosser level, the volume of air inspired at the start of a phrase reflects the amount needed to produce it before making the next inspiration at a suitable linguistic point (Lieberman and Lieberman, 1973; Lieberman, 1984; Winkworth et al., 1995). Finally, the muscular movements needed to produce a particular rate of air flow also vary according to body position, general activity levels, and the amount of liquid in the stomach (Bouhuys, 1974; Hixon et al., 1976; Lieberman, 1991). Taking all these factors together, human speech requires very fast, fine control of subglottal pressure which responds to cognitive factors and is integrated with control of the upper respiratory tract and other body changes. This makes considerable demands on the control of the respiratory muscles, for, as Campbell (1968, p. 137) said, "Moving air is easy, but controlling it is difficult."

Evidence that thoracic neural control is particularly important for the control of breathing during human speech

The main muscles involved in human breathing are the diaphragm, internal and external intercostals plus some abdominal muscles, rectus abdominis, and external and internal oblique muscles. All of these muscles, apart from the diaphragm, are thoracically innervated. Other muscles have also had a respiratory role attributed to them, such as the scalenes, sternocleidomastoid, trapezius, pectoralis major and minor, serrati, sacrospinalis, levatores costarum, transversus thoracis, erector spinae, subclavius, latissimus dorsi, and quadratus lumborum, but their role in breathing is more minor, including their role, if any, during speech (Campbell, 1968; Romanes, 1984; Sharp and Hyatt, 1986).

During quiet breathing the main muscles of inspiration are normally described as the diaphragm, the interchondral portion of the internal intercostal muscles, and the posterior external intercostal layer. Expiration

involves the action of the interosseous portion of the internal intercostals, together with passive recoil of the rib cage and lungs (Campbell, 1968, 1974; Borden and Harris, 1984). The role of the abdominal muscles in quiet breathing is less clear, although they have been reported to be active throughout inspiration and expiration (Gould and Okamura, 1974). However, this may only be the case when the body is in an upright standing position, but not when it is supine (Hoit et al., 1988). In the former circumstances, they could be acting to pull the contents of the abdomen inwards so that the costal fibers of the diaphragm are stretched and its mechanical efficiency is increased (Hoit et al., 1988). However, whatever the involvement of the abdominals during quiet breathing, both cervically and thoracically innervated muscles are involved.

From the evidence presented above, it is clear that the intricacies of human speech place demands on the neural control of muscles that are of a very different order from those of quiet breathing. However, analyzing the detailed muscle actions involved is problematic precisely because of their variability and subtlety. A further complicating factor is that different individuals appear to adopt different and sometimes inefficient muscular strategies to achieve particular aspects of speech (Ladefoged, 1968; Hixon et al., 1976; Hixon and Putnam, 1983; Hoit et al., 1990a; Winkworth et al., 1995). In addition, results derived from the use of different techniques such as monitoring the electrical activity of muscle groups with EMG (Draper et al., 1959; Taylor, 1960; Sears and Newsom Davis, 1968; Campbell, 1974), or deformations of the chest wall using kinematic observations (Hixon et al., 1976; Hixon and Weismer, 1995), or linearized magnemometers or respiratory plethysmography (Proctor, 1974; Hixon and Putnam, 1983; Hoit et al., 1990b, 1994; Winkworth et al., 1995) have sometimes been contradictory. Interpretation has also varied. In their now classic work, the Edinburgh group concluded that the intercostal muscles play a much more important role than abdominal muscles during conversational speech (Draper et al., 1959; Ladefoged, 1968). However, Hixon et al. (1976) and

Hixon and Weismer (1995) have criticized this view, suggesting a more central role for the abdominals. For present purposes, though, such differences are not particularly important, as both these sets of muscles are thoracically innervated.

There is general agreement that the intercostal muscles involved in inspiration for quiet breathing (i.e., the external intercostals, interchondral portions of the internal intercostal muscles) are active during the rapid inspirations required for speech. Hixon et al. (1976) also emphasized the importance of the abdominal muscles in this phase of the speech breathing cycle. They suggested that these muscles are tensed before an inspiration, which raises the diaphragm slightly, stretching its costal fibers and increasing its potential contribution to rapid inspiration. However, there is also evidence that the diaphragm is much less important during phonation than it is in quiet breathing (Draper et al., 1959; Taylor, 1960; Bouhuys et al., 1966; Campbell, 1974). Proctor (1974) even stated that the diaphragm is completely relaxed during most speech and singing. The external (or inspiratory) intercostal muscles may also continue to be active during the initial moments of speech expiration, particularly for soft speech (Draper et al., 1959). According to Draper et al. (1959), this enables the increase in subglottal pressure due to relaxation at the start of a speech sequence to be restricted appropriately. However, Hixon and Weismer (1995) have strongly criticized this interpretation.

Expiration during speech is initially the result of elastic recoil of the lungs, but at some point (precisely where is a matter of dispute) this is insufficient to maintain subglottal air pressure at the required level. At this stage the internal (expiratory) intercostal muscles and abdominal muscles become active, increasing the expiratory drive to maintain subglottal pressure (Draper et al., 1959; Hixon et al., 1976). This allows speech to be produced at a consistent volume throughout a phrase on a single breath. The same muscles can also increase subglottal pressure briefly for emphasis of a particular syllable or for the production of particular consonants (Mead et al., 1974; Borden and

Harris, 1984). The relative contribution of the two sets of muscles in regulating expirations during speech is still a matter of dispute, and it is unclear whether the apparently contradictory results produced emanate from the different experimental conditions used or the different measurement techniques (e.g., Draper et al., 1959; Hoit et al., 1988; Stathopoulos and Sapienza, 1993), or from different strategies adopted by different individuals.

Understanding of the precise muscular deployment in breathing control during human speech is clearly far from complete. However, it is reasonably well-established that the most important muscles involved, both in inspiration and expiration, are the intercostal muscles and a set of abdominal muscles, all of which are thoracically innervated, and therefore the more detailed differences in interpretation of results are not particularly important here. There is also general agreement that complex coordination of the movements of these muscles is required to produce the subtlety of control needed for the intricacies of human speech. This coordination may include load-compensating reflexes within the spinal cord, incorporating feedback from muscle spindles and tendon organs with which the intercostal and abdominal muscles are richly supplied compared to the diaphragm (e.g., Sears and Newsom Davis, 1968; von Euler, 1968; Newsom Davis and Sears, 1970; Campbell, 1974; Grassino and Goldman, 1986; Iscoe, 1998).

Central control of speech breathing is served by neural pathways that are functionally and anatomically distinct from those involved in the control of respiration for metabolic purposes (Phillipson et al., 1978). Metabolic respiration is controlled by the pons and medulla of the hindbrain, involving vagal and chemoreceptor reflexes, whereas the control of breathing for phonation is more complex, involving forebrain and midbrain pathways (Purves, 1979; Zhang et al., 1994; Davis et al., 1996; Murphy et al., 1997). At the level of the spinal cord, several descending tracts and reflex loops involved in the control of breathing are integrated (Newsom Davis and Sears, 1970; Milic-Emili and Zin, 1986). Reflexes originating from the proprioceptors of the lower

intercostals might also affect phrenic motoneurons, producing an excitatory effect on the diaphragm (Decima et al., 1967; von Euler, 1968). While the picture again is far from complete, there is clear evidence of significantly different and increased neural control of breathing for speech production in humans compared with that for metabolic respiration. And, at the level of the spinal cord, these differences occur in the thoracic region.

Human language compared with nonhuman primate vocalizations

Human language differs from the vocal communication of nonhuman primates in many ways. In broad terms, these can be divided into cognitive differences and differences in sound production, though clearly the two aspects must be interrelated for meaningful communication. As shown above, sophisticated control of breathing is very important to human speech, or the physical production of human language, and it is suggested that this control increased during human evolution. An important part of the evidence for this is the difference in the amount of thoracic innervation in extant humans and nonhuman primates. In addition, if the association made here between an evolutionary increase in thoracic innervation and breathing control is correct, then the breathing control required for nonhuman primate vocalizations should be substantially less than that needed for human speech. The evidence for this part of the suggested evolutionary picture is considered below.

Precise comparisons of breathing patterns during human speech and nonhuman primate sequences of vocalizations are difficult for a number of reasons. The most important of these is that most researchers who have worked on nonhuman primate vocalizations have not focused on breathing related to vocalization, and hence information in this area is often only available incidentally, or has to be estimated from sonograms selected and reproduced for other purposes. What evidence there is suggests that sequences of varied, discrete sounds are commonly produced by nonhuman primates on a series of both inspirations and expirations, with only

single sound units expressed on individual air movements (e.g., pant hoot, *Pan troglodytes* (Marler and Hobbett, 1975; Marler and Tenaza, 1977; Clark and Wrangham, 1993); sections of gibbon songs, *Hylobates* spp. (Geissmann, 1993; Gittins, 1984; Haimoff, 1983, 1984); whoop gobble, *Cercocebus* spp. (Waser, 1982); two-phase or roar grunt, *Papio* spp. (Andrew, 1963a,b; Byrne, 1981, 1982); gecker, *Macaca fuscata* (Green, 1975); loud low-pitched calls, *Callicebus moloch* (Robinson, 1979); grunt series, *Eulemur fulvus* and *Nycticebus coucang* (Andrew, 1963a); click-grunt, *Otolemur crassicaudatus* and *Perodicticus potto* (Andrew, 1963a)), rather than multiple units on extended expirations, which is the human pattern. This qualitative distinction implies that the interrelationship between vocalization and breathing is very different in our species.

Despite the paucity of direct evidence, it is possible to make a series of predictions of additional quantitative differences that would be expected if human vocalization does indeed involve greater breath control than that of nonhuman primates, and to test these largely using information that can be gleaned from the literature. These predictions are that nonhuman primates will have less extended exhalations during vocalizations than humans, more equal divisions of breathing cycles into the inspiratory and expiratory portions, and a drop in fundamental frequency through single expirations of more than a very short duration. In addition, it is expected that nonhuman primates will be limited in their rate of production of discrete sounds (particularly if this involves a series of inspirations and expirations), and restricted in the order in which sounds can be produced relative to the phase of the breathing cycle.

Compared with quiet breathing, during speech, humans take quicker inspirations with increased volume and they extend the exhalation phase of the breathing cycle (e.g., Borden and Harris, 1984). There is no good evidence that nonhuman primates modify the inspiratory phase, although occasionally it has been suggested (Larson et al., 1994; Davis et al., 1996). The duration of speaking breaths (expirations) in human speech normally ranges between about 2–6 sec (Hoit et al., 1994; Kien and Kemp, 1994; Mitchell et al., 1996), although it can be more than 12 sec (Winkworth et al., 1995). As far as it is possible to assess from published information (including estimations from published sonograms), the longest calls given by nonhuman primates on a single breath are much shorter than this, e.g., individuals of *Indri indri* and *Alouatta palliata* can produce calls of up to 5.0 sec and 4.8 sec, respectively (Table 4).

However, a comparison of the maximum degree to which the duration of a resting inhalation is extended during vocalizations is probably more important than a comparison of the absolute duration of calls. Resting breathing rate scales allometrically with body weight in mammals (Stahl, 1967) and is absolutely slower in larger species. Therefore, assuming that exhalations make up 50% of a breathing cycle, which is a reasonable approximation (see below), the duration of resting exhalations will be longer in larger-bodied species. Available data indicate that the majority of nonhuman primate species only extend the duration of exhalations to 2–3 times the resting duration, compared with humans who can produce a more than 7-fold increase (see Table 4). Some nonhuman species can extend exhalations to at least 4–5 times resting duration, e.g., some *Hylobates* spp., *Indri indri,* and *Alouatta palliata.* These species all have laryngeal air sacs (though *H. klossi* may be an exception; Geissmann, 1993), which humans lack. This adaptation could be an alternative means of increasing the duration of exhalation during vocalization (Fitch and Hauser, 1995), though one that is less powerful and less controllable in terms of variability of the rate of air release, in comparison with enhanced thoracic breath control in humans. The evidence indicates that humans can increase both the absolute and relative duration of exhalations during vocalization substantially more than any nonhuman primate, despite our lack of air sacs (see Table 4).

Mainly as a result of extending exhalations, humans are apparently unique among primates in the extent to which they can distort an even breathing cycle for vocalizations to a greater extent than any other

TABLE 4. *Respiratory data for call duration and call rate: examples from species of a range of body sizes and respiratory adaptations*

Species	Mean body weight[1] (kg)	Mean resting breathing rate[2] (min^{-1})	Duration of longest call[3] (sec^{-1})	Call length as a multiple of resting exhalation[4]	Call rate[5] (sec^{-1})	Call rate as a multiple of resting breathing rate[6]	References from which call duration and call rates were estimated
Without air sacs							
Galago senegalensis	0.19	82.4	0.5	1.4	3.0	2.2	Andrew (1963a), Zimmermann et al. (1988)
Tarsius spectrum	0.20	82.0	0.7	2.0	6.0	4.3	Haimoff (1986)
Otolemur crassicaudatus	1.2	51.1	0.7	0.6	2.3	2.7	Andrew (1963a), Zimmermann (1990)
Hylobates pileatus	5.45	34.4	2.1	2.4	2.0	3.5	Haimoff (1984, 1986), personal observation
Hylobates lar	5.6	34.2	2.8	3.1	2.0	3.6	Haimoff (1984), Raemakers and Raemakers (1985)
With air sacs							
Alouatta palliata	6.55	32.9	4.8	5.1	3.0	5.6	Sekulic and Chivers (1986)
Hylobates concolor	7.55	31.6	4.5	4.7	3.0	5.7	Deputte (1982), Haimoff (1984), Haimoff et al. (1987)
Indri indri	10.5	29.0	5.0	4.8	3.0	6.2	Haimoff (1986), Thalmann et al. (1993)
Pan troglodytes	45.9	19.8	1.6	0.6	4.0	12.5	Marler and Tenaza (1977), Clark and Wrangham (1993)
Gorilla gorilla	117.55	15.7	3.2	1.6	5.4	20.6	Harcourt et al. (1993)
With enhanced breathing control							
Homo sapiens	60.00	18.5	12.0	7.2	12–15		Lieberman et al. (1992), Winkworth et al. (1995)

[1] Body weight data from Martin and MacLarnon (unpublished data).
[2] Breathing rates estimated from body weight using the allometric formula, respiration rate = $53.5W^{-0.26}$, where W = body weight in kg (Stahl, 1967).
[3] Duration of longest calls given on a single breath calculated from published data, including sonograms. Breathing patterns either described in source or implied by definitions.
[4] Duration of resting exhalation calculated as 50% of duration of a single breathing cycle (see text).
[5] Fastest rate of call units given on sequences of inhalations and exhalations (call rate) calculated from published data, including sonograms. Breathing patterns either described in source or implied by definitions.
[6] Call rate as a multiple of resting breathing rate calculated by dividing the absolute call rate by the number of resting breathing cycles per second.

primates. In human speech, exhalations typically comprise 85% of each cycle (e.g., based on data in Borden and Harris, 1984; Mitchell et al., 1996). Published sonograms, and some published data, suggest that expirations usually fill between 35–65% of breathing cycles during the vocalizations of nonhuman primates, e.g., 55% for the pant hoots of *Pan troglodytes* (calculated from data in Marler and Hobbett, 1975), 67% for train grunts in *Gorilla gorilla* (calculated from Harcourt et al., 1993), and 33–57% for the woo-ah sequence of *Hylobates agilis* (estimated from sonograms in Gittins, 1984). During human speech, therefore, which is only produced on the expiratory phase, pauses in sound production for inspiration are minimized, and the length of expirations can be varied over a considerable range, enabling inspiratory breaks to be placed at linguistically suitable points (Winkworth et al., 1995; Davis et al., 1996; Mitchell et al., 1996).

The fundamental frequency (F_0) of sound production falls as subglottal pressure falls. Without breath control, expiration essentially results from the relaxation of the respiratory muscles, and vocalizations on such expirations would be expected to show a decline in F_0 through their duration. In humans, F_0 can be controlled voluntarily, as subglottal pressure can be controlled, and F_0 only falls in 63% of spontaneous utterances (Lieberman, 1983, as corrected by t'Hart, 1986, and cited in Hauser and Fowler 1992). A rise or fall in F_0 at the end of a phrase in human speech affects meaning; it may indicate a question or the end of an utterance, or it may facilitate (or prevent) turn-taking in conversation. Control of F_0 changes through an expiration is an important aspect of human speech and language.

Nonhuman primates commonly show a drop in fundamental frequency through a vocalization on one exhalation, e.g., the coos of rhesus macaques, the wrrs of vervets, and the girneys of rhesus macaques (interpreted from evidence in Andrew, 1963a; Hauser, 1991; Hauser and Fowler, 1992). However, there are other vocalizations produced on single expirations which have a flat or rising F_0 (e.g., segments of gibbon songs; Haimoff, 1984). In almost all cases, these are of very short duration (Hauser and Fowler, 1992), normally no longer than about 1 sec, and many are much shorter. In a survey of the literature, very few cases were found of longer vocalizations with a rising inflection. Usually, these are associated with the presence of air sacs, e.g. a long whoo of up to 4 sec given by a male *Hylobates concolor leucogenys* in response to a female song bout (Fig. 4.6 in Deputte, 1982). There are also a very few examples where air sacs are not present: e.g., *H. lar,* one rising note lasting approximately 2.8 sec (Fig. 5 in Raemakers et al., 1984), and *H. klossi,* a long, flat whoo lasting 2.5 sec (Fig. 2 in Tenaza, 1976), though neither of these is very extended. It is apparently broadly true to say that nonhuman primates do not produce substantially extended exhalations without a declining F_0, except by the use of air sacs, which humans do not possess. It is possible that nonhuman primates have no choice about this drop in frequency because they are unable to control their rate of breath release to the same degree as humans. There is also no evidence from nonhuman primates of the complex, fast-changing patterns of rising and falling F_0 on a single expiration that characterize human speech, and play a central role in conveying meaning, be it through tonal differentiation of phonemes, or intonation across a phrase.

As well as fundamental frequency, humans can also modify the volume or amplitude of speech to emphasize any syllable or part of a phrase, providing linguistically important flexibility. No evidence of such control has been reported in nonhuman primates.

Human speech is characterized by the production of rapid sound sequences which Lieberman et al. (1992) stated are 10 times faster than those of any nonhuman primate. This rate of sound sequencing is an essential element in rapid information transfer. Comparison between humans and nonhuman primates of the rates of production of discrete sounds is fraught with difficulties, mostly related to the definition of a "unit of sound." Human speech is usually partitioned into phonemes or syllables, units which are meaningful in terms of perception, and which are not defined solely by their acoustic properties. The units used to describe nonhuman primate vocalizations

are essentially acoustic, and there is no general agreement about their comparability between species, or between different studies, and in particular about their comparability to the units of human speech.

There are two main factors that together result in the rate of sound sequencing during vocalization: first, the number of sound units (e.g., notes, syllables, phonemes) produced on a single expiration or inspiration, and second, the breathing rate, i.e., the number of breathing cycles per second. Nonhuman species can produce sequences of sound units on a single breath using a number of mechanisms, though most of these are quite simple repetitions, which do not approach the highly varied sound sequences of human speech. Many species produce trills and quavers by simple tongue or lip movements, e.g., *Cercopithecus aethiops* (Hauser and Marler, 1992), *C. mitis* (Hauser et al., 1993), and *Macaca fuscata* (Green, 1975). Some species can produce more complex sound sequences on a single breath, e.g., two more distinctive units are produced in the waa-quaver of *Hylobates lar,* by opening and closing the mouth (Haimoff, 1984). More distinctive still, the bitonal scream of the siamang involves two sound units on a single expiration, produced by inflation and deflation of the laryngeal airsacs (Haimoff, 1984). The multimodulated squeals of Sykes' monkey, *Cercopithecus albogularis,* might involve independent and simultaneous vibrations of the vocal folds in the larynx and the vocal lip, using a combination of air flow from the lungs and air sacs (Brown and Cannito, 1995). The more complex sequences seem to involve the use of air sacs (which humans do not possess), and they are considerably less variable and flexible than the sound sequences which humans produce on a single breath by complex manipulations of the upper respiratory tract. Nonhuman primates are apparently severely limited in the extent to which they are able to divide a single expiration into clearly delineated sound units, something which Provine (1996) also suggested, based on the limitations on chimpanzees' ability to laugh. They therefore would not be capable of utilizing very extended expirations to produce complex sound sequences, as in human speech.

The second factor contributing to the rate of sound sequencing, i.e., breathing rate during vocalization, is therefore especially important, as nonhuman primates are apparently limited in the extent to which they can produce varied sounds on a single air movement. As mentioned previously, resting breathing rate is faster in smaller than larger species (Stahl, 1967). For a medium-sized primate of 5–6 kg, a 3–4-fold increase of resting breathing rate, well within the normal physiological range, would enable 2 or 4 sounds per sec, depending on whether sounds are produced on both inhalation and exhalation, or only one part of the cycle. A similar rate of sound production could require a 6–7-fold increase from resting breathing rate for humans, and more than an 8-fold increase for gorillas. Clearly, the physiological demands of producing fast breathing rates are greater for larger species. Air sacs may again have an important role here, and larger-bodied species that vocalize on breathing rates more than 3–4 times resting breathing rate generally have air sacs, e.g., *Pan* spp., *Gorilla,* larger-bodied *Hylobates* spp., a range of larger New and Old World monkey species, and *Indri* (see Table 4). Humans do not possess air sacs, but the ability of our species to produce fast sound sequences on single extended exhalations provides an alternative, and apparently much more effective, means of overcoming the physiological limitations of large body size.

The communicatory power of the vocalizations of nonhuman primates is further restricted because they normally only produce specific sound units on either exhalations or inhalations, but not both, which restricts their order of production. However, the sequence of note production definitely can be important in conveying meaning. For example, Mitani and Marler (1989) showed that playbacks of reordered sound sequences of the great call of *Hylobates agilis* produced no vocal response from individuals of the species. Particular sequences of sounds produced by nonhuman primates can convey a variety of information (e.g., Seyfarth and Cheney, 1992), such as the species or individual status of the caller, the type of approaching predator, mating interest, or terri-

torial claim. However, most authors agree that nonhuman vocalizations contain nothing approaching human syntactical constructions, the encoding systems enabling rapid and highly flexible information transfer. Cognitive differences between humans and nonhuman primates are no doubt of great importance here, but so are physiological and morphological differences. The latter include several features of the upper respiratory tract such as the much greater ability of humans to mould the pharynx and mouth structures to filter the spectrum of harmonics generated by the larynx in order to produce different phonemes. However, the importance of the human ability to produce extended, controlled expirations should not be underestimated. It is not known whether nonhuman primates could be trained to take on a more human pattern of exhalations, but there is no evidence from their habitual vocalizations that they would be capable of doing so.

Evidence of differences in the muscular control of breathing for human speech and nonhuman primate vocalizations

There are few detailed studies of breath control during vocalizations in nonhuman primates, apart from the extensive series of laboratory studies on respiratory muscle activity and the neural control of vocalizations in *Saimiri sciureus* (Jurgens, 1982, 1988; Jurgens and Kirzinger, 1982, 1984; Jurgens and Richter, 1986; Sutton and Jurgens, 1988; Jurgens and Schreiver, 1991; Kirzinger and Jurgens, 1994) and the studies on macaques (*Macaca nemestrina* and *M. fascicularis*) (West and Larson, 1993; Larson et al., 1994). These workers reported that vocalizations occurred only on exhalations and primarily involved abdominal muscles rather than intercostal muscles, which were active prior to vocalizations in the study of macaques by West and Larson (1993) and not consistently active during vocalizations in the studies of either genus. Jurgens and Schreiver (1991) speculated that the intercostal muscles in *S. sciureus* could be involved in supporting the thorax and providing anchorage against which the abdominal muscles could act, rather than producing respiratory drive. West and Lar-

son (1993) suggested that in macaques the diaphragm could have a central role during vocalizations similar to that of the intercostals in humans. This evidence suggests that the pattern of muscular recruitment during nonhuman primate vocalizations is very different from that involved in producing the air flow for human speech (as described above), in which the intercostals have a primary role, although the actions of the abdominal muscles may be more similar. However, all such comparisons are difficult because most of the vocalizations in the nonhuman primate studies were not produced naturally. Rather, they were elicited by stimulation of electrodes in the periaqueductal region of the midbrain, and all were of relatively short duration (100–600 msec). More definitive analysis of the relative muscular involvement during nonhuman primate vocalizations and human speech awaits further physiological research.

CONCLUSIONS

Evidence presented here on the size of the thoracic vertebral canal in a range of fossil hominids has been interpreted as showing that thoracic innervation among australopithecines and *Homo ergaster* (or early *Homo erectus*) was similar to that of extant nonhuman primates. Sometime later in human evolution, the grey matter in this part of the cord expanded, and Neanderthals and early modern humans had expanded thoracic innervation, like extant humans. It seems most probable that this increased innervation evolved to enable enhanced breath control, and the most likely functional reason for this was the evolution of human speech, i.e., the physical production of language. Full human language requires extended exhalations for vocalizations and increased control of volume, emphasis, and intonation compared with nonhuman primates and therefore presumably compared with early hominids. Such features require fast, intricate, flexible, and integrated neural control of intercostal and abdominal muscles.

Enhanced breath control, which is a necessary feature for fully modern language, therefore was not possible for earlier hominids up until at least 1.6 Mya, the time of *Homo ergaster* (or early *Homo erectus*).

TABLE 5. *Summary of suggested dates for evolution of language or contributory features*

Date	Features	Evidence	References
3.5 Mya or more recently	Increased brain size, increased size of particular brain parts, brain asymmetries	If the initial enlargement of the brain was important, language may have evolved at any time from about 2 Mya. However, more detailed features that have been associated with earlier language evolution require very careful interpretation in the light of recent findings.	Holloway (1983) Falk (1980) Aiello and Dunbar (1993) Walker (1993) Petersen et al. (1988, 1989)
1.6 mya–100,000 years ago	Enlargement of vertebral canal, indicating increased control of breathing	Absent in australopithecines and *Homo ergaster,* but present in Neanderthals and early modern humans	MacLarnon (1993) MacLarnon and Hewitt (1995) Present paper
400,000–300,000 years ago	Basicranial flexion present, indicating laryngeal descent and high pharynx	Present in some archaic *Homo sapiens* (e.g., Kabwe, Petralona), but not Neanderthals	Laitman et al. (1992) Lieberman (1984)
>300,000 years ago	Hypoglossal canal as large as modern humans, indicating tongue richly supplied with motor nerves and complex motor coordination possible	Absent in australopithicenes, but present in archaic *Homo sapiens* (e.g., Kabwe, Swanscombe, and Neanderthals) and early modern humans	Kay et al. (1998)
>100,000 years ago	Hyoid bone human-like	Kebara Neanderthal	Arensburg et al. (1990)
40,000 years ago	Cultural development of Late Stone Age and Upper Palaeolithic, indicating symbolic behavior (e.g., variety of materials used, variety of objects fashioned, including nonutilitarian objects, jewelry, grave goods, cave art)	Modern humans only	Isaac (1976) Noble and Davidson (1991) Mithen (1996)

However, this feature was present in hominids of 100,000 mya or less, including both Neanderthals and early modern humans. Many evolutionary changes, both cognitive and physical, were required for the development of fully modern language from our nonhuman ancestors. A range of paleontological and archaeological evidence has been interpreted as indicating the probable time or time range of their evolution (see Table 5). The present evidence from the thoracic vertebral canal suggests that the language abilities of early hominids were at most severely limited to short, unmodulated utterances, lacking rapid sequencing, perhaps something like the protolanguage of Bickerton (1990).

With such a long and important time gap between the most recent fossil hominid with an unexpanded thoracic canal and the earliest fossils with expanded canals, the evidence presented here can only make a limited contribution to the great debate over modern human origins, i.e., the single origin theory (Stringer and Andrews, 1988) vs. multiregionalism (Wolpoff et al., 1984). However, with the early date of about 1.8 mya now attributed to *Homo erectus* in the Far East (Swisher et al., 1994), it seems likely that the first major migration out of Africa was of hominids lacking the developed breath control necessary for modern human speech, like other African hominids up to at least 1.6 mya (KNM-WT 15000). Assuming such an evolutionary change would be highly unlikely to evolve twice, and that sufficient gene flow to carry it thousands of miles is very improbable, this seems to act against Asian *Homo erectus* being the ancestor of modern Asians, as the multiregional theory proposes. Based on the same types of assumption, the expanded thoracic canals shown by Neanderthals and early modern humans suggest that they had a common

ancestor after the evolution of thoracic expansion, more recently than 1.6 Mya, as genetic evidence now indicates (Krings et al., 1997). However, evidence from the vertebral canal does not enable more precise determination of how distant or recent this ancestor was. More fossil evidence from this "gap" is needed to clarify the more recent evolutionary history of this neglected aspect of the evolution of human language, the evolution of sophisticated neural control of breathing required for speech production.

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