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CHAPTER 12

Seafood, Diving, Song and Speech

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Abstract: In this paper we present comparative data, suggesting that the various elements of human speech evolved at different times, and originally had different functions. Recent work by Nishimura [1-6] shows that what is commonly known as the *laryngeal descent* actually evolved in a mosaic way in minimally two steps: (a) a descent of the thyroid cartilage (Adam's apple) relative to the hyoid (tongue bone), a descent which is also seen in non-human hominoids, and (b) a descent of the hyoid bone relative to the palate, which is less obvious in non-human hominoids, and which is accentuated by the *absence of prognathism* in the short and flat human face. Comparisons with other animals suggest that (a) the first descent might be associated with loud and/or varied sound production, and that (b) the second might be part of an adaptation to eating seafoods such as shell fish, which can be sucked into the mouth and swallowed without chewing, even under water. We argue that the origin of human speech is based on different pre-adaptations that were present in human ancestors, such as (a) sound production adaptations related to the descent of the thyroid cartilage associated with the territorial calls of apes, (b) transformation of the oral and dentitional anatomy including the descent of the hyoid, associated with reduced biting and chewing, and (c) diving adaptations, leading to voluntary control of the airway entrances and voluntary breath control. Whereas chimpanzee ancestors became frugivores in tropical forests after they split from human ancestors about 5 Ma (million years ago), human ancestors became littoral omnivores. This might help explain why chimpanzees did not evolve language skills, why human language is a relatively recent phenomenon, and why it is so strongly dependent upon the availability of voluntary breath control, not seen in other hominoids, but clearly present in diving mammals.

Keywords: Speech origins, language evolution, laryngeal descent, hyoid bone, thyroid cartilage, hominid diet, hominoid evolution, diving abilities, seafood, suction feeding, consonants, *Homo erectus*, song, musical abilities, comparative biology.

INTRODUCTION

The evolutionary origins of human language are still heavily debated. Here we attempt to explore some of the pre-adaptations that might have contributed to the origin of human speech. We use a comparative analytical approach, which is based on the assumption that most of the 'unique' features of a species (*in casu*, human speech) consist of more elementary features, which are less unique (*in casu*, breath control, laryngeal sound production, sound modification by the pharynx, and the specific morphology of e.g., the palate, the tongue and the lips, and our extreme musicality). We argue that since these features are inherited largely independently, and have or had specific and often overlapping and evolving functions, they provide information on present or recent past lifestyles through comparisons with other species with similar features. Even in those cases where we do not know the exact functions of certain features, comparisons with other animals with similar features can provide information on past lifestyles. Using this method, we attempt to reconstruct the different evolutionary pathways of human phonation abilities, especially after human ancestors split from the last common ancestors shared with the chimpanzees, about 5 Ma [7, 8].

Humans have several remarkable differences when compared to chimpanzees and other primates, not only in the nasal, oral, pharyngeal and laryngeal anatomy (Fig. 1, Table 1), but also in the neurological control of these structures (Figs. 2 and 3, Table 1). Because the nasal and dental differences are probably less important in speech production, we focus mainly on the oropharyngeal (mouth and throat) adaptations that distinguish humans from the apes.

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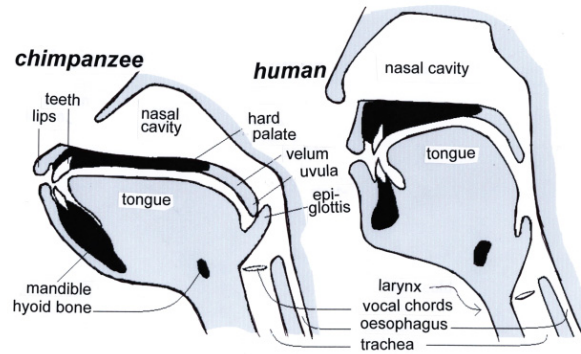


Figure 1: Midsagittal sections through chimpanzee (left) and human (right) head. Note the external nose, the absence of oral prognathism, the globular tongue, the short, vaulted, smooth palate, and the lowered hyoid in humans. In chimpanzees, air and food passages are separated in rest (not during *e.g.*, hooting and panting). In humans older than about four months, they overlap, probably due to the shortened oral cavity and the hyoidal descent (which the comparative data suggest might have been an adaptation for suction and/or underwater feeding). This overlap of air and food passages allowed the laryngeal sounds, generated by the vocal chords, to be permanently modified through mouth and tongue movements – a precondition to human speech.

Table 1: Unique features of human air and food passage entrances and their neurological control – possible convergences and functions

Characteristic	<i>Pan</i> : often the original situation?	<i>Homo</i> : mostly innovations?	References on <i>Homo/Pan</i> differences [11-14]	Examples of possible convergences in other animals	Possible functions (not mutually exclusive)
INTERNAL NOSE					
Olfaction	Rather poor	Very poor	[43]	Aquatic mammals	Atrophy: useless in water
Nasal passage	More direct	Long, inverted U	Fig. 1		Easier closure, keeping water out?
Plexus cavernosus on inferior concha nasalis	Absent: no erectile vascular tissue	Well-developed, nasal cycle 90 seconds	[44]	Diving cycle of sea otter	Shallow diving
EXTERNAL NOSE					
Size	Small	Large cartilages (esp. cartilago alaris maior)		Elephant, tapir, proboscis monkey, bladdermose seal	Semi-aquaticness <i>e.g.</i> , snorkel? Sound modification? Sexual selection?
Nostril form	Rounder	More slit-like			Easier closure
Nostril direction	Forwards	Downwards		Sea otter	Easier closure, keeping water out
Philtrum in upper lip	Absent	Fitting with septum between nostrils	[45]		Closure, see Fig. 6 of Chapter 7
MOUTH OPENING					
Lips	Less visible mucosa	Everted (red mucosa)			(Watertight?) fitting together. Kissing?
Opening size	Normal, wide	Small	[10]	Globicephalines	Suction feeding, prepared foods?
DENTITION					
Front teeth	Prognathism	Flat face, vertical incisors		Dusky titi, globicephalines	Less biting, suction feeding
Canines	Large + diastemata	Incisor-like, only slightly projecting			Larger cutting edge, <i>e.g.</i> , for frugivory? Tooth row closure, <i>e.g.</i> , for suction?
Tooth row	Parallel cheek teeth	Parabolic, closed tooth row		Dusky titi, parabolic tooth rows in aquatic mammals	Suction feeding of slippery foods, <i>e.g.</i> , fruits, seafoods
Enamel thickness	Thinner: reduced? (very thick in australopiths)	Thick		Capuchin, orangutan, sea otter	Durophagy, <i>e.g.</i> , feeding on nuts and/or shells
Occlusal relief	Higher relief	Bunodont (rounded cusps on cheek teeth)		Suids, sea otter	Harder food items: cracking rather than slicing foods?
Biting/chewing force	Stronger temporalis and masseter muscles	Weak (MYH16 inactivation)	[15]		Less biting: suction feeding?
Unerrupted teeth	Rare	Frequent in archaic <i>Homo</i> , M3 frequent in <i>H. sapiens</i>	[46]	Very frequent in <i>e.g.</i> , Globicephalines	Atrophy, <i>e.g.</i> , for suction feeding?

Table 1: cont....

ORAL CAVITY: TONGUE AND PALATE					
Palate length	Long	Short			<i>Cf.</i> hyoidal descent?
Palate form	Flatter	Vaulted		Dusky titi	Fitting tongue form, <i>e.g.</i> , for suction feeding?
Palate ridges (rugae)	5-15	2-8, restricted to the front, smooth palate		Aquatic mammals	Slippery foods, suction feeding
Tongue form	Flat, long	Globular, short, fitting in palate and tooth row			Versatile for suction feeding? For speech?
THROAT: HYOID AND LARYNX					
Hyoid bone localization	Undescended	Descended vs. mandible	[4, 22, 47]	Sea cows	Suction feeding?
Larynx position in rest	Connected to the nasal passage	Descended vs. hyoid: Adam's apple in adults	[48-50]		Phonation? Suction?
Larynx size	Normal	Well-developed, very muscular vocal folds	[49]		Singing, calling, speech
Laryngeal airsacs	Very large (liters)	Absent (vestigial laryngocele): atrophy?	[22, 47], Chapter 4	<i>Cf.</i> absence (reduced?) in gibbons	Hindrance to diving, especially in salt water? Hindrance to singing?
CEREBRAL CONTROL: BRODMANN'S AREA 4					
Hand, finger and thumb representation	Rather large, equally large as foot representation	Very large, many times Larger than (reduced) foot representation	[7, 8], Fig. 2 and 3	Fine hand movements, <i>e.g.</i> , in sea otters and raccoons	Fine manipulation of foods and/or tools
Mouth and tongue representation	Rather large	Very large, coordinated by Broca's area			Singing? Airway closure? Suction feeding? Hyperventilation? Speech?
Larynx representation	Small	Present, coordinated by Broca's area			Singing? Airway closure? Speech?
Representation of breathing muscles	Small or absent	Present, coordinated by Broca's area		Breathing control in diving mammals	Singing? Diving? Speech?

Most human differences with chimpanzees and other primates are obvious (*e.g.*, red lips, external nose) or described in Schultz [11] and Ankel-Simons [12]. Additional references are given in the fourth column. Not all items are discussed in this paper: see also our earlier publications [7, 8]. Differences between extant humans and chimpanzees-bonobos could evolve in the *Homo* or the *Pan* ancestral lineages at different times between ~ 5 and 0 Ma (if *Homo* and *Pan* split ~ 5 Ma), so that, for instance, thick enamel originally does not contradict enamel reduction in chimpanzees' ancestors (*e.g.*, for more herbivory?) and on the other hand masticatory muscle atrophy in human ancestors (*e.g.*, for more suction feeding?).

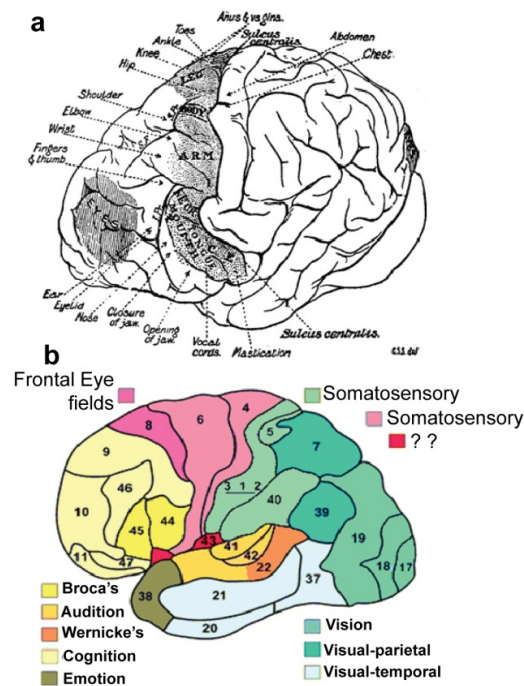


Figure 2: Sideview of **a)** chimpanzee cerebral cortex [Available at: <http://ahsmaill.uwaterloo.ca/~aktse/Brodman.gif>. Cited 2010 October 24]; **b)** human cerebral cortex, with Areas of Brodmann indicated on human cortex [Available at: http://commons.wikimedia.org/wiki/File:1911_EB_Chimpanzee_Brain.png. Cited 2010 October 24].

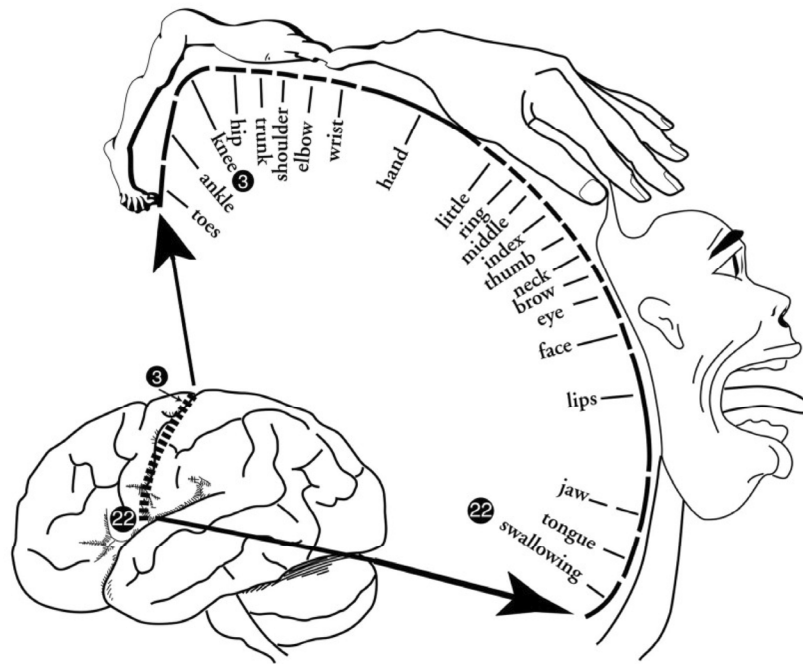


Figure 3: Representation of body parts in Brodmann's Area 4. [Available at: http://www.psywww.com/intropsych/ch02_human_nervous_system/02homunc.jpg. Cited 2010 October 24].

ORAL CAVITY

Humans have everted lips with exposed (red) mucosa, and a relatively much smaller mouth opening than other primates and than most tetrapods [9, 10]. This means that our biting possibilities are restricted, and this is also reflected by the possession of smaller front teeth, especially smaller canines. In general, carnivores have very large mouth openings with much larger canines than herbivores.

The human oral cavity is relatively much shorter than that of chimpanzees and the front teeth are less protruding (absence of *oral prognathism*) and are implanted vertically. The canines are incisor-like (more spatulated and not lengthened) and all the teeth are of nearly equal height so that the tooth row forms a closed dental arcade shaped like a parabola or semi-circle without diastemata (*i.e.*, gaps where the opposing canines fit) [11-14].

The strength of the human masticatory musculature is weakened by inactivation of the gene for *myosin heavy chain 16* (MYH16), a muscular protein that, at least in primates, is found only in the temporalis and masseter muscles of the jaw [15, 16]. Non-human apes, on the other hand, as most insect-, carni- and omnivorous terrestrial mammals, have prognathic muzzles and rectangular dental arcades with long, strong canines and large diastemata, protruding front teeth, and two parallel rows of cheek teeth (premolars and molars). Their hard palate (the bony part of the palate) is not highly vaulted, but rather long and flat (horizontal), with transverse ridges (*rugae palatinae*) that probably have the function of fixing the food so that it can be chewed without slipping away [11, 12]. Whereas the tongue of apes is long and flat, humans have a round, thick, globular, bulbous tongue that is very versatile and can be shaped to fit tightly at any place against the arched and smooth (ridge-poor) palate and the parabolic tooth row [11-14, 17, 18]. At least some of the differences of the human oral cavity, when compared to other apes, might be explained as adaptations to eating foods that can be sucked into the mouth and swallowed with minimal chewing (*e.g.*, soft fruits, grubs, eggs and/or slippery seafoods).

LARYNGEAL DESCENT

A conspicuous and often-mentioned difference between human and non-human primates is that humans have a *descended larynx*. The larynx or voice box (Adam's apple), housed in the thyroid cartilage, is an organ in the neck

of mammals involved in protection of the trachea and in sound production. In most terrestrial mammals the larynx at rest is positioned high up in the throat, but in humans (except babies) the larynx is positioned relatively low in the neck [13, 19]. In chimpanzees and even more so in other primates, the larynx connects with the nasal passage at rest and its entrance is within the nasal cavity, so that the food passes on both sides of the laryngeal tube in the centre of the throat: although in mammals the food passage and the air passage cross each other in the pharynx (Fig. 1), the food passage (from mouth to oesophagus) and the air passage (from nose to trachea) are fully separated most of the time, so that most mammals can swallow fluids (and some species even semi-solid foods) and breathe simultaneously [13, 19-21].

A lowered larynx is seen in a few aquatic mammals such as dugongs and manatees [22], but is probably less frequent in terrestrial mammals. Some mammals, like red deer, hammerhead bats, wolves and koalas, have a permanently low larynx, but have evolved (at least in red deer) a long and elastic *velum* (soft palate), which connects the nasal cavity with the larynx when at rest [19, 22-24]. This is lacking in humans. Thus, while most mammals, including all apes and human babies, can swallow fluids and breathe simultaneously, it is remarkable that humans from about the age of six months cannot.

However, recent work by Nishimura [1-6] shows that laryngeal descent is not so unique to humans among primates as once thought, and that laryngeal descent evolved in at least two steps during hominoid evolution. In human newborns, the hyoid (tongue bone) and the larynx are positioned as high as in other mammals, but postnatally the laryngeal skeleton descends relative to the hyoid, and the hyoid descends relative to the cranial base. In chimpanzee infants the larynx also descends relative to the hyoid, but the hyoid does not descend relative to the mandible, possibly due to the strong growth of the muzzle (oral prognathism). In both apes and humans the larynx moves independently from the hyoid, whereas in monkeys the *hyo-laryngeal complex* is a functional unit [2]. Nishimura [2] hypothesizes that the ability of apes and humans to move the larynx independently of the hyoid might have helped to prevent aspiration. In other mammals, however, a low larynx able to be moved independently of the hyoid appears to be associated with loud and varied calls. Male hammerhead bats, for instance, which sing loudly to attract mates, have an extremely low (in fact, intrathoracic) larynx they can move freely, and male deer and wolves have larynges which lower considerably during sound production. According to Fitch [19], laryngeal descent lengthens the vocal tract and produces lower-frequency formants in the calls, suggesting a large body size of the caller. It thus seems likely that the independently movable and descended larynx evolved in the early apes, before great apes and lesser apes split (~ 18 Ma), to allow the varied sound productions of the different ape species and especially the duets of the lesser apes (gibbons and siamang): “Gibbons are monogamous and they define their territories with characteristic, far-reaching, very melodic hooting songs” [12], although songs follow a relatively rigid pattern, unlike that of our species.

SINGING

Babies of two or three months are said to *vocalize*: they produce cooing sounds, which are performed using the vocal chords in the larynx without specific oral involvement. Soon thereafter, from about five months onwards, babies (even deaf) start *babbling*: they produce syllables that begin with a labial consonant plus vowel. In babies older than six months, the sound pattern resembles the native language, and *dialogues* with the mother, who addresses the child in ‘motherese’, stimulate the utterances [25, 26]. These early prelingual sounds, without symbolic meaning, follow a specific sequence of four phases that are also seen in young birds that learn to sing, *i.e.*, close listening, subsong, plastic song, and song crystallization [27]. Darwin [28] hypothesized that this prelingual sound production may correspond with the elaborate songs of non-human primates such as gibbons.

Well-developed musical abilities and duet singing are not only seen in some tropical monogamous birds in dense vegetation (*e.g.*, *Lanarius*, *Cossypha*, *Thryothorus*, *Cisticola*) [29], but also in several monogamous primates like indris, tarsiers, titi monkeys, and gibbons [26, 30]. Bonobos engage in group chorusing, and rival males of this species have been observed engaging in vocal duels [31]. For our own species, it is usually overlooked how powerfully music affects our emotions and can act as a territorial and pair- or group-binding behavior, *e.g.*, through anthems, hymns, marches and love songs [26]. It is known that musical training in young children induces an enlargement of the *planum temporale* and the auditory cortex in the left hemisphere of the neocortex, and improves the ability to hear absolute tones [32]. Intonation is an indispensable element of all spoken languages, and almost half of the world’s languages are still tonal, as the original languages, like extant KhoiSan, are thought to have been [33, 34].

In human infants between four and six months, the larynx starts to descend [35]. The comparative data suggest that the descent of the larynx *versus* the hyoid bone, which is also seen in chimpanzees, and presumably exists in other apes as well, has to do with sound production that includes lower formants (suggestive of large body size) [23]. Also, the loose connection between the larynx and the hyoid in hominoids (but not monkeys [2]) has probably to do with the development of varied sound production (singing).

SEAFOOD CONSUMPTION

Humans lack prognathism. They retain (possibly through *neoteny*) the short, flat face of the suckling infant, which may be an adaptive feature in order to more easily consume (slippery) seafoods later in life. The consumption of seafood might help explain the round tongue perfectly fitting in the smooth (*rugae*-poor) and vaulted palate, so that the tongue can obstruct the oral cavity at all possible places (*e.g.*, dental, palatal, velar, uvular), and not only keep the oral passage watertight, but also create the necessary low pressure required for the suction of small food items, both below and above the water. Indeed, most aquatic mammals are able to suction-feed to some extent, and have smooth, ridge-poor palates. Moreover, specialist suction feeders, such as walruses and globicephaline dolphins, have blunt heads, without beak-like mouths as in typical dolphins, and relatively small and round oral openings [36-39].

These features may be essential prerequisites to the evolution of spoken language, because obstruction of the vocal tract is an elementary requisite for the formation of *consonants*: complete obstruction in stops (*p, d, k etc.*) and nasals (*m, n etc.*), and partial obstruction in gliders (*v, z, sh etc.*). The sealing of the airways at the oral passage presumably overlaps with the abilities for suction feeding and for underwater feeding. The sealing of the airways at the nasal passage (Table 1) is not discussed in detail here.

Suction feeding is much rarer in terrestrial animals [37, 38]. It is seen in some primates, ursids and bats, who suck the juice from fruits and grubs with protruding lips forming very small mouth openings [24, 39-41]. Sloth bears, orangutans and chimpanzees can strongly protrude the lips creating a small oral opening, but nevertheless have long flat tongues and ridged palates. The typically human oral features such as flat face, small mouth, smooth palate *etc.* seem to be suited for suction of smooth aquatic foods more than for suction of terrestrial foods. We do not have to chew raw oysters, can swallow food under water, including small fish, and can swim with open mouth under water without swallowing or inhaling water. Feeding under water requires a fine co-ordination of the lips, mouth, tongue and throat in order to keep water out of the airways and prevent ingestion of too much (sea) water. Our extremely flexible globular tongue, in combination with the closed parabolic tooth row and smooth arched palate, is able to close the oral cavity at all possible places, but also manipulate objects within the mouth and help expel water from the mouth.

VOLUNTARY CONTROL OF SOUND PRODUCTION

The crucial step in the evolution of human speech might have been the linking of varied song production (as in gibbons) with voluntary breathing (as in diving mammals). Gibbon song, like bird song, is a territorial (emotional) behavior that is not under direct voluntary will.

Mammals that regularly dive, not only have to be able to seal their airways whenever necessary to prevent water entering the lungs, but also must be able to hyperventilate whenever and exactly at the moment they intend to dive, and to hold their breath under water. Terrestrial mammals automatically breathe deeper and faster when they exercise and need more oxygen, and this is directly regulated by the partial carbon dioxide pressure ($p\text{CO}_2$) at the respiratory centre in the brain stem. Such breathing reflex, however, would be catastrophic for a diving mammal, since their $p\text{CO}_2$ would be higher the longer they swim under water. Diving mammals need to have direct conscious (voluntary) control of their breathing musculature when they prepare to dive and when they re-surface.

When comparing human brain organization with that of the chimpanzee, the human voluntary breath control becomes apparent. In all primates and in many other mammals, fine and voluntary muscular skeletal movements are initiated in the *precentral cortex*, which in humans and other primates is called *Brodmann's Area 4* of the neocortex (Fig. 2). However, in humans – as opposed to apes and other terrestrial mammals – the breathing musculature is represented in the precentral cortex (Fig. 3). Thus, humans differ from other hominoids in that they are able to breathe whenever they want, *i.e.*, at free will.

Whereas cetaceans *only* breathe at free will (through the blowhole, the equivalent of our nostrils), humans possess *two* types of breathing: autonomous *abdominal* or diaphragmatic breathing through the nose, and free *thoracic* or chest breathing through the mouth. Most of the time we are not consciously breathing, and at rest we breathe automatically through the nose using our diaphragm and abdominal muscles, but when doing exercise we switch to open-mouthed breathing with thoracic musculature, using also the intercostal muscles of the rib cage. In the water, beneath the surface we hold our breath, and at the surface we breathe through the mouth, only using our thoracic muscles. Humans, unlike chimpanzees and other primates, not only have the laryngeal musculature represented in Area 4 of the neocortex, but also have a very large representation of the oral musculature in Area 4 (Fig. 3). (Interestingly, and as a consequence of this organisation, only in humans, damage of Area 4 produces muteness [42]).

Moreover, humans have direct fibers connecting Area 4 to the *nucleus ambiguus* (cortico-ambiguous connections), so they can voluntarily control the larynx muscles (nucleus ambiguus) and the breathing muscles (brain stem). When humans acquired this expansion of Area 4 to include breathing musculature (as required for diving), this would have encompassed or intensified the representation of the laryngeal musculature in Area 4, and brought laryngeal sound production under strong voluntary control.

This in turn would have made possible the production of laryngeal sounds (rhythmic tones, modified by the configuration of the lips, tongue and oral cavity into vowels) at free will, *i.e.*, influenced by connections to other neocortical centres such as the visual (Brodmann's Area 17 *etc.*) or auditory cortex (Area 41 *etc.*), thus making it possible to arbitrarily attribute a particular sound or melody to what was seen or heard.

When this voluntary control of laryngeal sounds was combined with the fine control of lips, tongue and velum, (initially developed) for suction feeding of slippery foods and/or underwater food manipulation (see above), this could have led to the introduction of consonants produced by brief interruptions of the airway by the tongue or lips at the labial, dental, palatal or velar regions of the oral cavity. In combination with the vowels, produced by the vocal chords and comparable to the sounds made by apes, consonants would have dramatically increased the number of possible *phonemes* (sound unities) available for communication.

CONCLUSIONS

Comparative studies between apes and monkeys indicate that the early hominoids well before the split of lesser and great apes (~ 18 Ma?) probably already had evolved a larynx that had descended in the neck relative to the hyoid bone and was able to move freely and independently of the hyoid bone, presumably for the production of loud rhythmical and melodic territorial duetting songs. After the *Homo-Pan* split (~ 5 Ma?), *Homo* populations apparently developed voluntary breath-holding abilities and the ability to close the airway entrances through the evolution of voluntary control of the oral musculature and of a round tongue, perfectly fitting in the smooth and vaulted palate, all unique among primates, and possibly explained as an adaptation to underwater and/or suction feeding on smooth seafood.

Indeed, the specific *Homo* characteristics are in our opinion best explained by assuming that sooner or later *Homo* populations dispersed to other continents along the coasts, where they collected littoral foods, not only through beach-combing and wading, but also through diving. Comparative data suggest that the consumption of slippery seafoods might help explain why human ancestors evolved flatter faces, smaller mouth openings, reduced dentition, smooth palates, round tongues, and descended hyoids. These innovations facilitated mouth closure at the labial, dental, alveolar, palatal and velar articulation places, allowing the production of consonants.

In combination with the song production already present in (some of) the early apes, this voluntary airway control made possible the extraordinary song capacities of the human species [26]. Later, the attachment of an arbitrary meaning to a musical phrase or utterance could have resulted in songs that conveyed free information, a precursor to spoken language. In addition, the diving-for-seafood scenario as an explanation for our voluntary breathing control and our flexible tongue and mouth coincides perfectly with the idea that the rapid expansion of the human neocortex came about as a result of an increase in the consumption of brain-specific nutrients such as DHA found in seafood (see Chapter 2).

In conclusion, on top of inherent song production as already present in early apes, the evolution of voluntary breath control, of increased oral musculature flexibility, of increased musicality and song production, and of very large

brains, all four explainable – directly or indirectly - as the consequences of seafood consumption, may explain why the human species is the only species on Earth to use spoken (grammatical) language.

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