



## Modern Human Origins Preadaptations to Language

Hugo Reyes-Centeno, Yonatan Sahle, Christian Bentz

17 January 2018, Lecture 9, Bentz



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## Readings for Lecture 9

Christiansen MH, and Chater, N. 2008. Language as shaped by the brain. In: *Behavioral and Brain Sciences* (31). **pp. 489-509.**

Klein, RG. (2017). Language and human evolution. In: *Journal of Neurolinguistics*.

Fitch WT. 2010. The evolution of language. Cambridge: Cambridge University Press. pp. 297-364.

## Course websites

<https://moodle02.zdv.uni-tuebingen.de/course/view.php?id=1932>

[http://www.christianbentz.de/teaching\\_humanOrigins2017.html](http://www.christianbentz.de/teaching_humanOrigins2017.html)



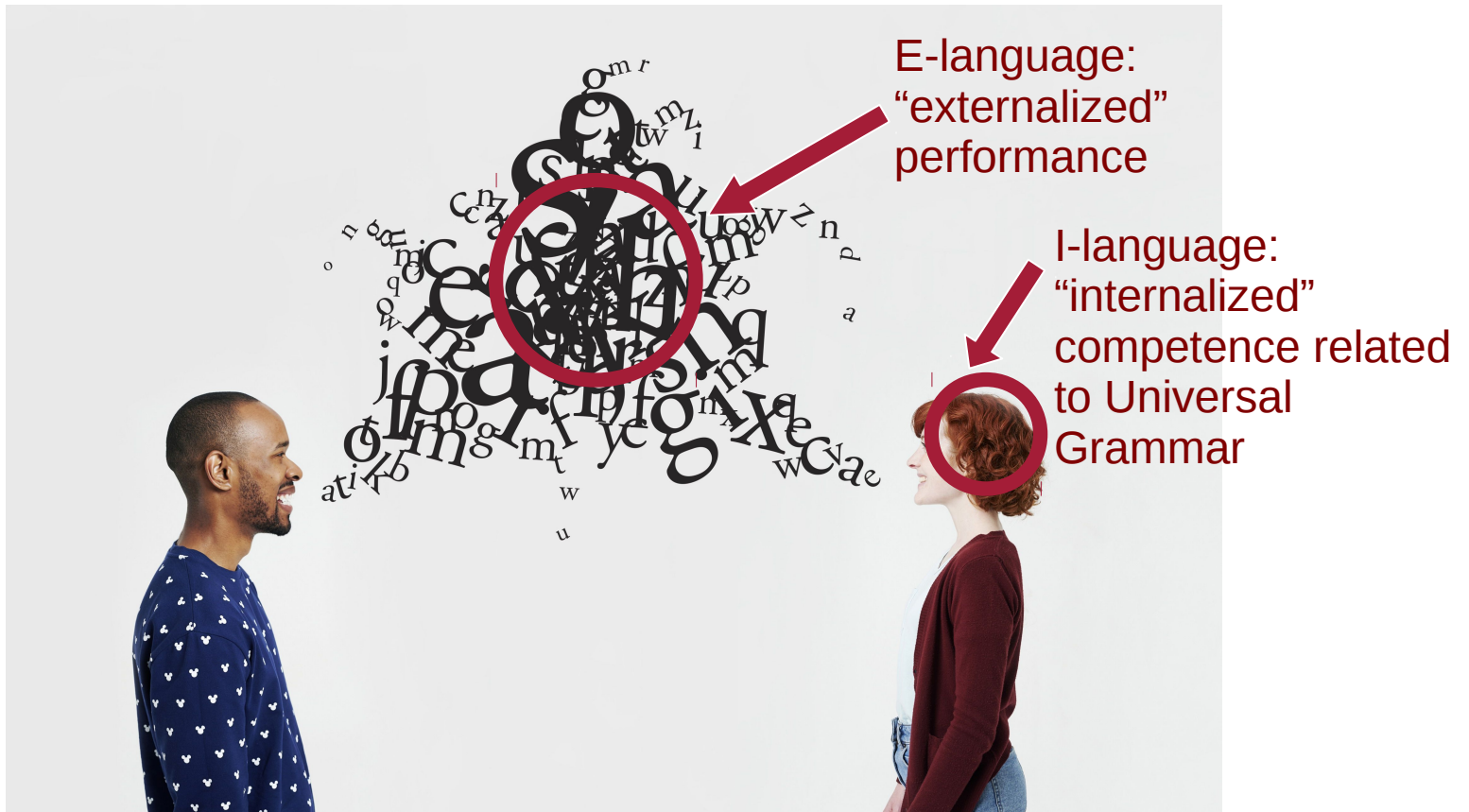
# Recap of Lecture 8

Language evolution: the hardest problem in science?

Christiansen & Kirby (2003)



## Question 1: What is „language“?



Chomsky (1965). Aspects of the theory of syntax.  
Chomsky (1986). Knowledge of language: it's nature, origin and use.



## Summary: Models of Language Evolution

Is language more like growing a wing or more like learning to play chess?



Saltational Account

Gradual Account

Co-evolution Account





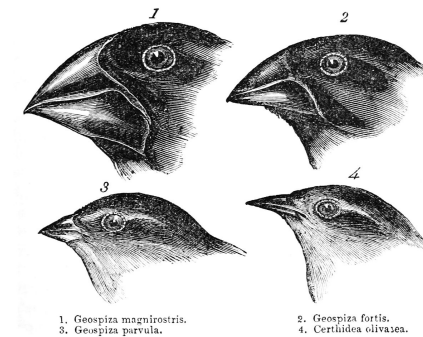
# Introduction

Adaptation, Preadaptation, Exaptation and  
Spandrels



## Terminology

- Adaptation
- Preadaptation
- Exaptation
- Spandrel



Fitch 2010, p. 63-64



## Terminology

### - Adaptation

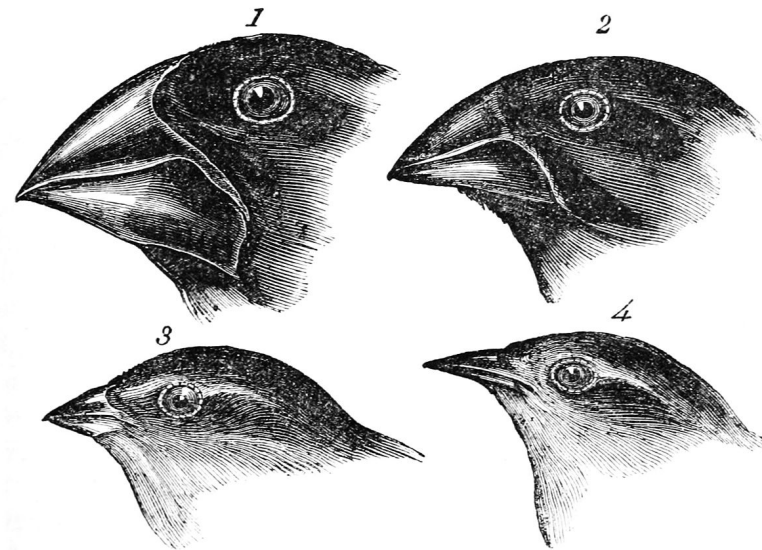
- Preadaptation

- Exaptation

- Spandrel

“**Random variability** is generated via recombination and mutation without any relation to function, and is followed by immediate **selection** in the context of whatever immediate problems an organism finds itself.”

Fitch 2010, p. 63



1. *Geospiza magnirostris*.  
3. *Geospiza parvula*.

2. *Geospiza fortis*.  
4. *Certhidea olivacea*.

Darwin, 1845. *Journal of researches into the natural history and geology of the countries visited during the voyage of H.M.S. Beagle round the world, under the Command of Capt. Fitz Roy, R.N.* 2d edition. 1.





## Terminology

- Adaptation
- **Preadaptation**
- Exaptation
- Spandrel

Darwin stressed “the highly important fact that an organ originally constructed for one purpose [...] may be converted into one for a widely different purpose” (Darwin, 1859). Such phenomena came to be termed preadaptations [...].”

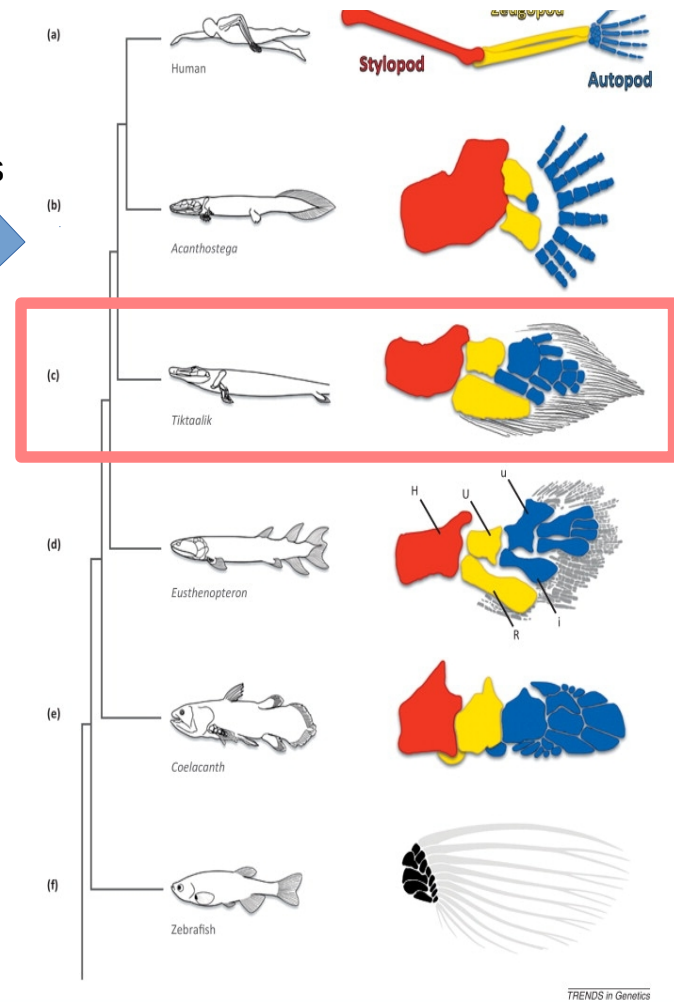
Fitch 2010, p. 63



# Terminology

- Adaptation
- **Preadaptation**
- Exaptation
- Spandrel

Boned fins as preadaptations to limbs



Schneider and Shubin (2013). The origin of the tetrapod limb: from expeditions to enhancers.



## Terminology

- Adaptation
- Preadaptation
- **Exaptation**
- Spandrel

[...] an important concept has no name in our lexicon (and unnamed ideas generally remain unconsidered): features that now enhance fitness but were not built by natural selection for their current role. We propose that such features be called **exaptations** and that adaptation be restricted, as Darwin suggested, to features built by selection for their current role.

Gould and Vrba (1982). Exaptation – a missing term in the science of form.

### Note also:

Objecting that the term “preadaptation” connotes foresight, Gould and Vrba suggested a new term, **exaptation**, to refer to **both the process of function shift and the end product of this process** [...]

Fitch (2010), p. 64.



## Terminology

- Adaptation
- Preadaptation
- **Exaptation**
- Spandrel

### Preadaptation vs. Exaptation:

[...] I will reserve the term “exaptation” for **the (typically brief) period during which an old trait is used in a new function**, but before it has been honed by selection to suit this new task

[...]

“Preadaptation” remains useful in this regard, retrospectively, to refer to the trait that provided the raw material for the process of exaptation.

Fitch (2010), p. 64.

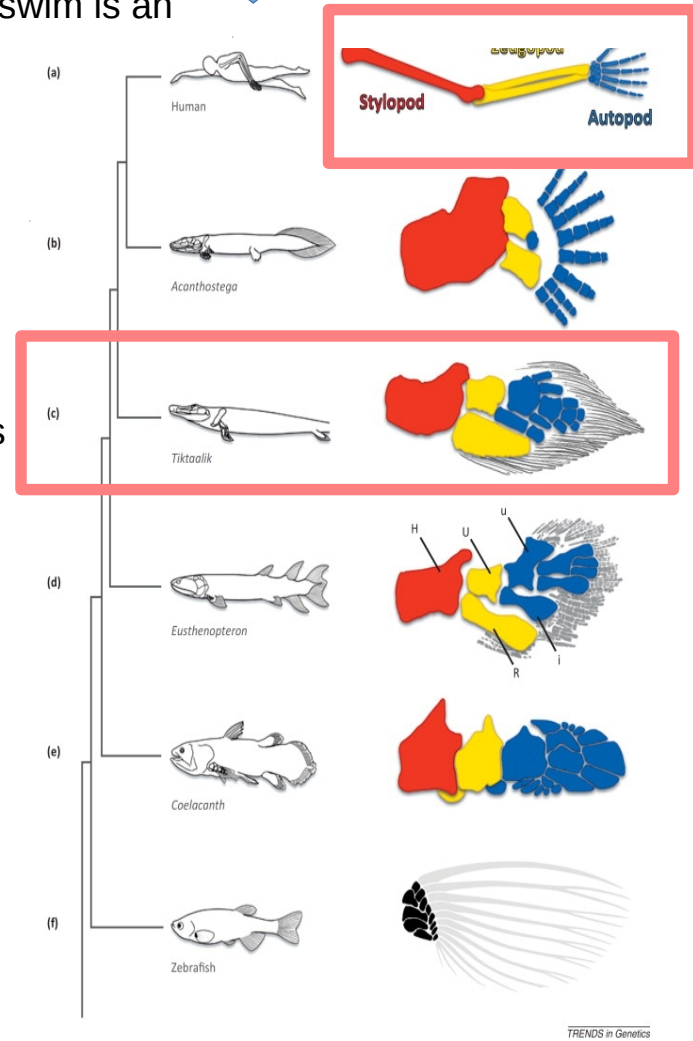


# Terminology

- Adaptation
- Preadaptation
- **Exaptation**
- Spandrel

Using limbs to swim is an **exaptation**

Boned fins as **preadaptations** to limbs ("raw material")





## Terminology

- Adaptation
- Preadaptation
- Exaptation
- Spandrel

“**Spandrels** - the tapering triangular spaces formed by the intersection of two rounded arches at right angles – are necessary architectural by-products of mounting a dome on rounded arches.”

Gould and Lewontin (1979). The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme.





## Terminology

- Adaptation
- Preadaptation
- Exaptation
- **Spandrel**

“Gould and Lewontin suggested that biological innovations may often occur via an analogous process, when selection on one trait leads to the appearance of some new feature as an automatic, unselected byproduct.

[...]

Such features [...] provide an alternative to the model discussed above, whereby an organ designed for one function shifts to another, because spandrels originally had **no function.**”

Fitch (2010), p. 65.



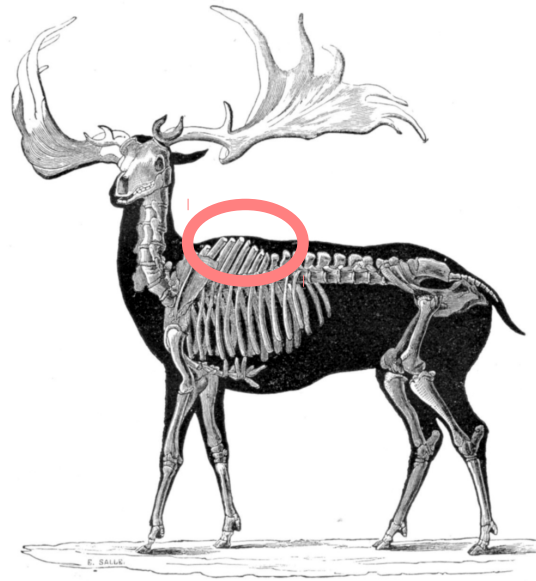
## Terminology

- Adaptation
- Preadaptation
- Exaptation
- Spandrel

## Example

“[...] the broadly raised area at the withers of the giant Irish deer (Megaloceros giganteus) – a spandrel produced by necessary elongation of the neural spines of the vertebrae [...] to hold up the massive head of this maximally horned deer – may become enlarged, altered in shape to a more prominent and localized hump, and festooned with distinctive colors, all (presumably) for coopted function in mating display.”

Gould (1997). The exaptive excellence of spandrels as a term and prototype.







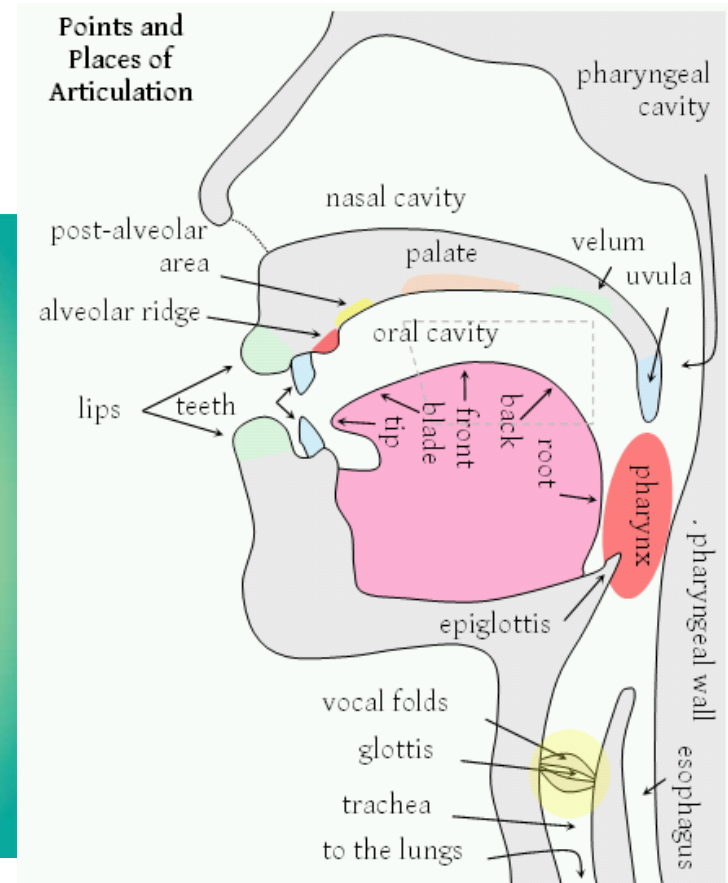
# Preadaptations for Language

- **The vocal tract**
- Speech perception
- Brain areas for language processing
- Genetics of language



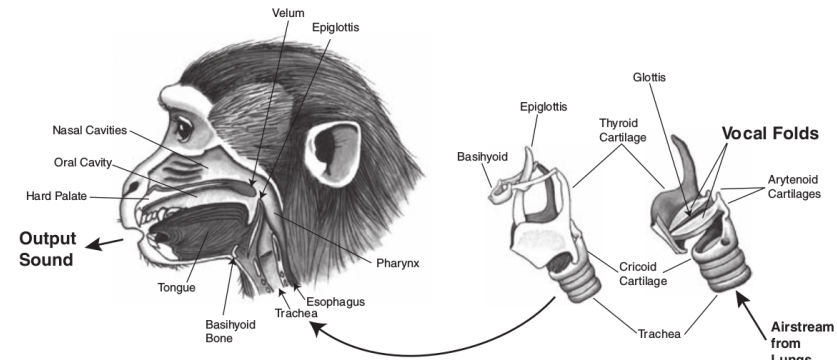
# Speech Production and Perception

A difference in **software**  
or **hardware**?



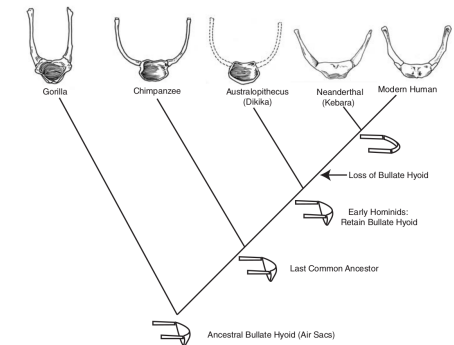
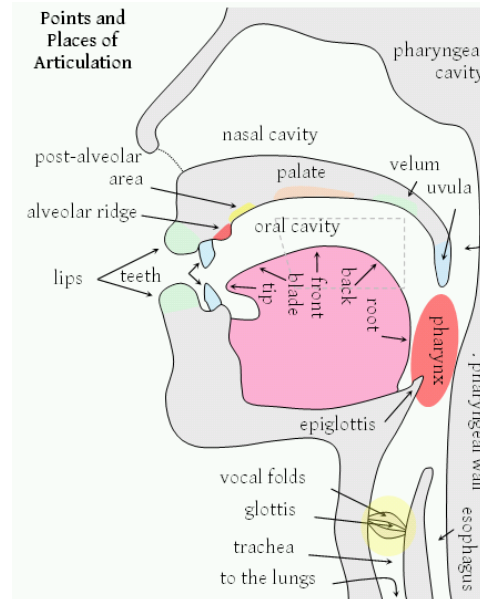
# The Vocal Tract

- The Larynx
- Hyoid Bone
- Air sacs
- Hypoglossal Canal
- Thoracic Canal



A. Filter: Vocal Tract

B. Source: Larynx



Fitch 2010, p. 297-337



# The Vocal Tract

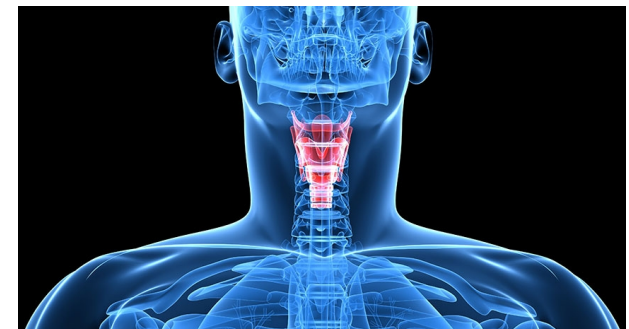
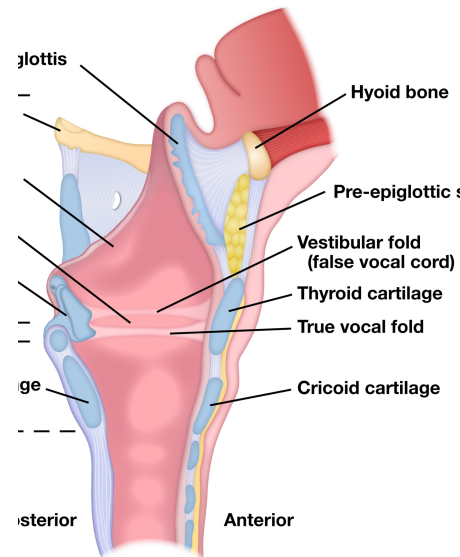
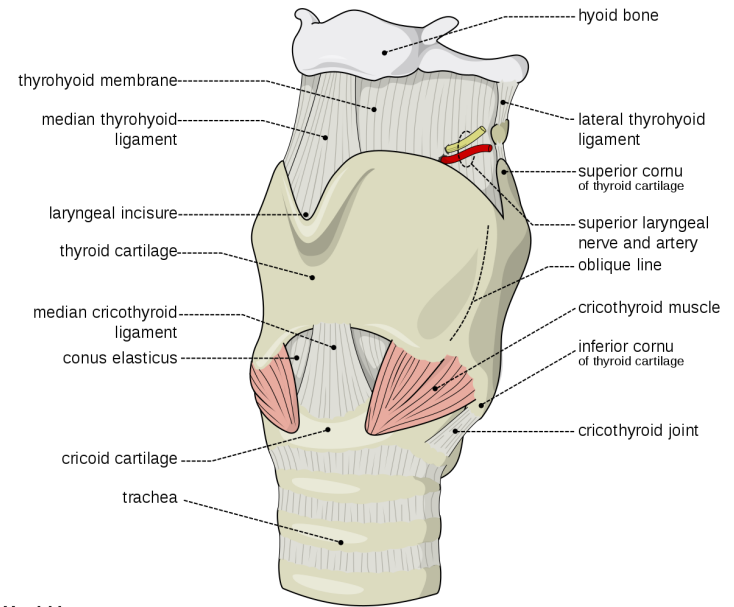
## - The Larynx

- Hyoid Bone

- Air sacs

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- Thoracic Canal





## The Vocal Tract

### - The Larynx

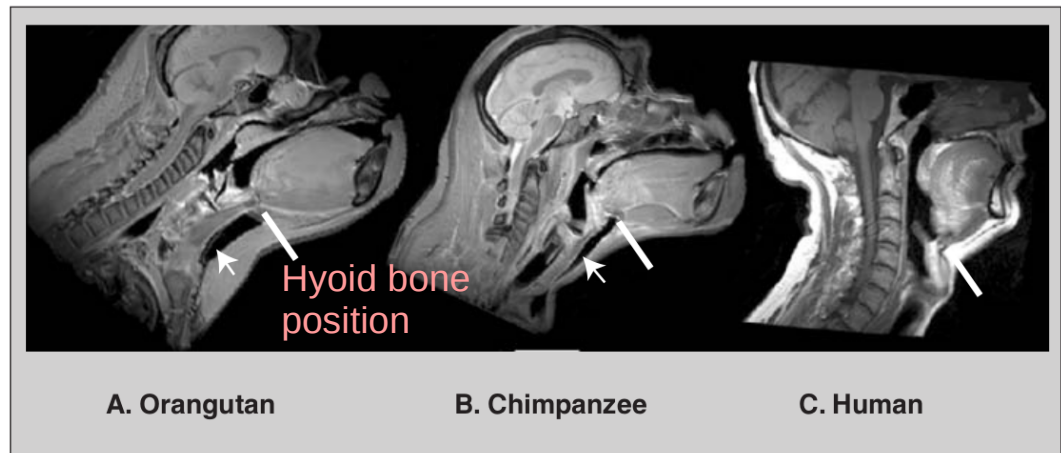
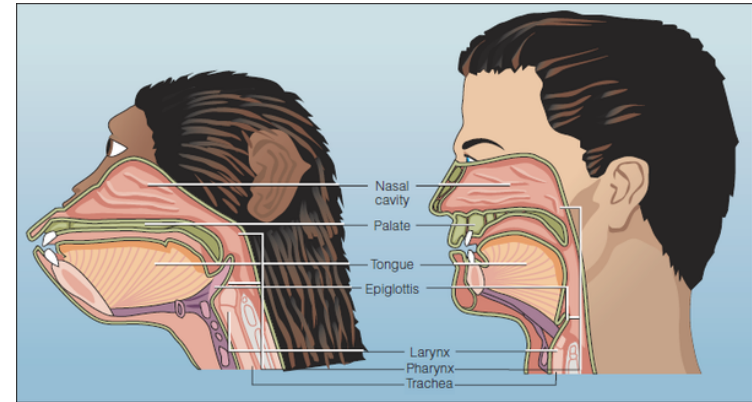
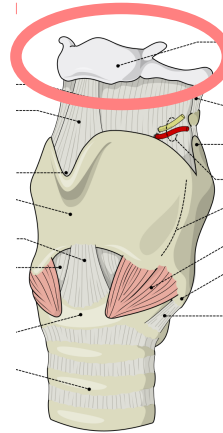
- Hyoid Bone

- Air sacs

- Hypoglossal Canal

- Thoracic Canal

### The descent of the larynx



Fitch 2010, p. 307 pp.



Video at 10:45

<http://www.dailymotion.com/video/x40jndd>



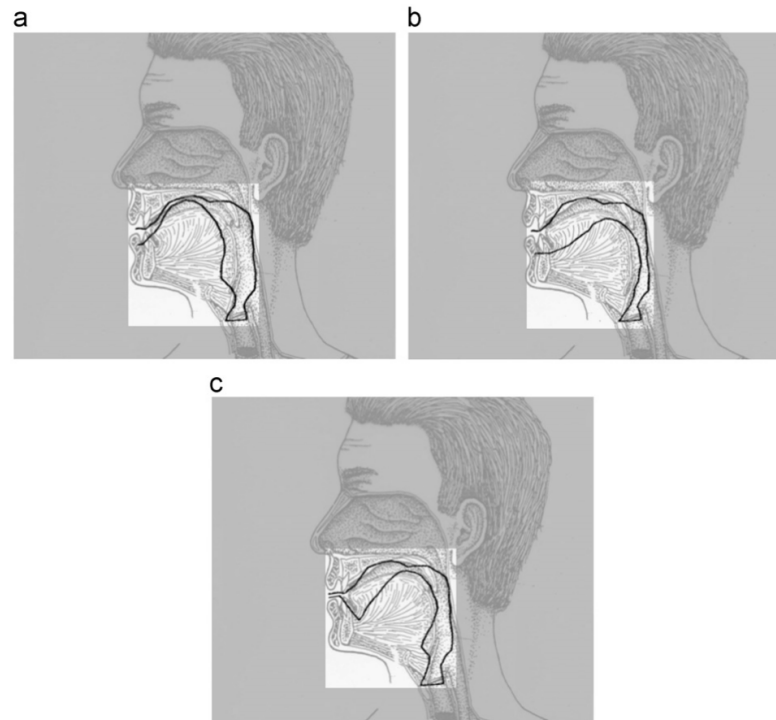
## The Vocal Tract

### - The Larynx

- Hyoid Bone
- Air sacs
- Hypoglossal Canal
- Thoracic Canal

Two opposing views still:

- 1) Specific vocal tract adaptations in humans extend the range of vowel formant frequencies to include the vowels [i], [u] and [a].



Lieberman (2012). Vocal tract anatomy and the neural bases of talking.



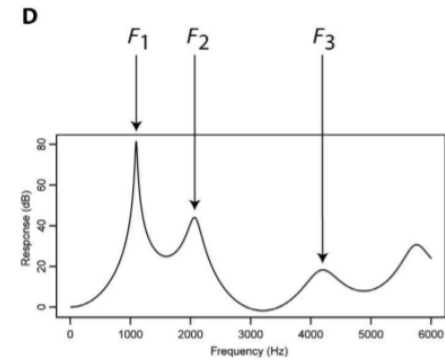
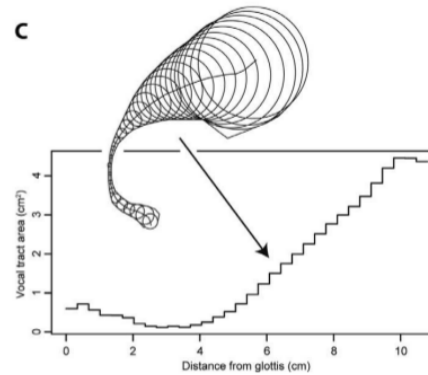
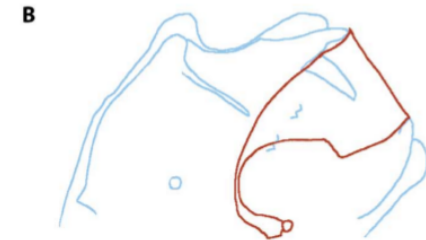
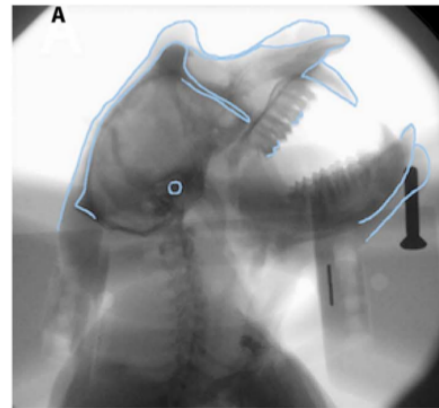
# The Vocal Tract

## - The Larynx

- Hyoid Bone
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- Hypoglossal Canal
- Thoracic Canal

Two opposing views still:

2) At least some other animals can produce all formants necessary for speech.



Fitch et al. (2016). Monkey vocal tracts are speech-ready.



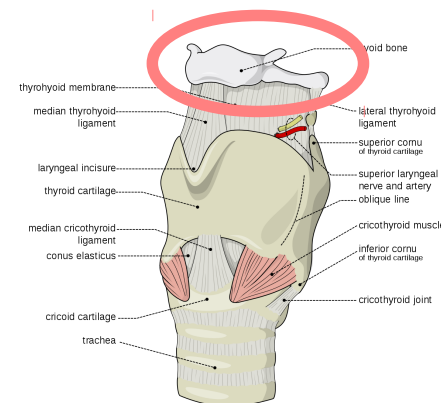
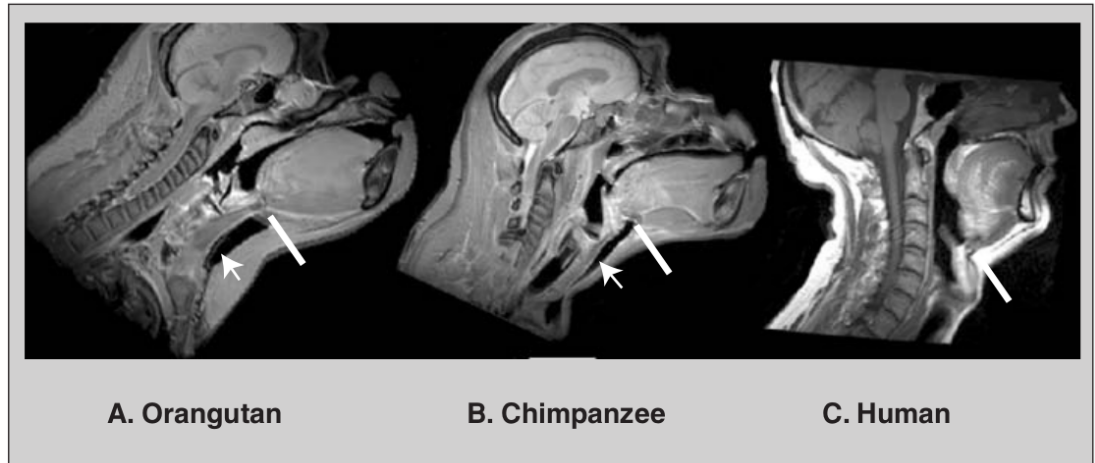


## The Vocal Tract

- The Larynx
- **Hyoid Bone**
- Air sacs
- Hypoglossal Canal
- Thoracic Canal

Indirect relevance for two reasons:

a) indicates the position of the larynx, potentially also in hominid fossils



Fitch 2010, p. 308



## The Vocal Tract

- The Larynx

- **Hyoid Bone**

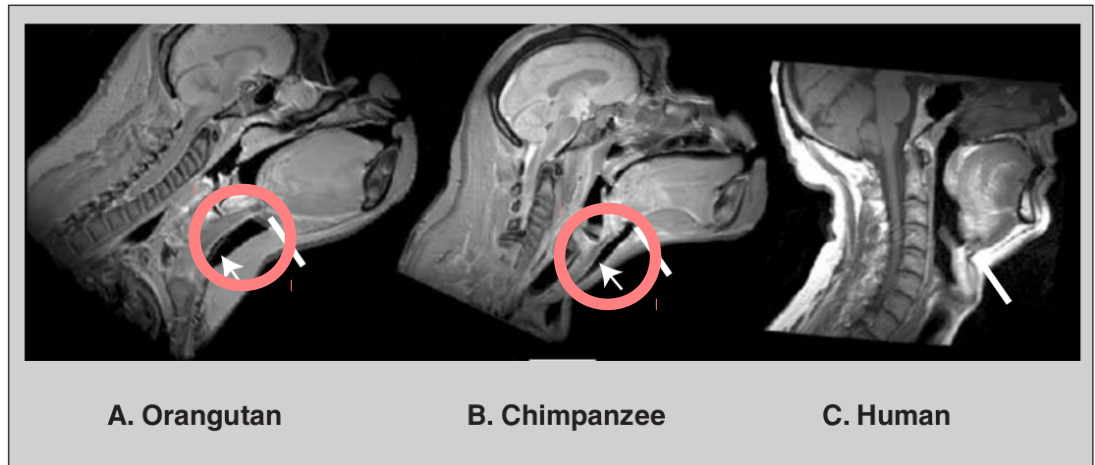
- Air sacs

- Hypoglossal Canal

- Thoracic Canal

Indirect relevance for two reasons:

b) indicates by its shape whether air sacs are present or not



Fitch 2010, p. 308



## The Vocal Tract

- The Larynx

- **Hyoid Bone**

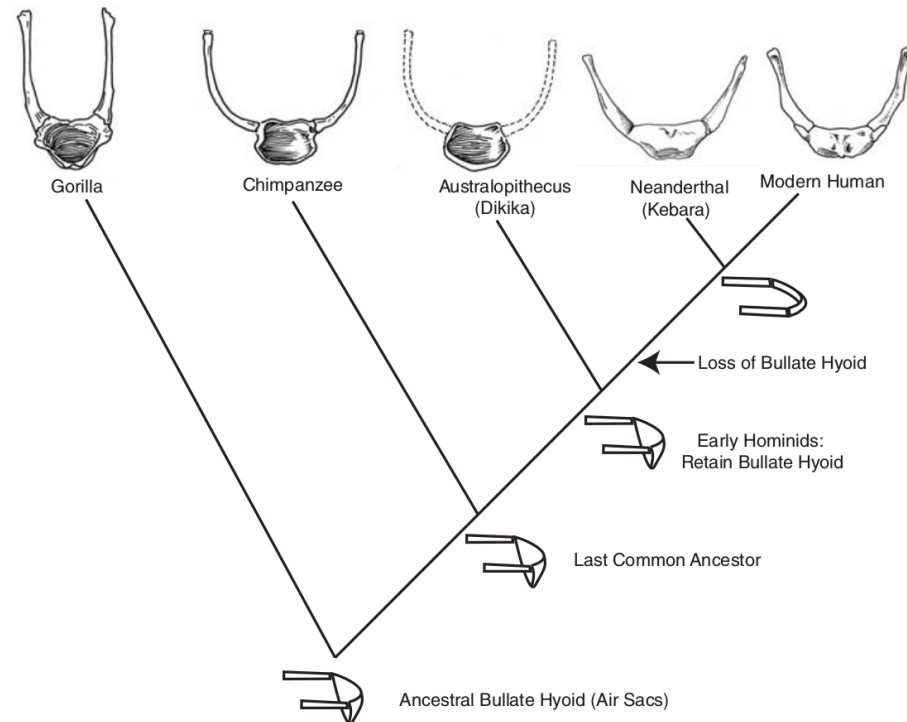
- Air sacs

- Hypoglossal Canal

- Thoracic Canal

Indirect relevance for two reasons:

b) indicates by its shape whether air sacs are present or not



Fitch 2010, p. 334

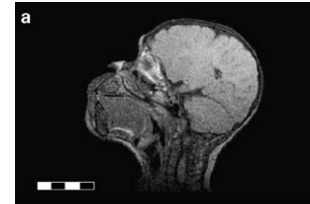


## The Vocal Tract

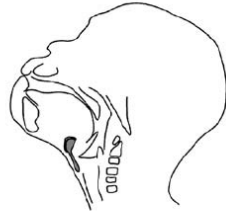
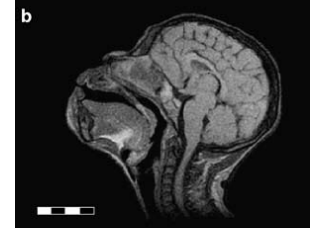
- The Larynx
- Hyoid Bone
- **Air sacs**
- Hypoglossal Canal
- Thoracic Canal

### Female chimp

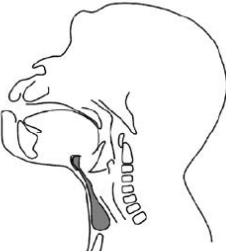
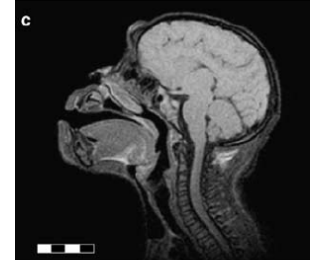
4 months



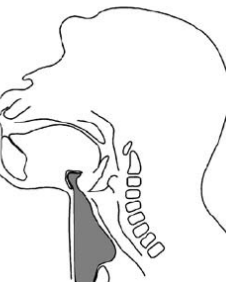
18 months



24 months



48 months

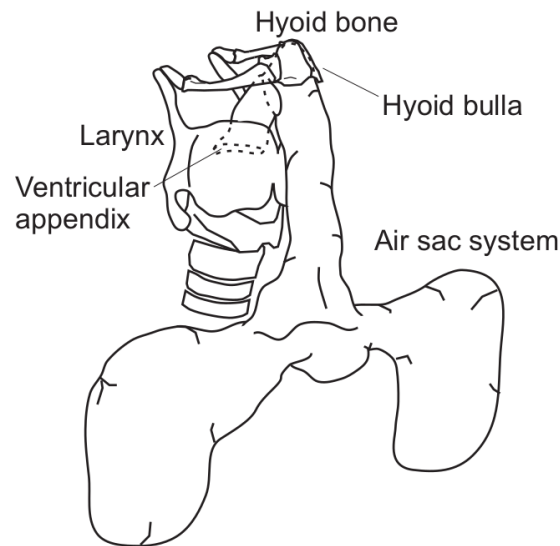
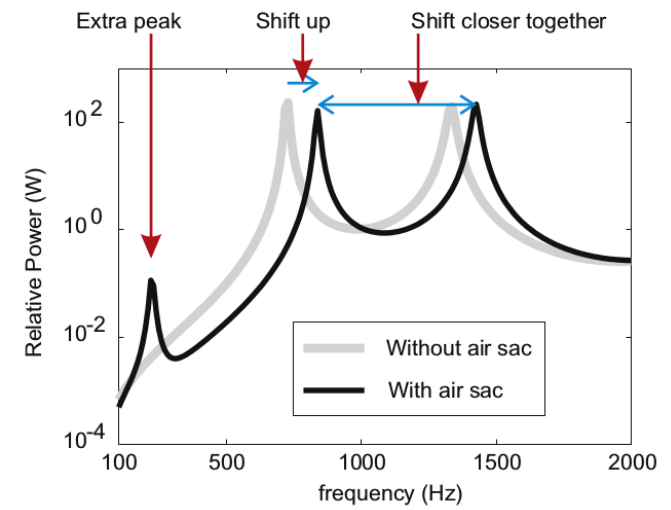


Nishimura et al. (2007). Development of laryngeal air sacs in Chimpanzees.



## The Vocal Tract

- The Larynx
- Hyoid Bone
- **Air sacs**
- Hypoglossal Canal
- Thoracic Canal



De Boer (2012). Loss of air sacs improved hominin speech abilities.

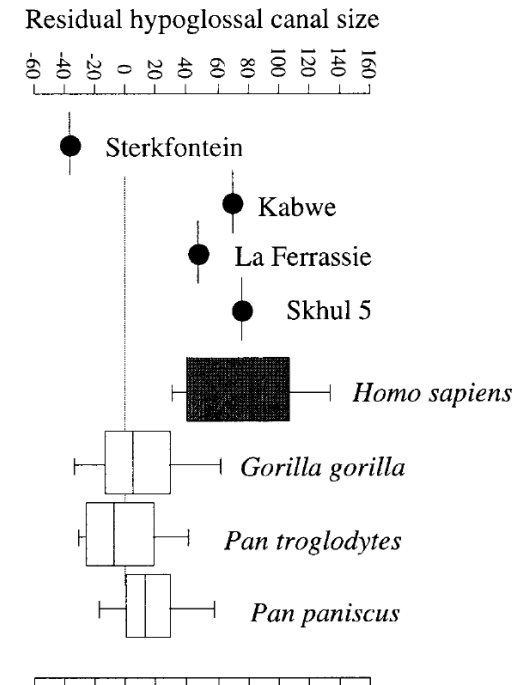
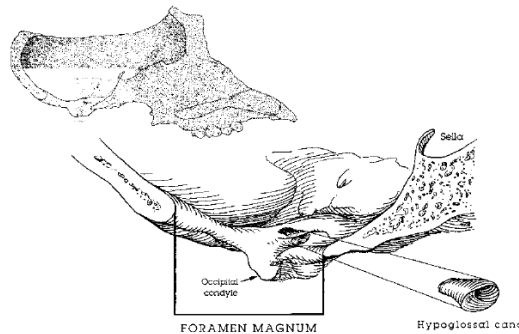
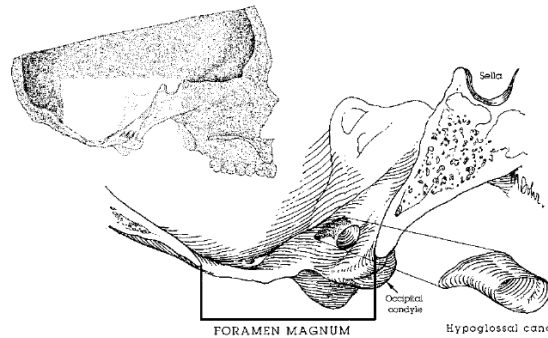


## The Vocal Tract

- The Larynx
- Hyoid Bone
- Air sacs

### - Hypoglossal canal

- Thoracic Canal



Kay et al. (1998). The hypoglossal canal and the origin of human vocal behavior.  
Fitch (2010), p.333-334.



## The Vocal Tract

- The Larynx

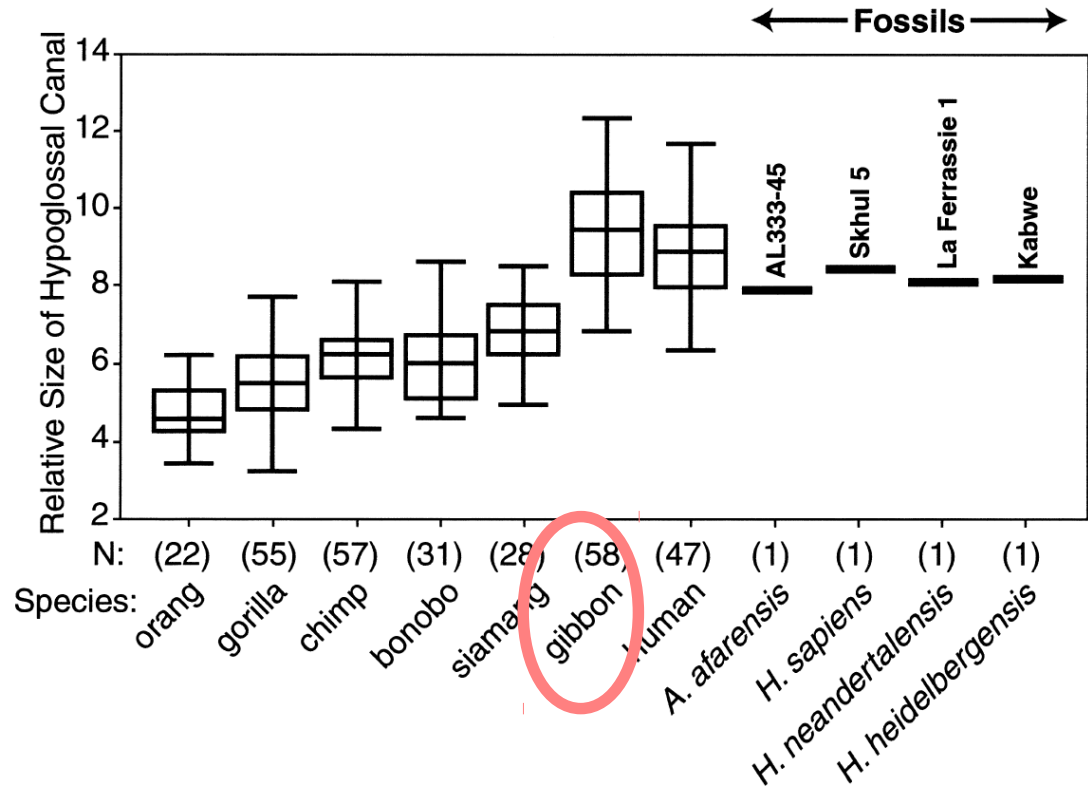
- Hyoid Bone

- Air sacs

- Hypoglossal canal

- Thoracic Canal

However (!)

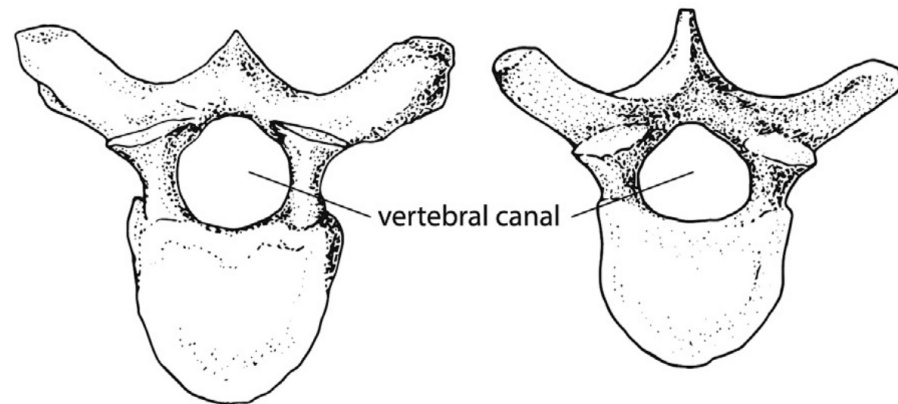
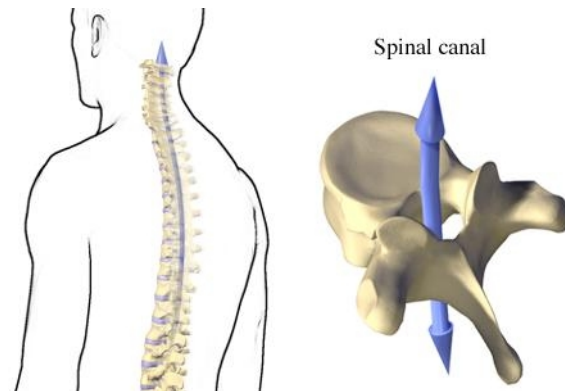


Jungers et al. (2003). Hypoglossal Canal Size in Living Hominoids and the Evolution of Human Speech.



## The Vocal Tract

- The Larynx
- Hyoid Bone
- Air sacs
- Hypoglossal canal
- **Thoracic Canal**



modern *Homo sapiens*

*Homo ergaster*  
(KNM-WT 15000)

Klein (2017), p. 7.

MacLarnon and Hewitt (1999). The evolution of human speech: The role of enhanced breathing control.



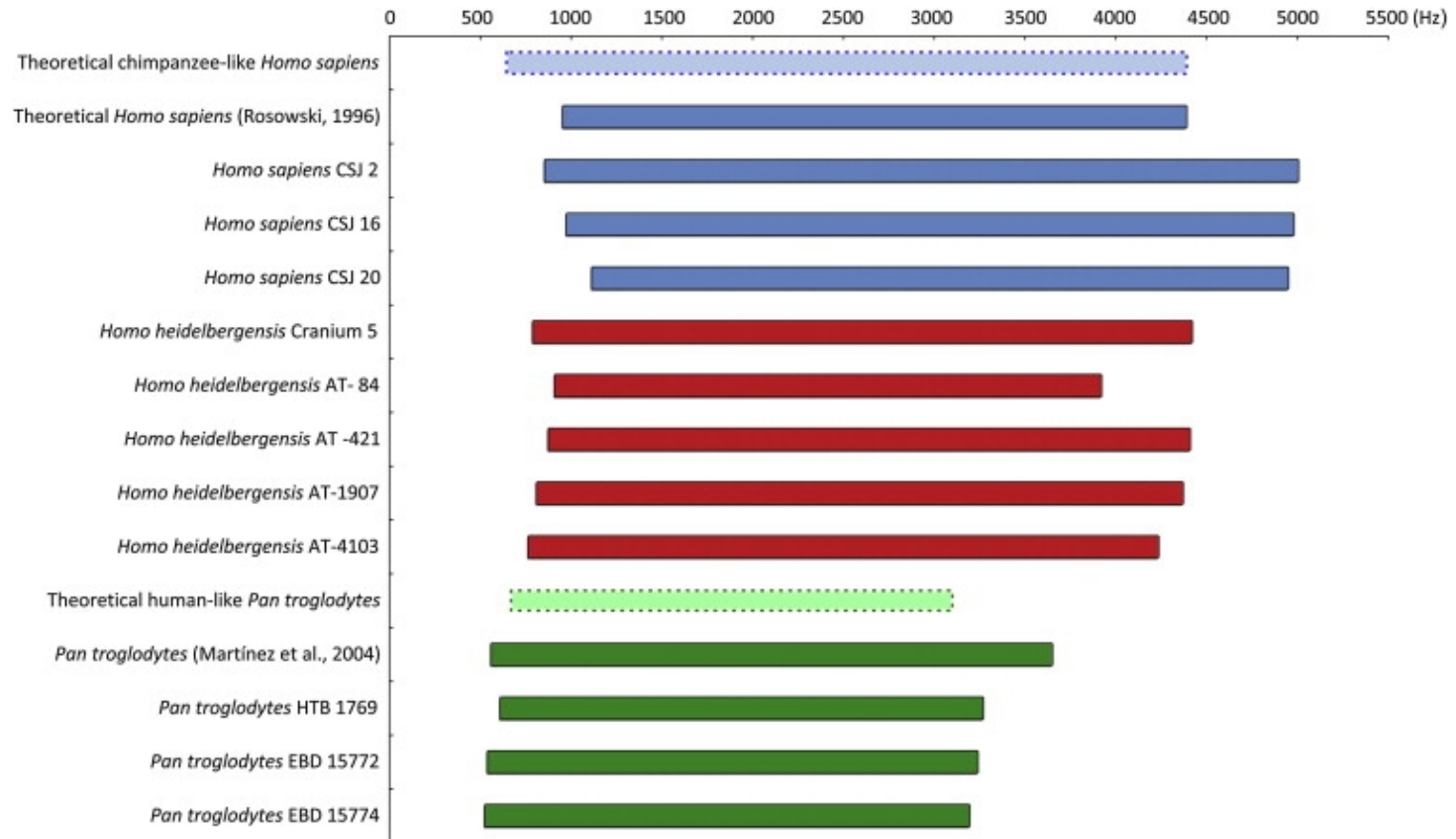


# Preadaptations for Language

- The vocal tract
- **Speech perception**
- Brain areas for language processing
- Genetics of language



# Speech Perception: Special in Humans?

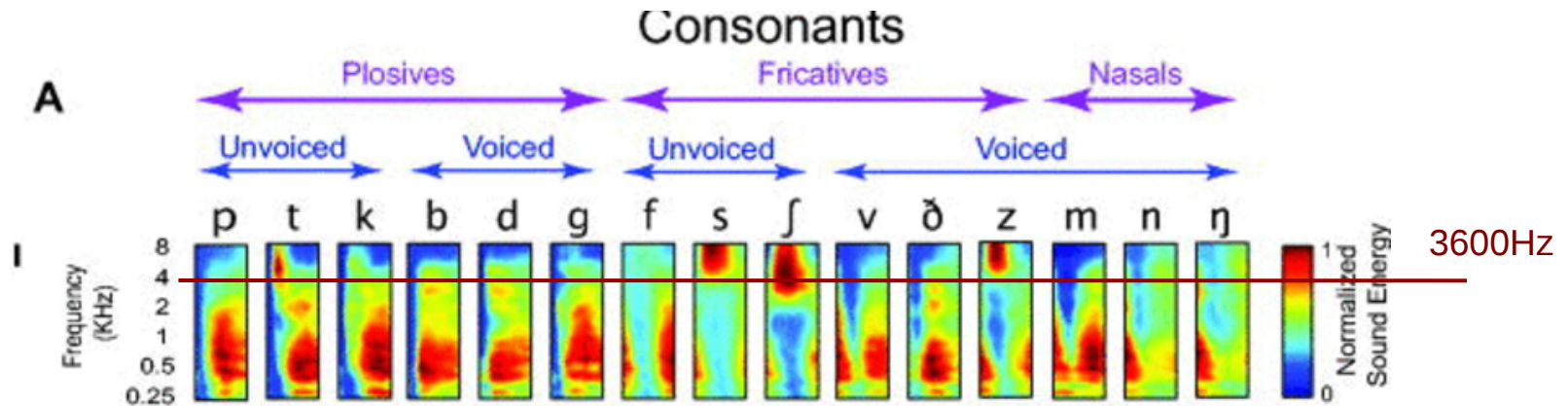
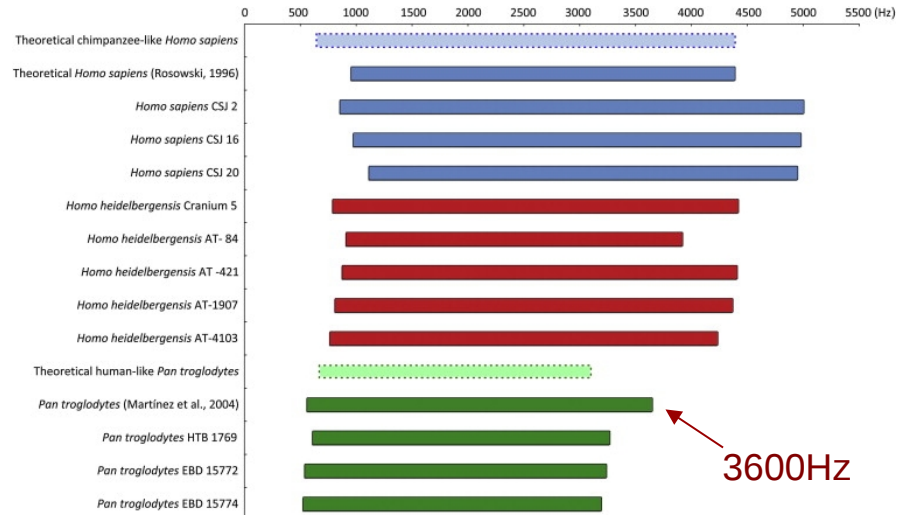


Martinez (2013). Communicative capacities in Middle Pleistocene humans from the Sierra de Atapuerca in Spain.



# Speech Perception

Chimps might not be able to perceive some fricatives and (partially) plosives.



Martinez (2013). Communicative capacities in Middle Pleistocene humans from the Sierra de Atapuerca in Spain.  
Mesgarani et al. (2008). Phoneme representation and classification in primary auditory cortex.

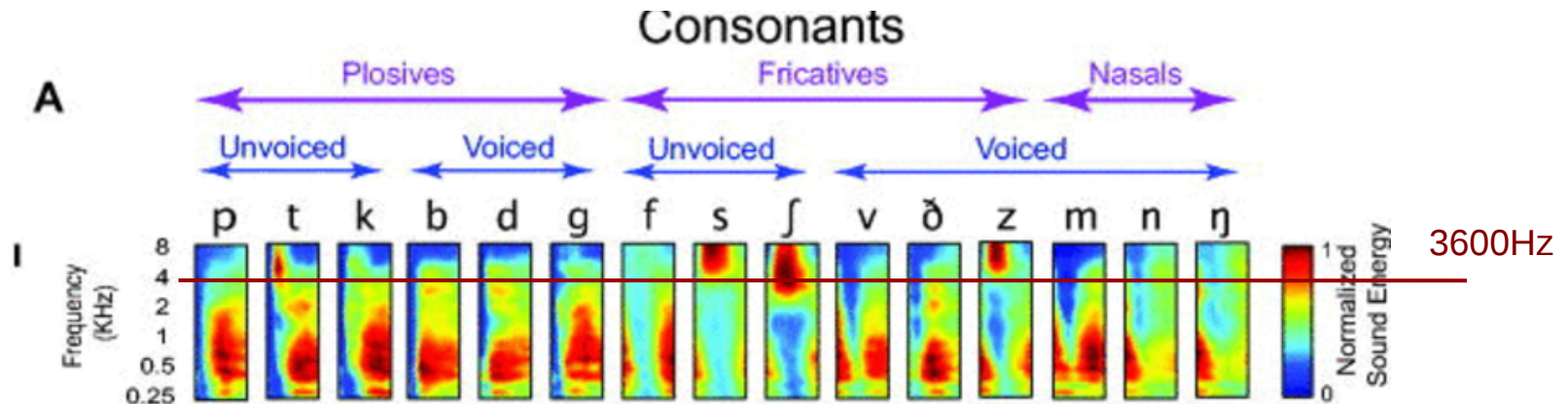
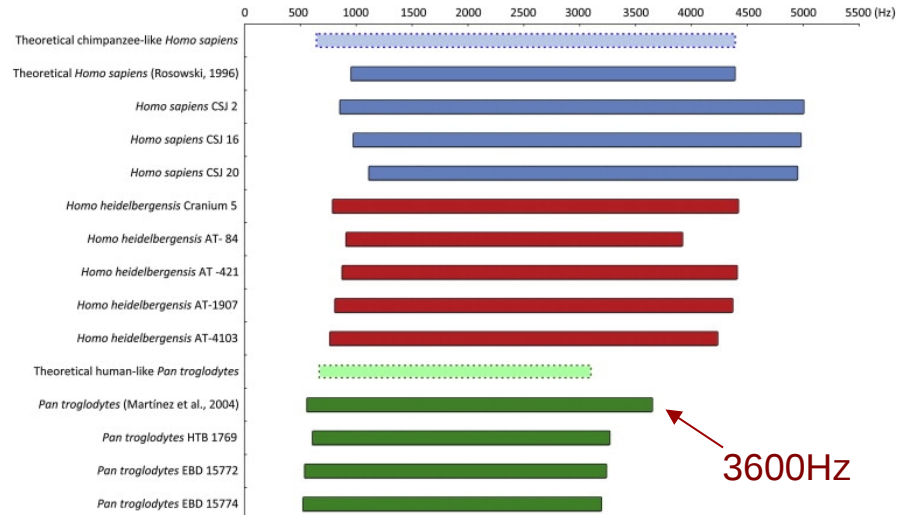


# Speech Perception

Chimpanzees might not be able to perceive some fricatives and (partially) plosives.

However:

Fitch (2010, p.325) gives completely different frequency ranges for chimpanzees (?)

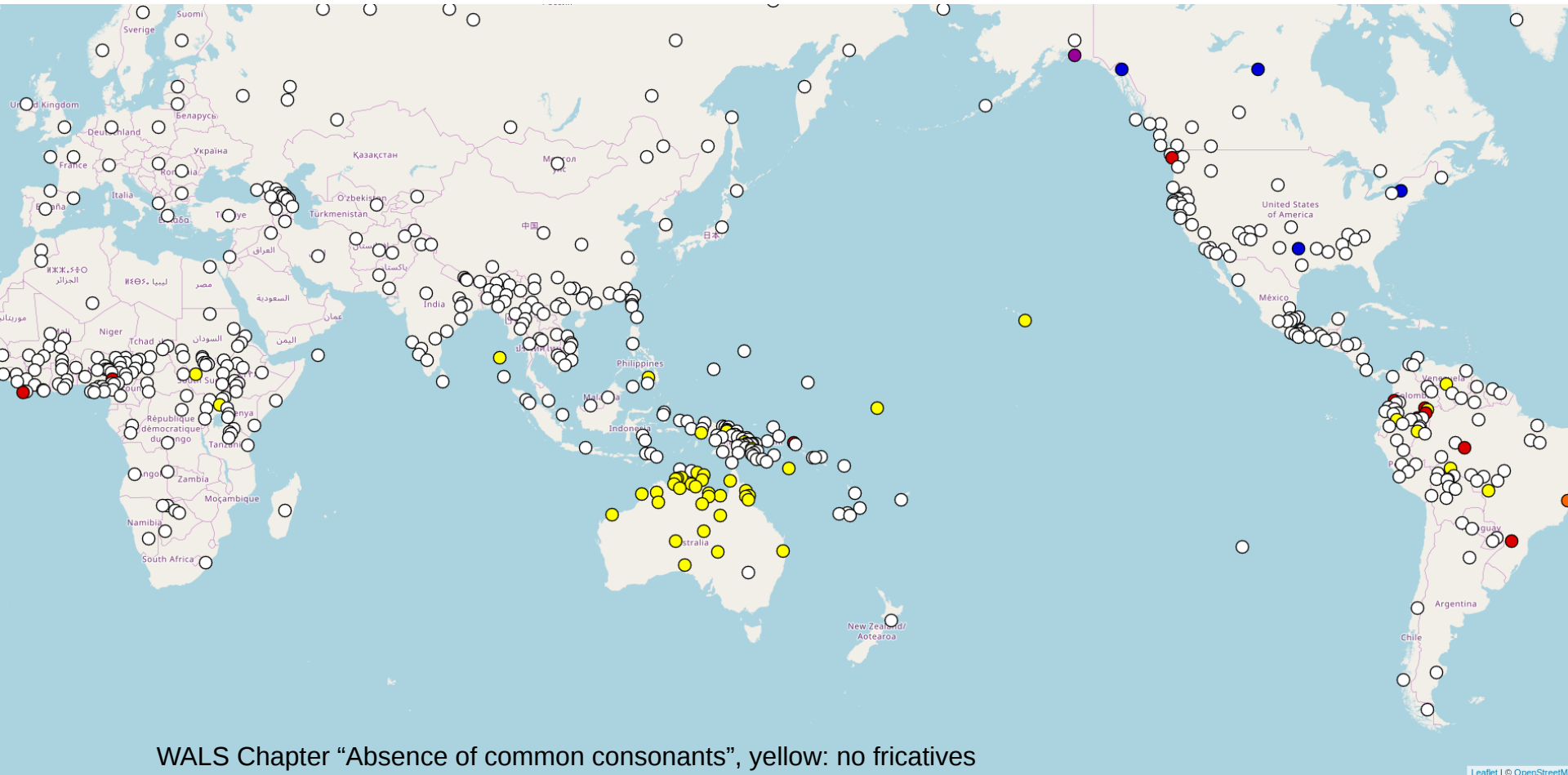


Martinez (2013). Communicative capacities in Middle Pleistocene humans from the Sierra de Atapuerca in Spain.  
Mesgarani et al. (2008). Phoneme representation and classification in primary auditory cortex.



# Speech Perception

Also: Languages can perfectly do without fricatives...

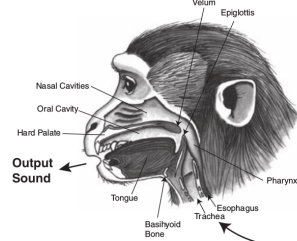
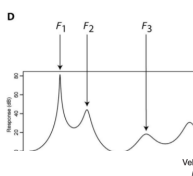
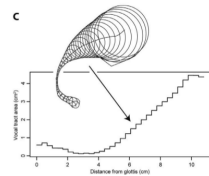
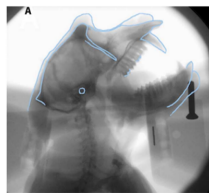
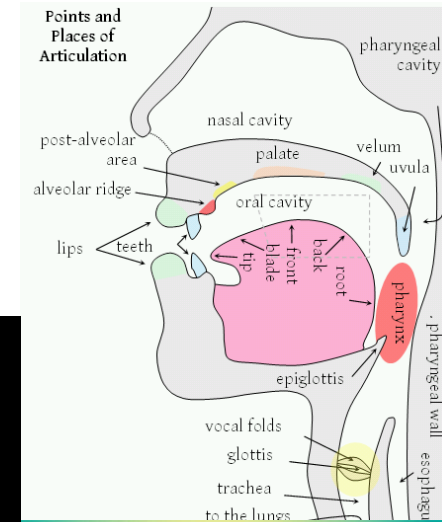




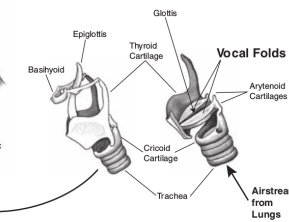
# Summary: Speech Production and Perception

There is **no strong** evidence that the vocal tract anatomy and perceptual abilities of animals – **the hardware** – prevents them from using speech.

The difference is more likely in the **software**.



A. Filter: Vocal Tract



B. Source: Larynx





# Preadaptations for Language

- The vocal tract
- Speech perception
- **Brain areas for language processing**
- Genetics of language



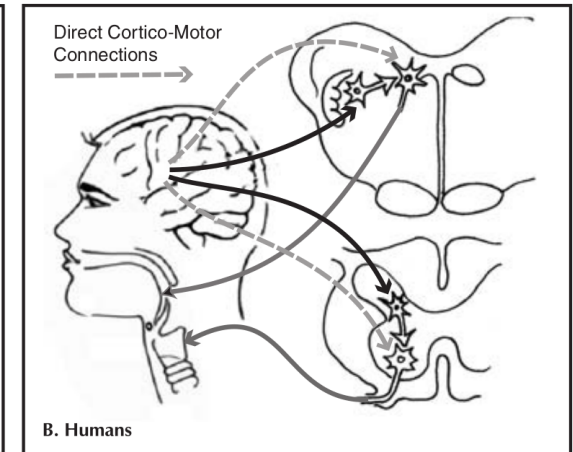
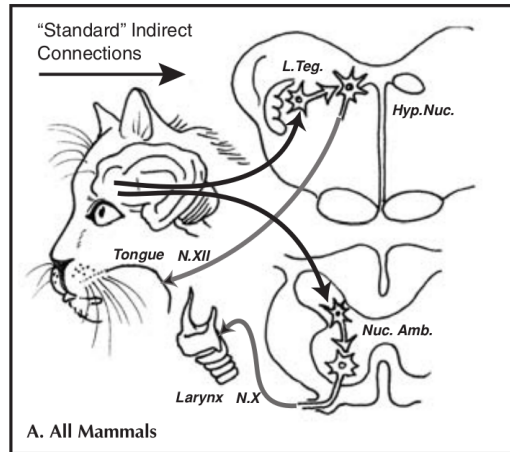
## Brain areas

### - cortico-laryngeal connections

- Broca's and Wernicke's area

- Update: Language networks

- Areas specific to syntax?



### Direct Cortico-Motor Connections: The Kuypers/Jürgens Hypothesis

Fitch (2010), p. 350-351

However...

"[...] the direct, cortical-to-laryngeal neural circuits that Deacon and Fitch believe account for human speech do not Exist."

Lieberman (2012). Vocal tract anatomy and the neural bases of talking.





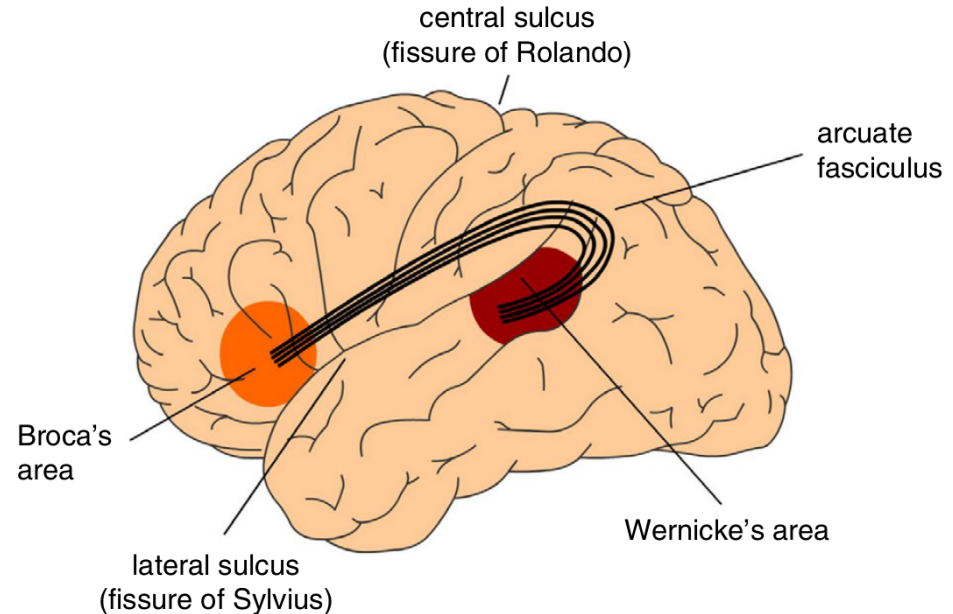
## Brain areas

- cortico-laryngeal connections

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Current Opinion in Neurobiology

The classical **Wernicke–Lichtheim–Geschwind model** of the neurobiology of language. In this model Broca's area is crucial for language production, Wernicke's area subserves language comprehension, and the necessary information exchange between these areas is done via the arcuate fasciculus, a major fiber bundle connecting the language areas in temporal cortex (Wernicke's area) and frontal cortex (Broca's area).

Hagoort (2014). Nodes and networks in the neural architecture for language: Broca's region and beyond.



## Brain areas

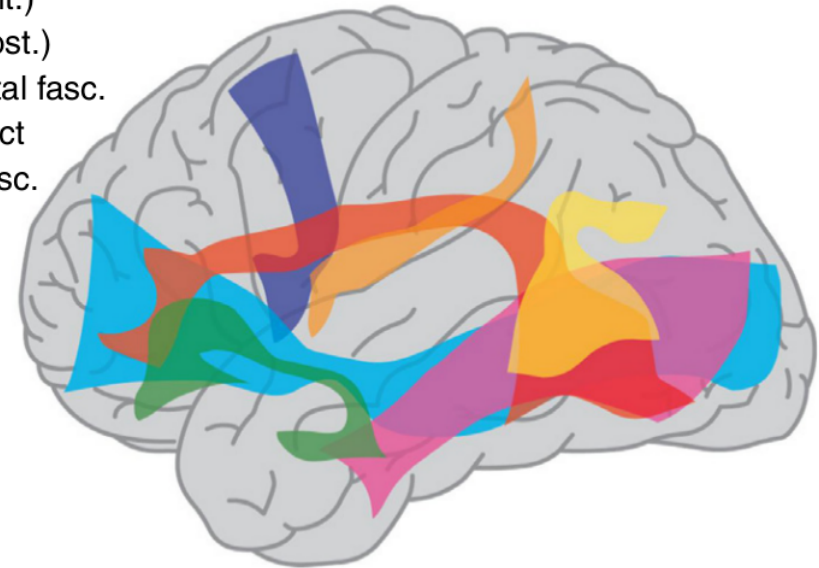
- cortico-laryngeal connections

- Broca's and Wernicke's area

- Update: Language networks

- Areas specific to syntax?

- arcuate fasc. (long)
- arcuate fasc. (ant.)
- arcuate fasc. (post.)
- inf.frontal-occipital fasc.
- frontal aslant tract
- inf. longitudinal fasc.
- uncinate fasc.



Current Opinion in Neurobiology

Hagoort (2014). Nodes and networks in the neural architecture for language: Broca's region and beyond

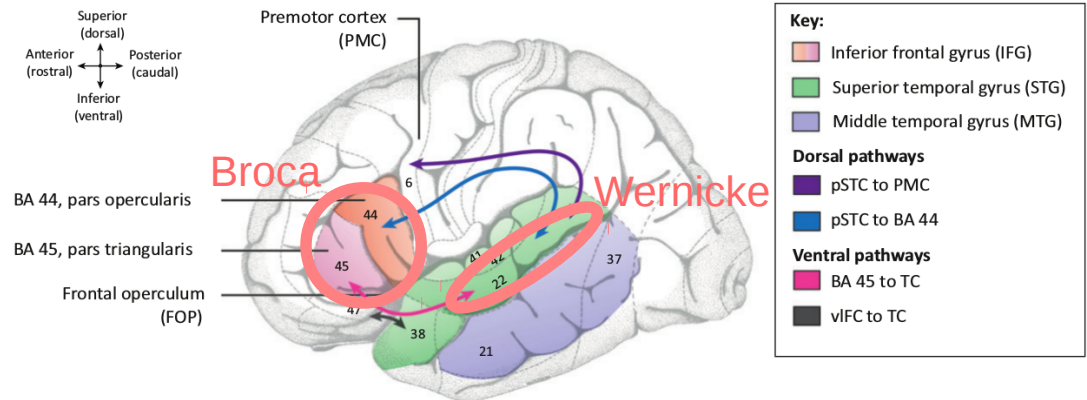
## Brain areas

- cortico-laryngeal connections

- Broca's and Wernicke's area

- Update: Language networks

- Areas specific to syntax?



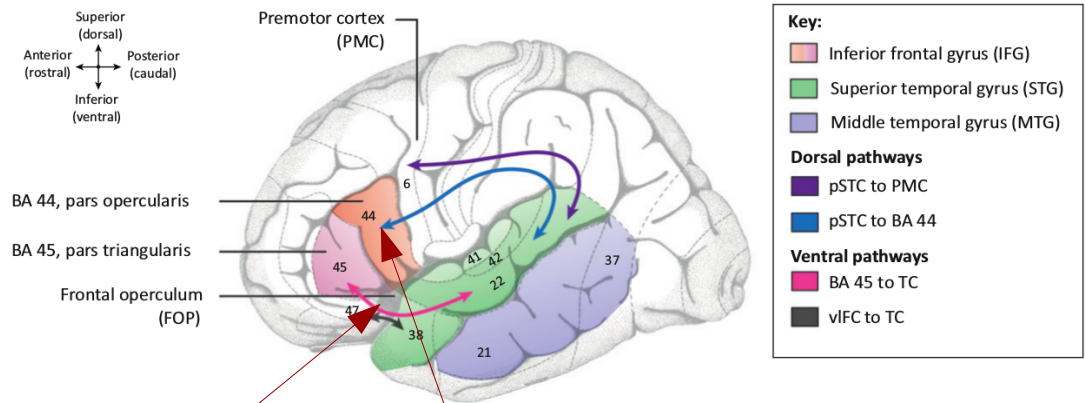
*TRENDS in Cognitive Sciences*

Berwick et al. (2013). Evolution, brain, and the nature of language.

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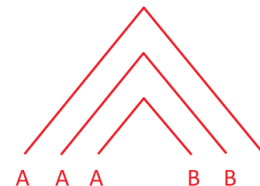


TRENDS in Cognitive Sciences

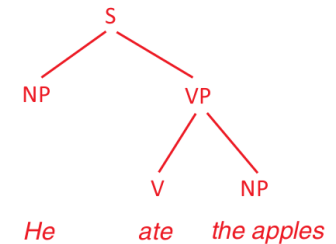
(a) (AB)<sup>n</sup> Sequence



(b) A<sup>n</sup>B<sup>n</sup> Sequence



(c) Natural language



TRENDS in Cognitive Sciences

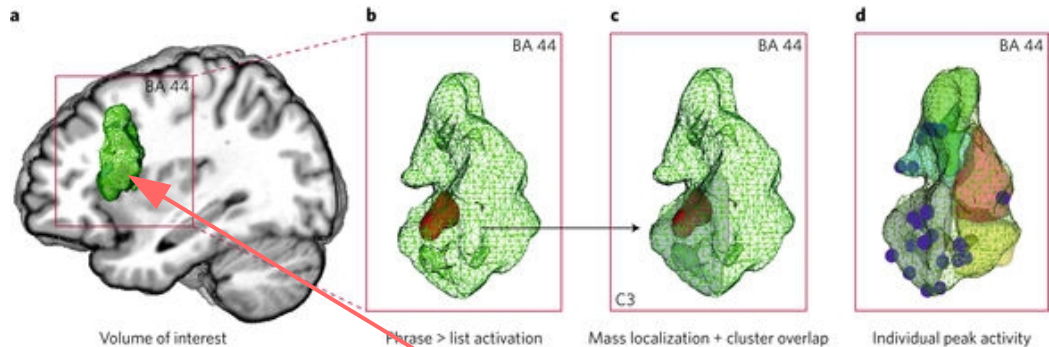
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## Brain areas

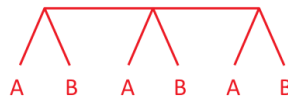
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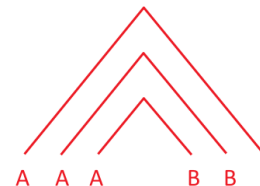
### Beyond preadaptations? "Real" language



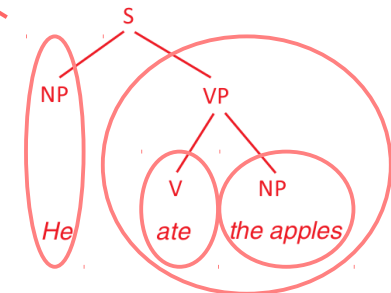
(a) (AB)<sup>n</sup> Sequence



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(c) Natural language



Merge operation

Friederici et al. (2017). Language, mind and brain.



# Preadaptations for Language

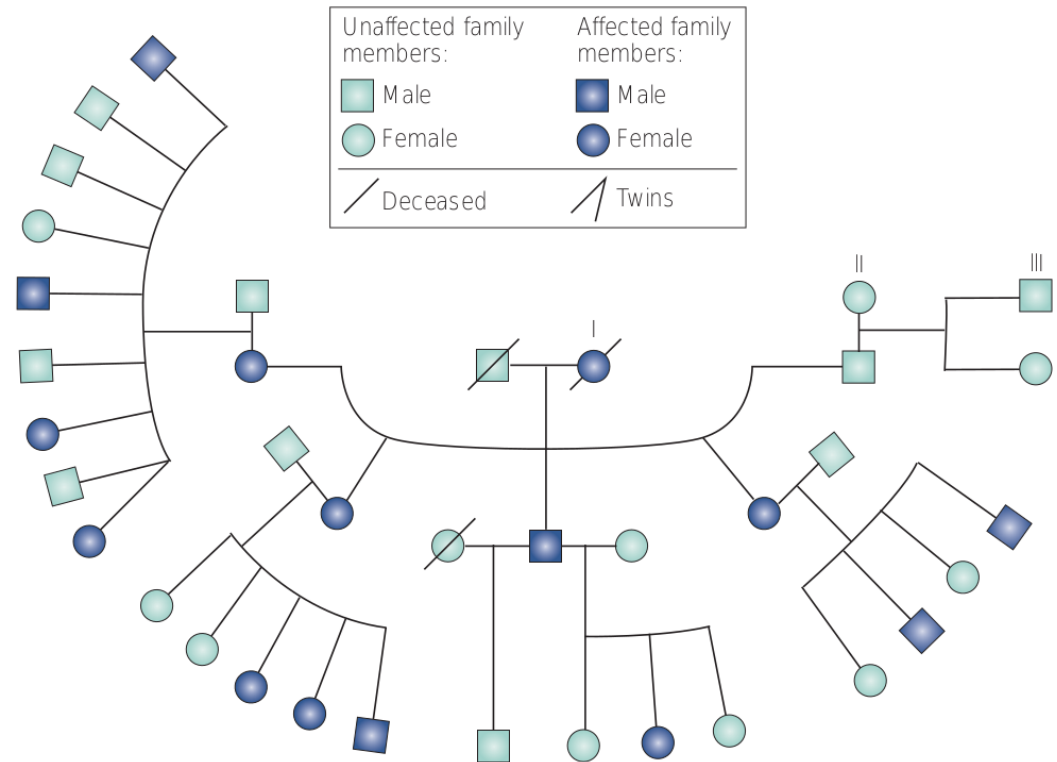
- The vocal tract
- Speech perception
- Brain areas for language processing
- **Genetics of language**



## Genetics: FOXP2

### - KE family

- Behavioral effects
- Expression in the brain
- Time of evolution



Vargha-Khadem et al. (2005). FOXP2 and the neuroanatomy of speech and language.



## Genetics: FOXP2

- KE family

- Behavioral effects

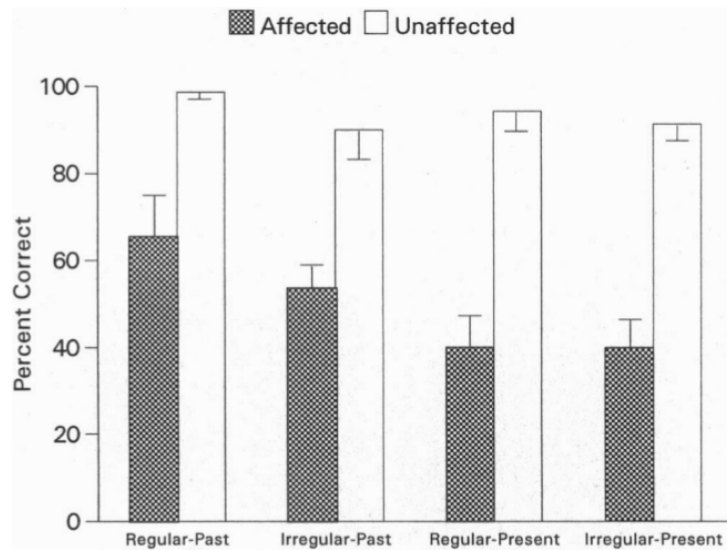


FIG. 2. Production of tenses. Scores are means  $\pm$  standard errors. See Table 2 for examples of test items.

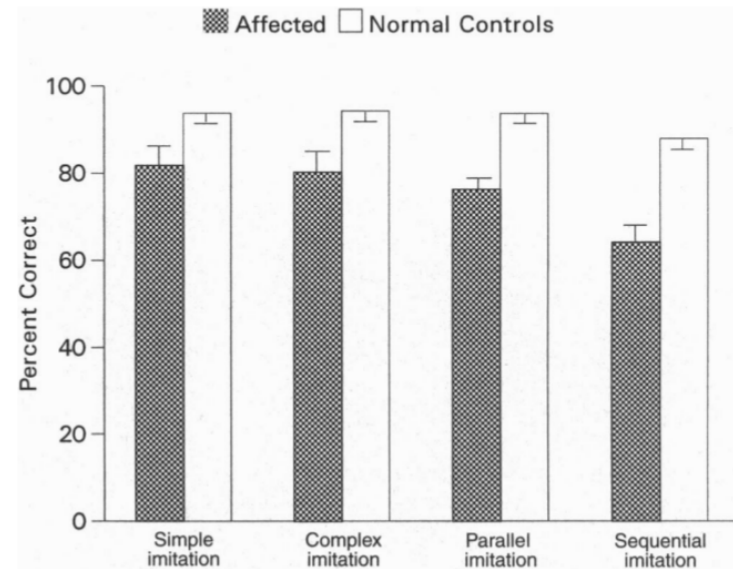


FIG. 3. Imitation of oral and facial movements. Scores are means  $\pm$  standard errors.

Vargha-Khadem et al. (1995). Praxic and nonverbal cognitive deficits in a large family with a genetically transmitted speech and language disorder.





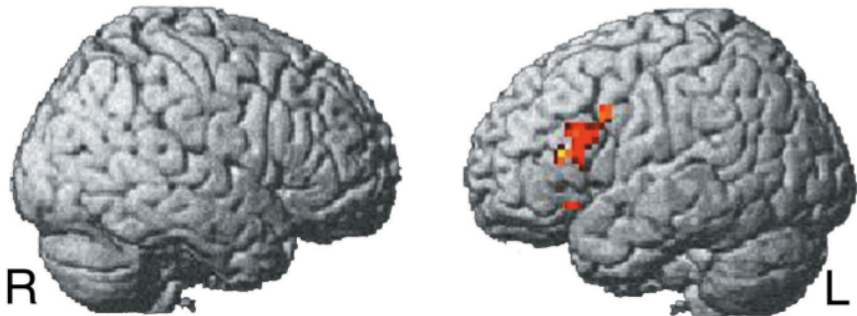
## Genetics: FOXP2

- KE family

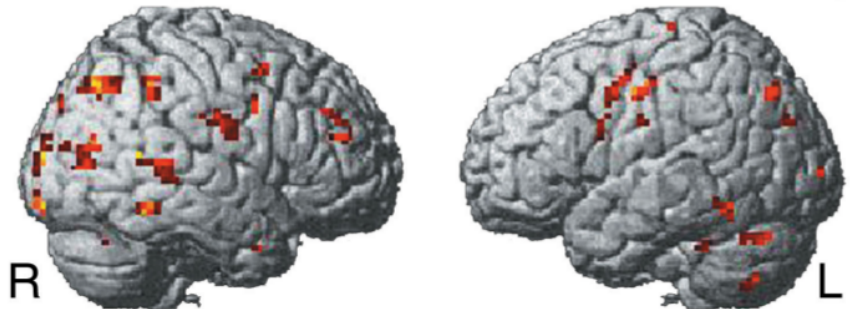
- Behavioral effects

“Ten members of the KE family (5 affected, 5 unaffected) and two groups of control participants, individually matched on age, sex and handedness to each member of the family, performed an fMRI task that required the covert generation of verbs in response to hearing nouns.”

Unaffected group



Affected group



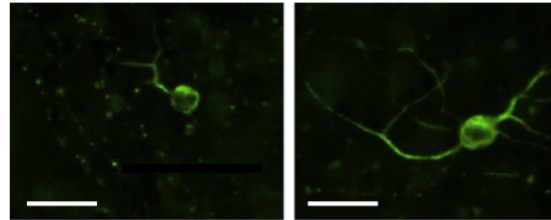
Liégeois et al. (2003). Language fMRI abnormalities associated with FOXP2 gene mutation.



## Genetics: FOXP2

- KE family
- Behavioral effects
- Expression in the brain (mice)
- Time of evolution

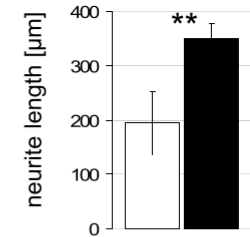
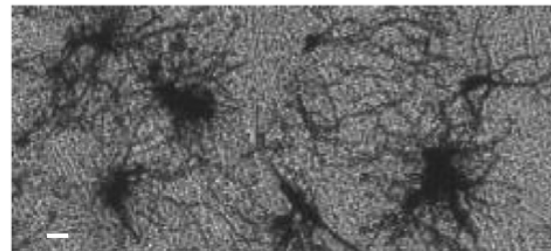
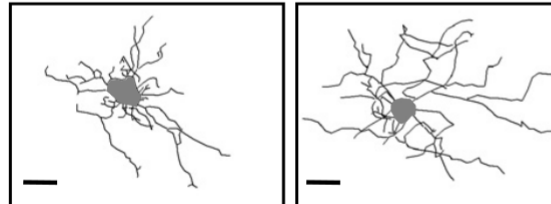
**A** *Foxp2*<sup>WT/WT</sup> *Foxp2*<sup>hum/hum</sup>



WT: wild-type

hum: humanized

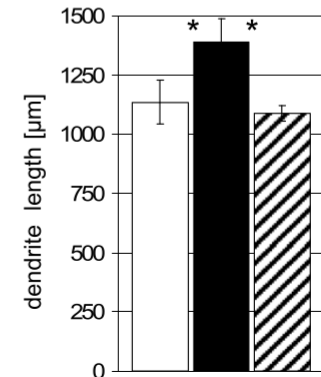
**B** *Foxp2*<sup>WT/WT</sup> *Foxp2*<sup>hum/hum</sup>



□ *Foxp2*<sup>WT/WT</sup>

■ *Foxp2*<sup>hum/hum</sup>

▨ *Foxp2*<sup>WT/KO</sup>



Enard et al. (2009). A humanized version of Foxp2 affects cortico-basal ganglia circuits in mice.



Video at 41:50

<http://www.dailymotion.com/video/x40jnnd>



# Genetics: FOXP2

- Expression in the brain (mice)

- Time of evolution

Krause et al. (2007). The derived FOXP2 variant of modern humans was shared with Neandertals.

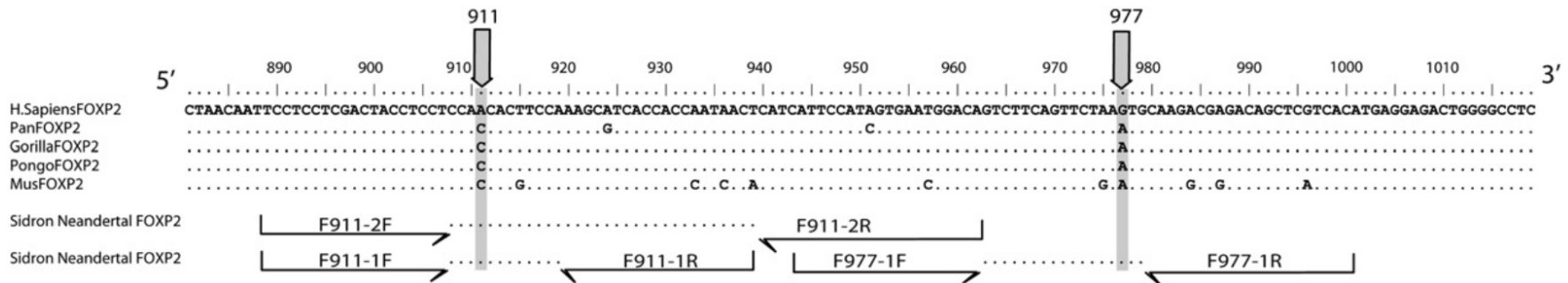


Figure 1. Sequence Alignment of Nucleotide Positions 880–1020 from the *FOXP2* Gene

The two nonsynonymous nucleotide substitutions on the human lineage are indicated by arrows. Identical positions in the alignment are given as dots. The three primer pairs used to retrieve the two substitutions from the El Sidrón Neandertals are indicated by arrows.





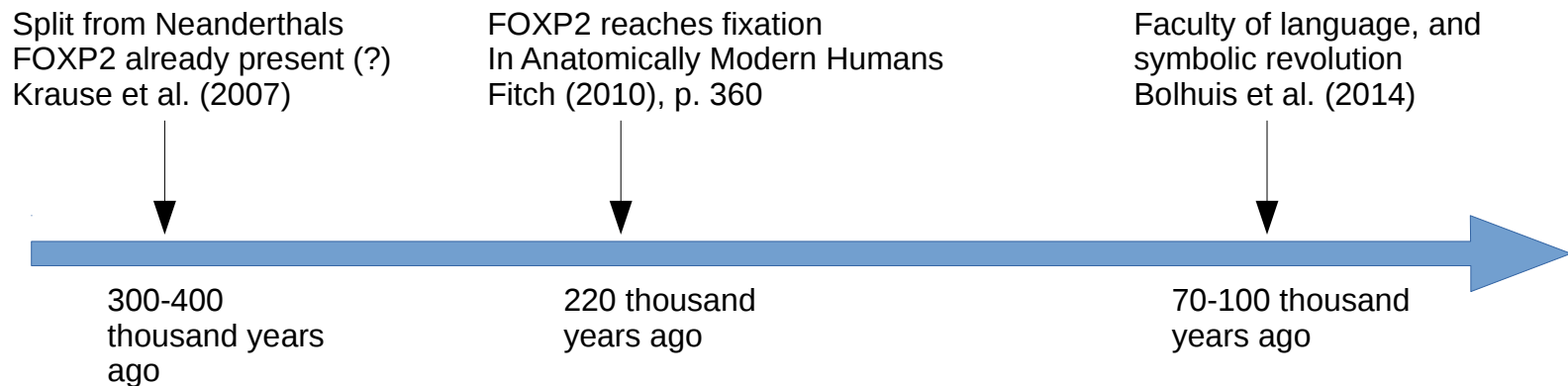
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## Is FOXP2 a “Great Leap Forward”?

*When and who made this „leap“, and how is it expressed in behavior?*





Contact:

**DFG Center for Advanced Studies**

“Words, Bones, Genes, Tools”

Rümelinstraße 23

72070 Tübingen · Germany

Phone: +49 7071 29-76548

[monika.doll@ifu.uni-tuebingen.de](mailto:monika.doll@ifu.uni-tuebingen.de)