EBERHARD KARLS
UNIVERSITÄT
TÜBINGEN

Center for
Advanced Studies

DFG

Modern Human Origins

Preadaptations to Language

Hugo Reyes-Centeno, Yonatan Sahle, Christian Bentz

14 January 2019, Lecture 9, Bentz

Readings for Lecture 9

Dediu, Dan, and Morten H. Christiansen. 2016. Language evolution: constraints and opportunities from modern genetics. *Topics in Cognitive Sciences*, 8: 361-370.

Fitch, Tecumseh W. 2017. Empirical approaches to the study of language evolution. *Psychonomic Bulletin & Review*, 24: 3-33.

Fitch, Tecumseh W. 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

Recap of Lecture 8

Language evolution: the hardest problem in science?

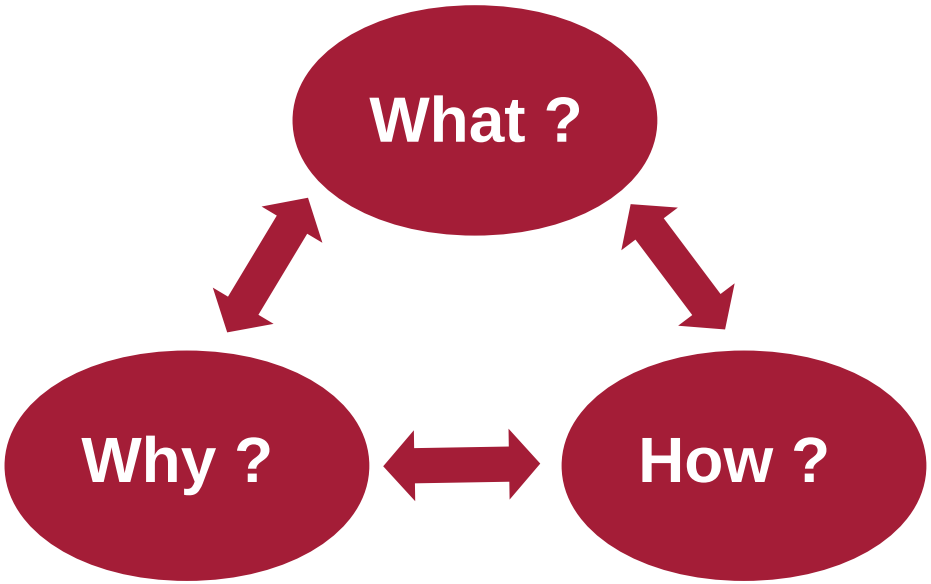
Christiansen & Kirby (2003)

Three interdependent questions:

1) **What** evolved, i.e. what is “language” in the first place?

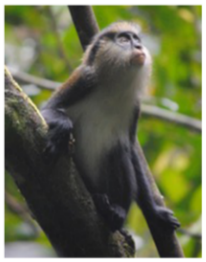
2) **Why** did it evolve, i.e. did it have particular function(s)?

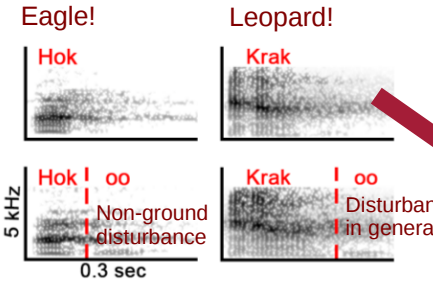
3) **How** did it evolve, e.g. suddenly via mutation, gradual, etc.?



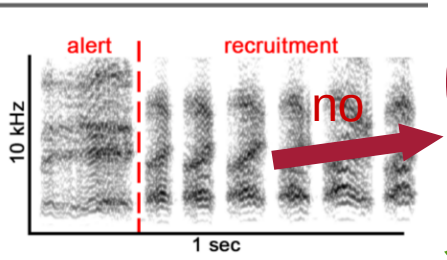
Is there a **decision algorithm** that would tell us from empirical data whether “language” is present?

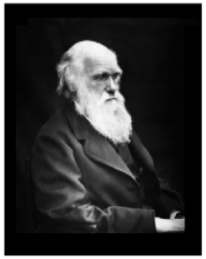
Campbell’s monkeys

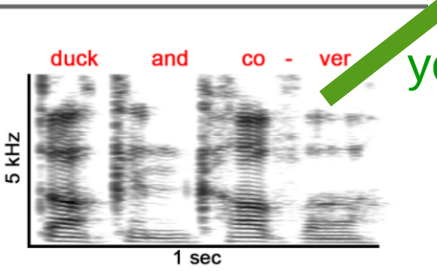




Pied babblers







no

no

yes

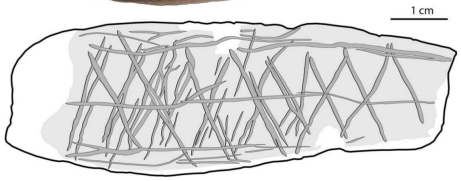
Language

no

no

yes

yes



Townsend et al. (2018). Compositionality in animals and humans.

Summary: Models of Language Evolution

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

Saltational Account

Gradual Account

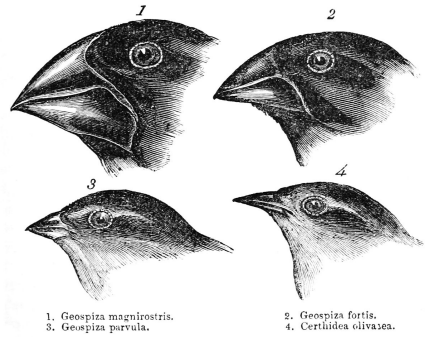
Co-evolution Account

Preadaptations to Language: Introduction

Adaptation, Preadaptation, Exaptation and Spandrels

Terminology

- Adaptation
- Preadaptation
- Exaptation
- Spandrel



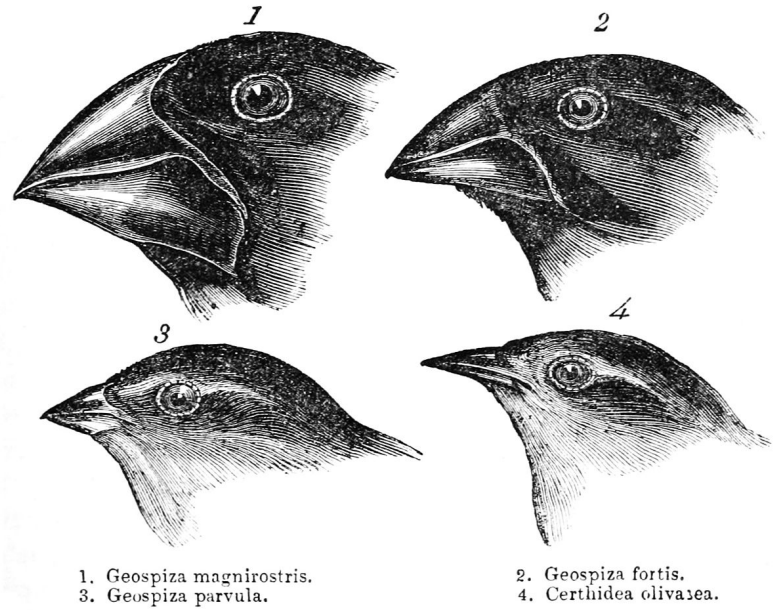
Fitch 2010, p. 63-64

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



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

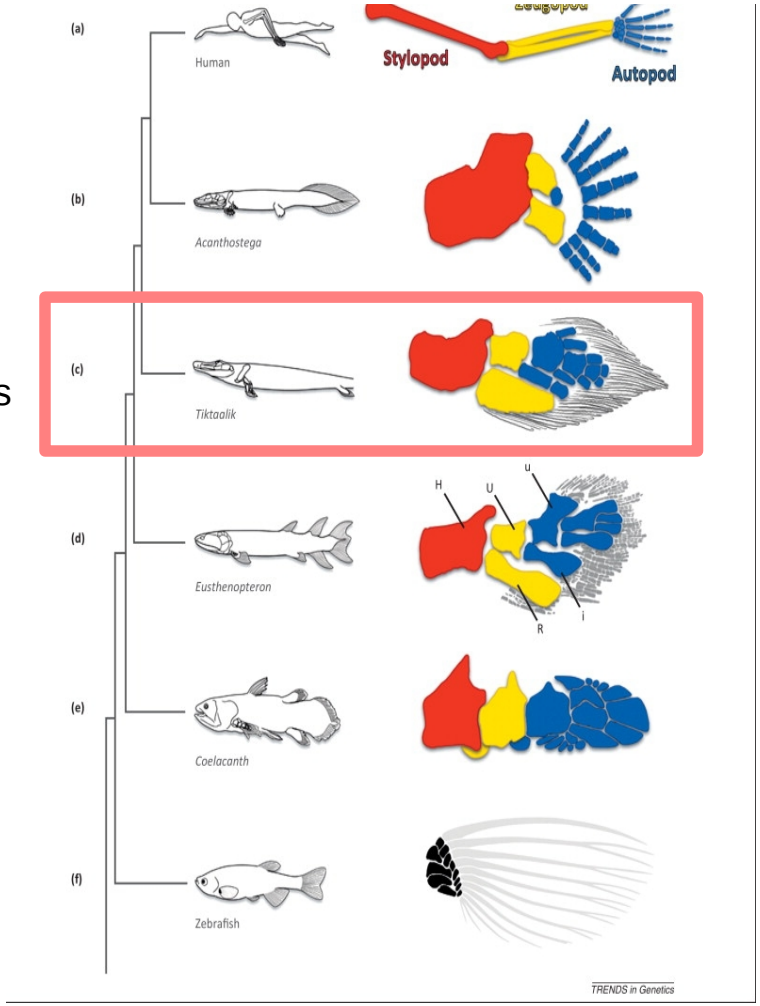
“Darwin stressed “the highly important fact that an organ originally constructed for one purpose [...] may be converted into one for a widely different purpose” (Darwin, 1859). Such phenomena came to be termed preadaptations [...]”

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."

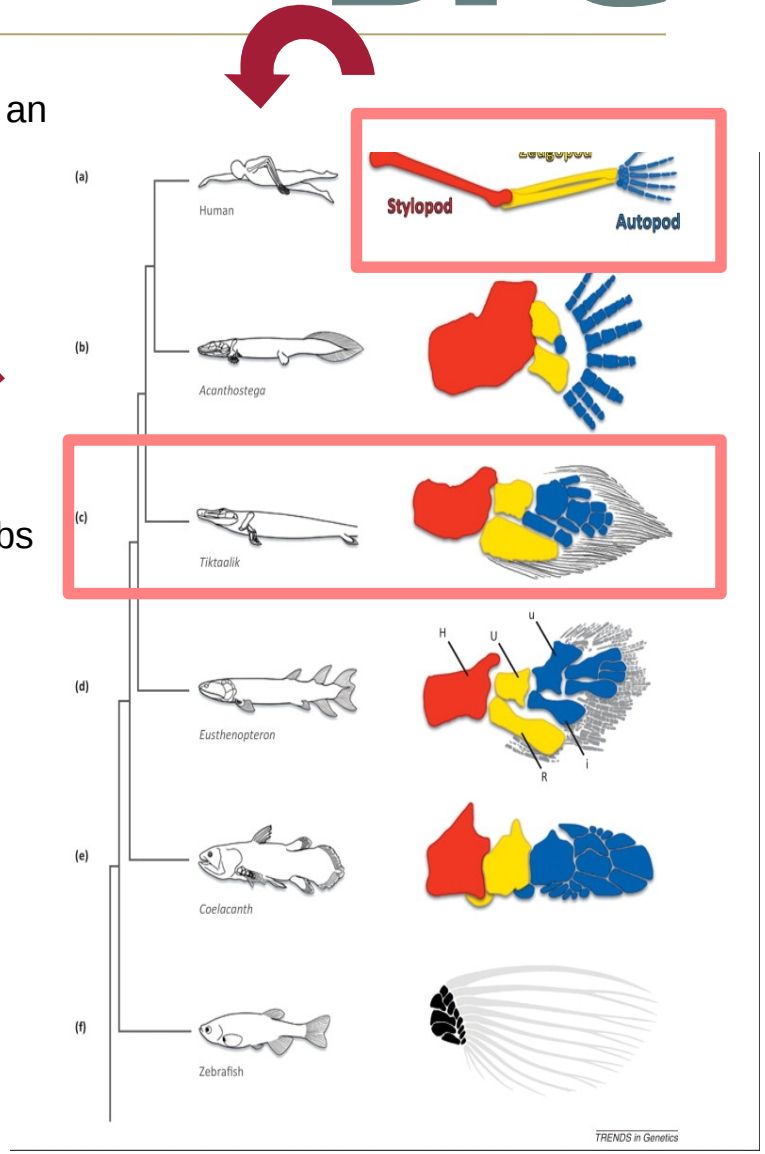
Fitch (2010), p. 64.

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.

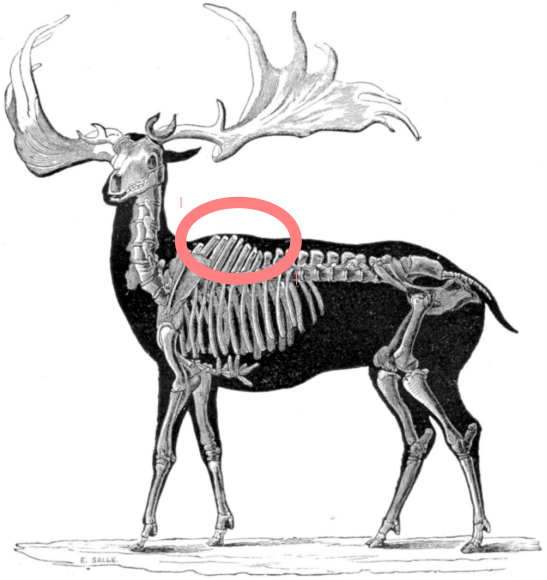
Terminology

- 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.

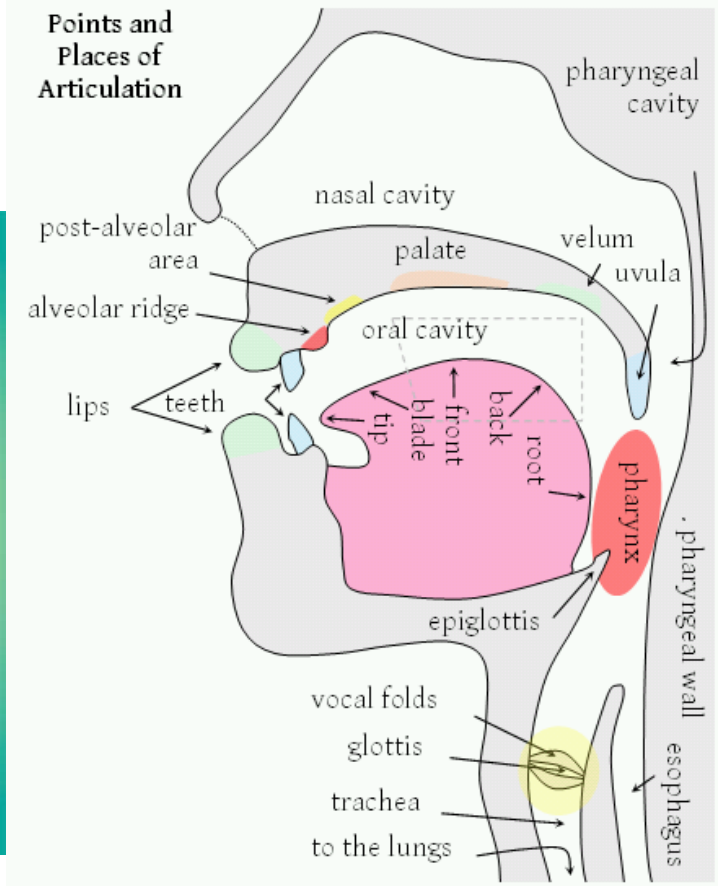


Preadaptations for Language

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

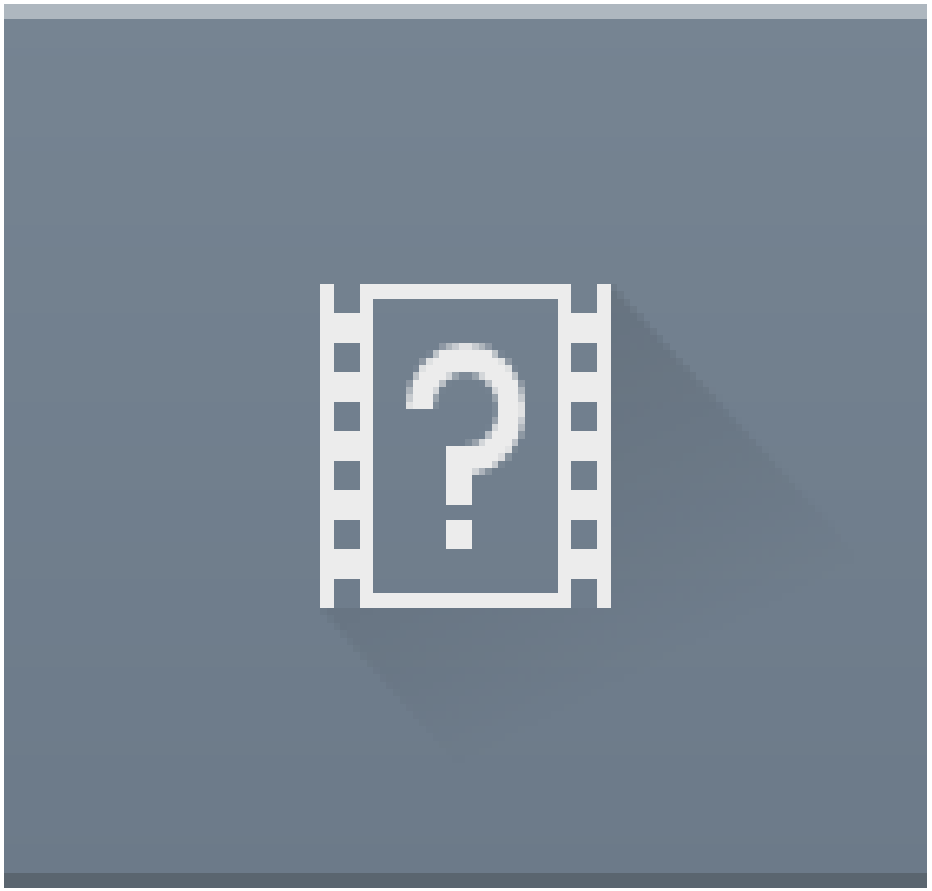
Speech Production and Perception

A difference in software
or hardware?



Speech Production

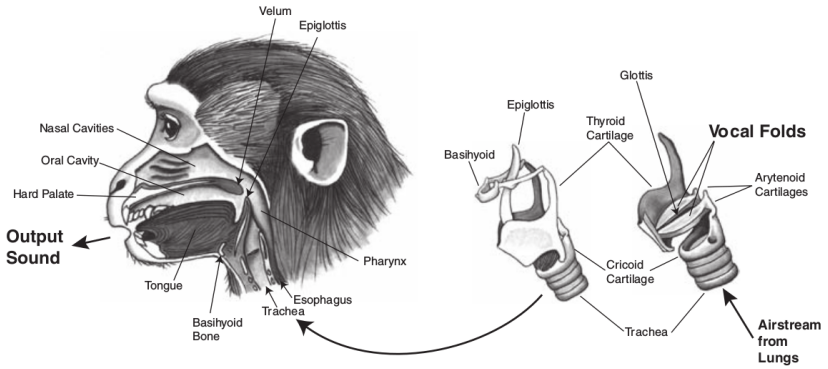
Max Planck Institute for Biophysical Chemistry

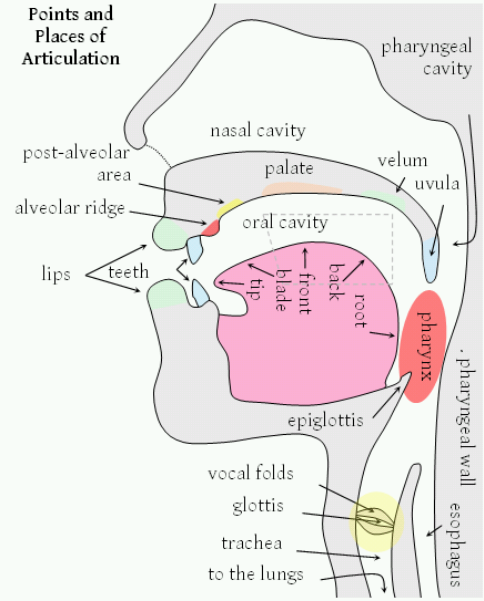


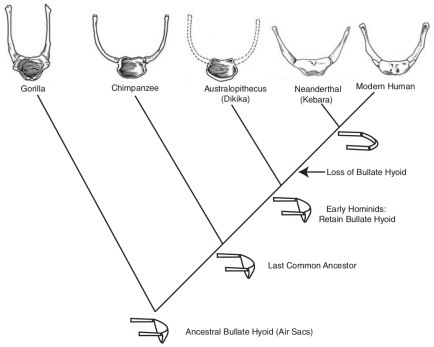
https://www.youtube.com/watch?v=6dAEE7FYQfc

The Vocal Tract

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







Fitch 2010, p. 297-337

The Vocal Tract

- **The Larynx**
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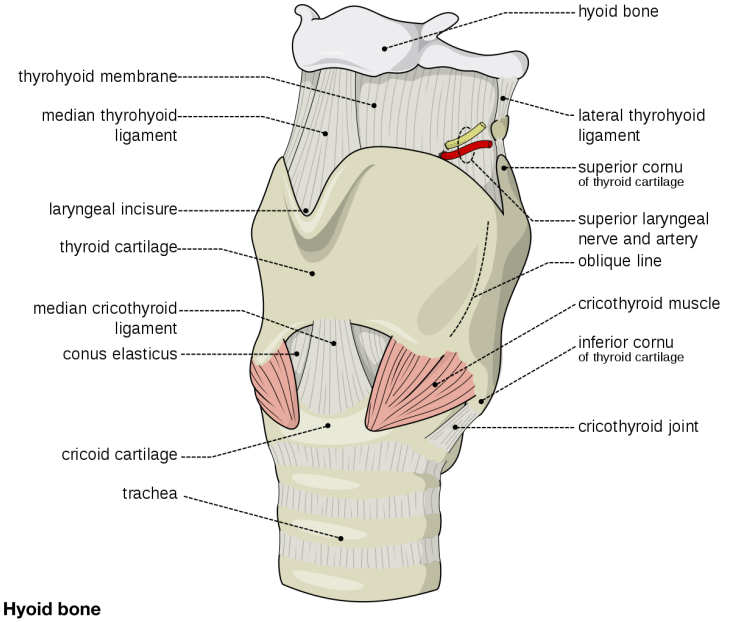

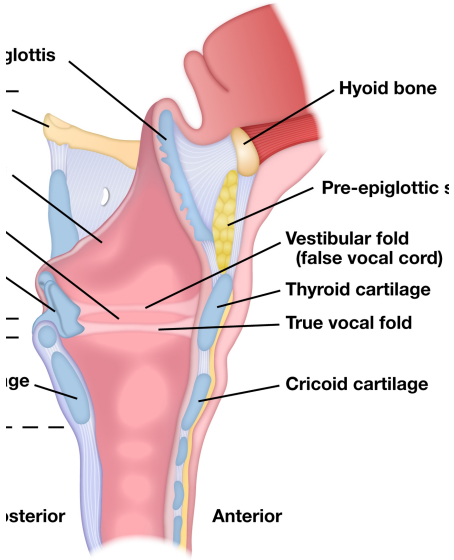

The Vocal Tract

- **The Larynx**
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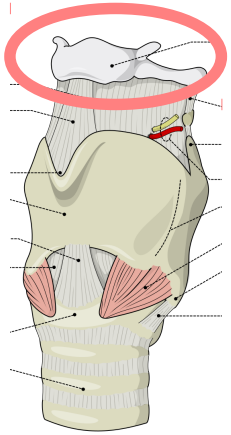
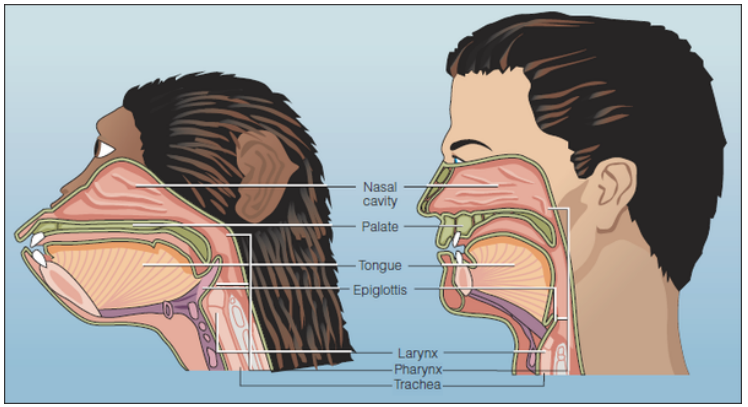
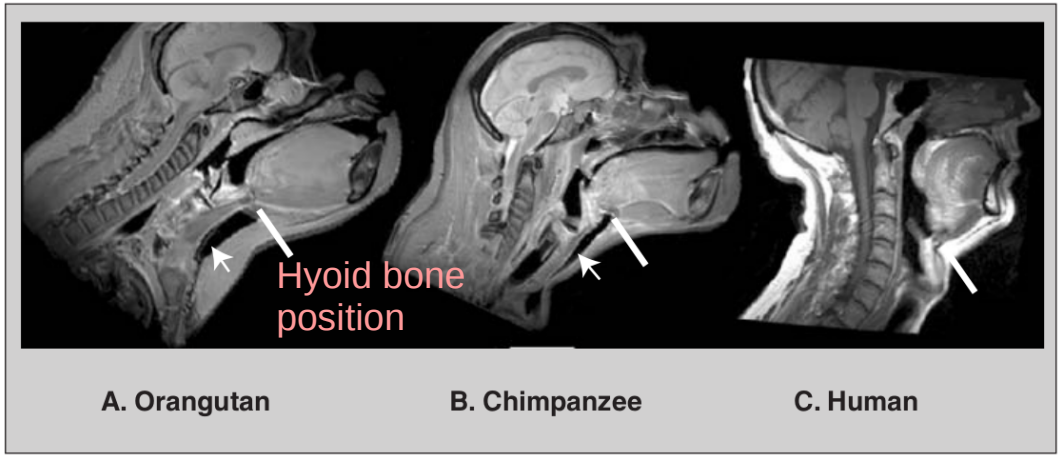
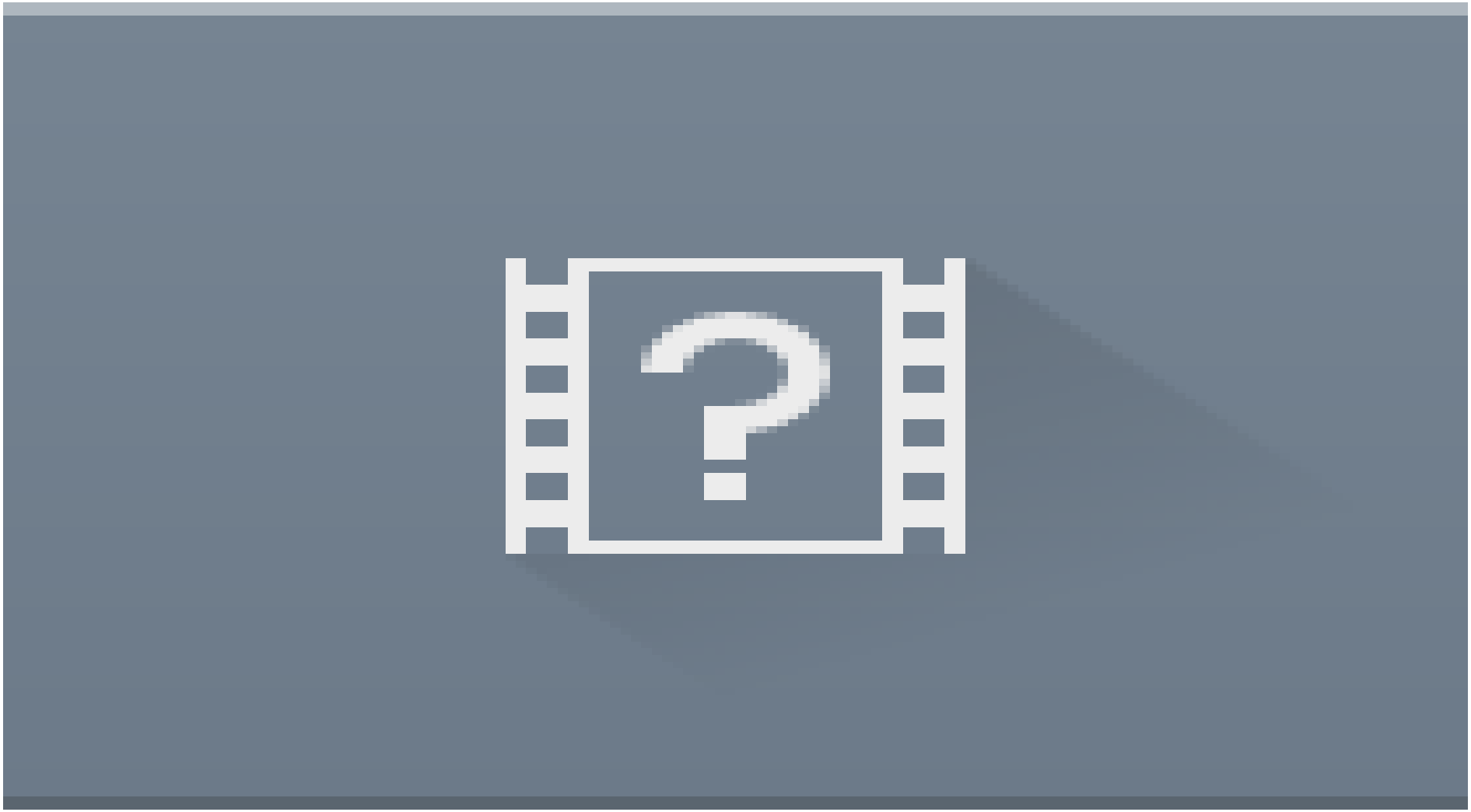
The **descent** of the larynx







Fitch 2010, p. 307 pp.



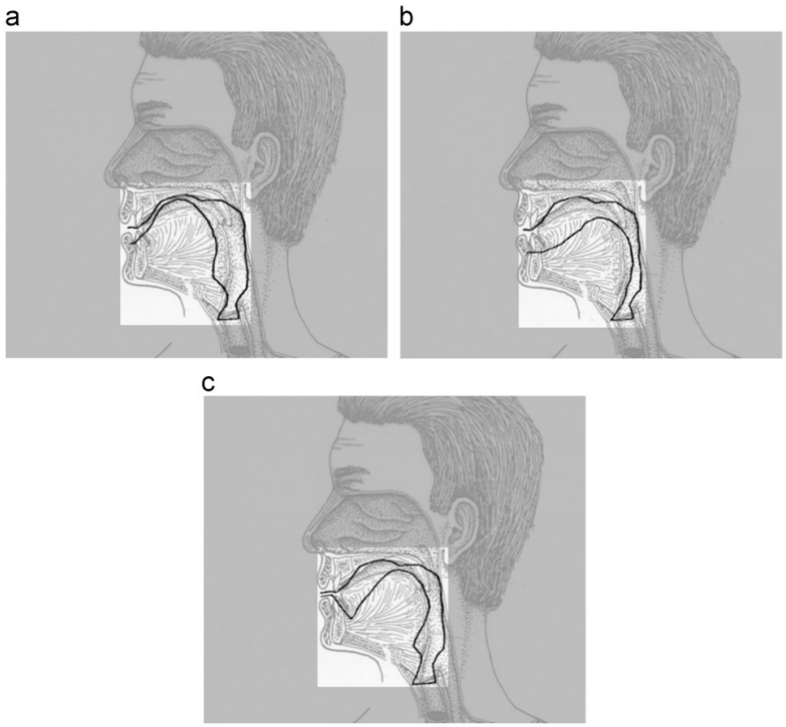
BBC Horizon at 10:45 – 15:00 http://www.dailymotion.com/video/x40jndd

The Vocal Tract

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

Two opposing views still:

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



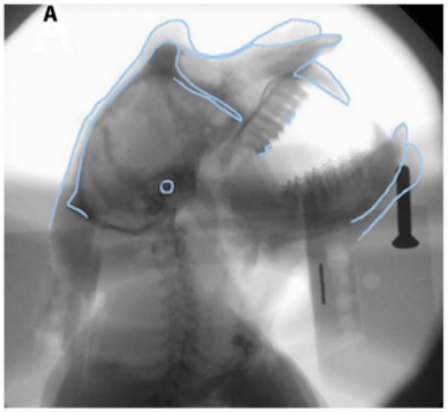
Lieberman (2012). Vocal tract anatomy and the neural bases of talking.

The Vocal Tract

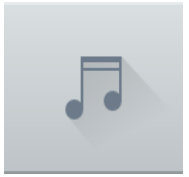
- **The Larynx**
- Hyoid Bone
- Air sacs
- Hypoglossal Canal
- Thoracic Canal

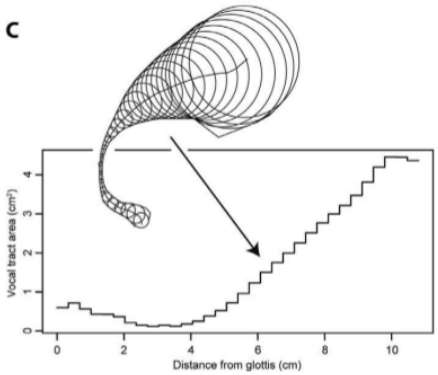
Two opposing views still:

At least macaques can produce all formants necessary for speech.

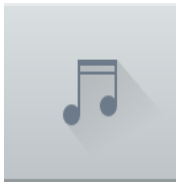


Human voice





Macaque voice



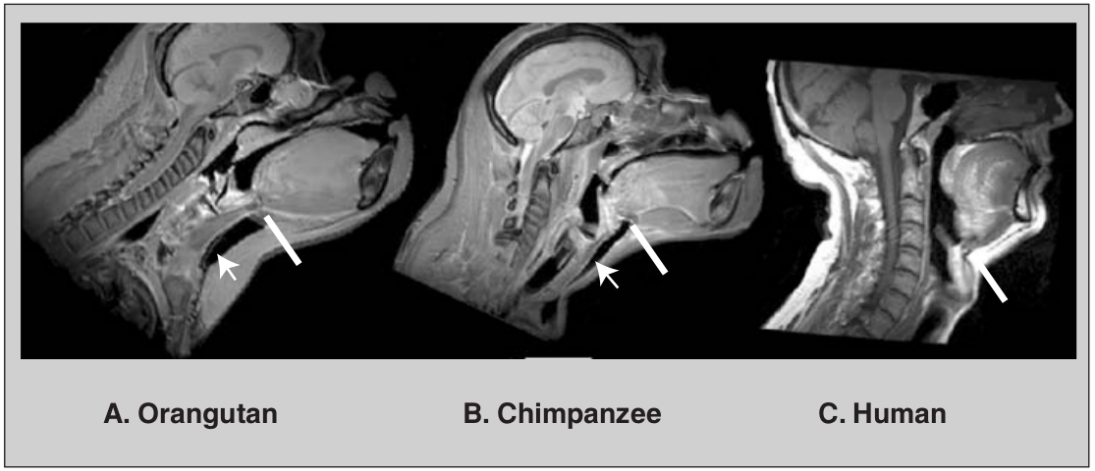
Fitch et al. (2016). Monkey vocal tracts are speech-ready.

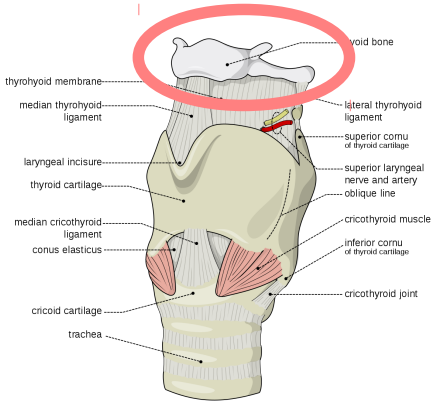
The Vocal Tract

- 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





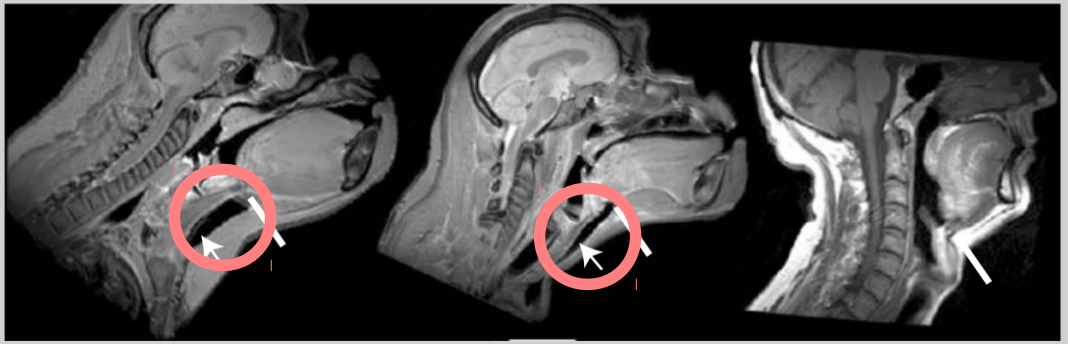
Fitch 2010, p. 308

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

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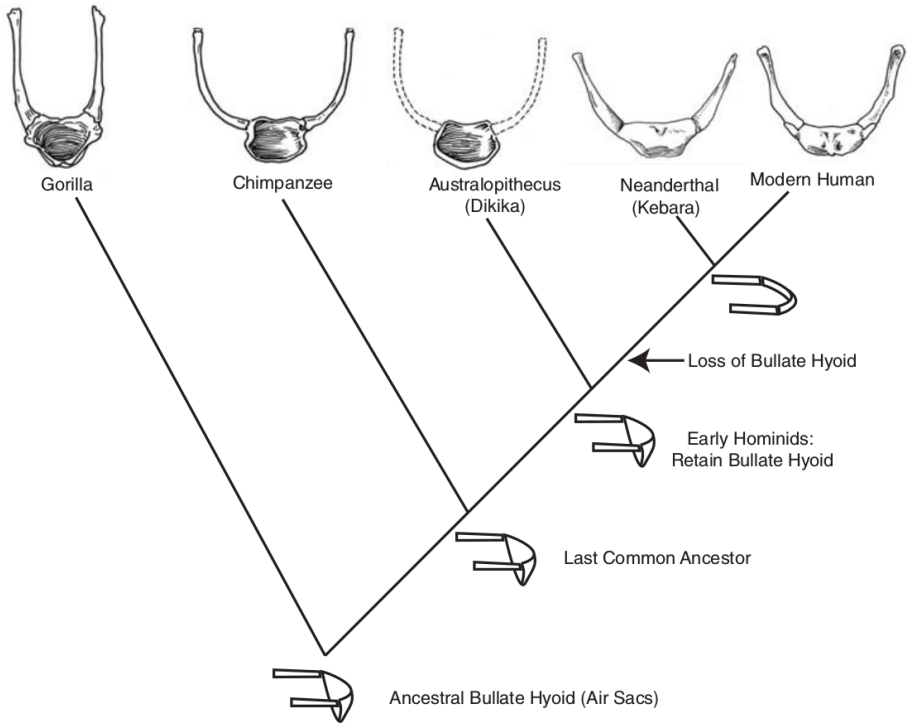

Fitch 2010, p. 334

The Vocal Tract

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

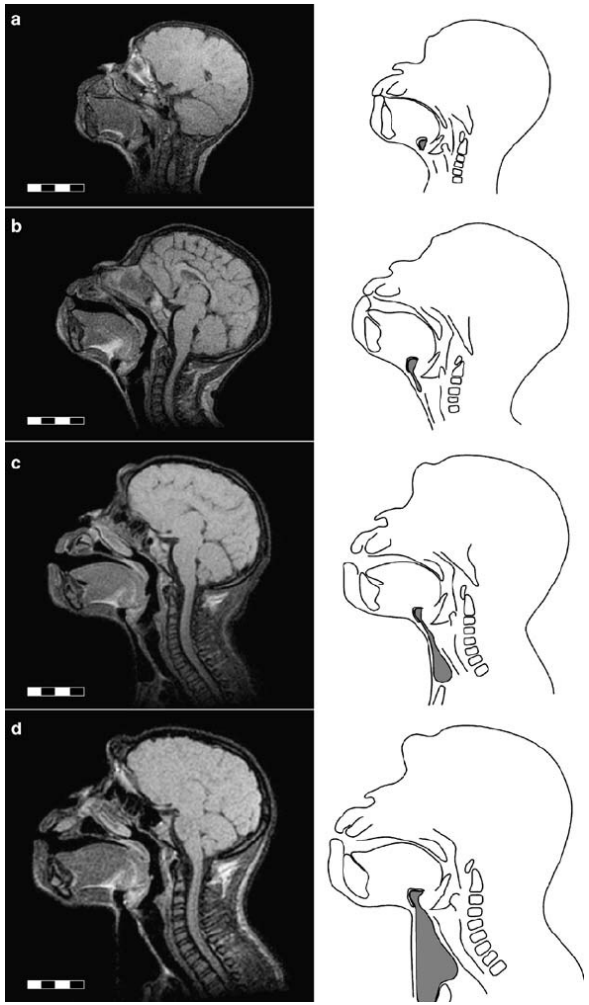
Female chimp

4 months

18 months

24 months

48 months



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

The Vocal Tract

- The Larynx
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- **Air sacs**
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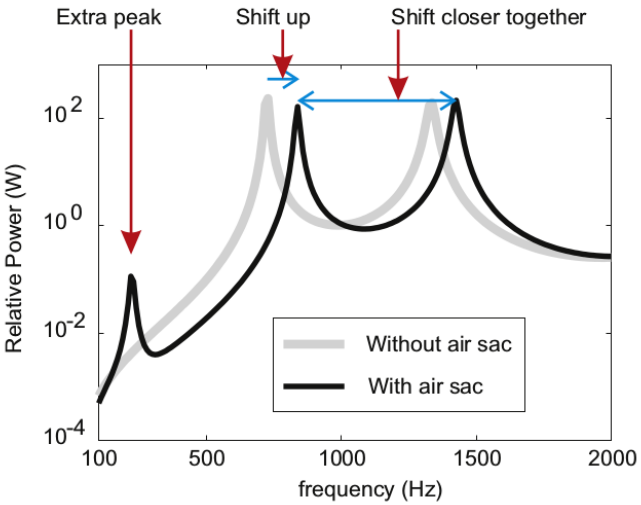
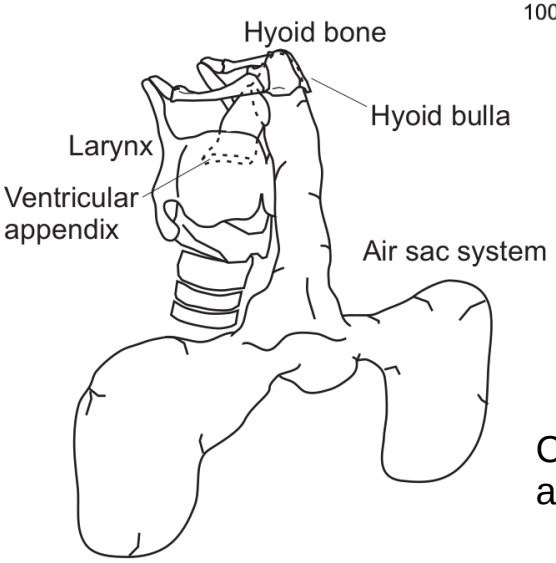
- Thoracic Canal

Power spectra of the signal predicted for the articulation [a] without (gray line) and with (black line) an air sac





Chimpanzee air sac anatomy

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

The Vocal Tract

- The Larynx
- Hyoid Bone
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- **Hypoglossal canal**
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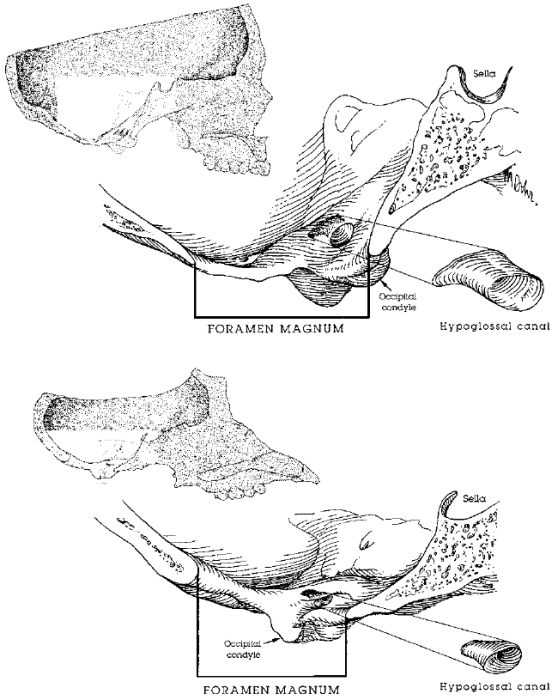
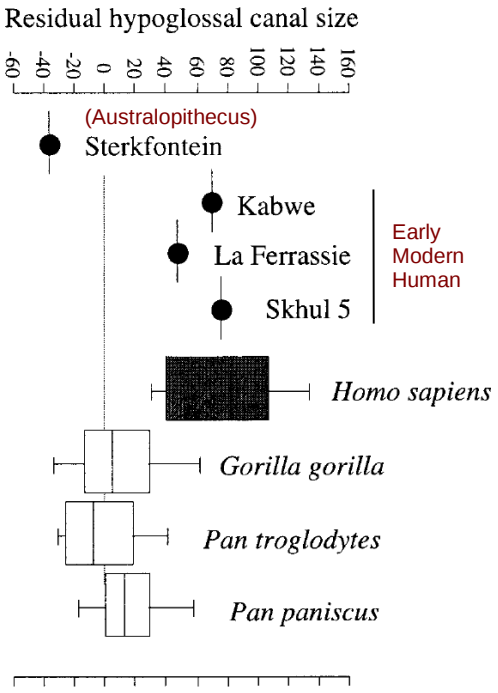




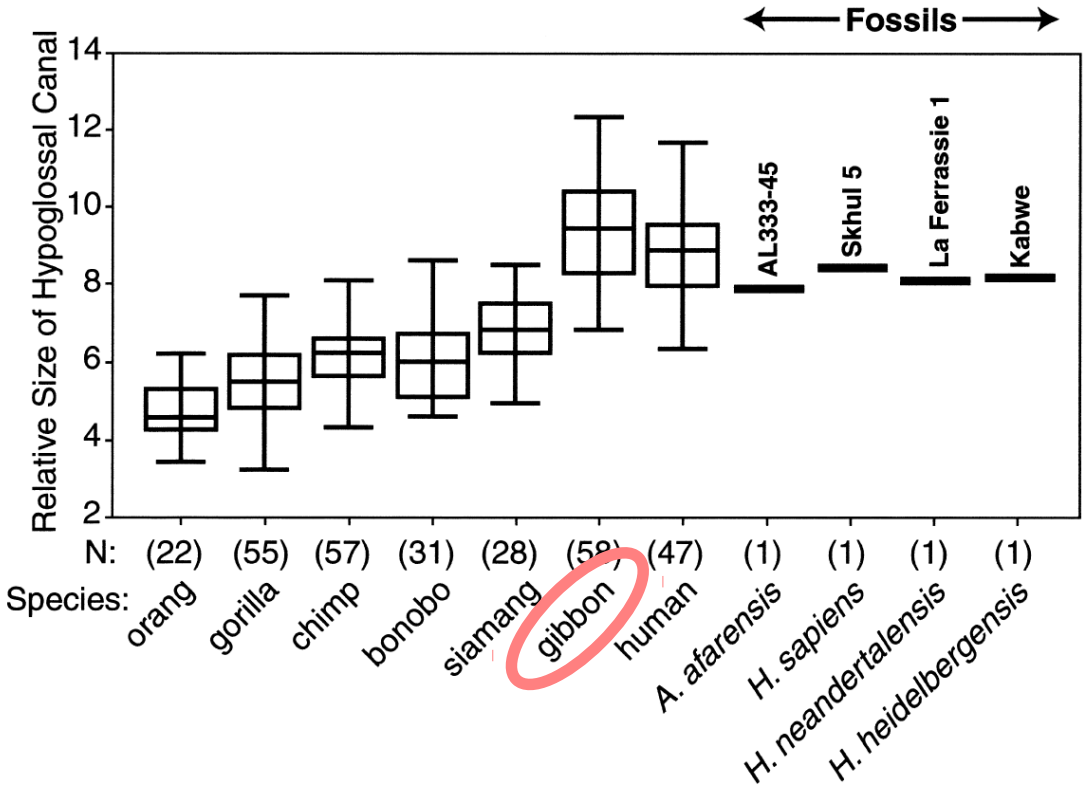
"We hypothesize that the human tongue is supplied more richly with motor nerves than are those of living apes and propose that **[hypoglossal] canal size** in fossil hominids may provide an indication about the motor coordination of the tongue and reflect the evolution of speech and language."

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 ...



"We conclude, therefore, that the relative size of the hypoglossal canal is neither a reliable nor sufficient predictor of human-like speech capabilities […]."

Jungers et al. (2003). Hypoglossal canal size in living hominoids and the evolution of human speech.

The Vocal Tract

- The Larynx
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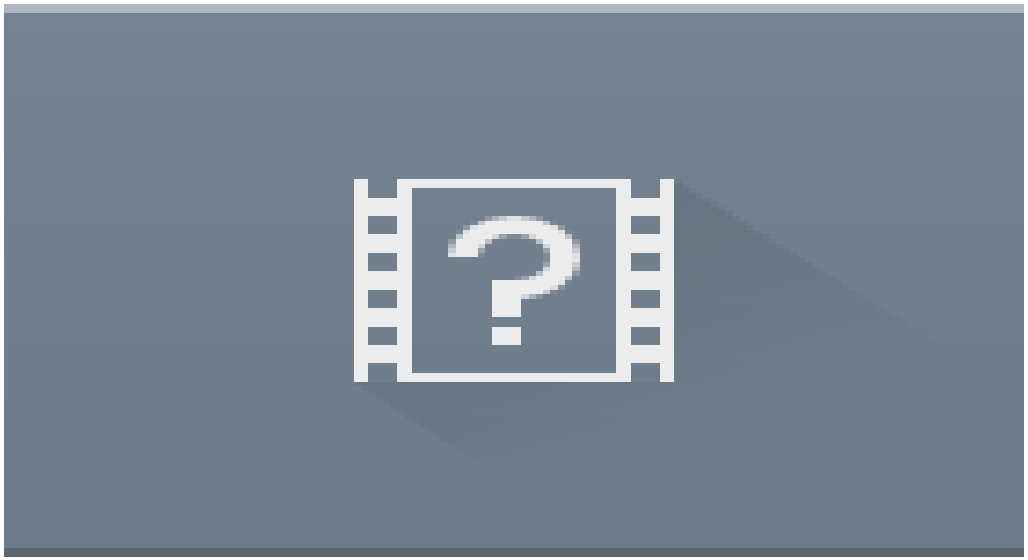
- **Hypoglossal canal**
- Thoracic Canal

… However ...



"We were interested in gibbon songs because, apart from human speech, these vocalisations provide a remarkable case of **acoustic sophistication and versatility in primate communication**. Individuals combine a finite number of call units into structurally more complex sequences in rule-governed ways, hereby conveying different contextual situations."

Clarke et al. (2006). The syntax and meaning of Wild Gibbon songs.

The Vocal Tract

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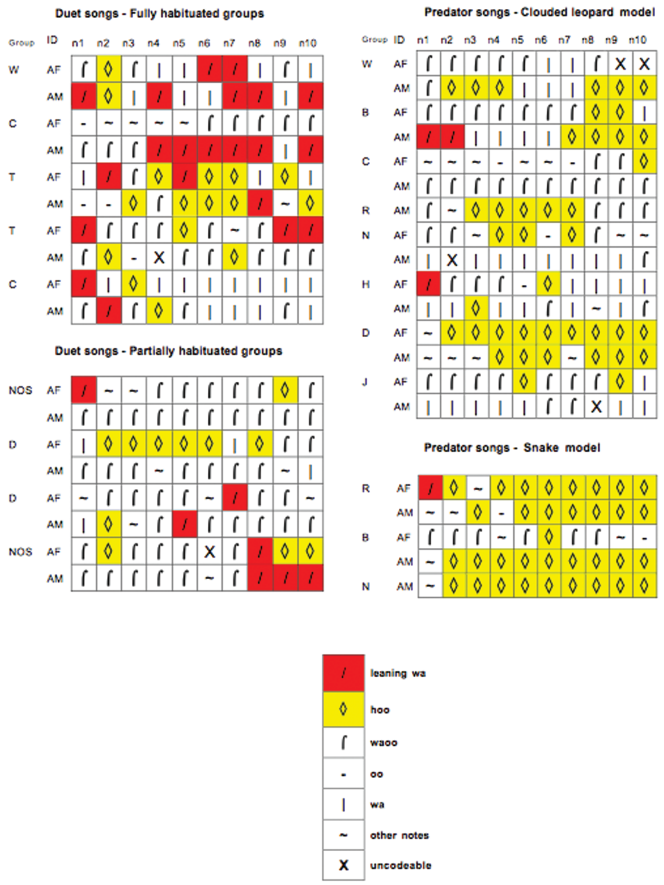

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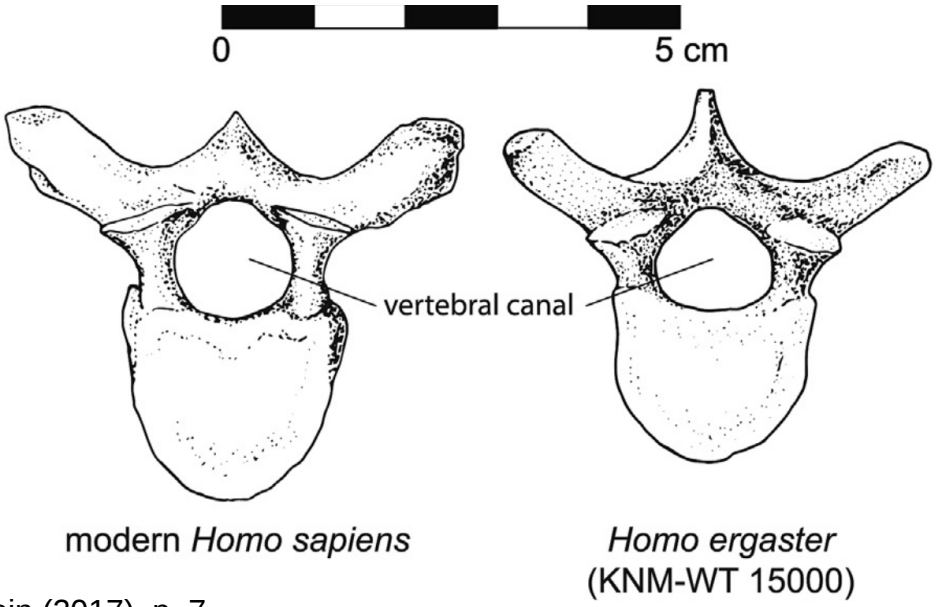
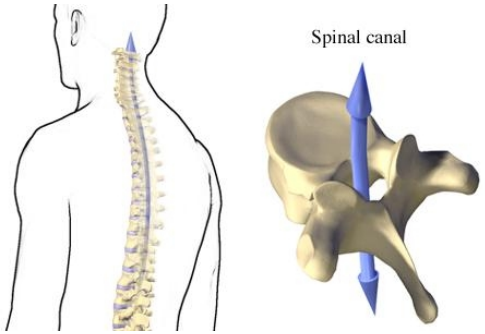
- Hypoglossal canal
- **Thoracic Canal**

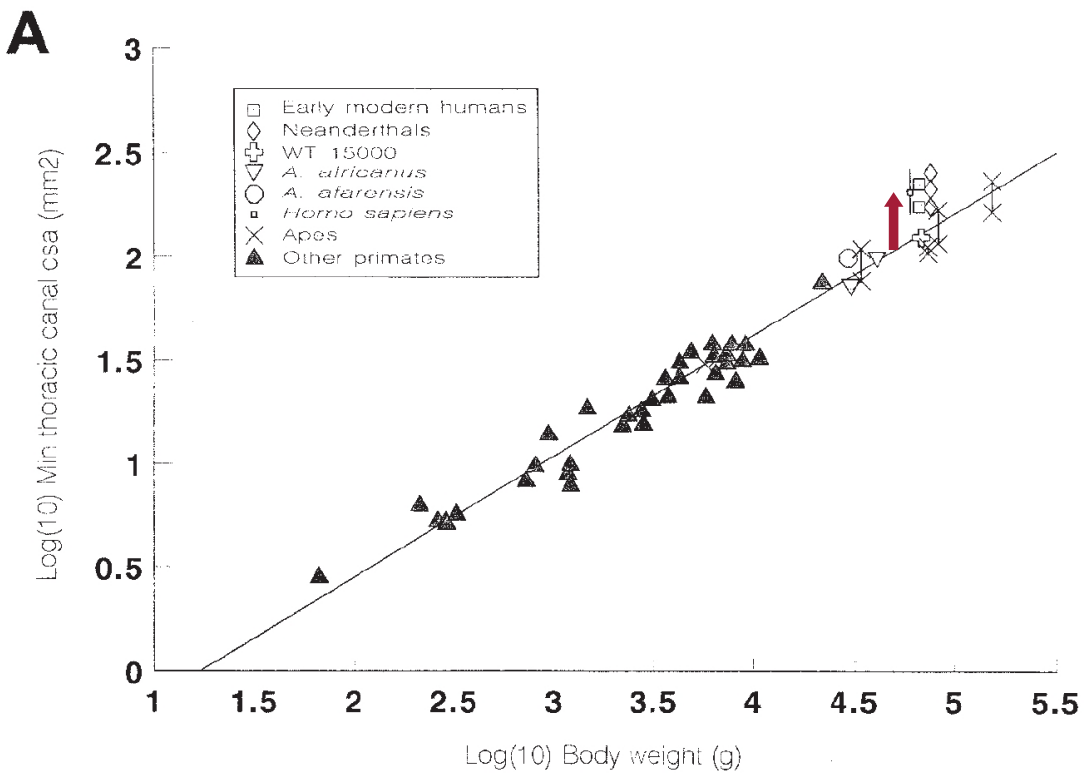


Klein (2017), p. 7.



The Vocal Tract

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

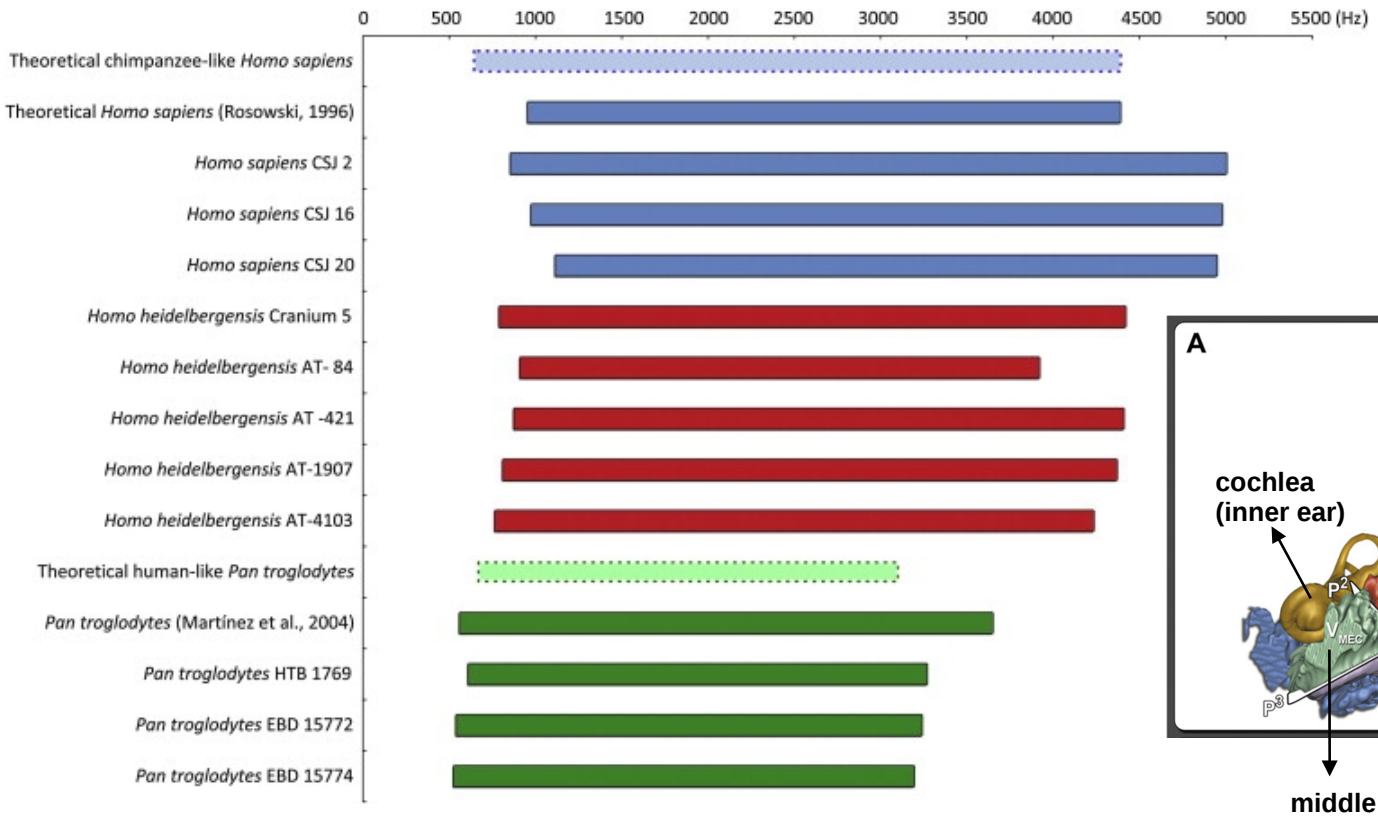


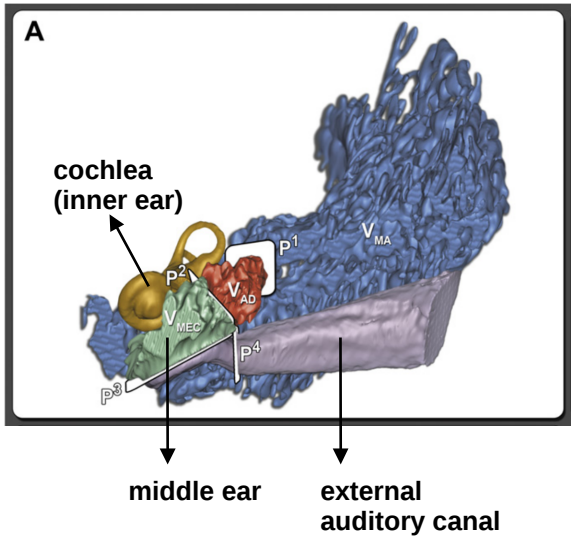
MacLarnon and Hewitt (2004). Increased breathing control: Another factor in the evolution of human language

Preadaptations for Language

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

Speech Perception: Special in Humans?



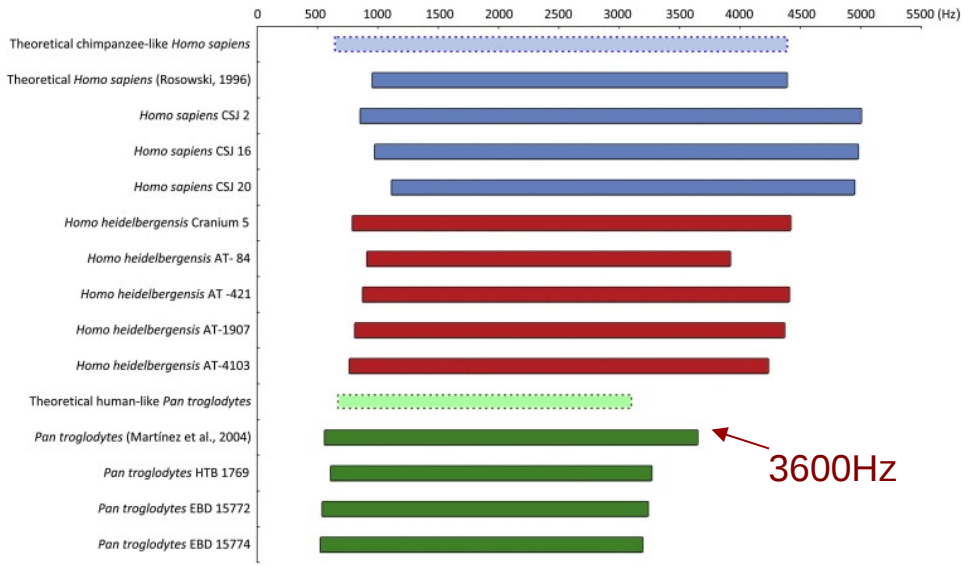


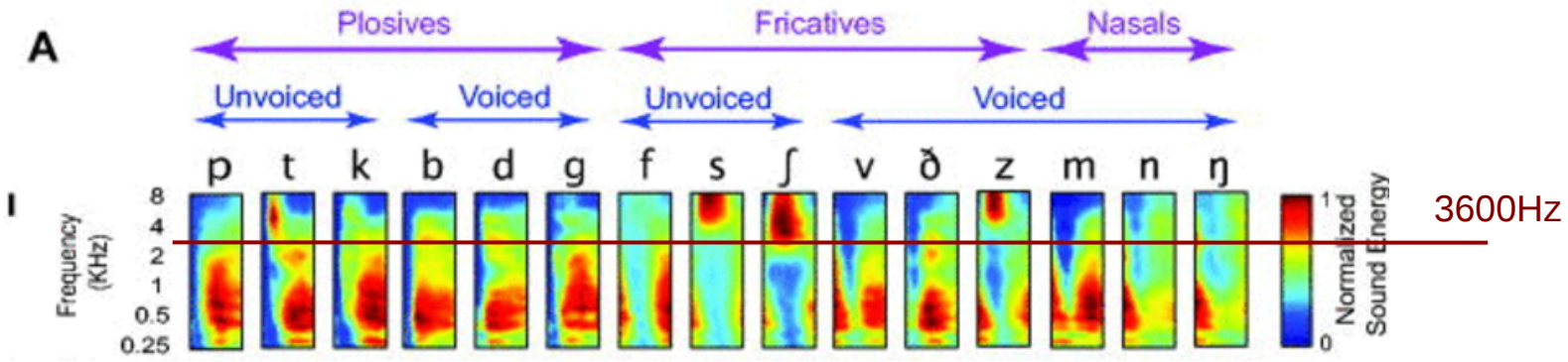
"The pattern of sound power transmission was studied through the **outer and middle ears** in five individuals from the Sima de los Huesos, four chimpanzees and four modern humans."

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

Speech Perception

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





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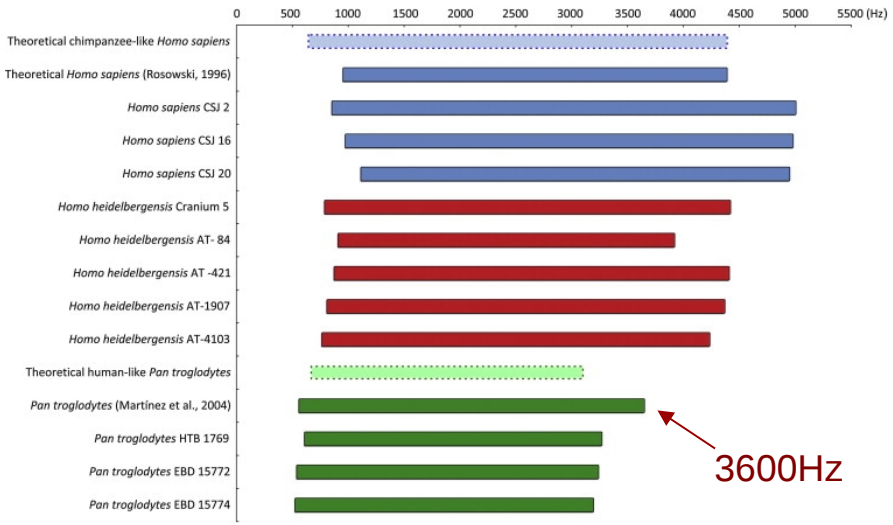
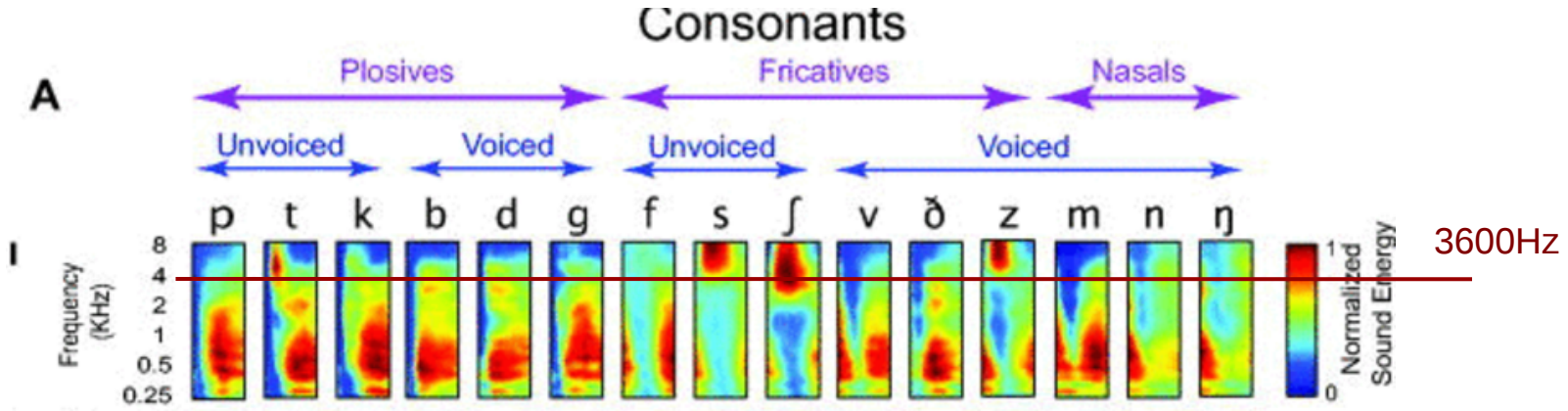




Martinez et al. (2013). Communicative capacities in Middle Pleistocene humans from the Sierra de Atapuerca in Spain.
Mesgarani et al. (2008). Phoneme representation and classification in primary auditory cortex.

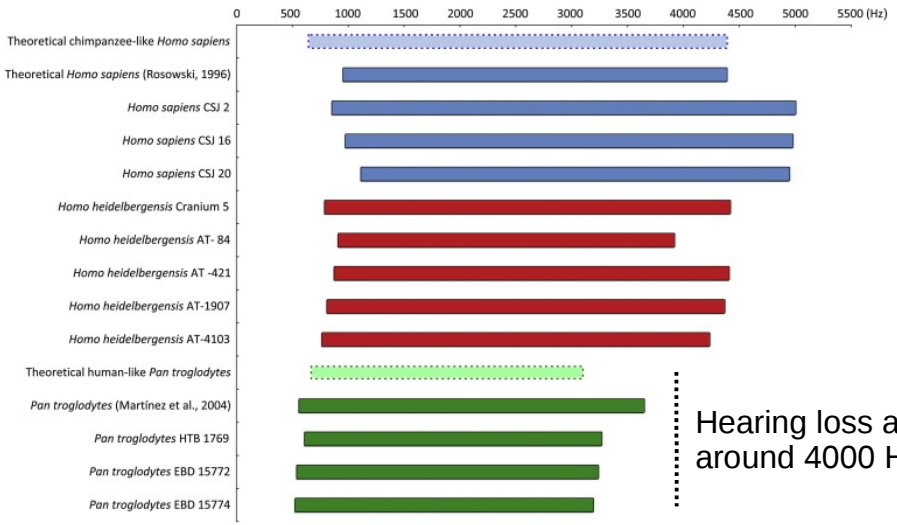
Speech Perception

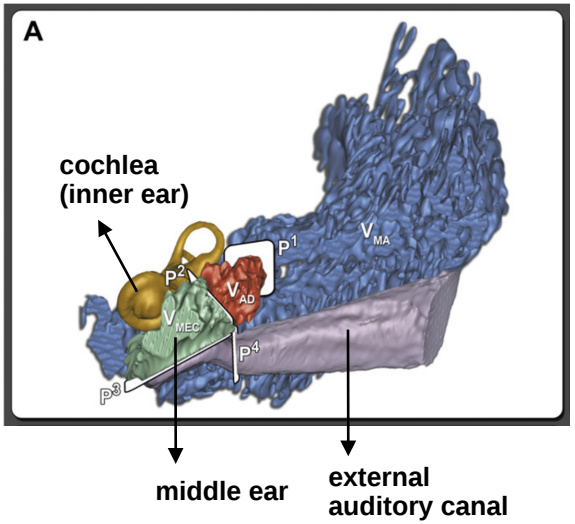
However ...

"[…] the primary determinant of hearing range and acuity is the **cochlea**, not the outer or middle ears [...]"

"Captive housed animals often suffer **noise-induced hearing loss**, caused by exposure to loud vocalizations in a reverberant concrete environment, which may explain this "divot" in adult sensitivity."

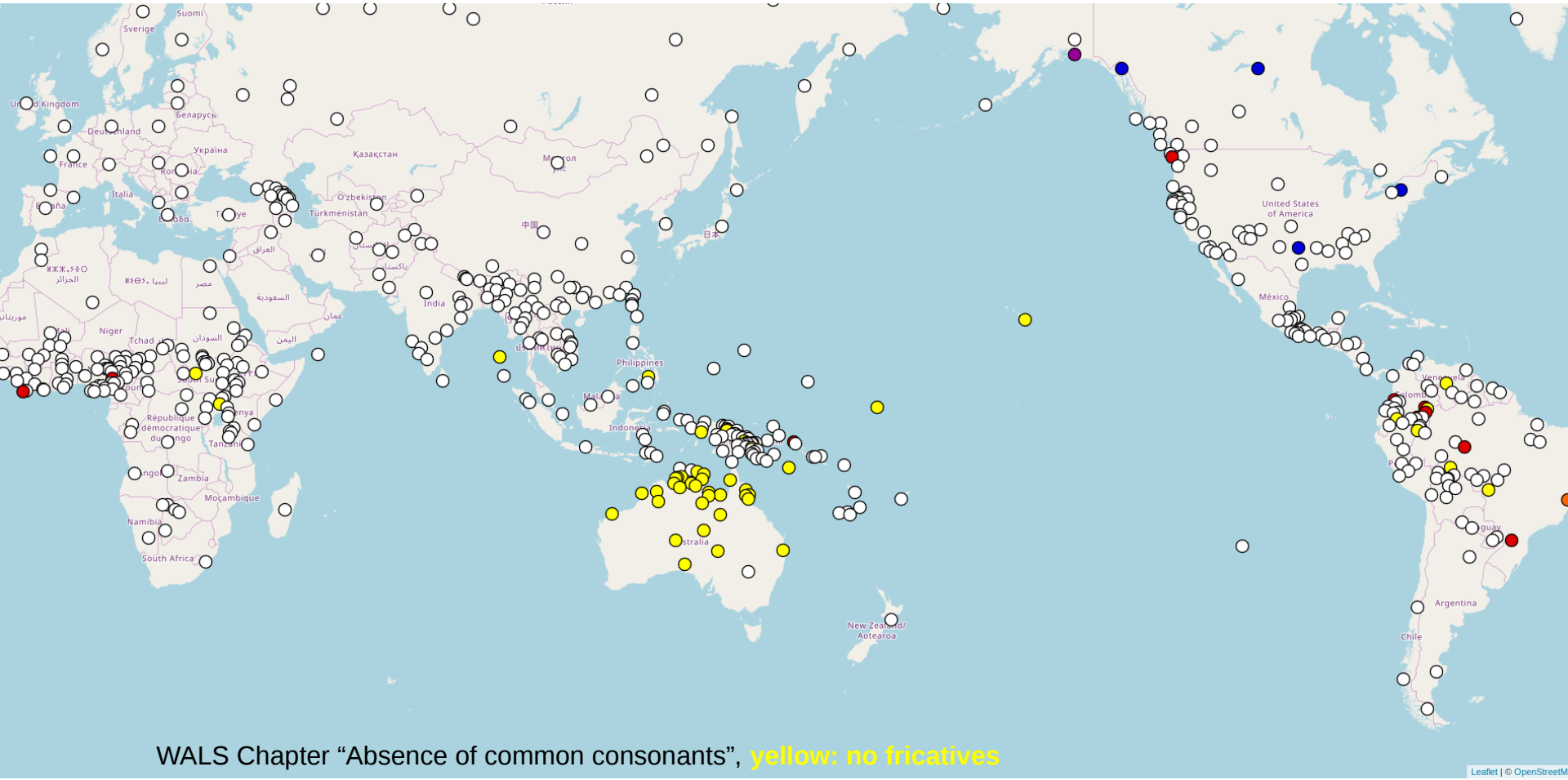
Fitch (2017), p. 5





Speech Perception

Also... languages can perfectly do without fricatives alltogether ...

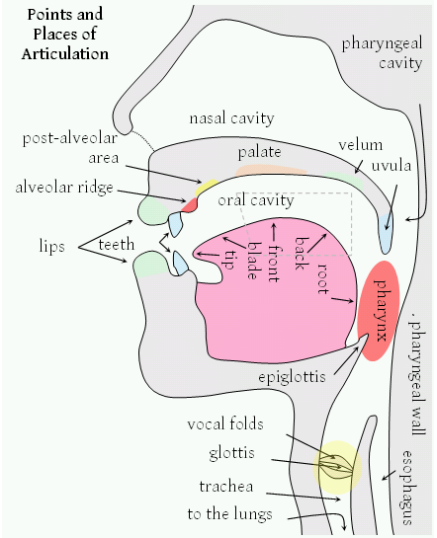


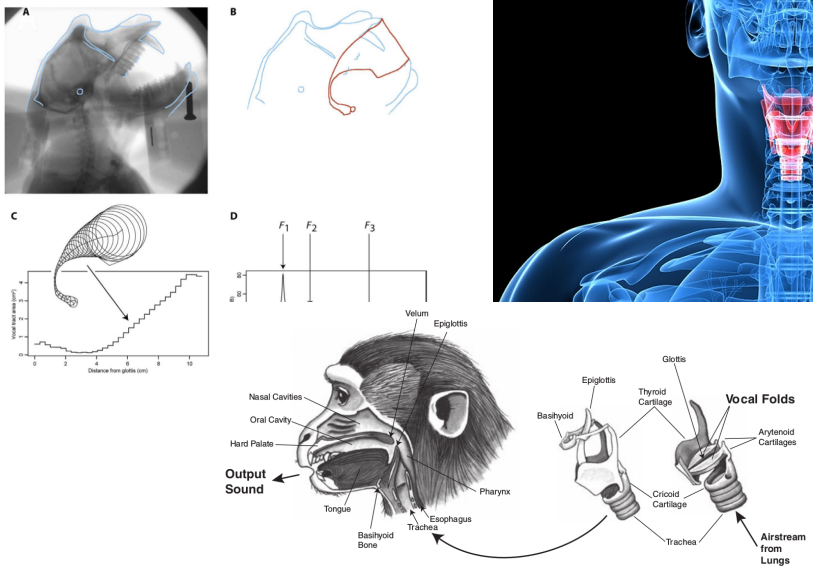
WALS Chapter “Absence of common consonants”, **yellow: no fricatives**

Summary: Speech Production and Perception

According to Fitch (2010, 2017) 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 - i.e. neural circuitry.**





Preadaptations for Language

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

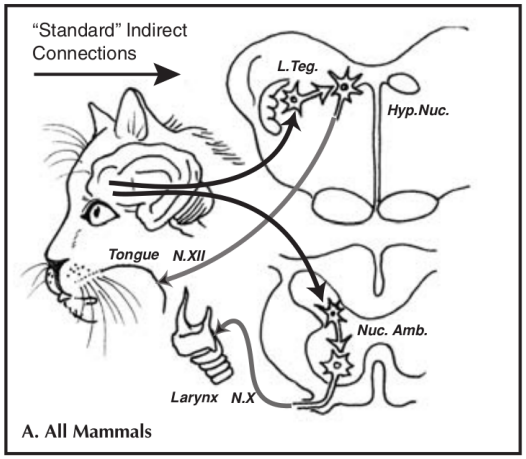
Brain areas

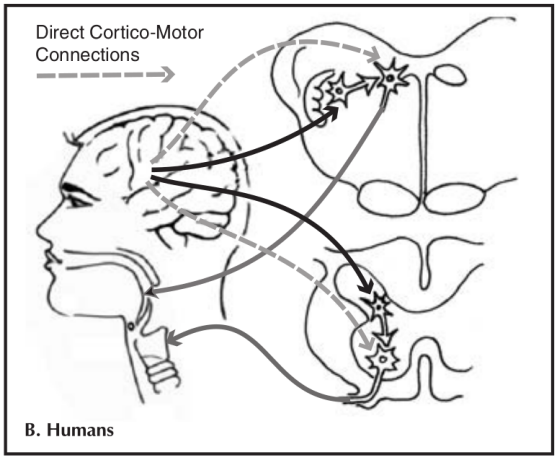
- cortico-laryngeal connections

- 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.

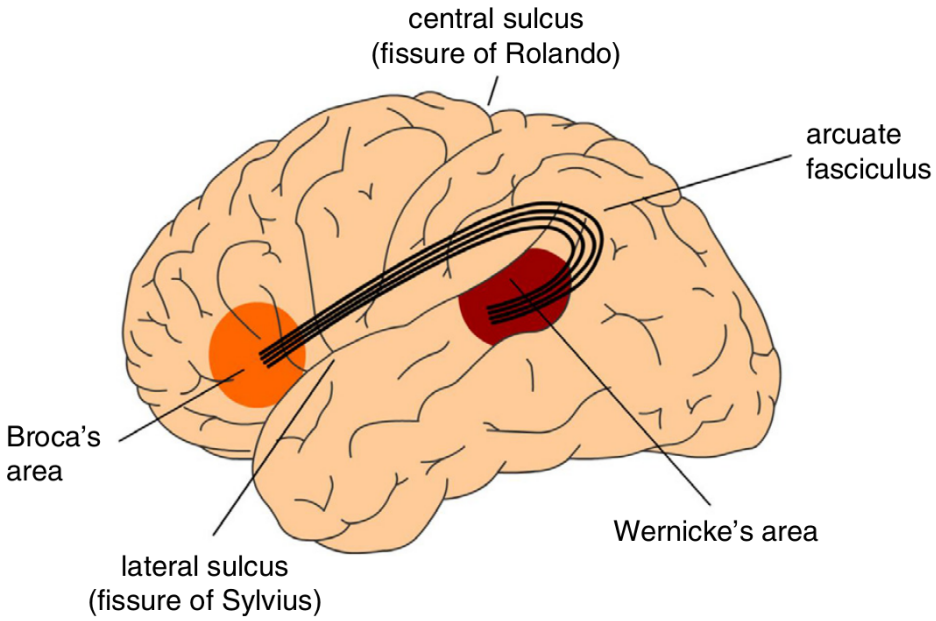
Brain areas

- cortico-laryngeal connections

- Broca's and Wernicke's area

- Update: Language networks

- Areas specific to syntax?



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

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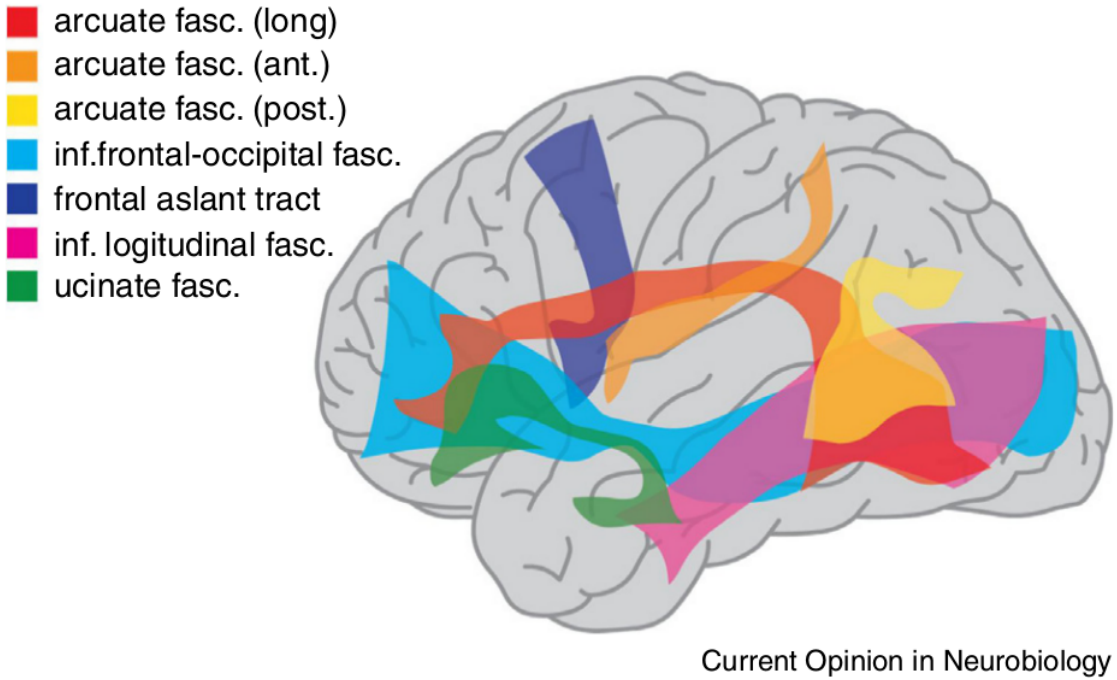
- Update: Language networks

- Areas specific to syntax?



Current Opinion in Neurobiology

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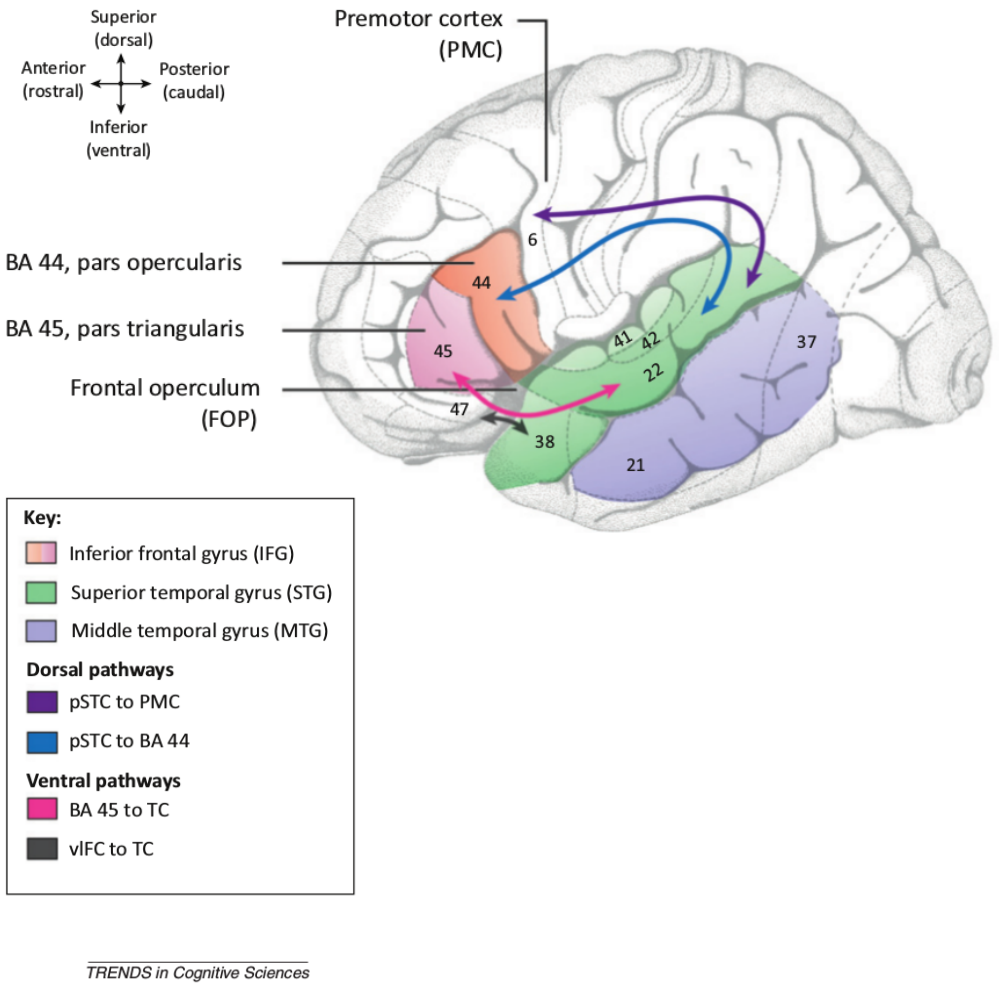

Berwick et al. (2013). Evolution, brain, and the nature of language.

Brain areas

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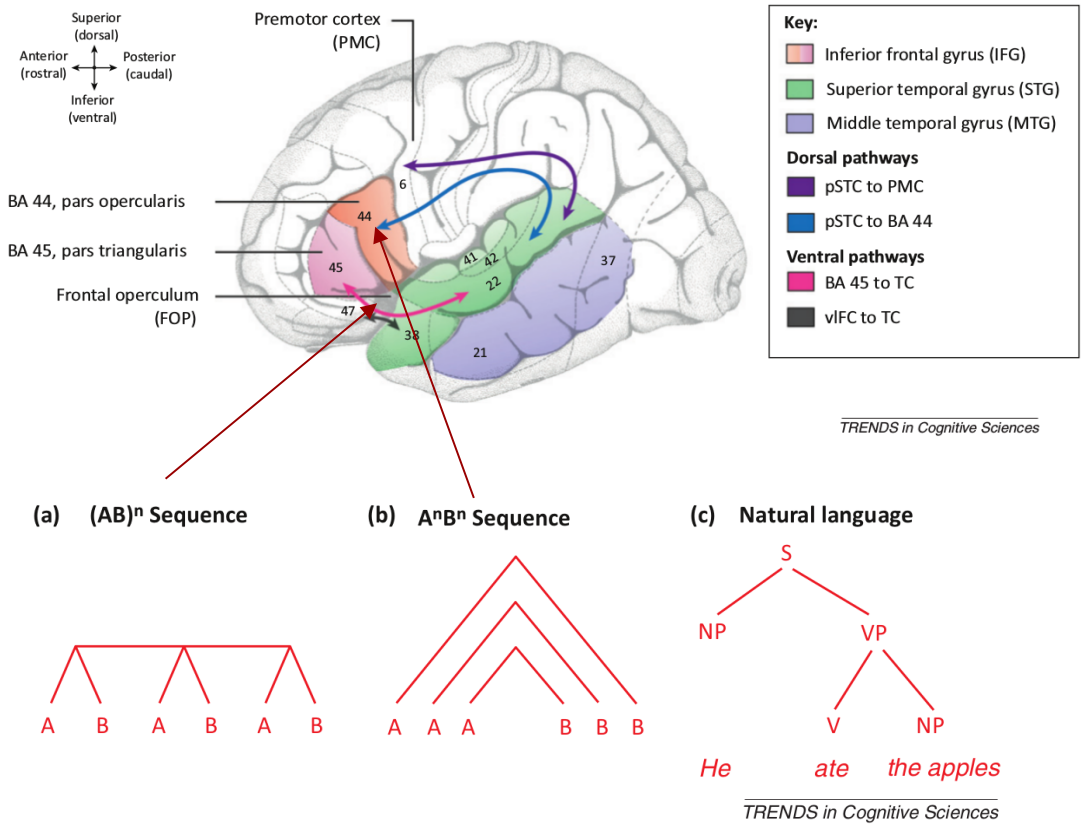

Berwick et al. (2013). Evolution, brain, and the nature of language.

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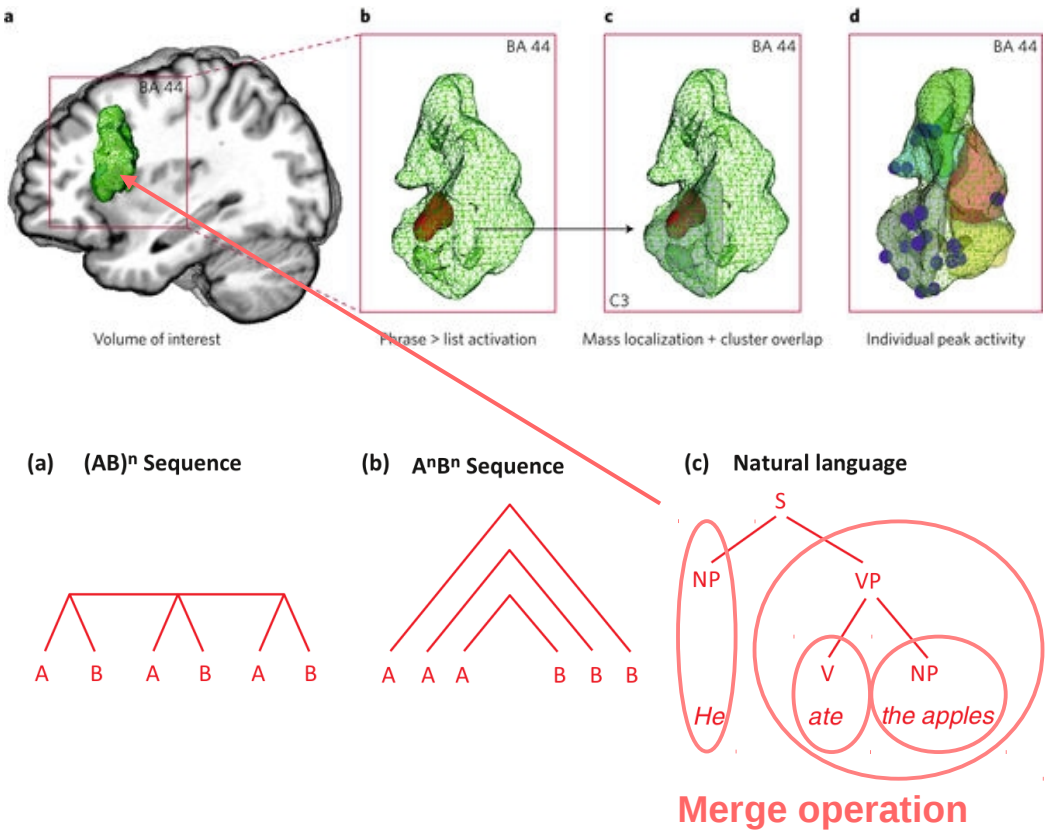
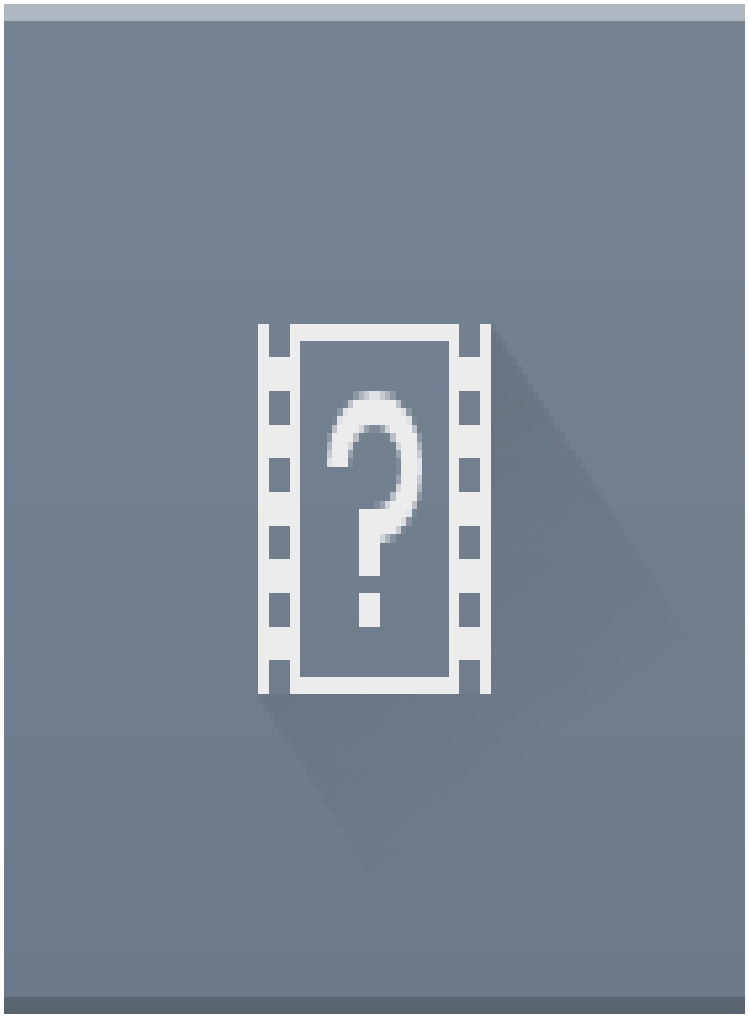
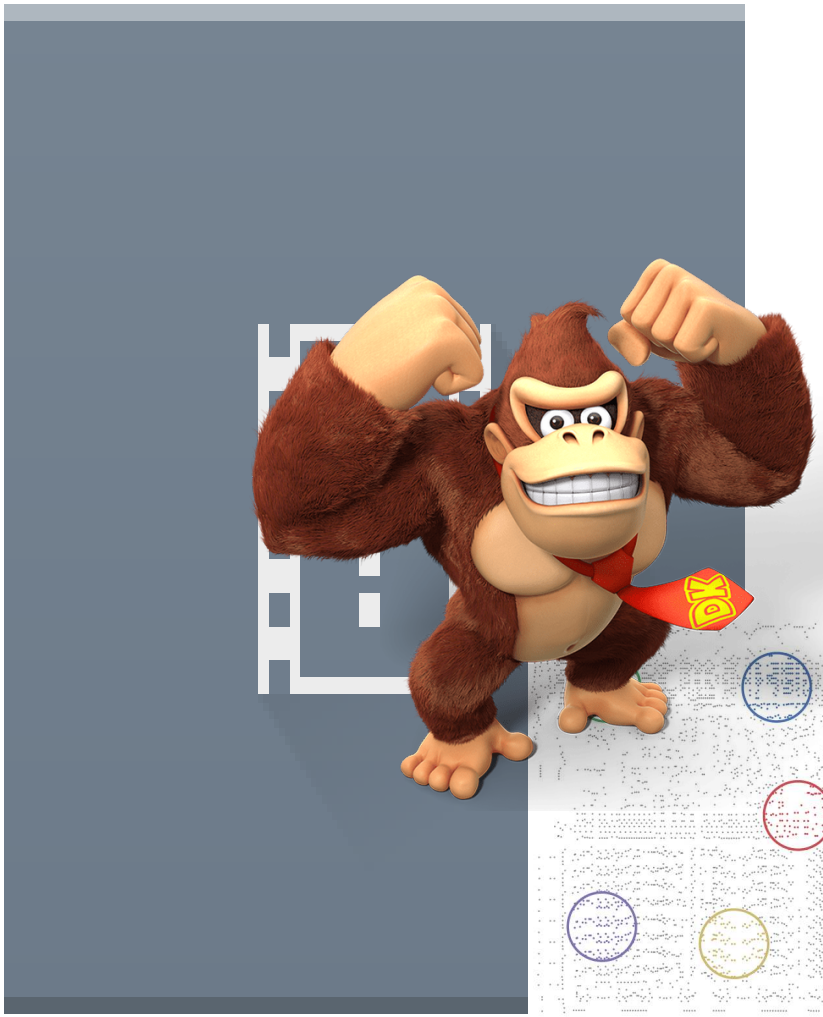
Beyond preadaptations? "Real" language



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



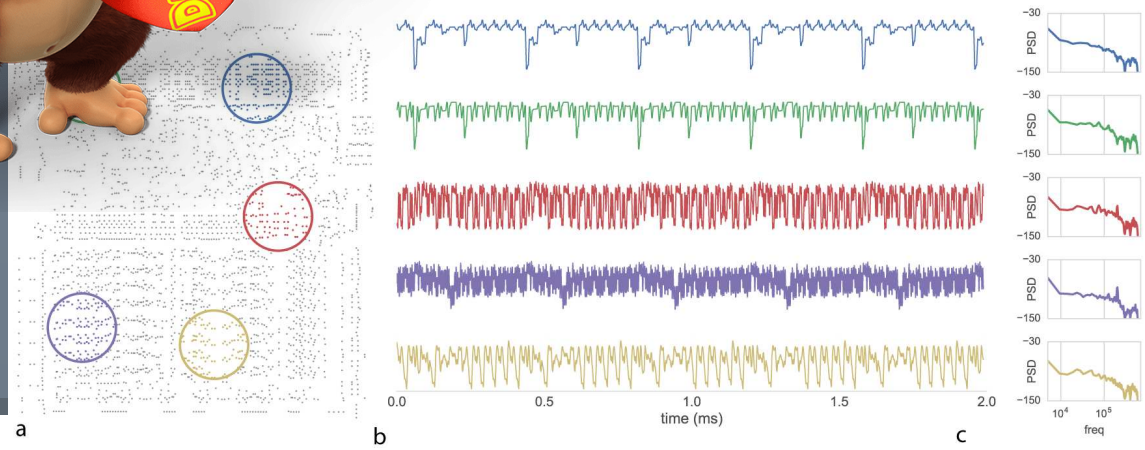
Excursion: What might this be?



Strong limitations on interpretability of neuroscientific data?

We show that the [standard neuroscientific] approaches reveal interesting structure in the data but **do not meaningfully describe the hierarchy of information processing in the microprocessor**. This suggests current analytic approaches in neuroscience may fall short of producing meaningful understanding of neural systems, regardless of the amount of data.

Jonas & Kording (2017). Could a neuroscientist understand a microprocessor?

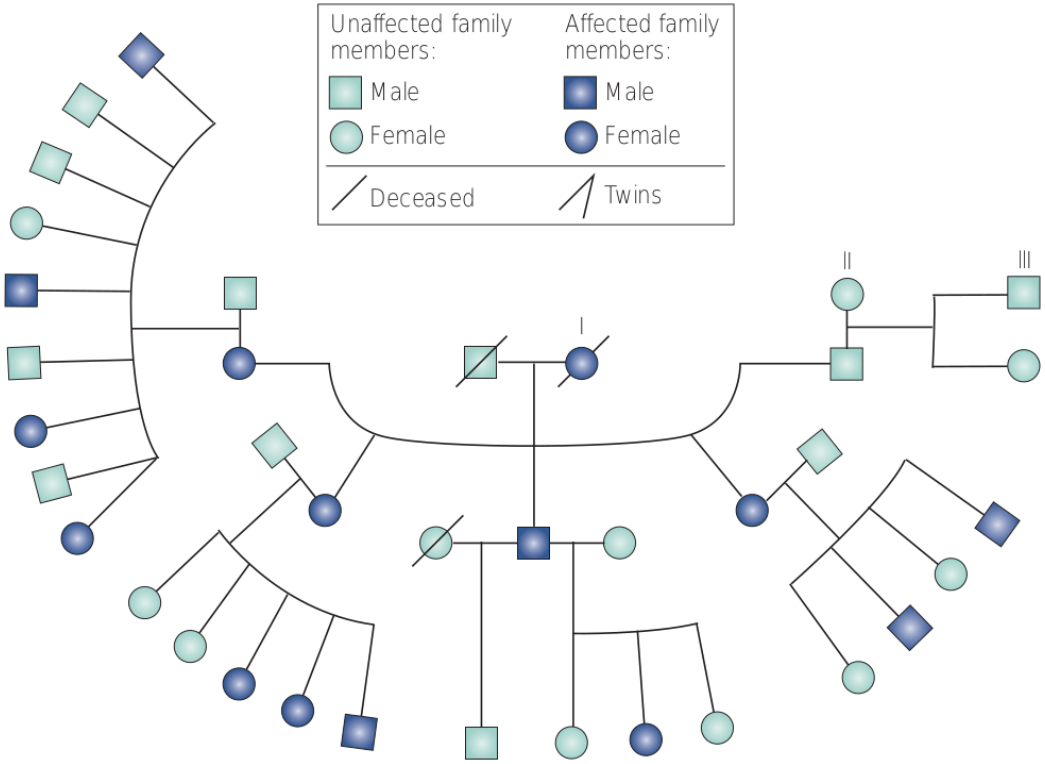


Preadaptations for Language

- 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**

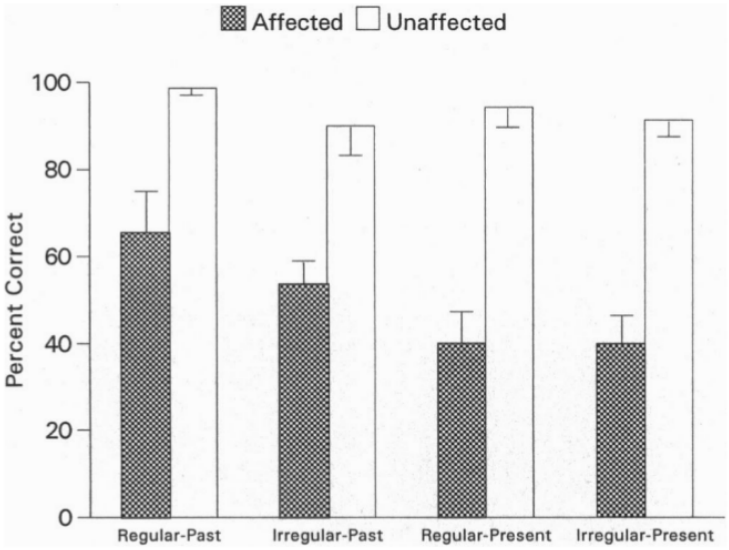


FIG. 2. Production of tenses. Scores are means ± standard errors. See Table 2 for examples of test items.

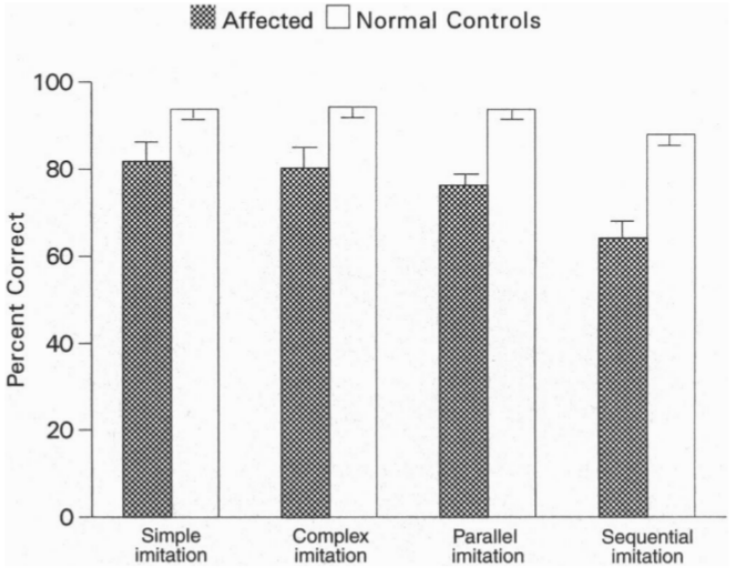


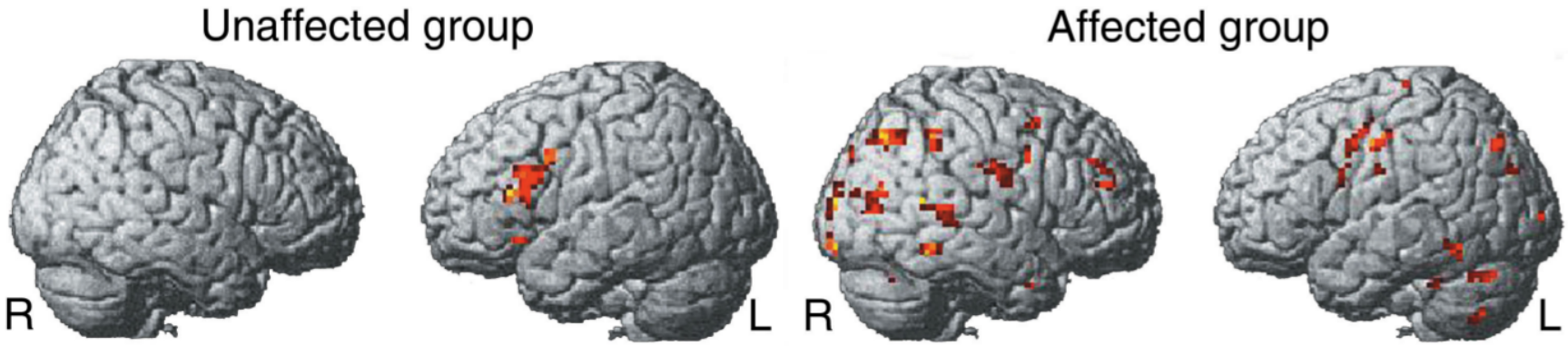
FIG. 3. Imitation of oral and facial movements. Scores are means ± standard errors.

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**

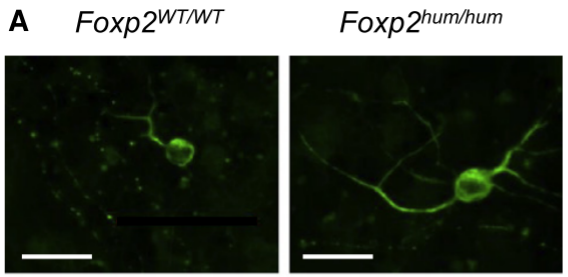
"Ten members of the KE family (5 affected, 5 unaffected) and two groups of control participants, individually matched on age, sex and handedness to each member of the family, performed an fMRI task that required the covert generation of verbs in response to hearing nouns."



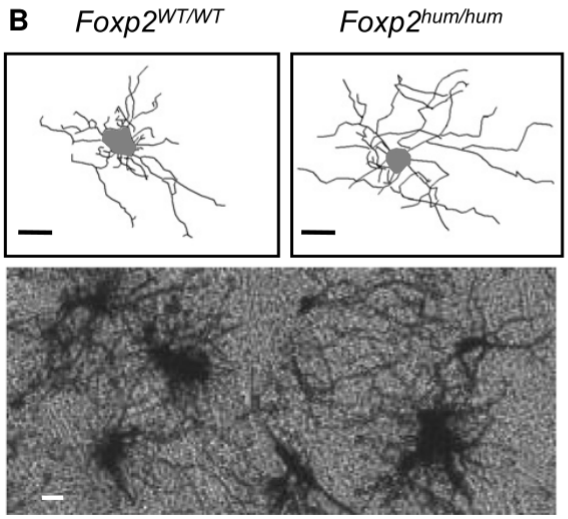
Liégeois et al. (2003). Language fMRI abnormalities associated with FOXP2 gene mutation.

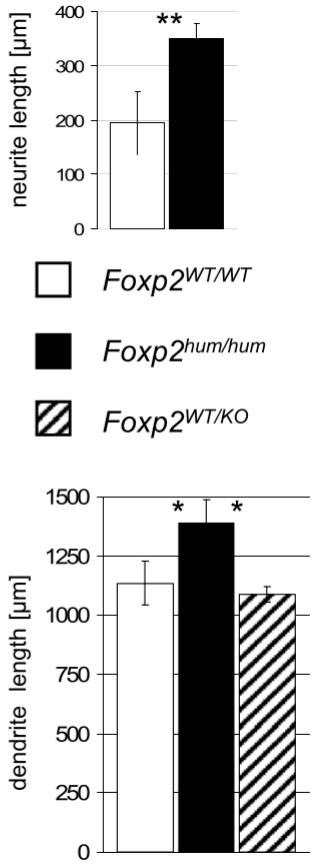
Genetics: FOXP2

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

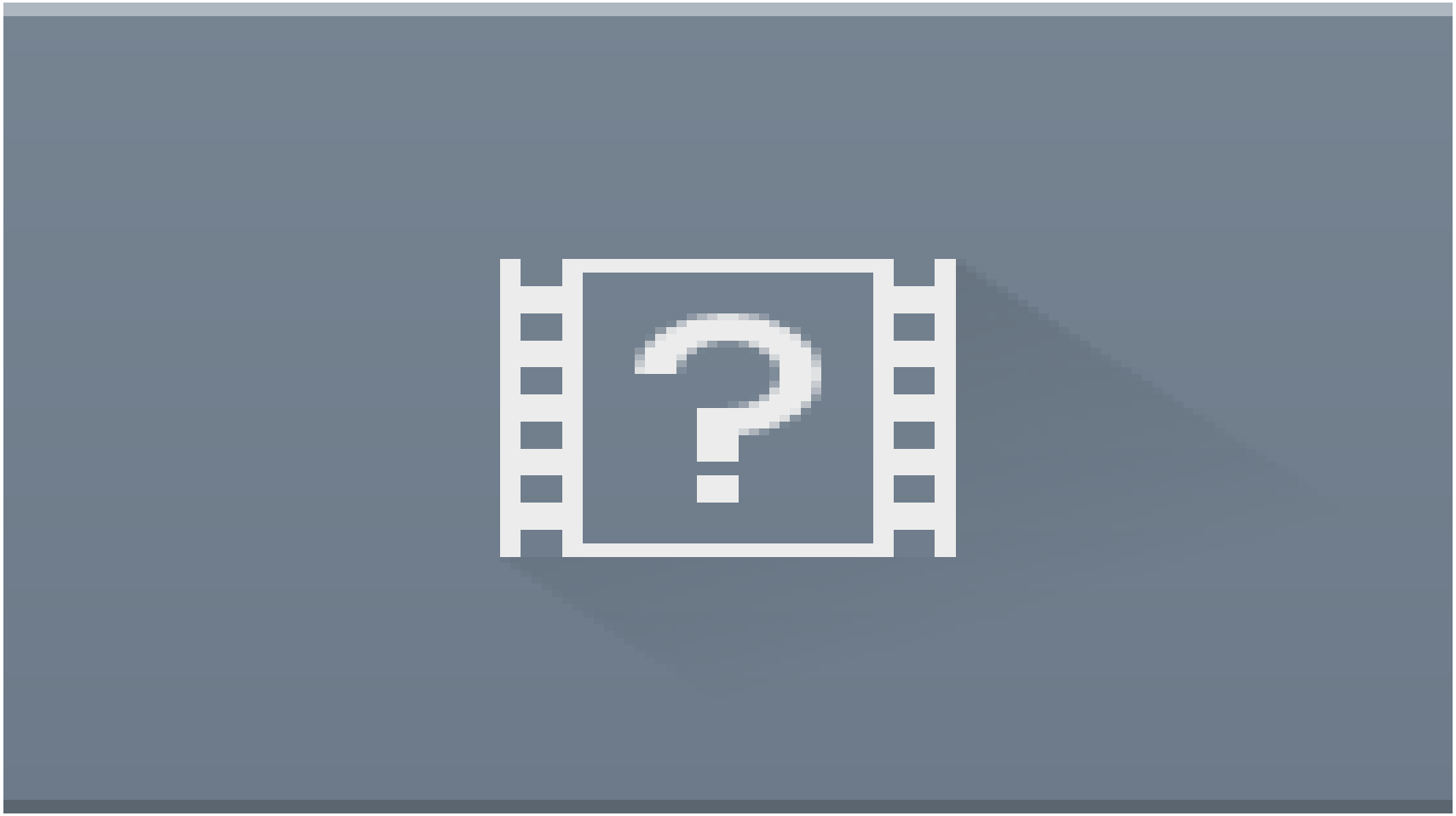


WT: wild-type hum: humanized





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



BBC Horizon at 41:50 – 47:00 http://www.dailymotion.com/video/x40jndd

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.

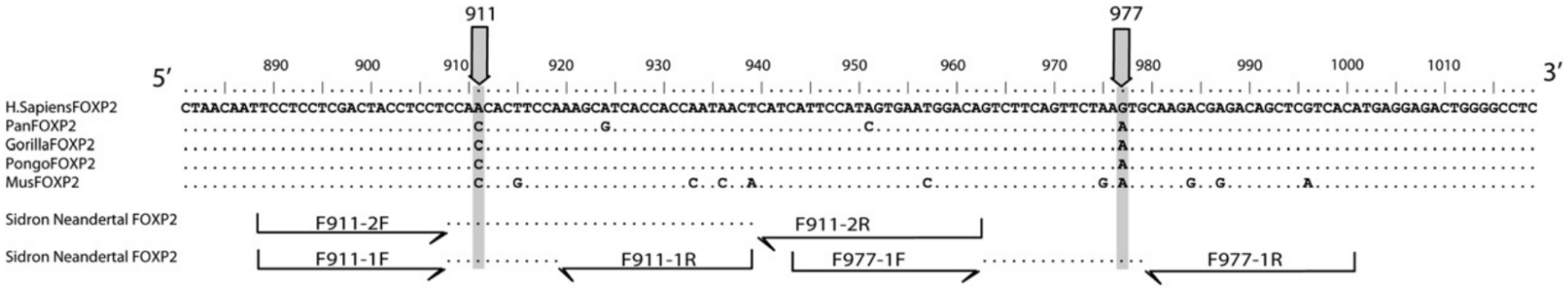
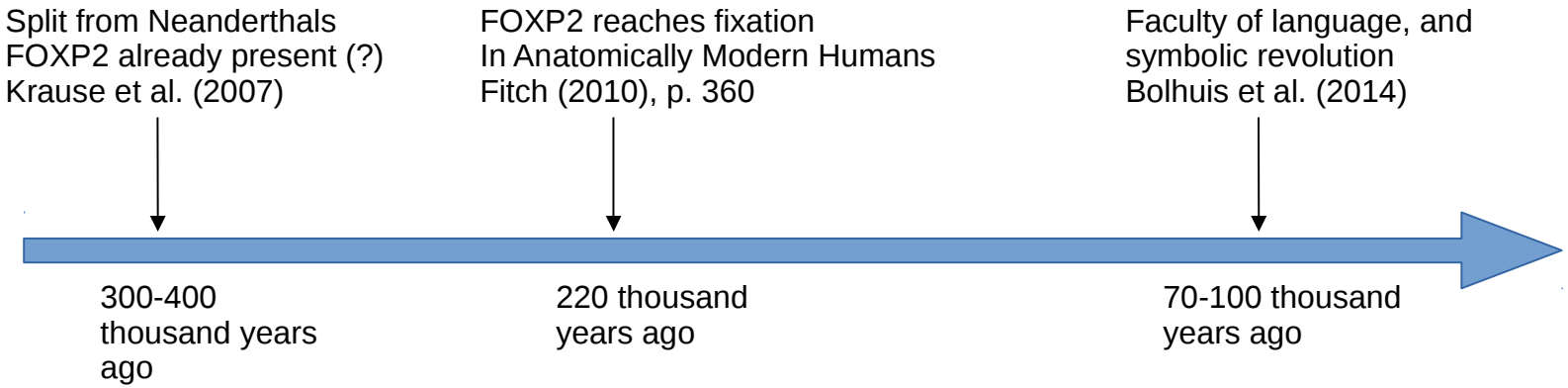


Figure 1. Sequence Alignment of Nucleotide Positions 880–1020 from the *FOXP2* Gene

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.

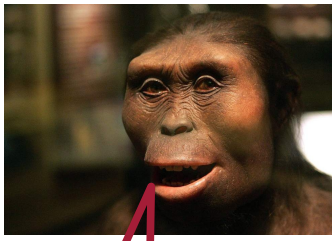
Is FOXP2 a “Great Leap Forward”?

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

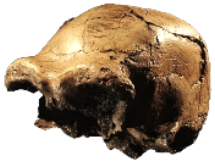


Summary: An evolutionary model according to Fitch

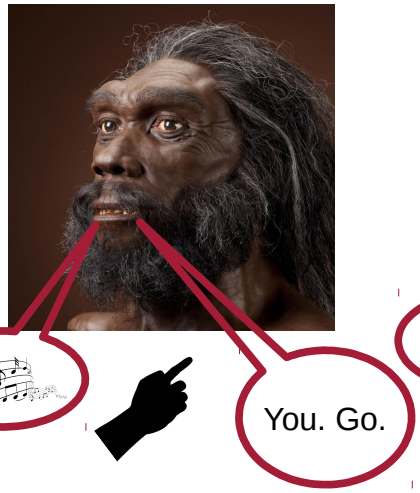
Singing
Australopithecus



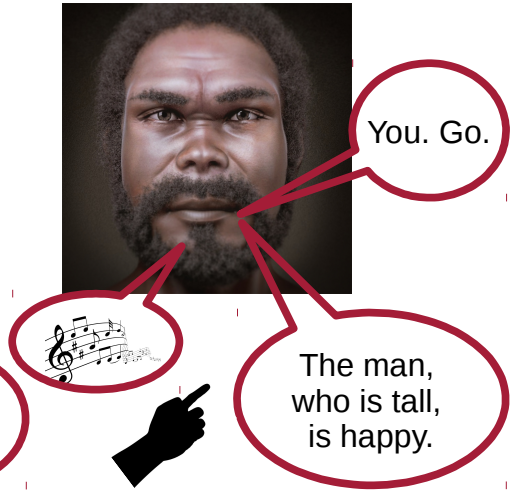
Mimetic
Homo erectus



Semantic
Homo antecessor
(heidelbergensis)



Syntactic
Homo sapiens



Fitch (2017). Empirical approaches to the study of language evolution.

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72070 Tübingen · Germany
Phone: +49 7071 29-76548
monika.doll@ifu.uni-tuebingen.de