

**SUBSTANCE-FREE
LOGICAL PHONOLOGY**
in **EVOLUTIONARY PERSPECTIVE**

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Background

- Twenty(-plus) years since the publication of Chomsky's "Three Factors in Language Design" and the FLN vs. FLB distinction by Hauser et al., and since I started thinking about what an evolutionarily plausible theory of phonology might look like
- At roughly the same time, SFP and what we now call LP were coming onto the scene, creating the first (and still only) truly M/minimalist theory of phonology
- In the interim, huge amounts of ink spilled over recursion/Merge, and almost zero interest in phonology from within the field of (bio-)linguistics
- I/we used to rely a lot on analogy to build the case for evolutionary plausibility: if birds/bats/whales could evolve this, so could we.
- Luckily, researchers in animal cognition started to ask many interesting questions in interesting ways, and it turns out the picture of our ape relatives was very incomplete
- Part 1: newer behavioral evidence; part 2: {paleo, epi, neuro}genetics to reconstruct the rest of the story
- The upshot: I think the LP kind of phonological system is well supported (less in the sense of disambiguating it from other theories than as a sanity check)

What is going on here?



Part 1: cognitive abilities & behavioral evidence

Prerequisites for phonology

Martins, Samuels & Boeckx 2015, Samuels 2009, Yip 2006

- Perceiving, producing, and categorically distinguishing discrete sounds (ignoring anatomical differences) \approx vocal learning
- Vowels and consonants
- Grouping sounds into chunks
- Phonotactics; learning/producing rule-governed alternations
- Computing different types of identity (natural classes)
- [Preference for and ability to produce] contrast and rhythmicity
- Basic numeracy
- + LP Operations: search, copy, unify, delete, concatenate (or some variation on this)

Pre-2005 settled-ish science

- Categorical perception / “perceptual magnet effect” is widespread, and some common phoneme boundaries coincide with mammalian perceptual biases
- Discreteness of phonological units is “a matter of signal detection theory, not of biology... comes by virtue of ‘natural law’” (Jackendoff 2011, but dating back to Hockett)
- Hierarchy/phonological syntax in singing species
- Basic counting and ratio comparison
- Learning/producing simple rule-governed alternations
- Prosody: discrimination of unfamiliar languages
- Old view: The animals with phonology most like ours are birds and whales. Phonology popped up out of nowhere in our species - alone among apes.

Recent developments/in progress

When the right questions are asked in the right way, and not in BIZARRE settings...

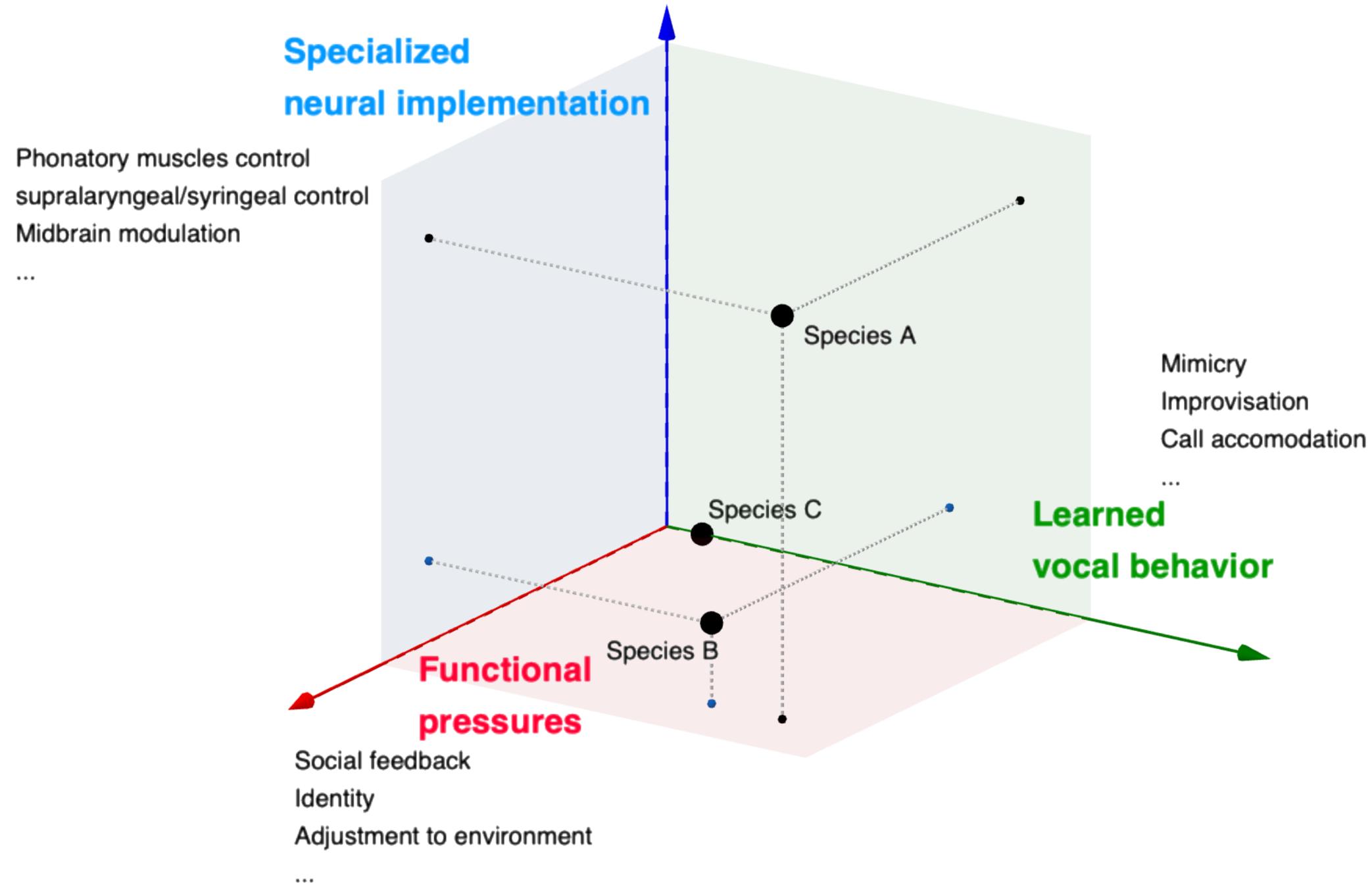
- Vocal learning in primates + connection to rhythmicity
- Consonants, vowels, and features
- Hierarchy and rhythmicity in apes
- Computation of identity + use of transitional probability
- Phonotactics / rule-governed alternations
- LP operations

Vocal learning in primates

- Martins 2020 dissertation: whether a species “has” vocal learning is not a categorical yes/no and it’s not a linear continuum. Building on Janik & Slater 1997:
 - Vocal comprehension learning: associate response to a particular sound
 - Vocal usage learning: learn the context in which a vocalization can be used
 - Vocal production learning: modify vocalization on the basis of experience
 - NB1: mimicry is over-emphasized and only constitutes a subset of VPL
 - NB2: in a lot of cases we just have not asked the question, or asked in the right naturalistic way, whether a particular vocalization is learned or innate

Vocal learning in primates

Martins & Boeckx 2020



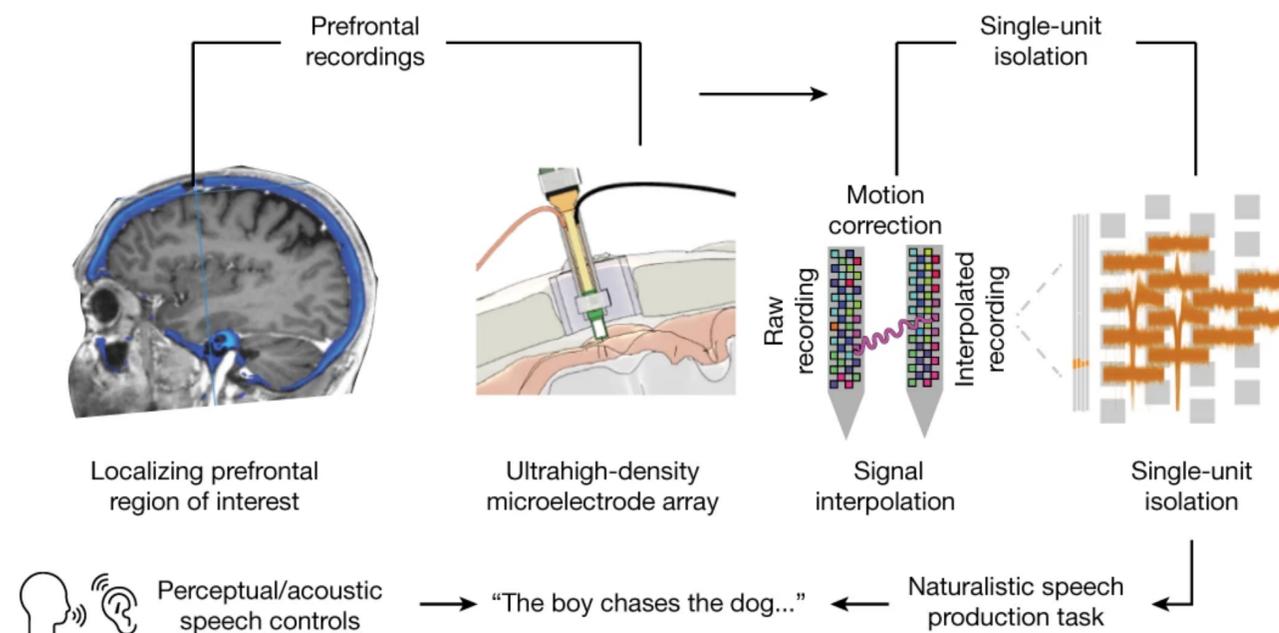
Vocal learning in primates

- Ani Patel hypothesis: vocal (production) learning and nonvocal rhythmic synchronization abilities are neurobiologically connected via strong integration of auditory regions and dorsal premotor region that controls the larynx - serendipitously also more deeply connected auditory cortex to adjacent nonvocal premotor regions.
- Primates turn out to be much better vocal learners than was thought, despite lacking fine laryngeal control (we will come back to the neural part) - reviewed in Martins & Boeckx 2018
 - Orangutans spontaneously learn to whistle (Wich et al. 2009) - more on their vocal behaviors later
 - Some primates will modulate their calls with their hands or with a leaf (Lameira et al. 2011)
 - Chimpanzee repertoire: bigrams with noncompositional meaning, meaning modification/clarification/addition. Ordering of elements can matter. (Girard-Buttoz et al. 2025)
 - Marmoset vocalization development involves acoustic changes not entirely explained by their physical growth and parental/conspecific behaviors affect it (Ghazanfar et al. 2019)
 - Growing literature on turn-taking and volume adjustment behaviors (reviewed in Ghazanfar et al. 2019)
 - In general: primate calls are under voluntary, intentional control and used strategically to facilitate social interactions, and the audience's mental state is taken into account (Cheney & Seyfarth 2018, Ghazanfar et al. 2019, Lameira 2017)

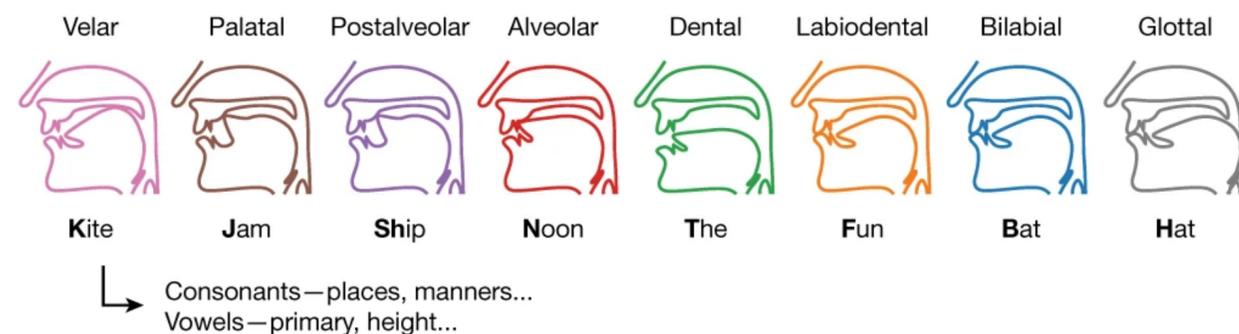
Phonological features

- Mesgarani et al.: much work on single-neuron encoding of particular qualities of speech sounds, in humans and paralleled by animals, e.g. naïve ferrets

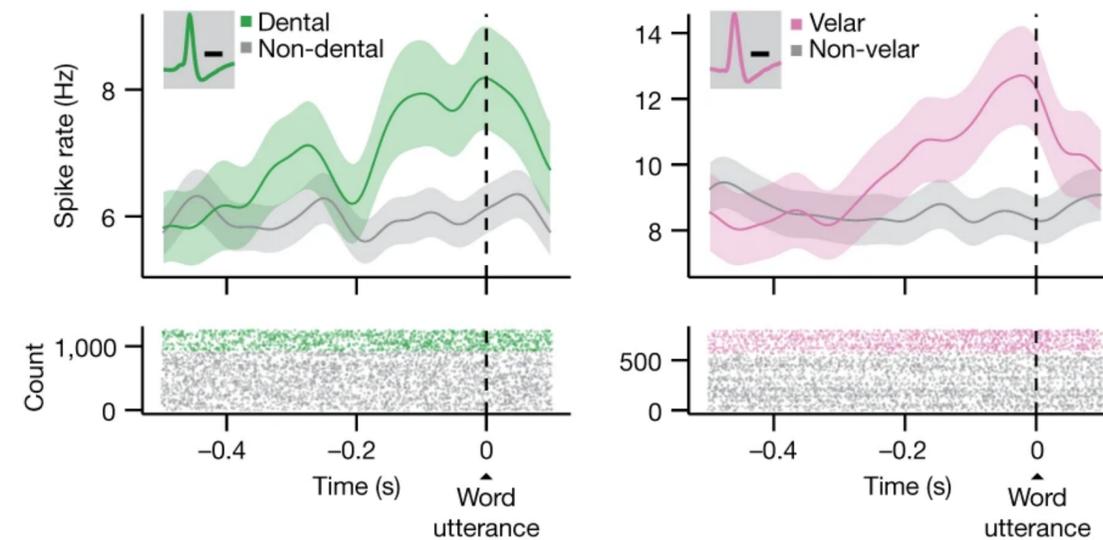
a Ultrahigh-density single-neuronal recordings in the human prefrontal cortex



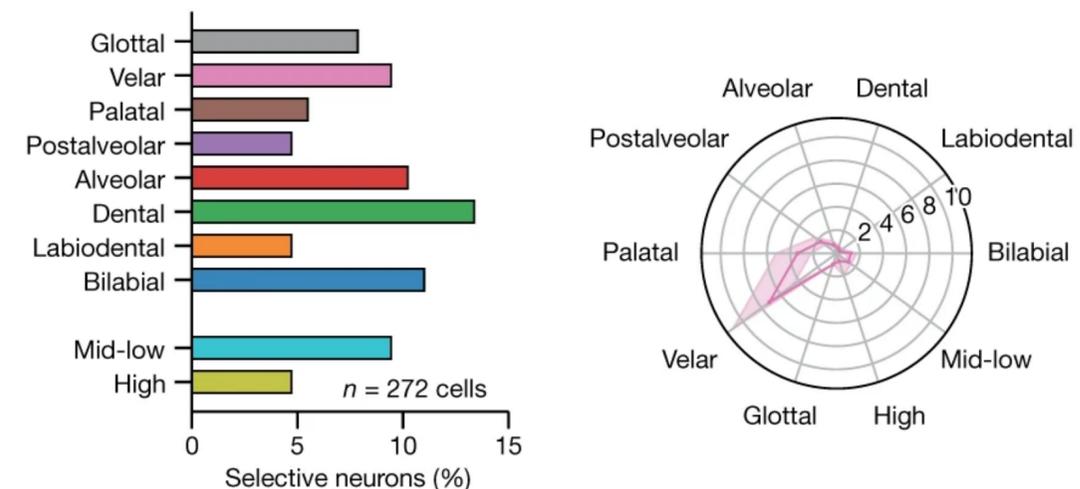
b Tracking the phonetic composition of words during natural speech production



d Single-neuronal activities before word utterance



e Selectivity of single neurons to planned phonemes

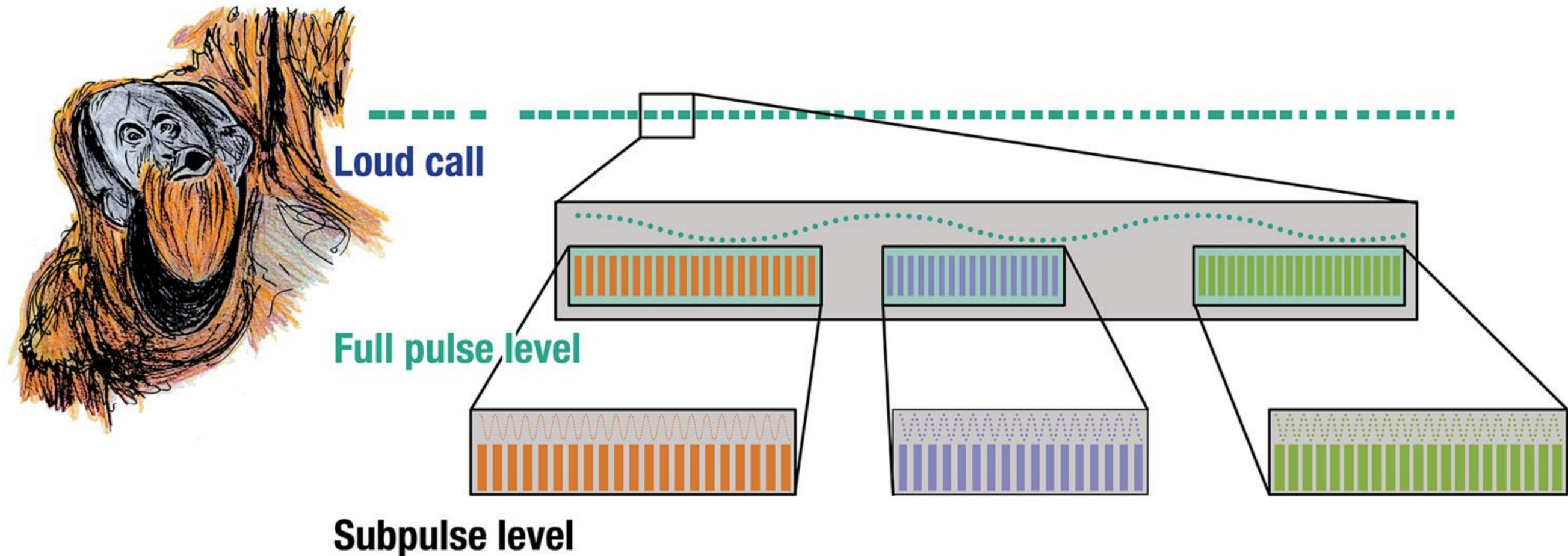


Identity + C/V asymmetry

- Rodents have been tested on ability to extract rules that depend on knowing the classes C and V (de la Mora & Toro 2013)
- Rats outperform humans in certain conditions:
 - BAKASI, KISIBOE, SOEBOEKA vs. BAKISOE, KISABOE, SOEBIKA
 - SIKABOE, BISOEKA, KABISOE vs. KOEKIBA, SASOEKI, BIBASOE
 - Rats will extend to new Cs or Vs; humans don't extend to new Cs
- This kind of study has not been done on primates to my knowledge
- Martins, Samuels & Boeckx 2015: even species like baboons and gelada monkeys that can produce Cs and Vs don't organize their vocalizations such that there are C-V asymmetries. As far as we understand it now, this functional difference is unique to humans:
 - C for lexical info, V for structural/functional info (cf. Toro et al. 2008)
 - Different attentional rhythms (4 Hz vs 8 Hz) for C vs V also key to processing of facial expressions, time, visual scenes in addition to speech

Hierarchy in call sequences

Lameira et al. 2024



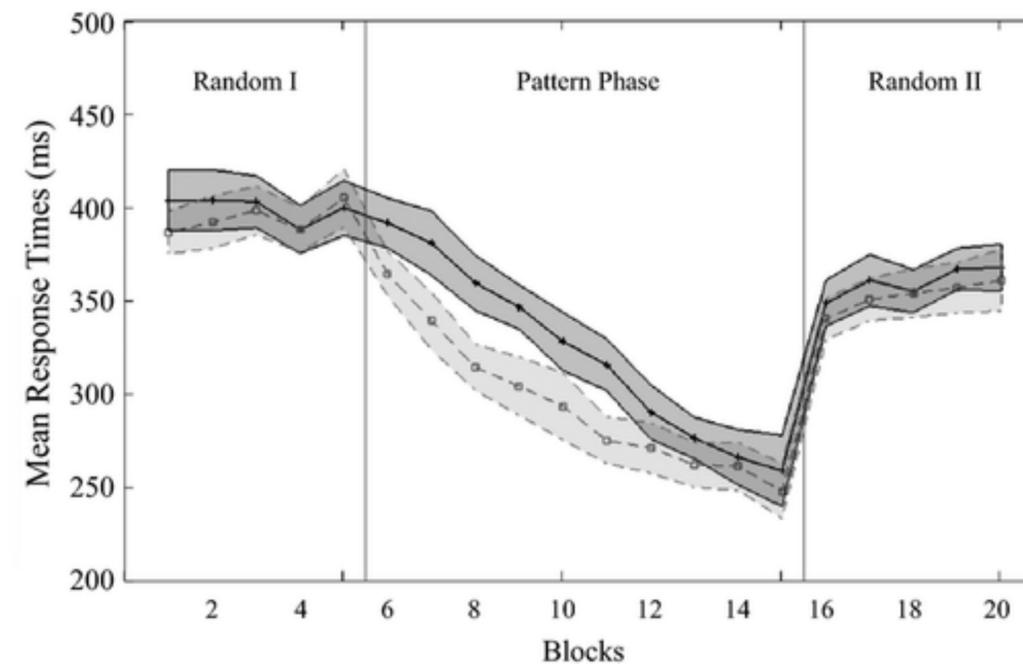
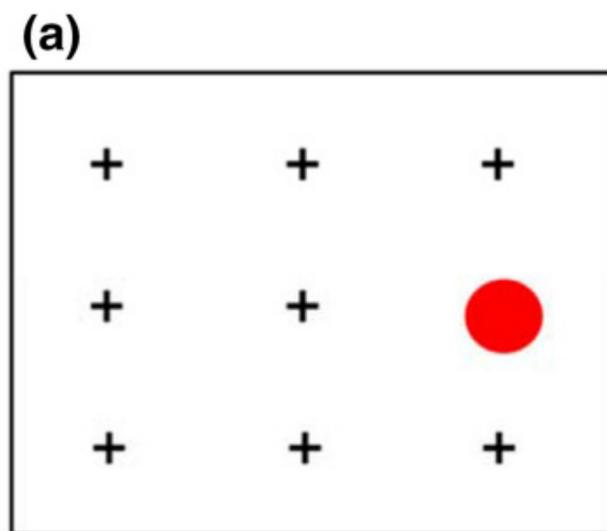
Pulses are composed of 1 of 3 possible subpulses of different tempi repeating at a constant interval

Hierarchy processing in the brain: inferior frontal gyrus & posterior temporal cortex plus hippocampus - in humans and other animals (overview in Scholz et al. 2023)

Transitional probabilities

Minier et al. 2016: First-order TPs ($A \Rightarrow B$) in baboons

Touch patterns of 9 dots, first random then 2000 trials of 3 x 3-touch “words”



Rey et al. 2022: Extended to second-order ($AB \Rightarrow C$) TP

If response time to 3rd touch decreases, they have learned 2nd order TP
(Response time to 2nd touch will not change because 1st is not informative)

A second experiment with a block with switched last element ruled out some alternative interpretations

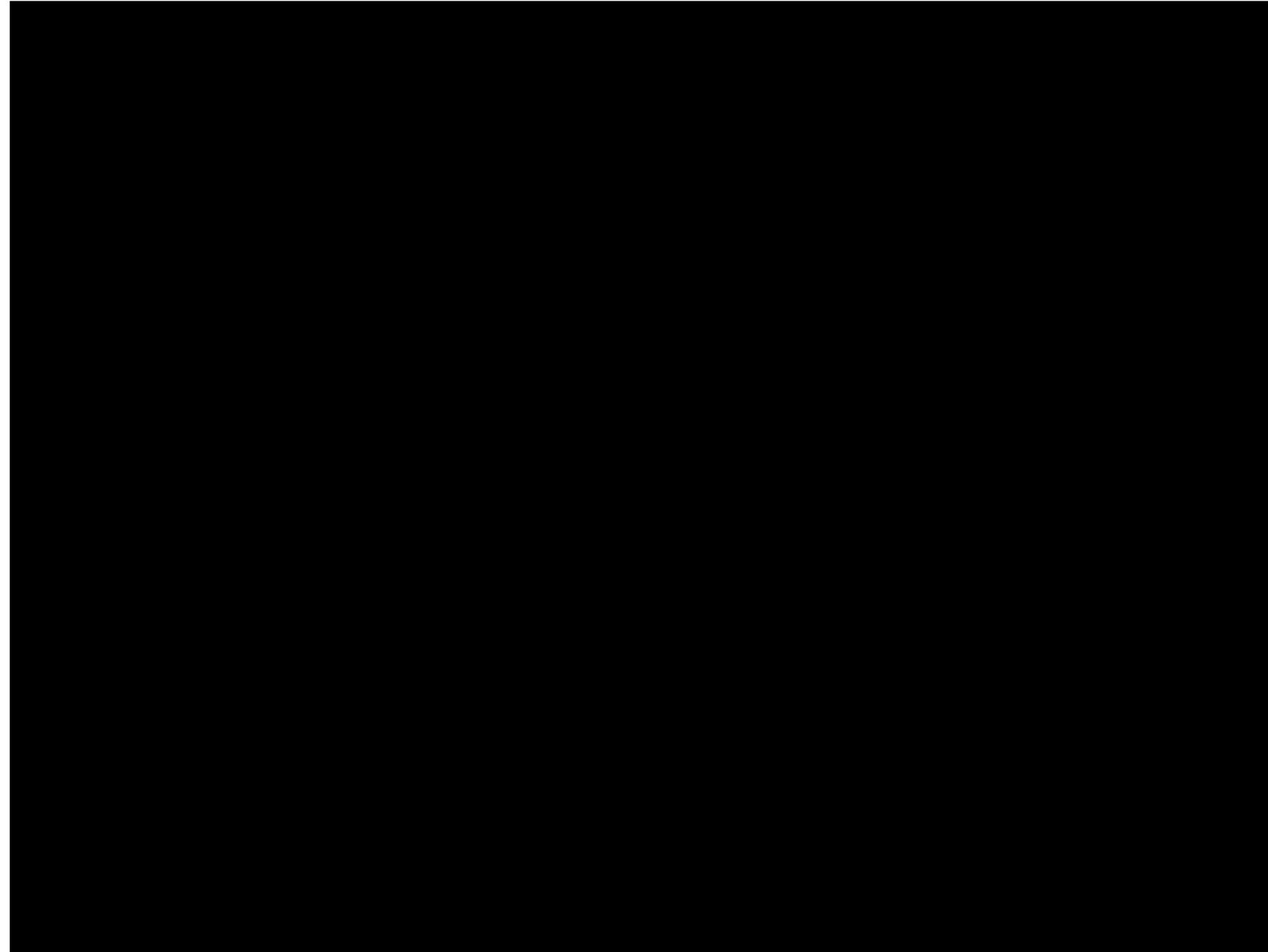
Arbitrary patterns / alternations

- Santolin et al. 2023: rats familiarized to rising, falling, or plateau syllable type - then distinguish Rise vs Fall, Plateau vs Rise
- Watson et al. 2020: Comparison of marmoset, chimp, human learning of adjacent & non-adjacent dependencies (A-B, C-D, A-X-B, C-X-D) concluded all species could recognize these, adding to literature on tamarins, squirrel monkeys, various other primates + birds in both auditory & visual modalities



Search, copy, concatenate, unify

Sequential + collective search strategies (Conway & Christiansen 2001)



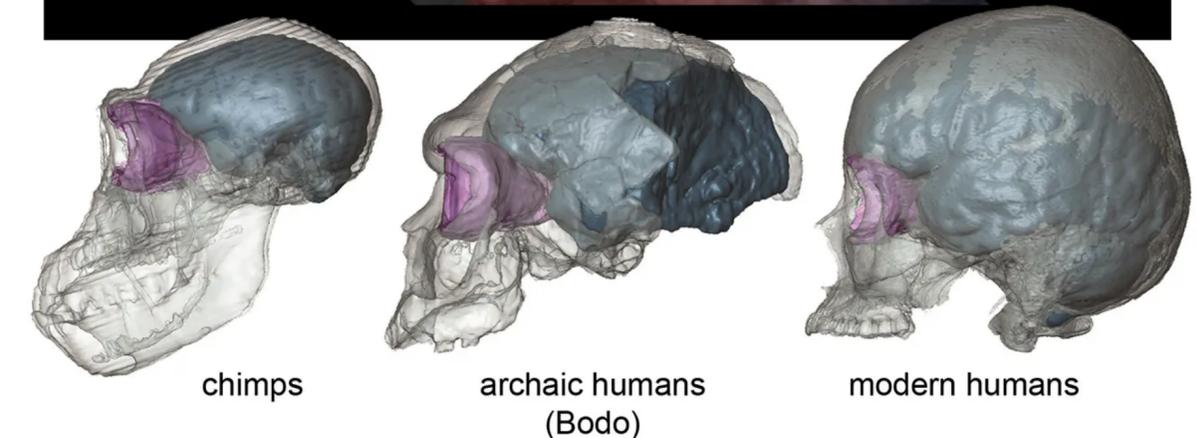
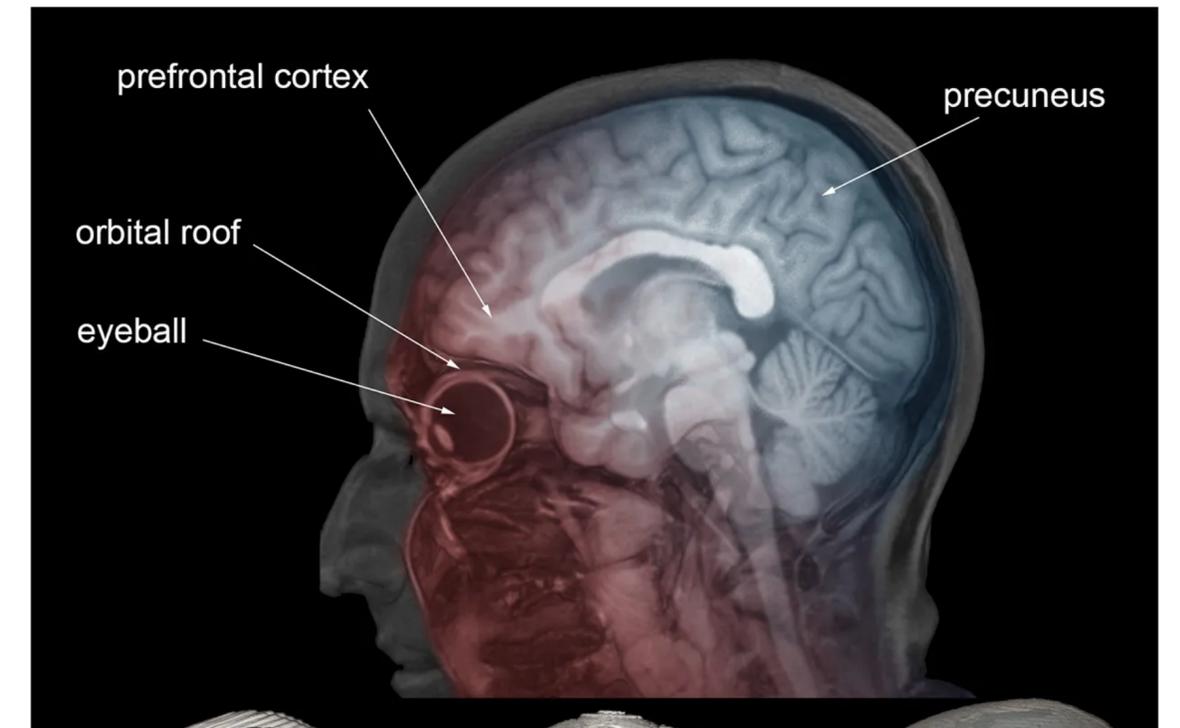
Search, copy, concatenate, unify

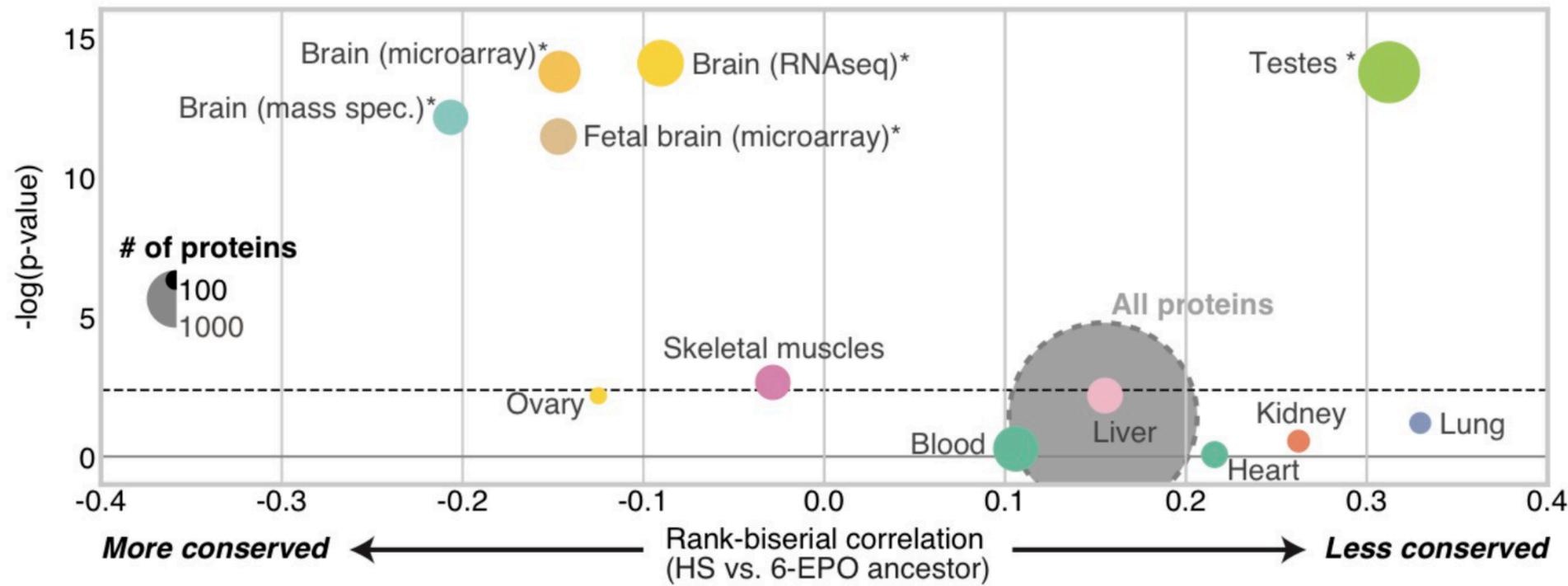
- Morris Halle: “from **memory** to speech and back”
- One driver of searches in phonology is underspecification - are there any parallels to this e.g. in visual perception? Is this forced by the interface with syntax?
- Concatenate, unify, delete - related to our number sense? Primates, rats, and birds can count, add, and subtract small numbers (reviewed in Gallistel & Gelman 2005)
 - Chomsky (2008): Merge can define addition via the recursive successor function (every number N has a unique successor, $N+1$); see also Hiraiwa (2017) on Merge integrating our small precise + large approximate number systems. But concatenate is not Merge!
- Seyfarth et al. 2005: baboon social knowledge is representational, discretely valued, linear-ordered, rule-governed, open-ended, modality-independent, combinatoric/concatenative, propositional, and linearly hierarchical

Part 2: neuroscience & genetics

The human cognitive mosaic

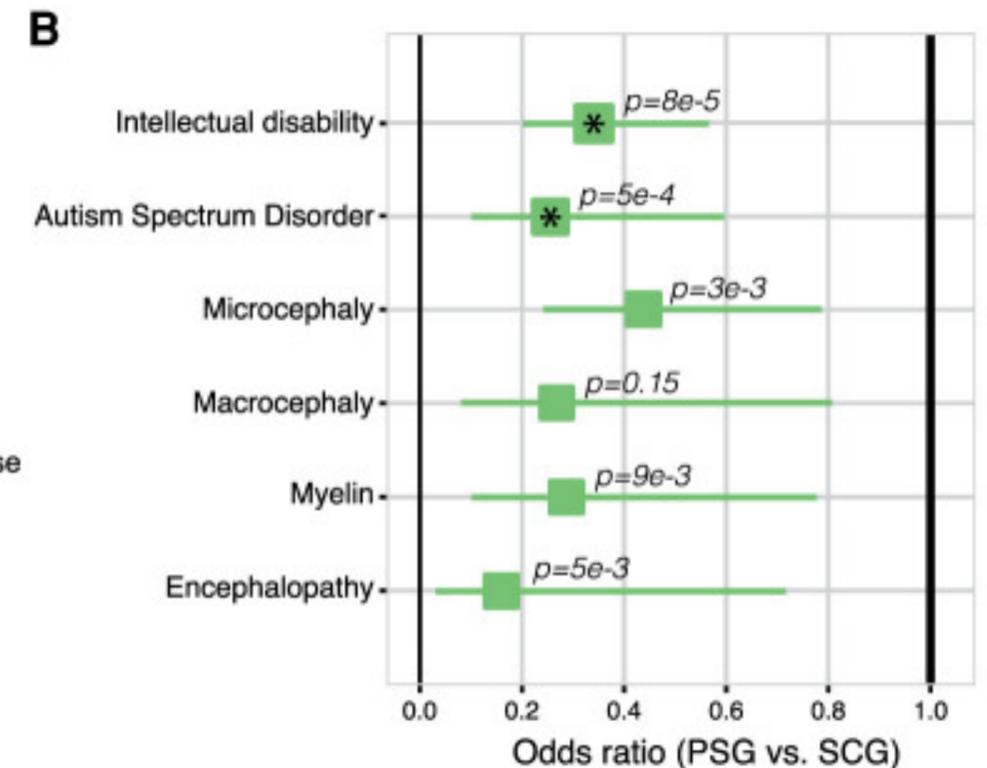
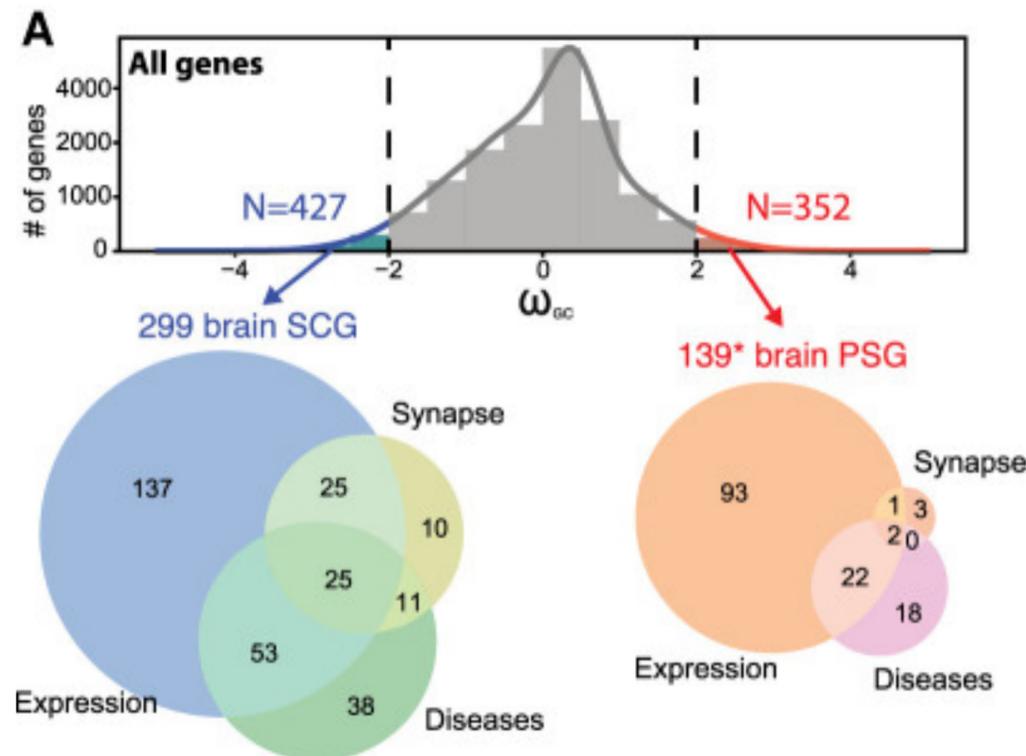
- Anatomically modern humans developed a mosaic of traits at different times
 - Brain expansion
 - Globularization of skull/brain supporting connectivity
 - Facial reduction
 - Vocal learning improvement along different axes
 - Hormonal changes (oxytocin +)
 - Changes in brain metabolism
- Fine-tuning to many genes' expression: different timings, locations, levels (not just changes to their sequences/proteins)



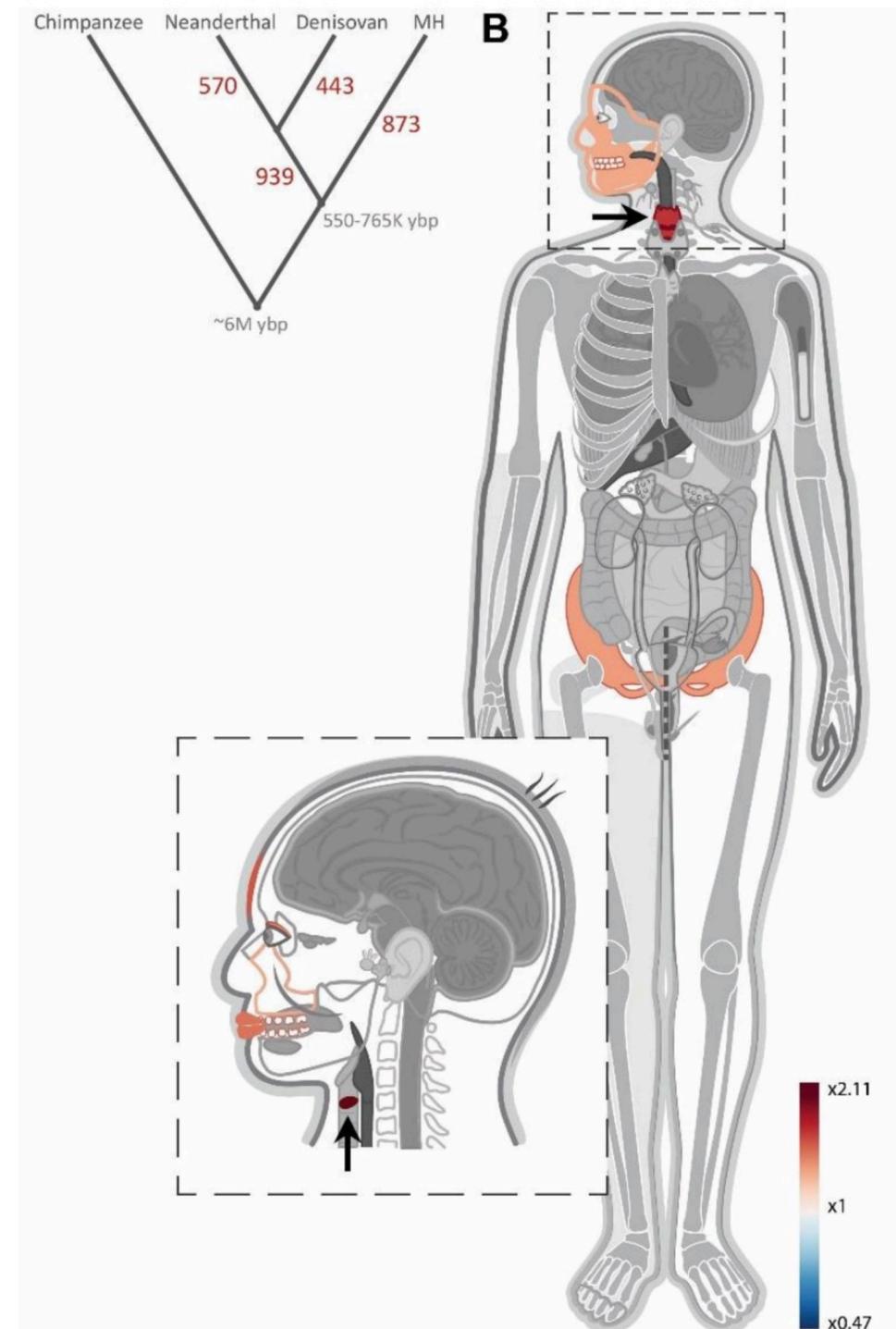


In modern humans vs. archaic humans and non-human primates, brain proteins are the most highly conserved

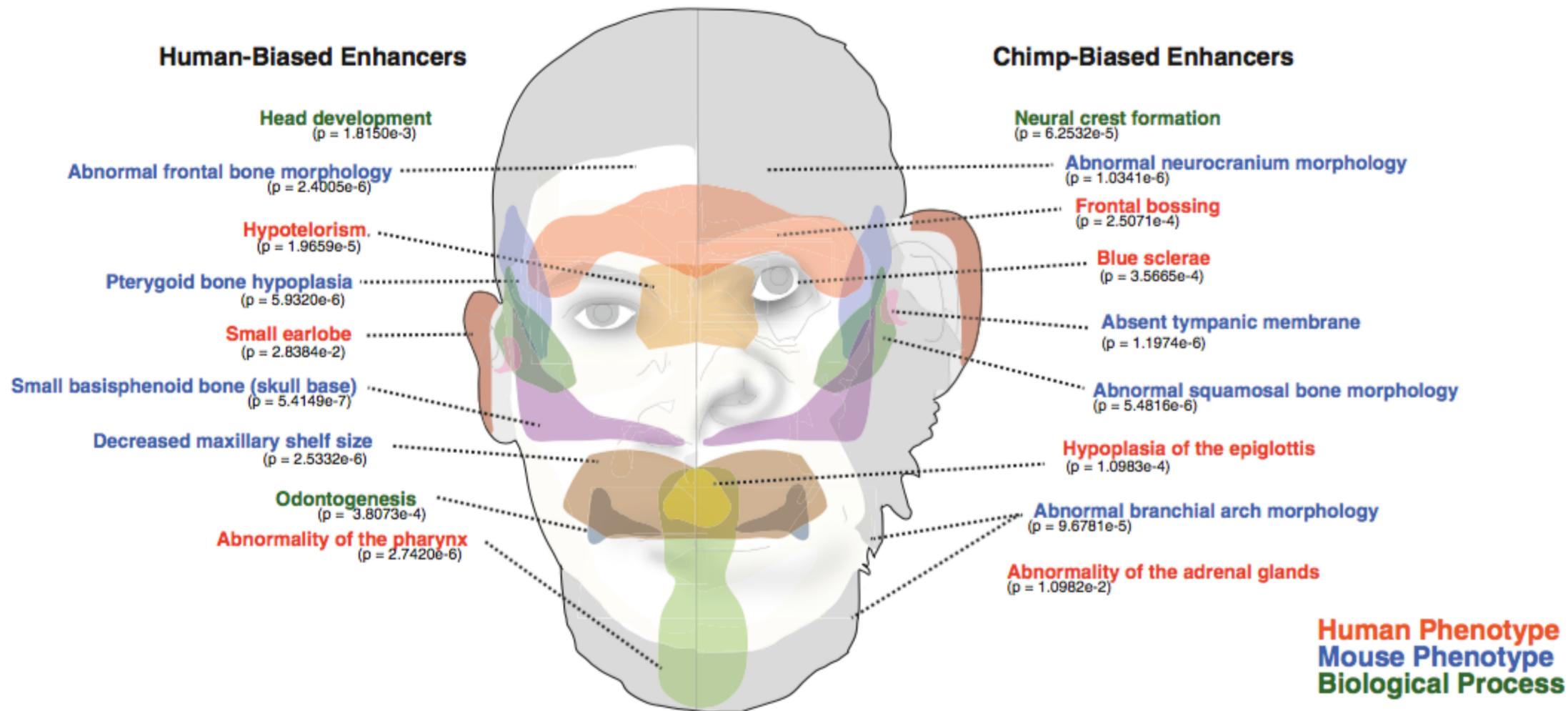
but a subset have been under positive selection, especially related to brain/skull size, fine motor control, social cognition, some disorders



The face and larynx are evolutionary hotspots



Epigenomic divergence in primates



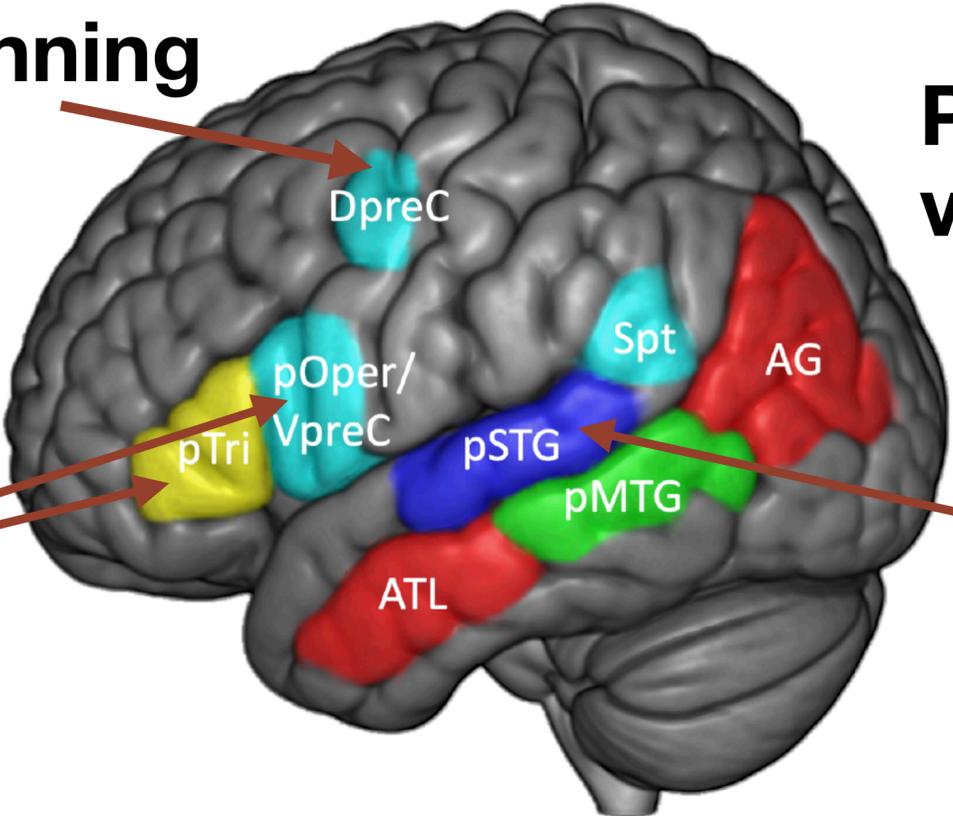
**“Higher order”
prosodic planning**

**Production & Comprehension -
ventral stream**

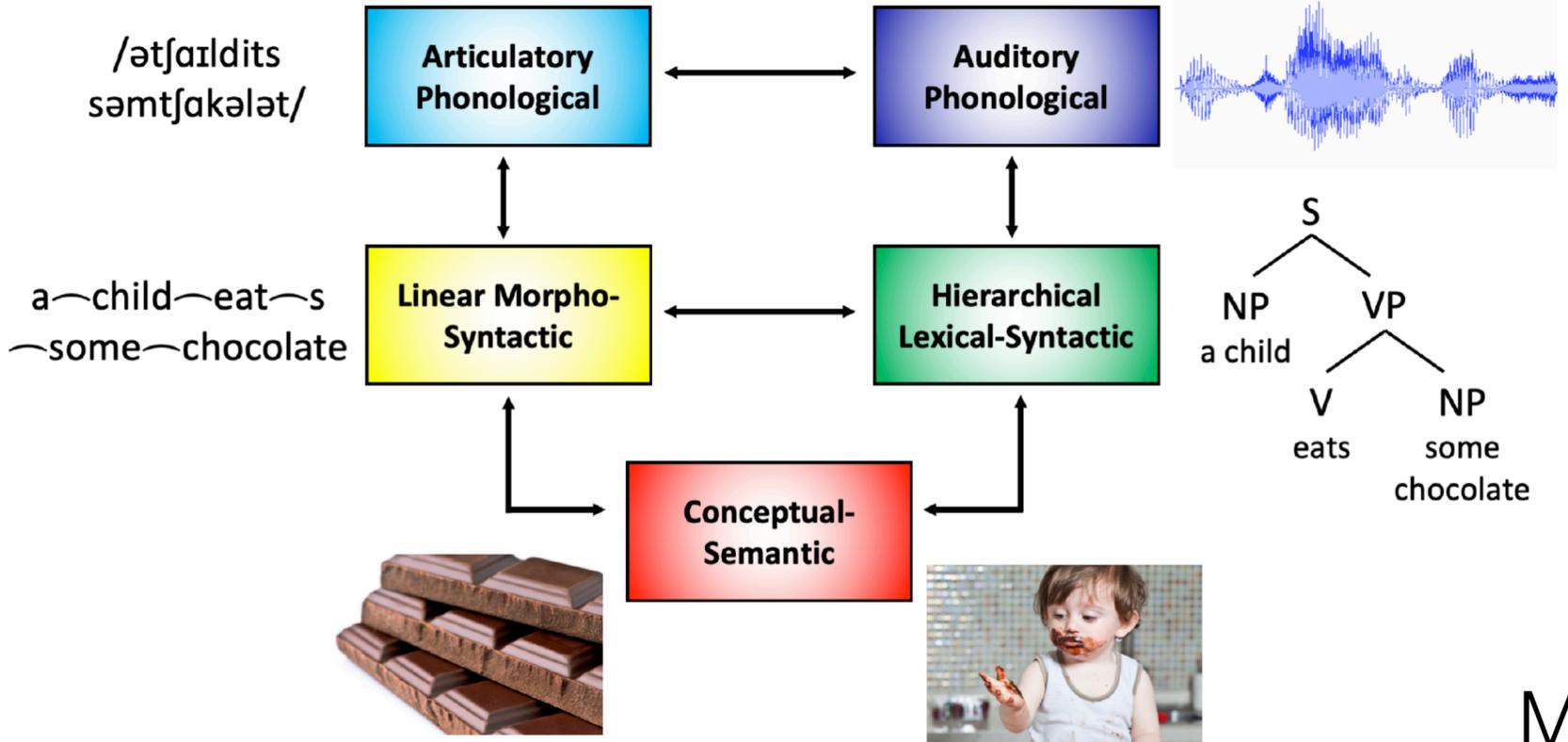
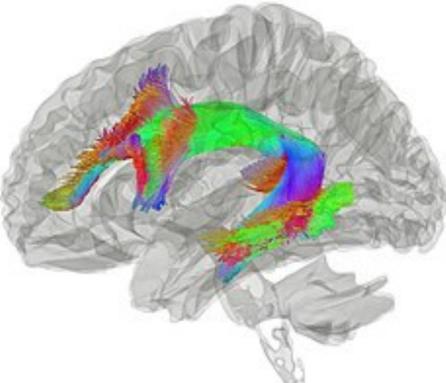
**Production (mostly) -
dorsal stream**

Broca’s area
(inferior frontal gyrus)
“agrammatical aphasia”

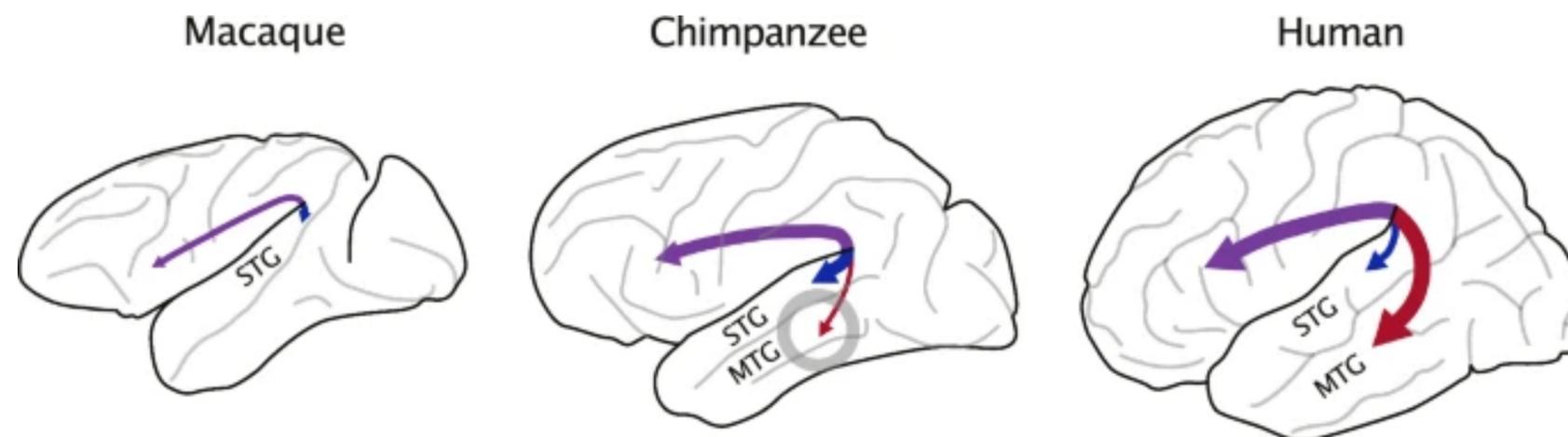
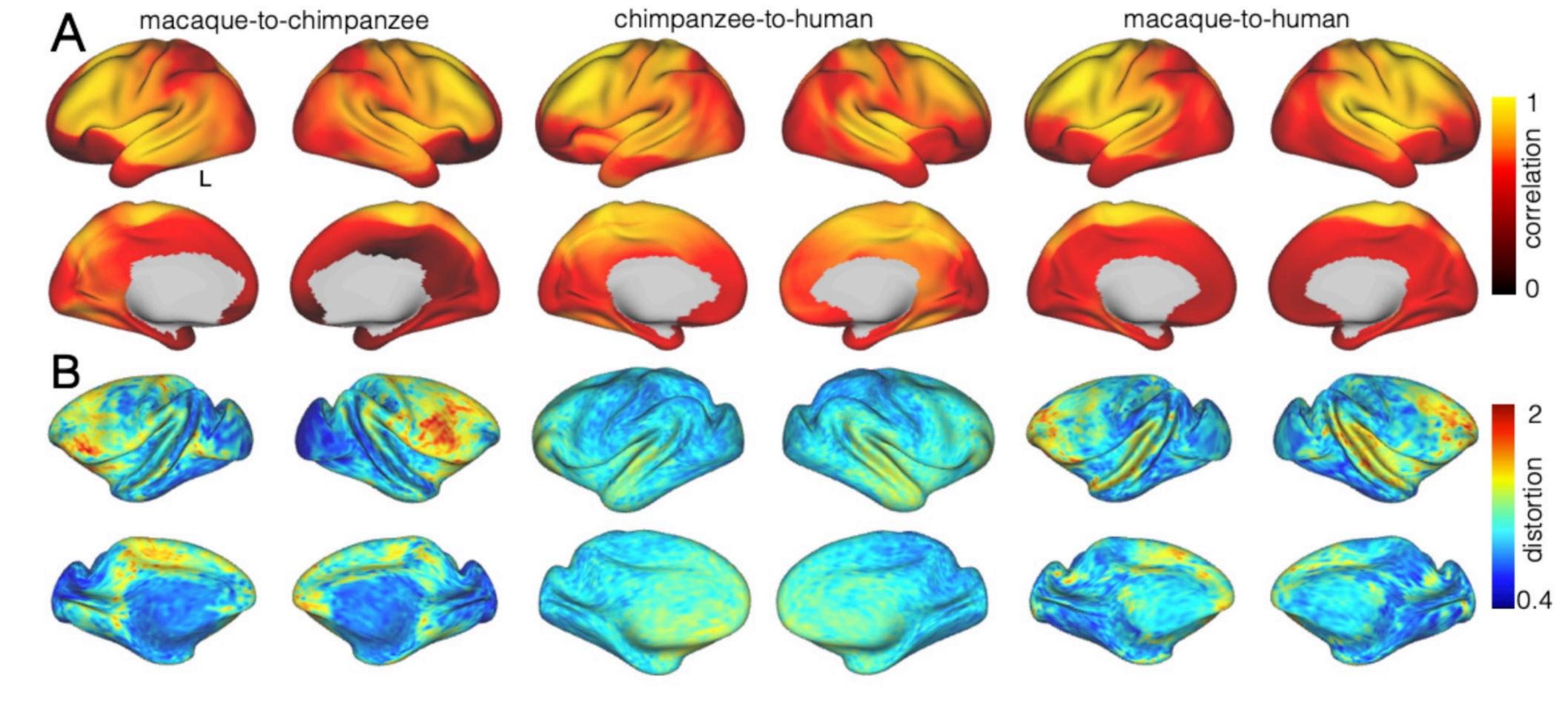
Wernicke’s area
(posterior superior
temporal gyrus)
“fluent aphasia”



**White matter tract
connecting
these two streams =
arcuate fasciculus**



Changes in connectivity to language areas

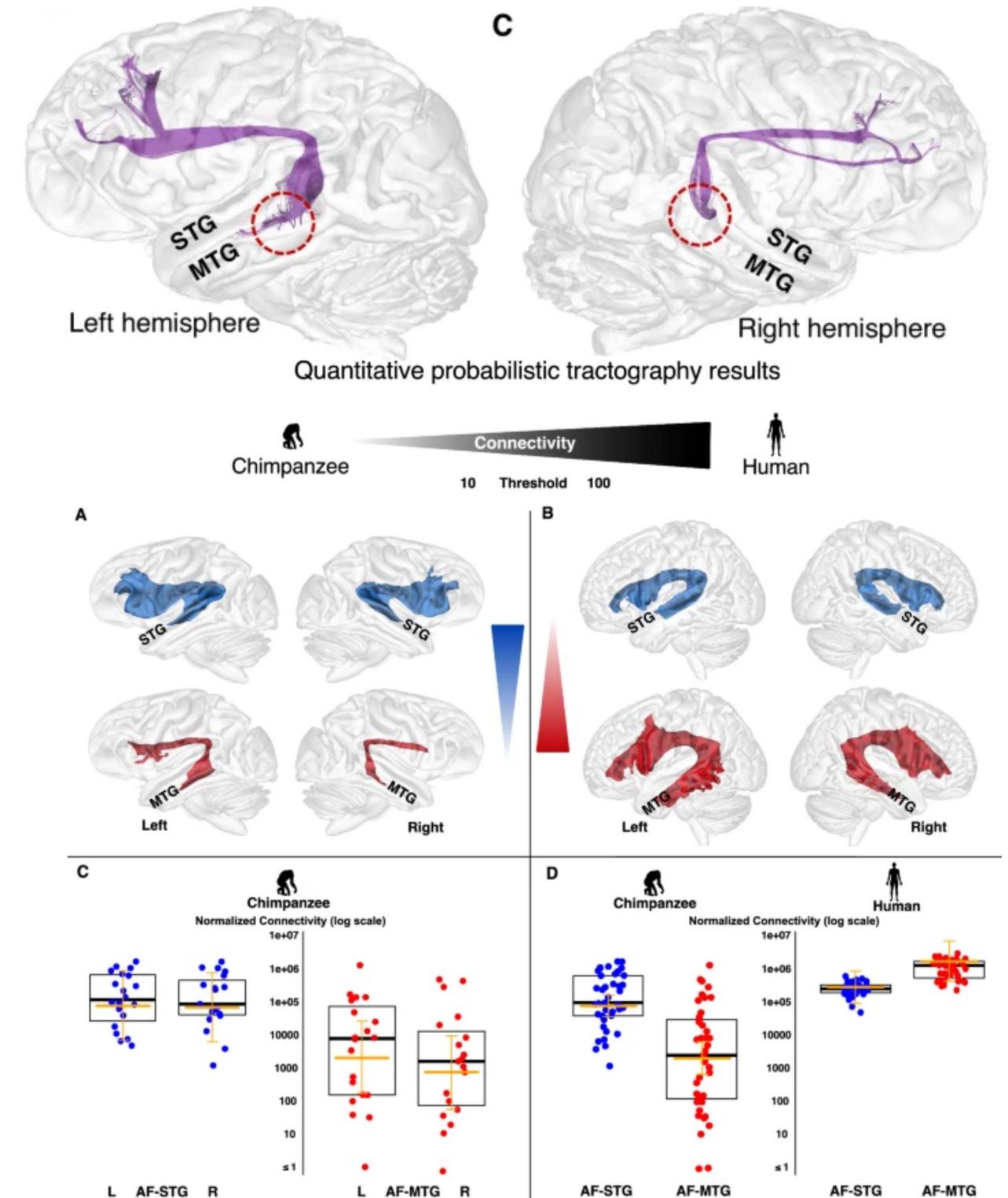


Eichert et al. 2019
Becker et al. 2025

Changes in connectivity to language areas

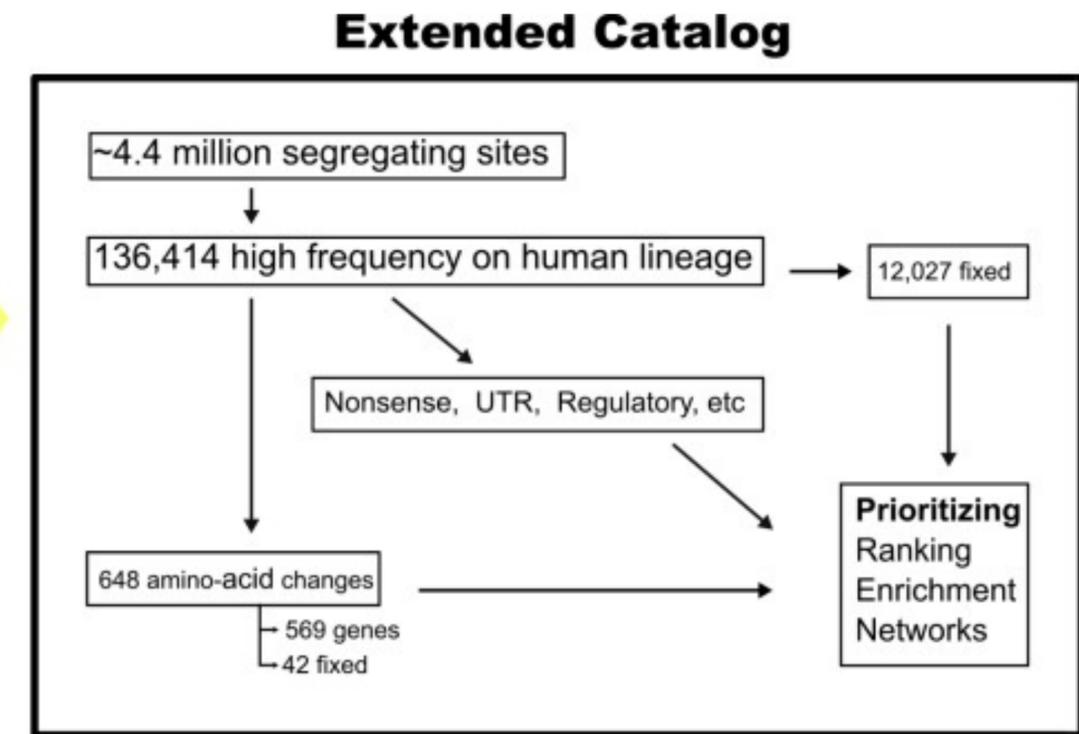
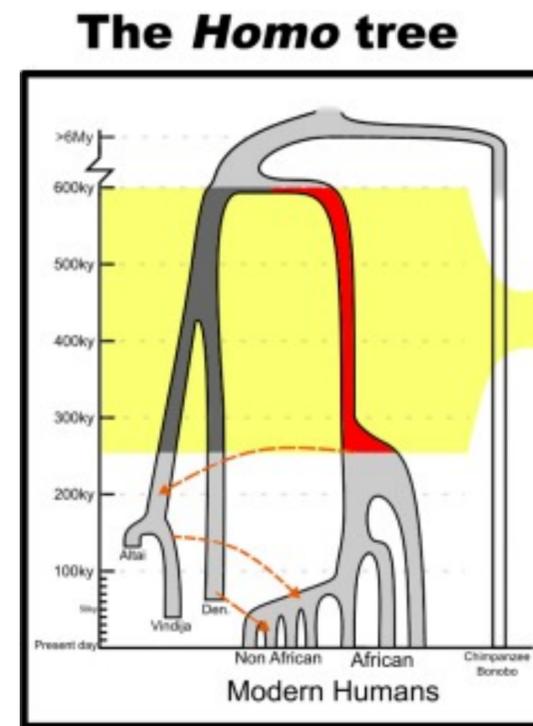
Hecht et al. 2025, Becker et al. 2025

- Arcuate fasciculus is larger and more left-lateralized in humans
- On an individual level, chimps with larger & more left-lateralized AFs produce more attention-getting sounds (raspberries, kisses, grunts) + manual gestures
- It's known that apes have connection between AF and STG that subserves auditory-motor mapping, but was thought they lack connection between AF and MTG subserving semantics/syntax
- Strength & lateralization is stronger in humans, but present especially in zoo-housed chimps



Further micro-level changes

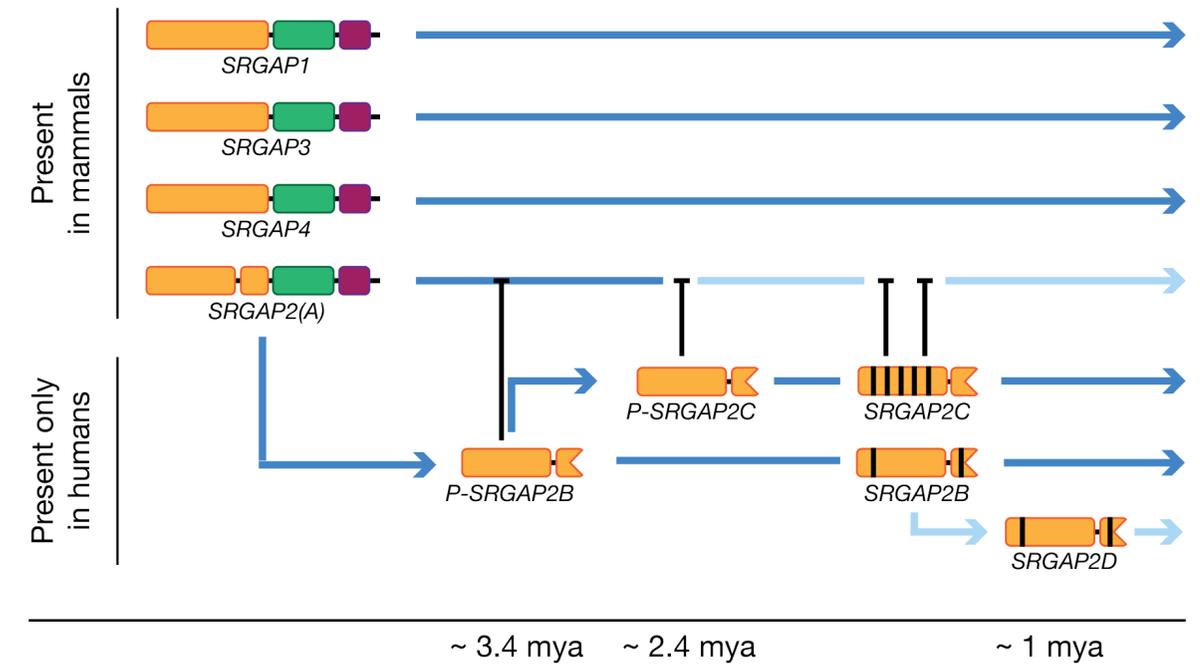
- Peyregne et al. 2017: selective sweep regions
 - SLIT2, ROBO2 - axon guidance, vocal learning, vocabulary growth, dyslexia
 - DCX - neuronal migration, double cortex/lissencephaly
 - Synapses, neuronal membrane
- Kuhlwilm & Boeckx 2019: Cell cycle genes influencing number of neurons; axons, myelin sheath, and synaptic transmission; brain growth; craniofacial morphology



Kuhlwilm & Boeckx 2019

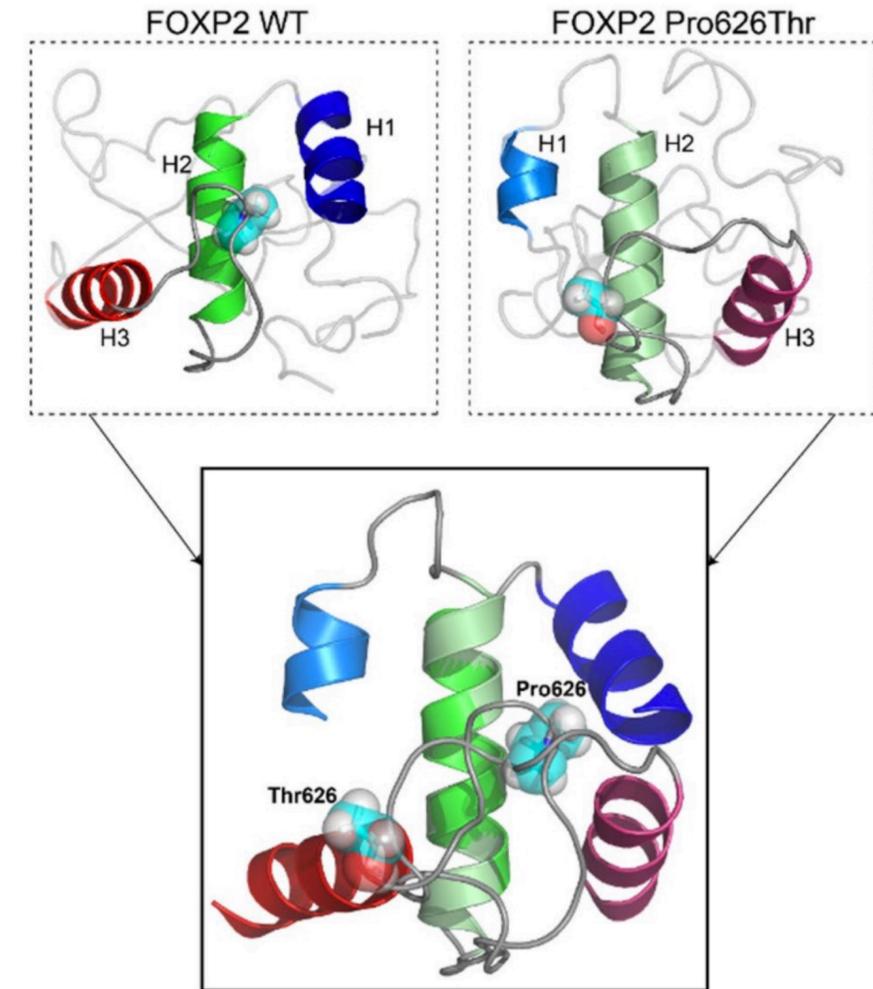
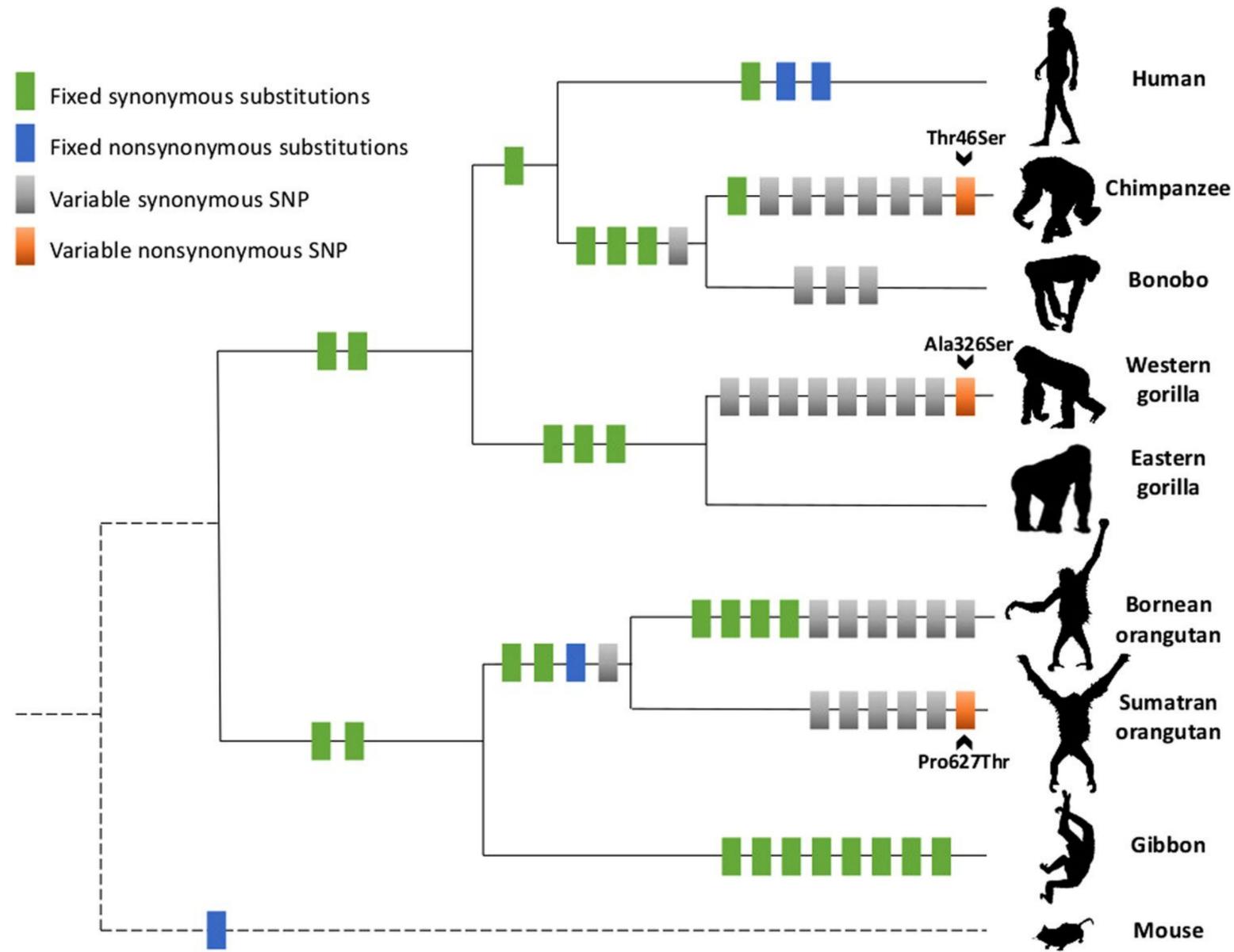
SRGAP2 gene duplication

- SLIT-ROBO GTPase 2 (SRGAP2) highly conserved among mammals
- SRGAP2C paralog w/accumulated mutations found in AMH, Neanderthals, Denisovans
- SRGAP2C inhibits “original” SRGAP2A
- Effect 1: slowing of cortical dendritic development leading to longer period of neuroplasticity via downregulation of SLIT1
- Lower SLIT1 level also in song production area of vocal learning birds
- Effect 2: modulation of axon guidance. Potential effect on cortico-laryngeal connection of vocal learning circuit
- Cortico-syringeal connection in vocal learning birds – convergent evolution 3x
- Effect 3: higher neuronal density



Stone Technology	Lomekwian	Oldowan	
New genus and species	Australopithecus	H. habilis H. erectus	H. neanderthalensis et al.
Brain volume (cc)	475	900	

Foxp2 in orangutans



Summary

- Our understanding of animals' cognitive abilities has advanced substantially, especially when it comes to primates (and setting aside avian controversies)
- Paleogenetics and various genomic analyses are giving much new insight into how anatomically modern humans emerged, and much of the action was certainly related to cognition and probably also speech
- The core representational and operational components of SFLP seem well supported from an evolvability standpoint, even though there remains a fairly large gap between neural/genetic studies and phonology
- What would it take to give us evidence for SFLP over other theories?

Thank you!

Special thanks to Cedric Boeckx & Pedro Martins

References:

