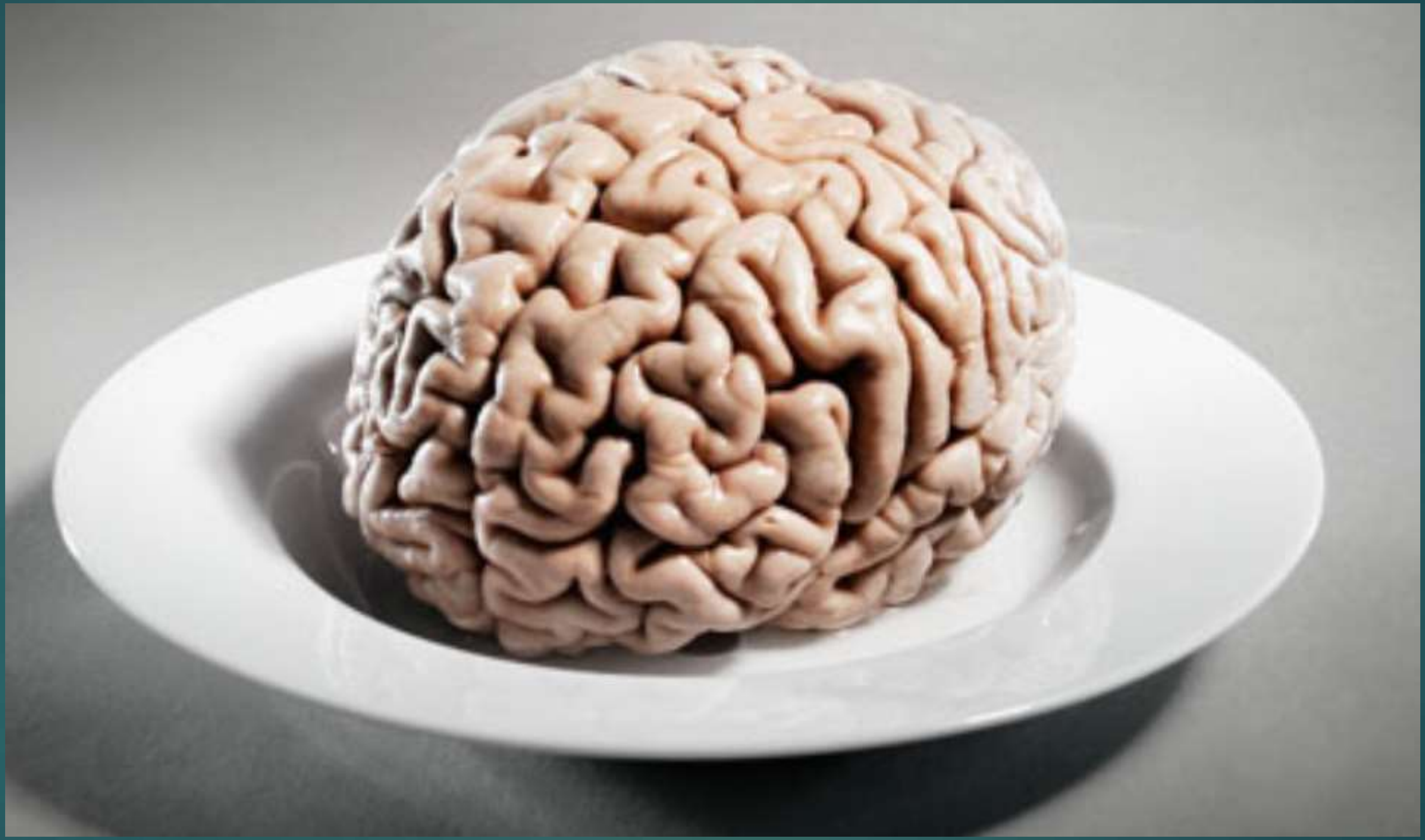
Mind’s Big Bang: Hominid Brain Evolution

CHARLES J. VELLA

FEBRUARY 3, 2016

THANKS TO JOHN S. ALLEN, HENRY J. PETER RALSTON, GEORGE F. STRIEDTER

Humans have a Large Brain



Nothing in biology makes sense except
in the light of evolution.

Theodosius Dobzhansky

Topics to be covered – Jan 26 & Feb 18

- History of theories of brain evolution
- Role of the nose in evolution
- Invertebrate vs vertebrate brain evolution
- Hominid brain evolution
- What’s special about humans
- Human brain size
- Encephalization
- Mosaic evolution: brain reorganization
- Rodent brain as classical model of brain differences
- Evolution of prefrontal & parietal regions
- Regional reorganizations
- White matter connectivity
- Von Economo neurons
- Theories of Causation of Brain Enlargement: Radiator Theory, Smaller Facial Muscles & Bones, Sociality, Environment, Weather, Endurance running, Diet, Genetic mutation
- Evolution of language
- Art and Culture


OCTOBER 9, 2006
www.time.com
ANDREW SULLIVAN ON BLIND FAITH ■ LEO & JACK & MATT & MARTY
TIME
HOW WE BECAME HUMAN
Chimps and humans share almost 99% of their DNA. New discoveries reveal how we can be so alike—and yet so different

The Darwinian Theory of Evolution – “Descent with Modification”

- There are **inherited differences** between individuals
- These include random variations
- Resources are not unlimited
- Some individuals will flourish more than others and produce more offspring
- Natural selection occurs if a population changes over generations because of this

Evolutionary survival is based on the selective advantages that particular observable characteristics or behaviors confer to some individuals within a given environmental context.

If the target of selection is adaptive, then genes replicate and produce a long line of descendants.

Brains, like genes, are not the direct targets of selection. Behavior is the target of selection.

Darwin & Huxley vs. Owen: Evolution in Human Brains

- Darwin never wrote much about the brain, but Darwin's nemesis, Richard Owen, tried in 1861 to protect humans from Darwin's threatening ideas by arguing that human brains differ fundamentally from those of other apes.
- This argument provoked a spirited attack by Darwin's "bulldog," Thomas H. Huxley.
- Darwin did not comment publicly on this controversy, but for the second edition of his Descent of Man, Darwin asked Huxley to write an essay "on the resemblances and differences in the structure and the development of the brain in man and apes."

Huxley: brains are like those of apes

- In this chapter, Huxley laid to rest Richard Owen's earlier argument that human brains are outliers among mammalian brains.
- Instead, Huxley argued that our brains resemble the brains of other apes in all fundamental respects.
- He even downplayed the greater size of human brains, noting that brain size is quite variable among humans.
- Importantly, Huxley did not deny that our brains must somehow differ from the brains of other apes, for he could see no other way to explain our unique cognitive capacities, most notably language.
- This essay was a forceful attack on Owen's argument and showed convincingly that human brains are like fairly typical ape brains, although larger.
- Thus the Darwinians began to contemplate evolving brains.

Changing views of neuroanatomy and brain evolution

- Although brain studies began in ancient Egypt, speculations on vertebrate brain evolution occurred only much later, after the publication of Darwin's *Origin of Species* in 1859.

- Subsequently, views of brain evolution have been shaped by a complex interplay of theory and technique.

- Darwin's theory allowed the variation in brain size and complexity to be re-interpreted within an evolutionary context, albeit an erroneous pre-Darwinian context based on scala naturae (great chain of being with humans at the pinnacle).

R. Glenn Northcutt

Brain evolution theory

- With the development of histological techniques, research shifted to descriptions of cellular structure, cellular aggregates and their putative interconnections. In spite of these technical advances, brain evolution continued to be viewed within the context of scala naturae.

- Following the publication of *The Comparative Anatomy of the Nervous System of Vertebrates* by Ariëns Kappers, Huber, and Crosby in 1936, there followed a period of stasis
- Then biological views of evolution were radically altered by the confluence of genetics, paleontology, and systematics, termed the Evolutionary Synthesis. (J. Huxley, Ronald Fisher, Theodosius Dobzhansky, J. B. S. Haldane, Ernst Mayr. (Check Ian Tattersall – *Fossil Trail*)

Brain evolution theory

- Against this background, the development of new experimental techniques for establishing neural connections resulted in a new flowering of comparative neuroanatomy.

- While comparative descriptive and experimental studies of brain organization continue, the additions of embryology and genetics is fueling a new renaissance that promises to increase our understanding of brain evolution and its genetic basis.

3 ways brains evolve: natural & sexual selection; mutation

- Natural selection: Organisms who reproduce successfully pass more genes on to the next generation.
  - Natural selection increases or decreases the frequency of genes that already exist. It cannot create change without novel material that provides an evolutionary advantage
- Sexual selection: sexual characteristic can give you mating & reproductive advantage
- Mutation: Change in the chemical make-up of a gene (DNA) that produce small effect on anatomy and physiology; caused by: toxins, natural or artificial radiation, errors during duplication and cell division; mutations are only rarely "good"

Some theories to account for brain expansion in humans

1. Your brain is a Swiss Army knife

2. Your brain is a scheming despot

3. Your brain is a culture medium

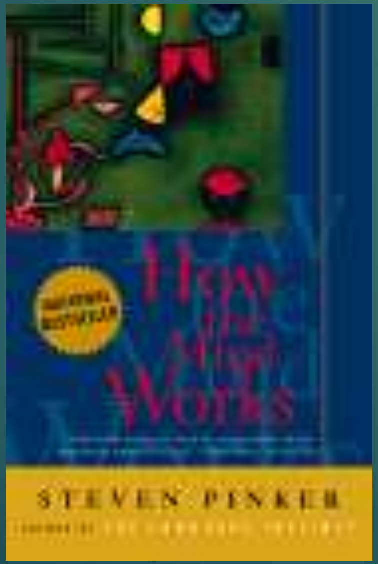
4. Your brain is a Las Vegas hotel suite

Your brain is a Swiss Army knife

- Your brain is a <u>collection of specialized cognitive devices that are designed to solve specific problems</u>

- This is the <u>predominant view of evolutionary psychologists</u>

- Brain processes, once developed, <u>may be co-opted for other means</u>



Steven Pinker has popularized this view

Your brain is a scheming despot: Social Machiavellianism

- Primates are distinguished from all other animals by their scheming, Machiavellian politicking, thieving, lying and murderous deception.
- Much of this notion is driven by observations of primate social behavior
- There are no better schemers than us
- Theory is that our great cerebral hemispheres (especially perhaps the frontal lobes) have evolved help us with 'social intelligence' – a euphemism for Machiavellian scheming.

Niccolo Machiavelli
"No enterprise is more likely to succeed than one concealed from the enemy until it is ripe for execution."

Your brain as a culture medium

- At some point in our evolutionary history, we crossed a threshold when we had enough cerebral 'stuff' to produce culture.
- Culture can be thought of as a kind of unit of mind that is independent of bodies (meme: an idea, behavior, or style that spreads from person to person within a culture. Supporters of the concept regard memes as cultural analogues to genes in that they self-replicate, mutate, and respond to selective pressures).
- Culture and the brains that support it entered a kind of positive feedback cycle – brains better at propagating memes succeeded.

E. O. Wilson – originator of sociobiology, the forerunner of evolutionary psychology

Your brain as a Las Vegas hotel suite

Geoffrey Miller
"*The Mating Mind*"

Sexual selection

- It's no good surviving if you don't have sex
- To have sex you need to attract a mate
- If there is variability in mating success, then the traits that promote that success will be strongly selected for
- What if many of the things that we consider to be uniquely human were sexual ornaments like the tail of the peacock?
- This would mean that such traits would not have to have direct relationships with finding fruit or fleeing lions

Probably not sexual selection

- Geoffrey Miller, an evolutionary psychologist, suggested that big brains are a result of sexual selection: The large size of the brain evolved because mates (in most cases females) favored a mate (in most cases males) with increased abilities to produce such aspects of culture as art, creativity, storytelling, humor, wit, music, fantasy, and morality

- However, Miller's hypothesis is not supported by:
  - the actual development of the human brain, which does not display the characteristics of a sexually selected trait.
  - lack of sexual dimorphism
  - actual growth of the brain. Male brains do not significantly differ from female brains
  - And if the brain were a sexually selected feature, it would become more prominent after puberty. This isn't the case
  - The human brain weighs about 25% of its adult weight at birth, and it doubles in weight in about 6 months. At puberty, there isn't another of these types of gains. The brain completes most of its development within the first few years of life.

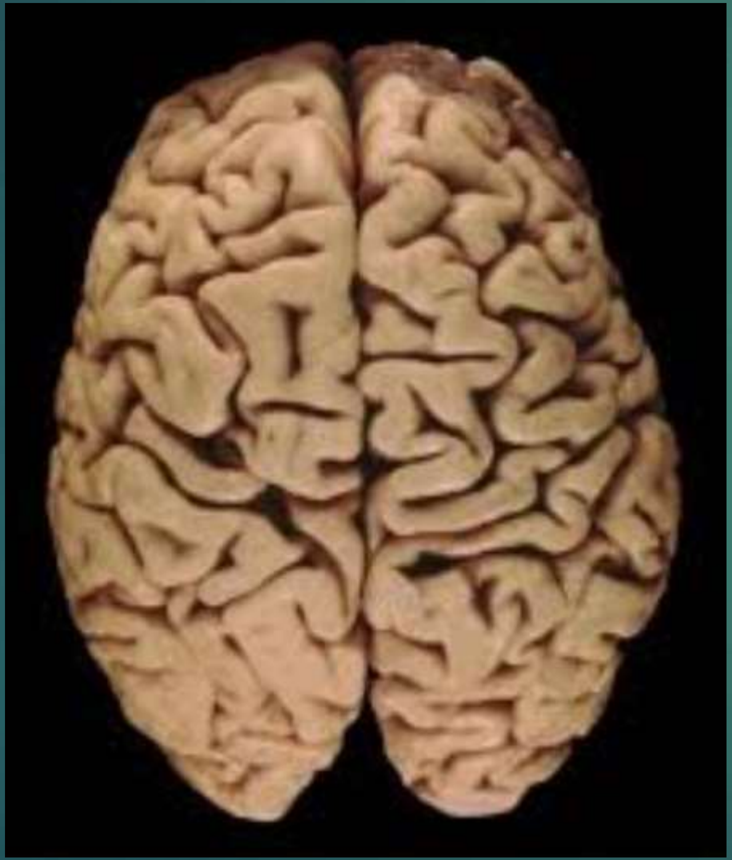
Spandrels (not everything is produced by natural selection): Stephen Jay Gould

Spandrels or exaptations are features of an organism arising as byproducts, a shift in function, that originally have no clear benefit for the organism's fitness and survival, but eventually serve the organism, i.e. changes in the brain may not have been produced by natural selection, but were a side effect.

Spandrels/exaptations are **side effects** of natural selection

Current Evolutionary Neuroanatomy Methodology: structure of the brain

Macrostructure



Methods

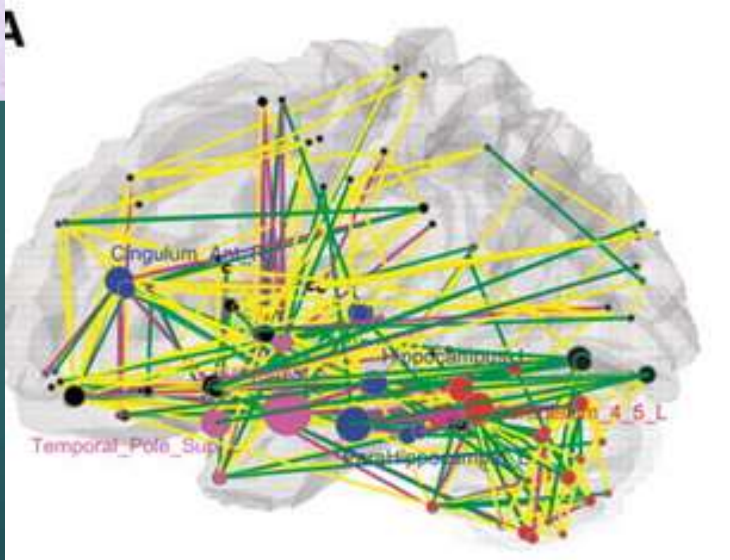
- Gross observation
- Dissection
- Magnetic Resonance imaging (MRI)
- Geometric morphometrics
- Voxel-based morphometry
- Endocasts

Features

- Study of brain surface anatomy
- Shape analysis
- Gross anatomical scale
- Limited to large regions

Methodology - structure of the brain 2

Microstructure



Methods:

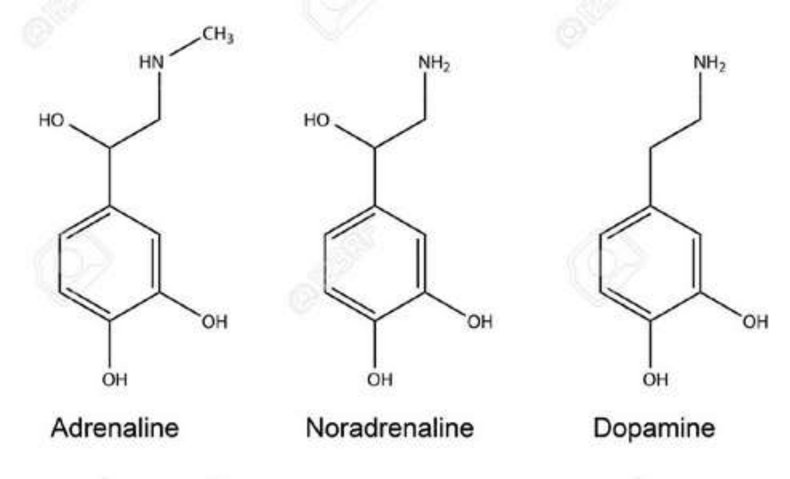
- Histology
- Diffusion Tensor Imaging

Features:

- Finer anatomical scale reveals underlying cellular structure of brain regions
- Can show connectivity between regions

Methodology: Molecular biology

Neurotransmitters, receptors and other molecules

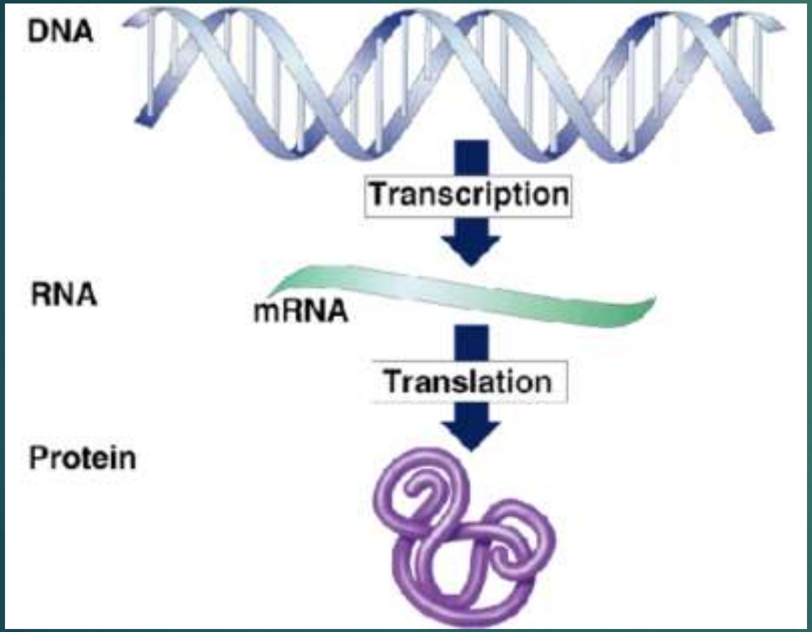


Methods
- Immunohistochemistry
- Western blotting
- Proteomics

Features
- Use antibodies to stain neurons or glia
- Identify specific cell types
- Can identify cells that use specific neurotransmitters

Methodology: Molecular biology 2

Genetics



Methods:

- Comparative genomics
- RNA-sequencing
- PCR
- Microarray
- Transgenic/knockout organisms

Features:

- Allow for comparison of genetic material
- Can show changes in gene expression
- Reveals molecular differences in development

Function of the brain: buffer vs. environmental variability

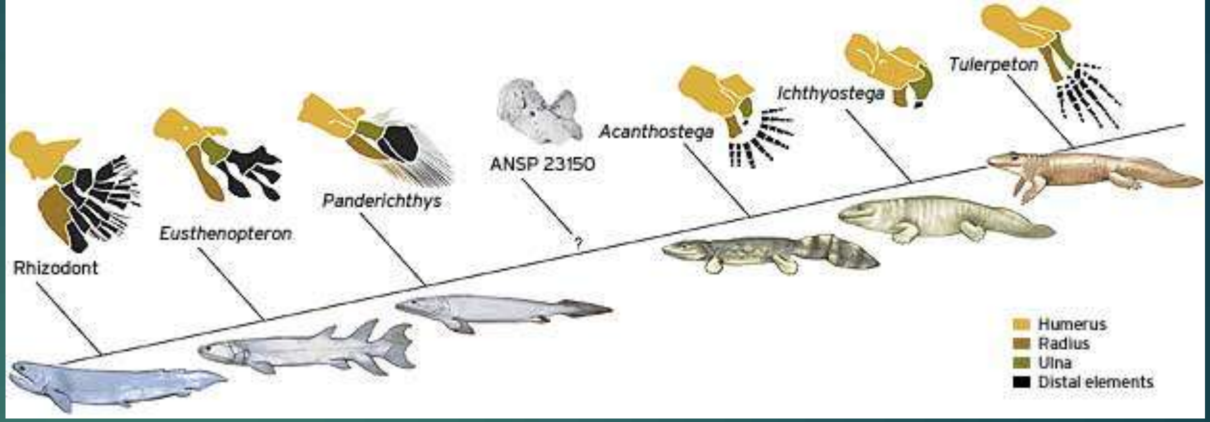
- Main function of a brain is to protect against environmental variability through the use of memory and cognitive strategies that will enable an organism to find the resources necessary to survive, esp. during periods of scarcity.

Function of the brain 2

- Lots of ideas why brain size increased.

- They can be boiled down to idea that the language-mediated, increasingly complex social and technological world occupied by genus *Homo* place a premium on both storage capacity and behavioral flexibility in response to quickly shifting environmental conditions.

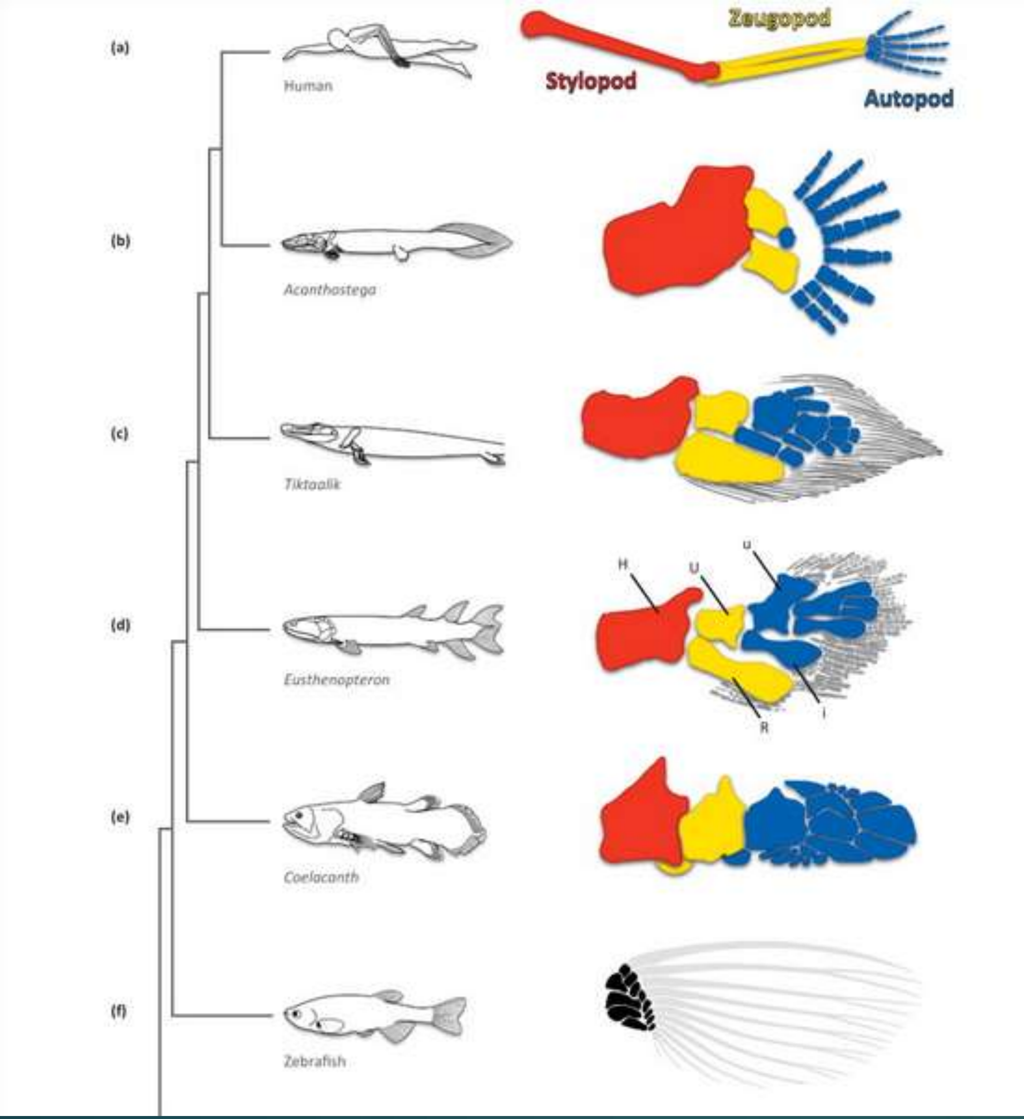
The Role of Constraint



- Natural selection can only work on pre-existing variation
  - Because of the incremental nature of this variation, the existing structures and behaviors of an organism constrain the possible solutions to an adaptive problem.

- Nature rarely starts from scratch
  - It is far easier to tweak an existing system.

Evolution is conservative – Tetrapods: from fish fin to 5 digits.



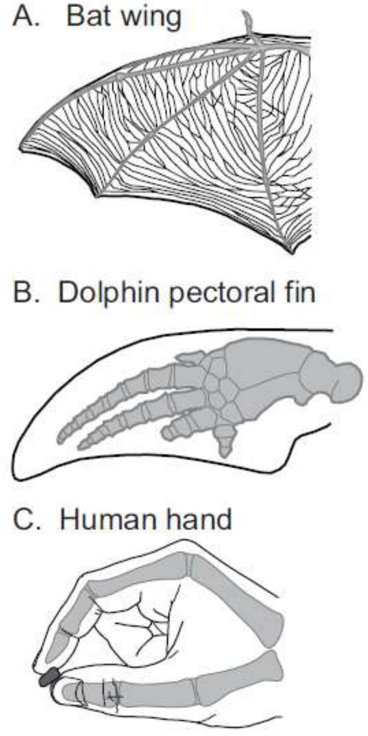


FIGURE 6.4 The wing of a bat (*A*), pectoral fin of a dolphin (*B*), and hand of a human (*C*) are examples of homologous morphological structures that have undergone remarkable specialization in different lineages and serve different functions. Although they are used for very different purposes, they are organized around the same basic skeletal frame (gray).

The Role of Constraint

- Exaptation
  - When faced with adaptive problems, existing structures commonly evolve new functions, i.e. feathers – from thermal regulation to flight
    - Brain exaptation
      - Hippocampus – smell memory and spatial maps co-opted to declarative memory formation
    - Cognitive exaptation
      - Facial recognition – from mate recognition and assessment to complex social communication

Neural System: Not much has changed in the last billion years…

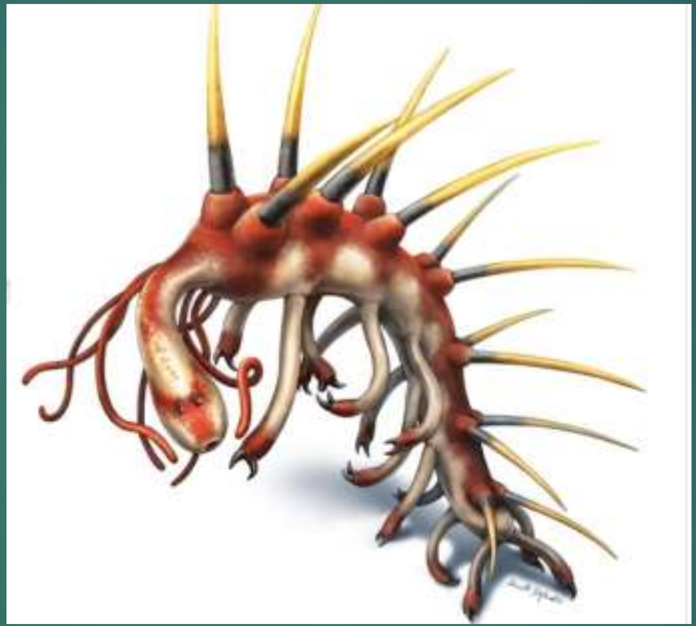
- Find food; avoid predation; in a changing environment
- Basic input-output organization
- Sensory apparatus
- Movement (effector) apparatus
- More or less complex links between perception and action
- Closeness of mouth & brain: brain arose as the gut's way of controlling intake; still have genes that control both formation of gut & forebrain
- Slightly elaborated in humans…

Ediacaran period (635 and 542 MYA): Metazoan animals that were bags. No mouth, no gut and no anus. No enemies.

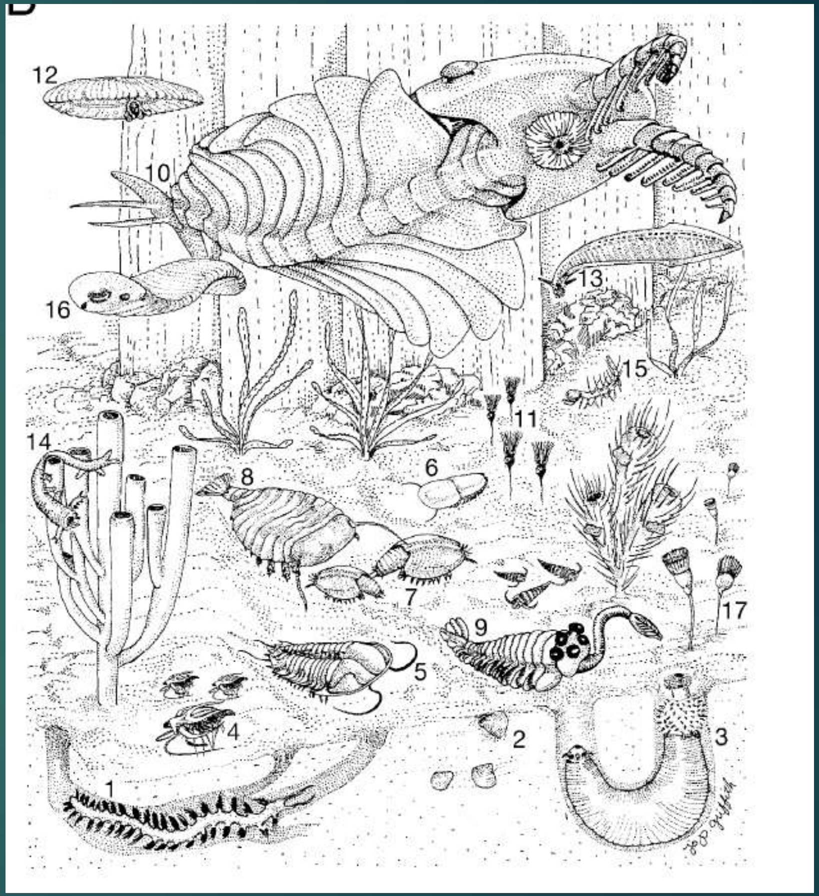
Arose after end of Snowball earth glaciations & increase in global oxygenation

Evolution's Big Bang = Cambrian Explosion: The blood bath – first arms war; Predation requires nervous systems

Anomalocaris: up to 2 meters

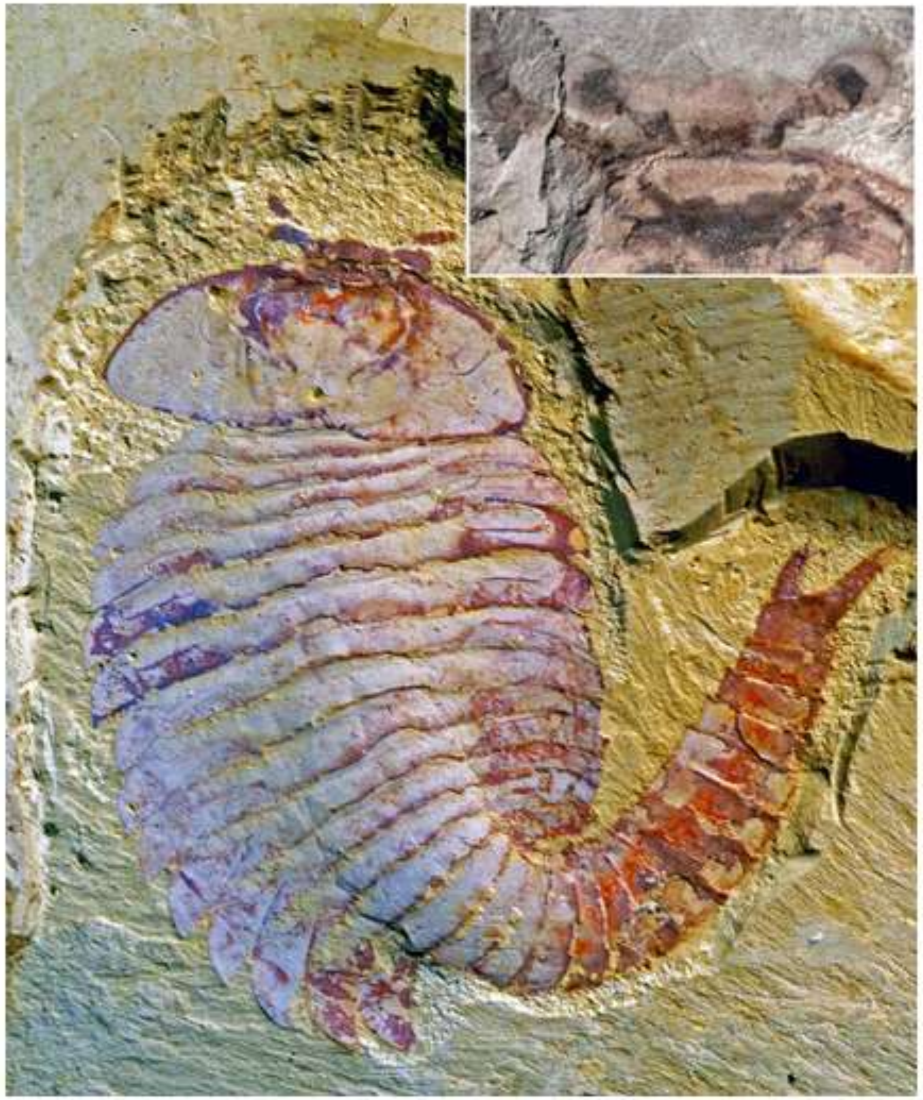


Hallucigenia: teethy smiling worm



Bilaterians: bilateral animals — body plans that have a left and right side, a top and bottom, and a mouth and anus. Mostly predators.

First fossil arthropod discovery with neural network: 520 MYA



3-inch, 520-million-year-old fossil of Fuxianhuia protensa. Insert shows dark features associated with putative 'brain' structure like that in modern organisms (Credit: Xiaoya Ma, insert: Nicholas Strausfeld).

Fuxianhuia protensa

Ma et al., *Current Biology, 2015*

Key Events in Evolution

- 10-16 bya - formation of universe.
- 4.5 bya - formation of Earth.
- 3.5 bya - microorganisms.
- 600 mya - multicellular organisms: serotonin
- 520 mya – invertebrates: axonal action potential, homeobox genes, smell & hippocampus,
- 460 mya – vertebrates: neural tube, myelin
- 360 mya - terrestrial amphibians.
- 260 mya - reptile-like mammals.
- 200 mya - true mammals: cortex
- 100 mya - marsupials and placentals
- 65 mya - mass extinction of dinosaurs and most mammals.
- 45 mya - anthropoid primates: color vision, mirror neurons, facial expression
- 7-4 mya - first hominids: large brain
- 200 K – *Homo sapiens:* language, culture

Neurotransmitters are ancient

- Many of the molecules found in neuronal synapses, especially within the postsynaptic density, predate the evolution of neurons.

- Serotonin: 95% in our intestinal brain, where it originated to regulate nervous system cells ~ 600 MYA; amazingly conserved
  - Regulates how neurons respond to other neurotransmitters;
  - increases during active movement;
  - influences prosocial behavior

- Reducing strength of S modulation:
  - increases motivational drive & sensitivity to risk and reward;
  - Low S found in people with depression, impulsive disorders, a history of suicide attempts, and in the brains of suicide victims.

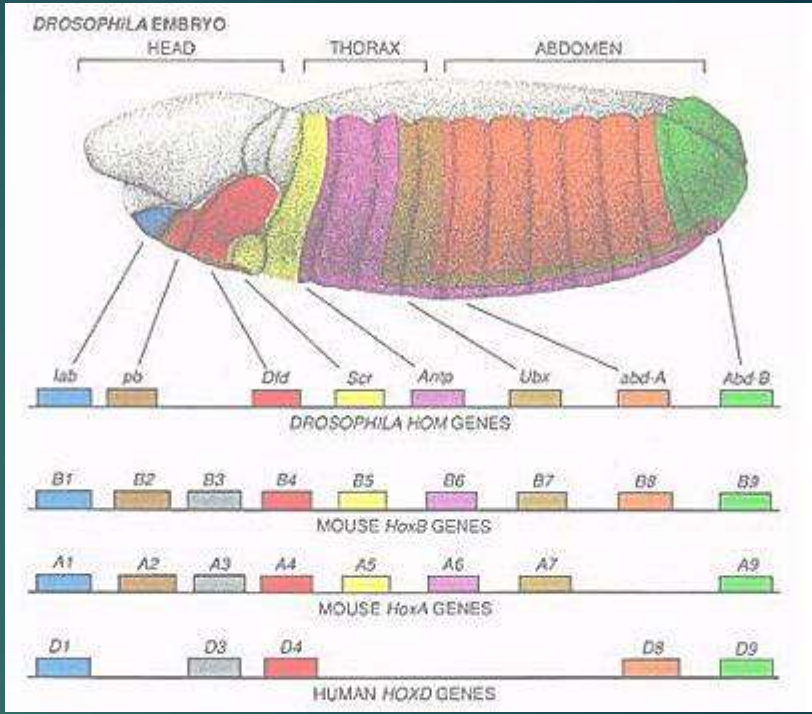
Origin of Brain Cells and Brains

Despite the age of the Earth (4.5 billion years), brain cells and brains are quite recent adaptations

- First forms of life: 3.5-4.0 billion years ago
- First brain cells: 700 million years ago
- First nervous systems: 500 million years ago
- First human-like brain: 3-4 million years ago
- Modern brain: 1-.2 million years ago

How did the Brain Evolve? Gene Duplication

- **Homeobox genes** – genes that control the development of different segments of the body (and brain)
- From fly to human – homeobox genes ("hox" genes) are very similar
- During evolution, some of these genes have been duplicated to give rise to similar structures
- This is how the hindbrain emerged from the spinal cord, the midbrain from the hindbrain, the forebrain from the midbrain, and so on



Evolution of nervous system

- R. Glenn Northcutt concludes that the last common ancestor of all bilaterian animals, living 600–700 Mya, probably had a diffusely organized nervous system.

- Cephalic neural ganglia apparently evolved soon thereafter and were retained in many lineages.

- Truly complex brains evolved even later and did so 3 or 4 times, in mollusks, arthropods, and chordates (including vertebrates).

Evolution of nervous system

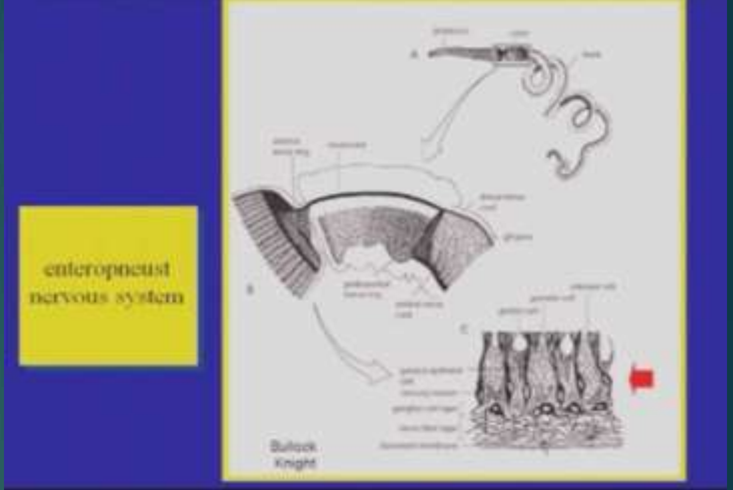
- Different conclusions of other researchers: similarities in developmental gene expression patterns among vertebrate, insect, and annelid nervous systems. To them, these similarities must represent homologies. That is, they argue that similar gene expression patterns must have existed in the last common ancestor of fruit flies, vertebrates, and worms.

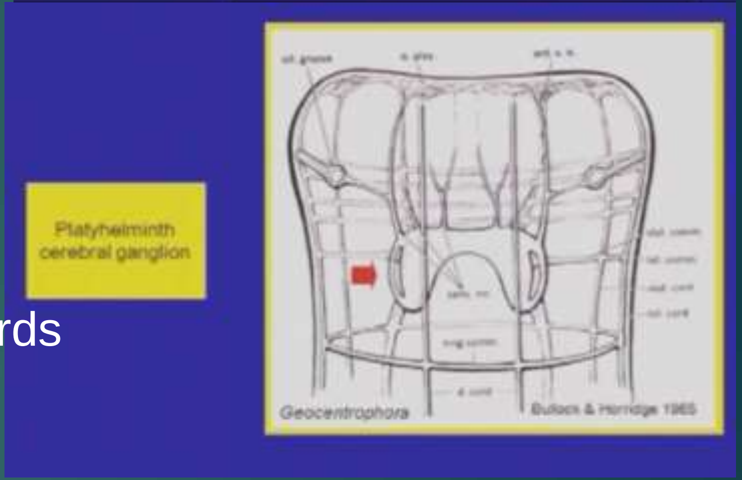
- Northcutt argues that the expression of these genes in brains is caused by convergent evolution, perhaps by the co-option of gene networks that predate brains. This debate will require more data for a full resolution.

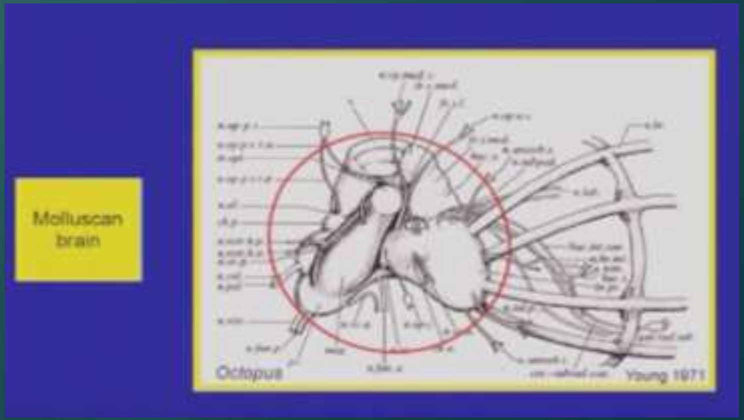
3 types of nervous systems

NEURAL CHARACTER STATES:

- D – diffuse nerve net or subepidermal nerve plexus. Neurons along epidermis
- C – simple cerebral ganglion. Neurons attached to neural chords
- B – central collection of neural centers (brain) with distributed functions. Brain with functional modules

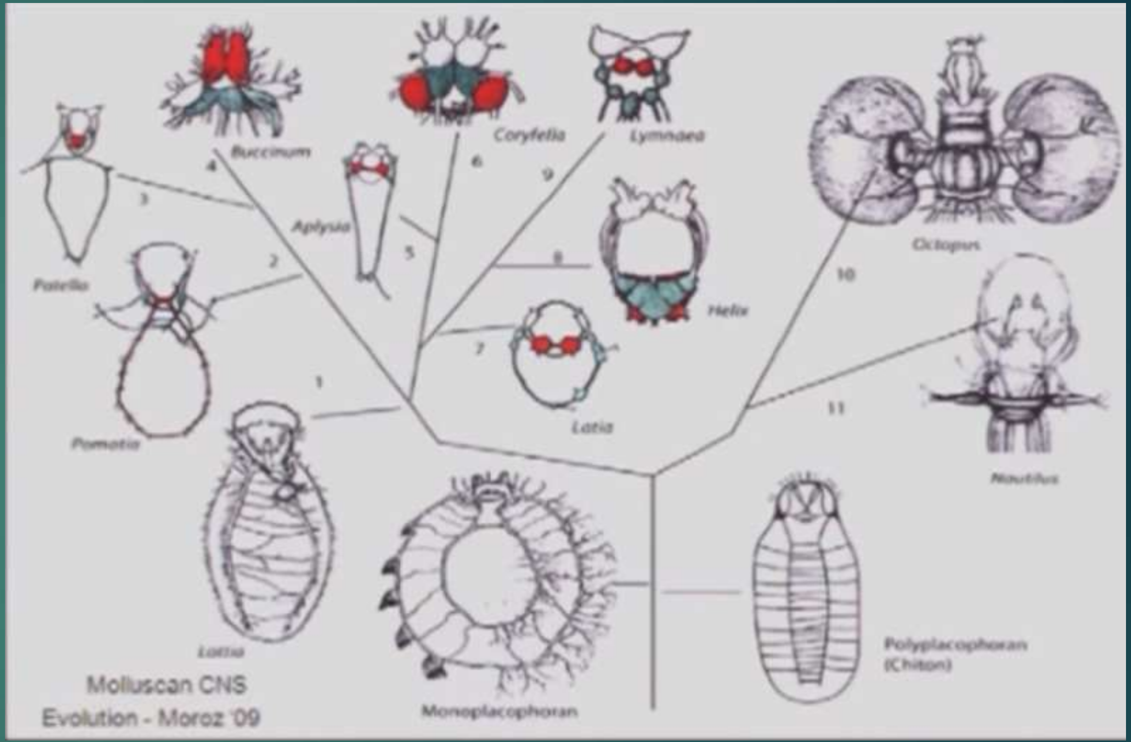


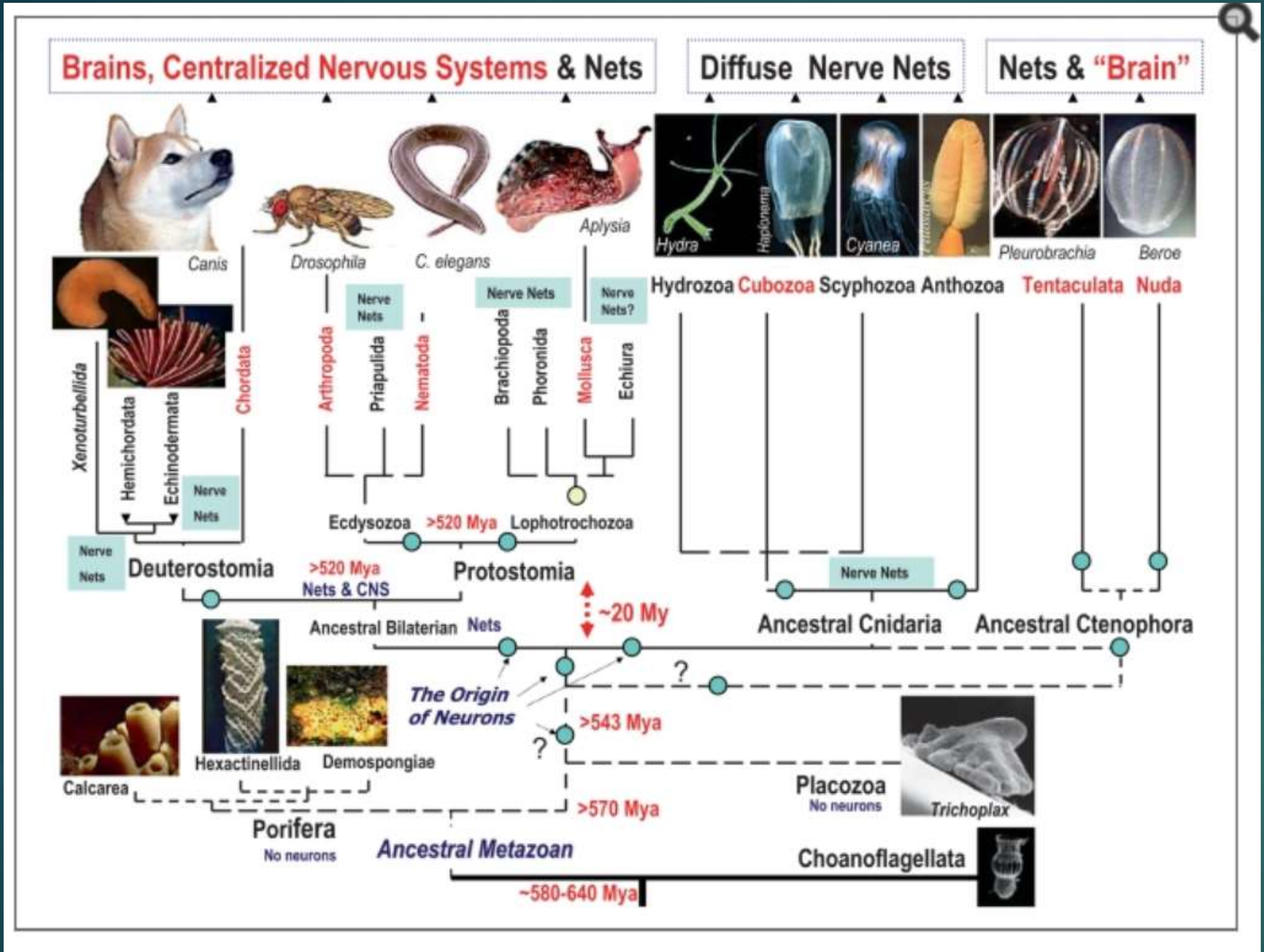




Independent, multiple evolution of brains

<u>Cladistic analysis</u> within encephalized phyla Indicates <u>brains have evolved independently within each phylum (same body plan)</u>





Not all animals have brains: Metazoan sponges (non-centralized, diffuse nervous systems that superficially can be termed 'nerve net(s)'.)

Leonid L. Moroz, Brain Behav Evol 2009;

Evolutionarily distinctive characteristics of human psychology

1. Folk physics w/ 'deeper' causal understanding.
2. Folk biology
3. Mind-reading
4. Language
5. Sophisticated imitation
6. Complex skills through practice
7. Motivation to guide social learning
8. Desire for status to promote successful social interaction
9. Personal attachments to kin, friends, mates
10. Normative capacities
11. Gossip
12. Capacity to reason about social exchanges and detect cheaters
13. Sense of humor
14. Interest in narrative
15. Music, rhythm, dance, ritual
16. Exact numerical cognition (numbers greater than 4)
17. Hypothetical thinking (pretend play)
18. Creativity
19. Analogy, metaphor, applying info. from one domain to another
20. Scientific reasoning (inference to best explanation)
21. Indefinitely flexible practical reasoning
22. Capacity to reflect upon and modify one's own reasoning capacities

Carruthers (2006) *The Architecture of the Mind*

Cambrian Revolution: 542-580 Mya

- In 40 M years:
  - All animal phyla appeared
  - 75% still with us
  - No new phyla since
  - All used olfaction
  - No complex behavior before
  - After, complex sensory systems, especially in predators
  - Movement beyond just reaction to stimuli
  - Then ability to learn, ability to predict, ability to control
  - Cambrian bloodbath of predator eating predator that probably supplied the selective force necessary for the evolution of the first brains.
  - Development of olfactory navigational system, which could map spatial valences, lead to an arms race between predators and prey

Early brain evolution and olfaction

- Brains first evolved underwater in a world defined by chemicals:
  - 1st system in all animals
  - The only universal
  - Largest investment (olfactory genes)
  - Only involved remote sensing via molecule detection

How The Brain Evolved From The Nose

From chemotaxis to the cognitive map: The function of olfaction - Lucia F. Jacobs:

The mammalian cortex evolved from the olfactory forebrain of primitive vertebrates, which was preadapted for complex input; ideal substrate for evolution of associative learning

1 From chemotaxis to the cognitive map: The function of olfaction - Lucia F. Jacobs, Dept. of Psychology, UCB
2 How Brain Evolved from a Nose –Lucia Jacobs; UCSF Neurology grand round presentation 9/19/2014

Evolution from chemotaxis to associative learning: Spatial cognition & odorants

- Chemotaxis: movement of an organism in response to a chemical stimulus in environment.

- The most universal of cognitive traits, the ability to orient in space.

- All mobile animals, vertebrate or invertebrate, must track the locations of prey, predators, mates and competitors and they do so in similar ways, particularly in their use of odorants.

Lucia Jacobs

Olfaction

- The need to orient in space to maximize fitness by acquiring resources and avoiding competition and predation is universal.

- Olfaction is also universal: “chemicals are probably the original stimuli, since they can participate directly in biochemical reactions without needing a sensory transduction step. This may be the reason that chemicals seem to be the most universal of stimuli. Indeed, it is possible that all organisms make use of chemical stimuli”

- Hence the primacy of olfaction, i.e., olfactory-guided navigation, as the ancestral function of the forebrain

- Olfactory gene variation: which can range from 1,500 chemosensory receptors in the nematode worm (Caenorhabditis elegans), 130 in Drosophila melanogaster, 900 in the laboratory mouse, to 350 in humans

Brains and olfaction

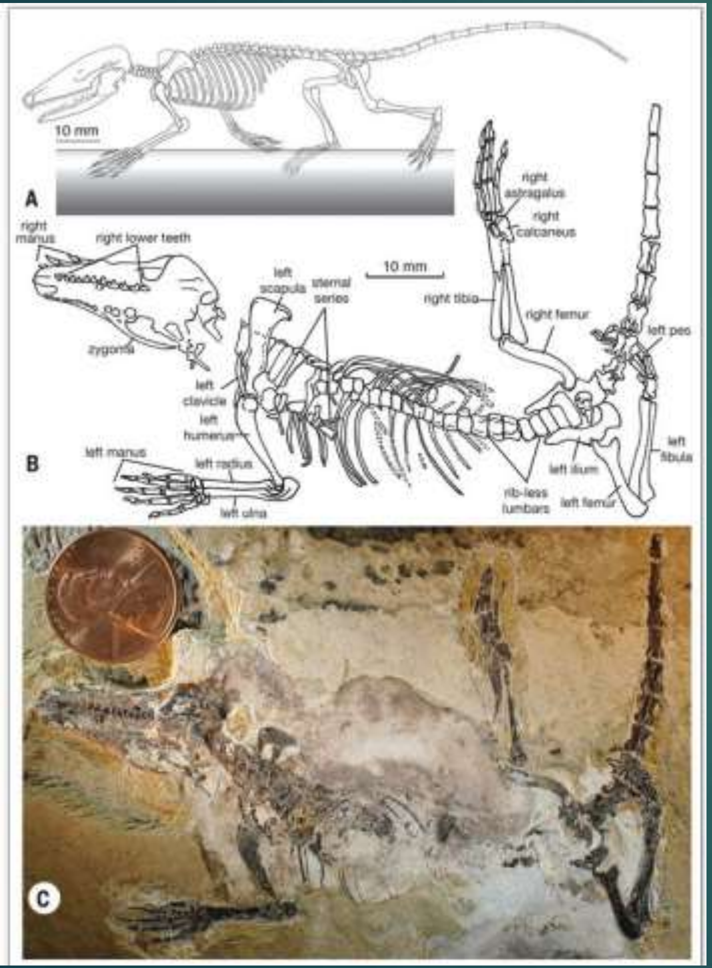
- Brains haven't changed much, especially in vertebrates. Gotten bigger, but few new structures in last 300 million years.
- The <u>ancestral mammal was probably an olfactory predator eating small prey, such as invertebrates</u>
- <u>Absolute size of the olfactory bulb size covaries with that of the hippocampus.</u>
- <u>Olfactory bulb size is independent of remaining brain size in mammals; Olfactory bulb & hippocampus is 3% of brain; more predatory, more olfactory</u>

The nose was first

- Osorio et al. concluded in 1994: “the mammalian neocortex with its protean powers has evolved from the olfactory forebrain of primitive vertebrates”

- The close relationship between the olfactory system and the hippocampus in mammals has long been recognized; indeed, olfaction was once believed to be the primary function of the hippocampus

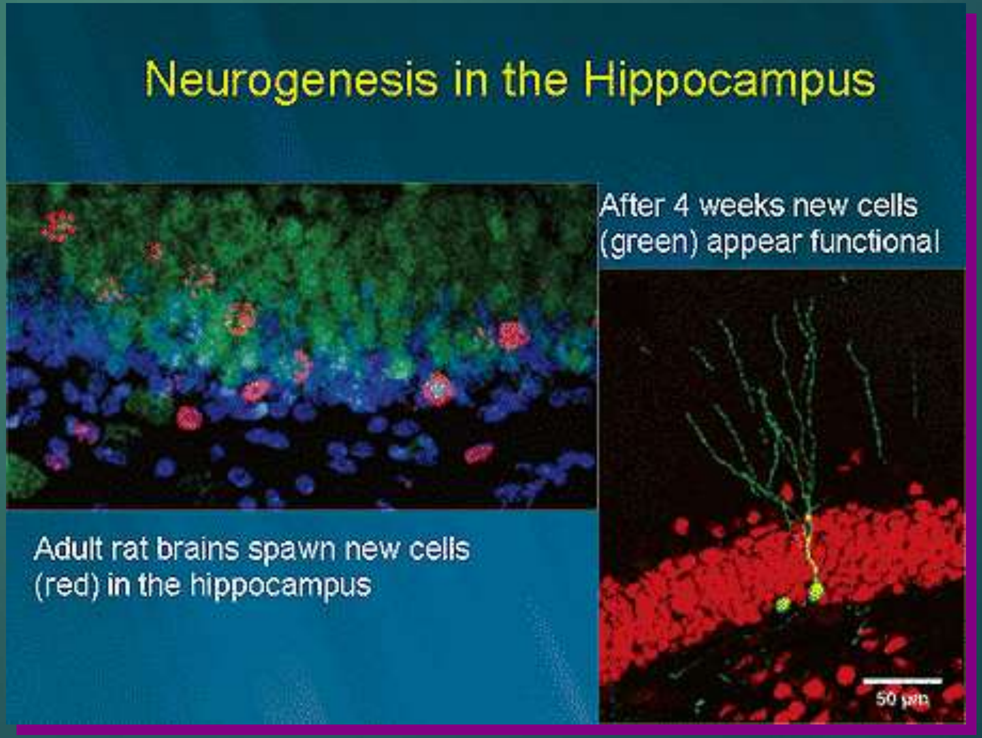
Oldest mammal fossil (China): 165 MYA - Agilodocodon scansorius - Mother of us all



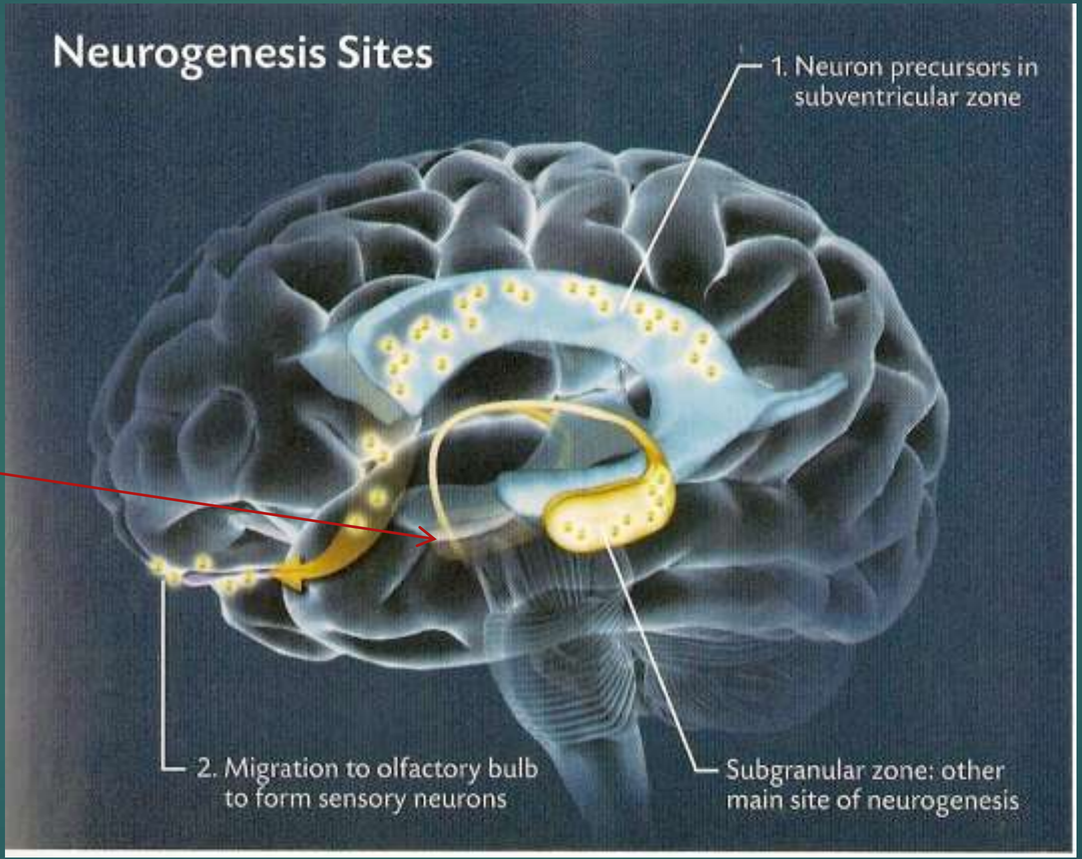
Mammalian nocturnal insect eater during age of dinosaurs

Neurogenesis

- Neurogenesis: growth of new neurons in the adult brain; Stem cells become new adult neurons



Neurogenesis: 3 major sites



Interneurons in Striatum

1400 new neurons per day, enough to replace all the neurons in the dentate gyrus of the hippocampus over a lifetime; needed for new memories

Function of Neurogenesis

- Most stem cells die
- Those involved in new learning survive
- Decreased by: / Increased by:

Decreased by:	Increased by:
Stress (Cortisol)	Environmental enrichment
Depression	Exercise
Aging	Antidepressants
Alzheimer’s	Alzheimer’s
	Seizures

Neurogenesis: new stem neuronal cells

- Olfactory bulb and hippocampus (esp. dentate gyrus) (needed for bearing map) are only brain areas with lifelong adult neurogenesis in all vertebrates

- Adult neurogenesis is found widely in animals but in vertebrates it is always found in the OB and the medial pallium (hippocampus/dentate gyrus in mammals).

- Thus, the two structures necessary for the Olfactory spatial system are also the only locations in which adult neurogenesis is found in all vertebrates, including mammals.

Neurogenesis

- OB neurogenesis increases with new odorant presentation, whereas hippocampal neurogenesis increases with spatial exploration.

- This vertebrate pattern of neurogenesis suggests its ancestral function was related to mapping and encoding the spatial distributions of novel odorants.

- Running increases hippocampal neurogenesis (spatial memory), but not OB neurogenesis; odor enrichment has opposite effect (odor memory)

Odorants can give both directional & positional cues

- Chemical odorants are a directional cue with repeated sampling of elements, using a concentration gradient, produces a vector (quantity having direction as well as magnitude, especially as determining the position of one point in space relative to another) and simultaneously being a positional cue where any one mixture can be perceived as a unique whole (landmark); can detect location by relation to these mixtures; add valency (positive and negative pull)
- Evolution later adds other stimuli (geomagnetic fields, light, vision) to increase bearing mapping ability, predation ability, body size; increases cognitive map; being able to map resources in environment gives you large selective advantage
- This evolution of associative learning may have been a major factor for the Cambrian explosion

Hippocampal place cells

- Hippocampal GPS: Pyramidal cells (place cells, border cells, and grid cells) have been implicated as the neuronal basis for cognitive maps within the hippocampal system.
- Individual place cells within the hippocampus correspond to separate locations in the environment with the sum of all cells contributing to a single map of an entire environment. The strength of the connections between the cells represents the distances between them in the actual environment
- Most emotionally encoded memory is olfactory

Hippocampus

- Hippocampus (medial pallium in animals): turtles, mouse, lizard, chickens, etc.
- Dentate is ancestral (bearing maps/directional)
- Derived only in mammals and birds
- Anterior/dorsal/ventral hippocampus = bearing map (Euclidean; only directional cues activate) (larger place cells)
- Posterior hippocampus = sketch map (topological; only positional cues activate)

Origin of Olfaction

- Same olfactory gene program development of forebrain, both in mouse and worms (invertebrates)
- Genetic sequences are homologous; implies origin from 1 species in Cambrian which then expanded
- Implication: primary function of olfaction is navigation
- Limbic system originated for navigational function to map space

Brain evolution

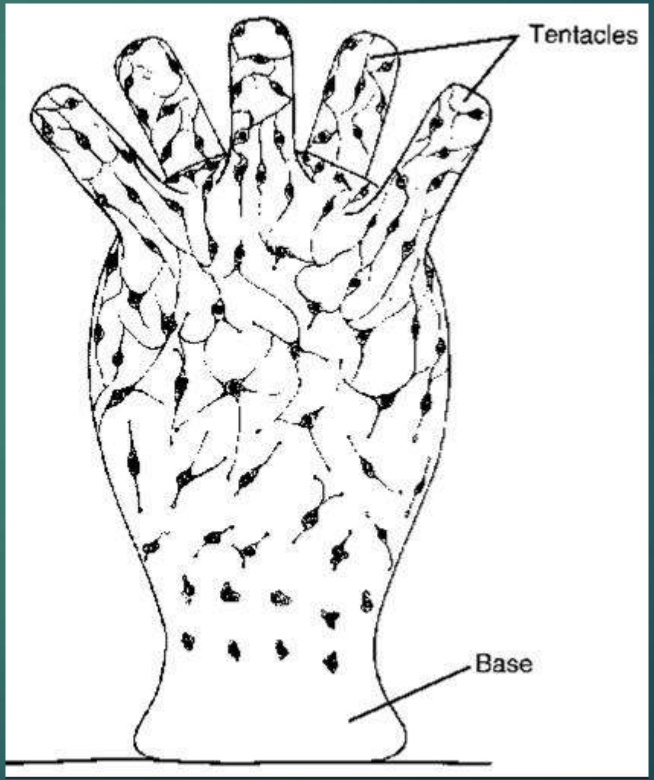
- Evidence of mammals evolving more sophisticated spatial cognitive abilities:
  - with increases in OB size accompanied by
  - increases in hippocampal size and olfactory cortex size
  - with eventual increases in brain size.
- The mammalian brain may thus have evolved first via mosaic evolution for olfaction, then via concerted cortical evolution
- Carnivorous predators, whether diurnal theropods or nocturnal terrestrial mammals, are olfactory predictors, and require an enhanced OS system to track mobile, dispersed prey

Proust & his Madeleine: Olfaction and Memory

"I raised to my lips a spoonful of the tea in which I had soaked a morsel of the cake. No sooner had the warm liquid mixed with the crumbs touch my palate than a shudder ran trough me and I sopped, intent upon the extraordinary thing that was happening to me. An exquisite pleasure invaded my senses..... And suddenly the memory revealed itself. "

Invertebrate Nerve Net

Sensory and motor neurons

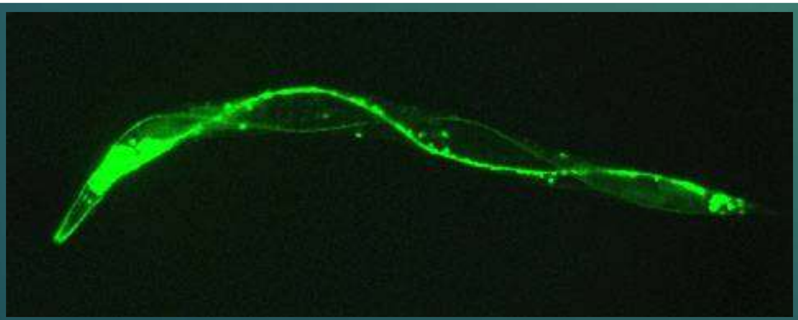


Anemone

Invertebrates

- <u>Segmented nerve trunk</u>:
  – <u>Divided into a number of parts</u>
  – <u>Bilaterally symmetrical</u>

- <u>Ganglia</u>:
  – <u>Collection of nerve cells that function somewhat like a brain</u>

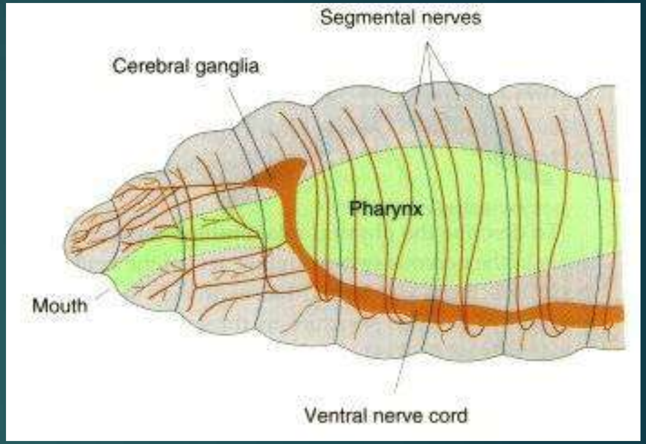


C. elegant

Ascidian

Invertebrate vs. Vertebrate Nervous System

- **Invertebrate**
  - Nerve nets, segmented nerve trunk, ganglia
  - Nerve cord and giant axons
  - Identifiable neurons (e.g., *Aplysia*)
  - Stimulus/response, receptor/effector
  - Reflexes, conditioned responses
  - Structure for processing smells & storage of olfactory memories (later becomes telencephalon (embryonic structure from which the cerebrum develops)

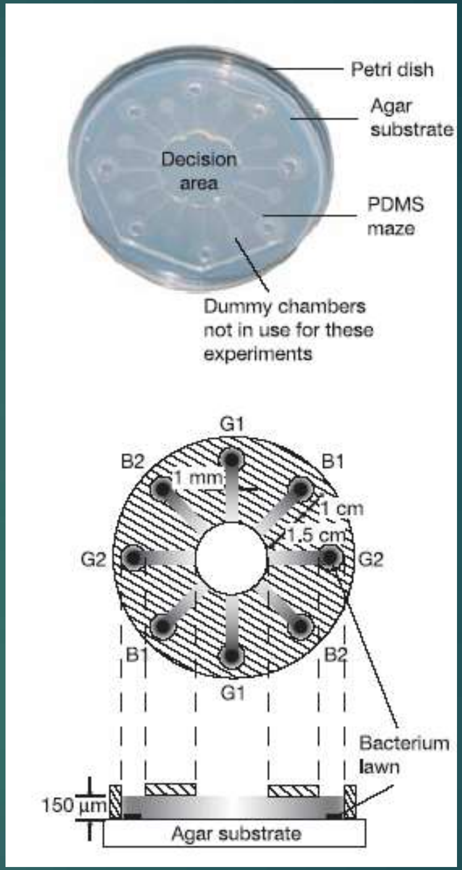


Earthworm – invertebrate

- **Vertebrate**
  - Brain and spinal cord encased in cartilage/bone
  - Myelin arose to enhance new predation ability
  - Crossed organization: Each hemisphere controls the opposite side of the body
  - Spinal cord is dorsal (at the back of the heart and gut)

Response to environment: Worms can learn, too

- Worms are the simplest organisms to have a central nervous system
- Roundworms learn by sense of smell and will avoid "bad" bacteria that make them sick
- "Shocking worms": Can they learn to avoid the shock?



Zhang, et al, Nature 438 Nov.10 2005

Planaria "flatworms" learn to avoid the side where shock was administered

Without a brain

- Different parts of the worm nervous system can function independent of the brain

- Can perform many types of behaviors including locomotion, mating, feeding, even maze learning without a brain

Insect Brains

- Giant fiber systems allow rapid communication between brain and muscles (precursor to spinal cord)
- 850,000 neurons
- The head region is dominant, and the body cannot survive without the head (unlike worms)

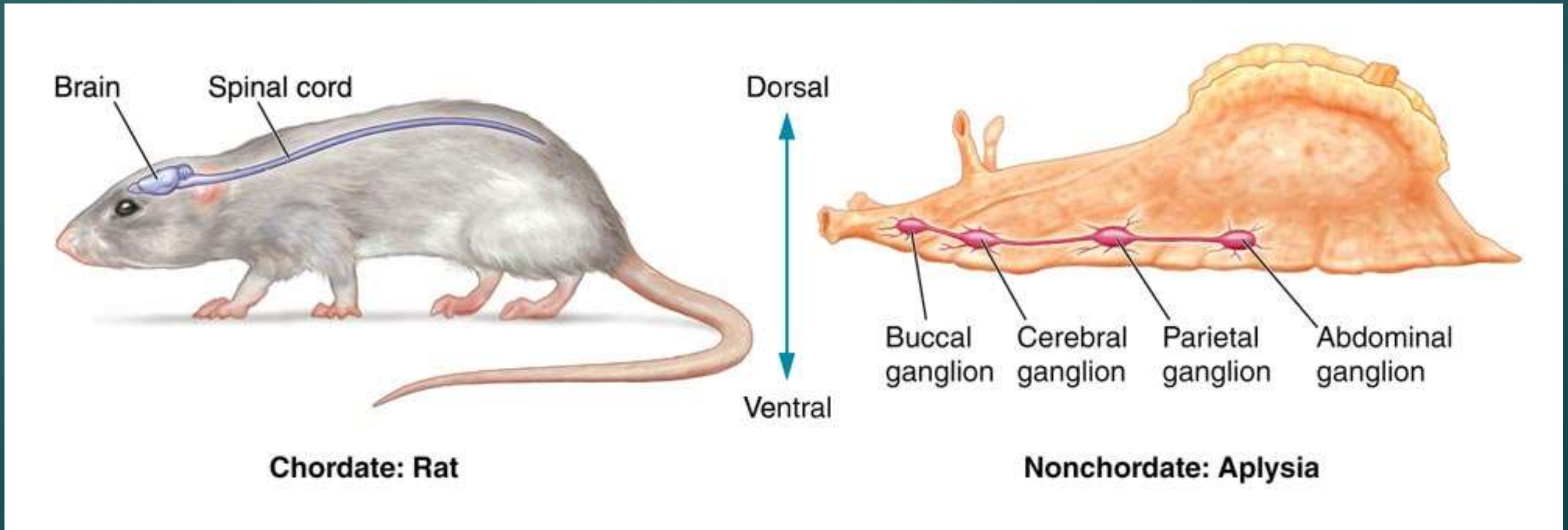
- Honeybees use olfactory cues to locate nectar sources
- Forms olfactory "memories" which can be used to find nectar in the future
- Language? Back at the hive, they perform a waggle dance that tells other bees where to find the nectar

Nonchordates & Chordates

Neural nets were followed by ganglia in the head region

Nonchordates: nervous systems that typically run along the ventral (underside) part of the body.

Chordates (possessing a notochord, a hollow dorsal nerve cord): true brains and spinal cords that run along the dorsal part of the body (easier to protect neural tissue)



http://genomics.biotech.ufl.edu/aplysia/images/aplysia_d.jpg

Vertebrates

- Common plan of organization of the CNS in all vertebrates is due to homeobox genes.
- Progressive pattern of gene expression in the developing brain of chordates and vertebrates.
- Birds & mammals have large cerebral hemispheres, derived from the embryonic forebrain.
- Orderly topographic representation of body structures (*e.g.*, limbs, retina, cochlea) in the brain, but those representations are altered to reflect function (*e.g.*, large representation of the hands in primates).

Vertebrate Nervous System

- Neural tube
- Bilateral symmetry
- Segmentation
- Hierarchical control
- Separate systems
- Localization of function

Brain Organization

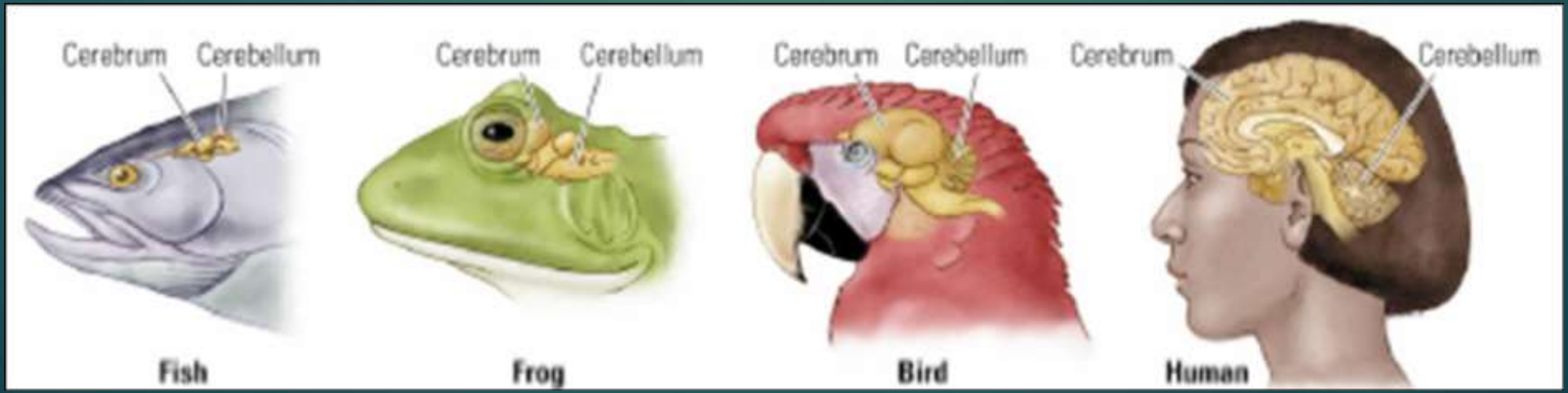
- The vertebrate brain has 3 basic components
- **Hindbrain** – most of the brainstem and the cerebellum. The oldest and so-called “reptilian” brain because it is especially prominent in reptiles
- **Midbrain** – part of the brainstem that evolved most recently
- **Forebrain** – the limbic system and the cerebral cortex

Evolution of Vertebrate Nervous System

- Behavioral complexity is correlated with the evolution of ***cerebral hemispheres*** and ***cerebellum***:

– Cerebellum: originally used for stabilizing retinal images; involved in the coordination of motor and other cognitive processes

– Increased size and folding of cortex (to fit more tissue into the skull & reduce wiring length)



Cerebral cortex is convoluted cover over the brain

Human cerebral cortex much larger.

Rat’s cortex = postage stamp

Monkey’s = post card

Chimpanzee’s =

page of printer paper

Human’s = four pages

Gyrification in humans

Brain scaling in mammalian evolution as a consequence of concerted and mosaic changes in numbers of neurons and average neuronal cell size

- Based on an analysis of the shared and clade-specific characteristics of 41 modern mammalian species in 6 clades, and in light of the phylogenetic relationships among them,
- Found:
  - An addition of neurons that is accompanied by a
  - decrease in neuronal density
  - and very little modification in glial cell density,
  - implying a significant increase in average neuronal cell size in larger brains,
  - allocation of approximately 2 neurons in the cerebral cortex and 8 neurons in the cerebellum for every neuron allocated to the rest of brain.

Suzana Herculano-Houzel, Paul R. Manger and Jon H. Kaas, 2014

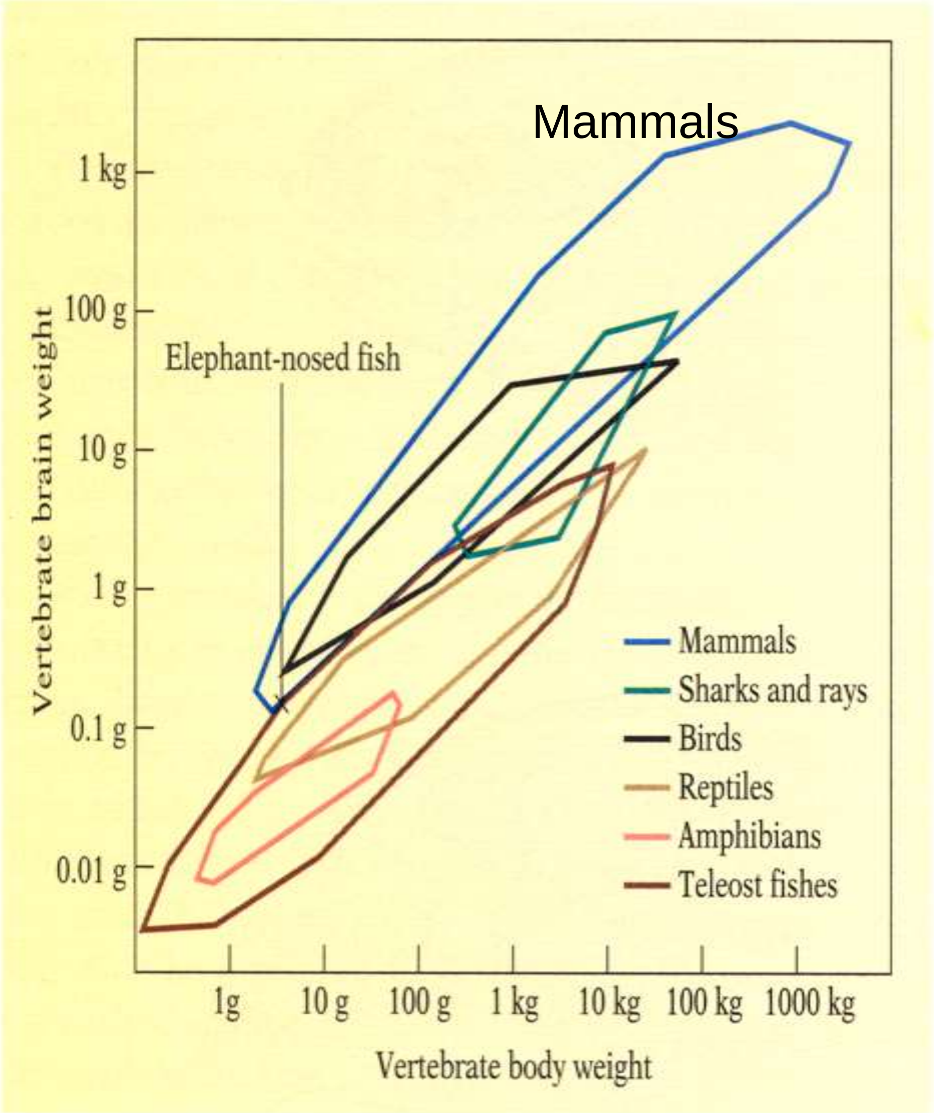
What are the changes that occurred between less to more complex vertebrates?

- Changes in size (encephalization factor)
- Changes in relative size of different parts of the brain–cerebral cortex, cerebellum
- Changes in representation of the body on the sensory cortex and locomotion
- Cortical specialization: functional organization in different regions
- Complexity of circuits
- Vascularity
- Variety of non-neuronal cells
- Changes in time course of development

What do you need in order to develop a big brain?

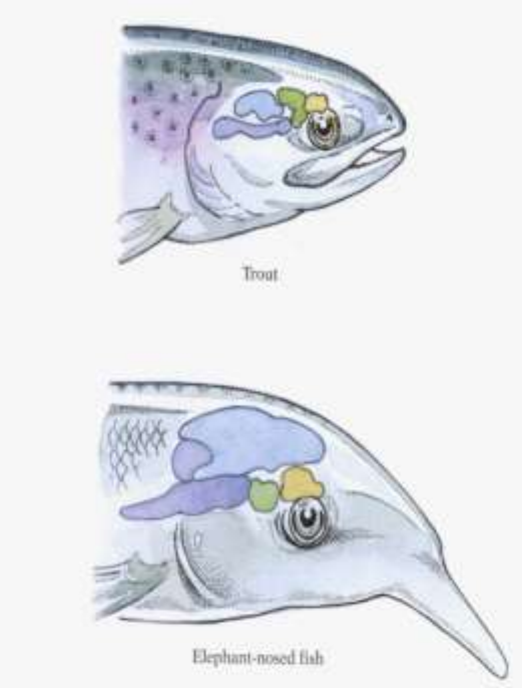
- Cortical folding ability
- Increased wiring and shorter wiring routes
- Myelin for speed
- Cooling system – the veins
- Better vasculature
- Functional units
- Climatic instability to drive need for change
- High energy utilization, better quality diet & smaller gut
- Solid memory storage & behavioral flexibility for foraging
- Long development requires parental dependency
- Larger social groups & extended families
- Longevity: memory for environmental crises & grandmothers

Relationship between brain and body weight:
bigger bodies need bigger brains for somatic maintenance

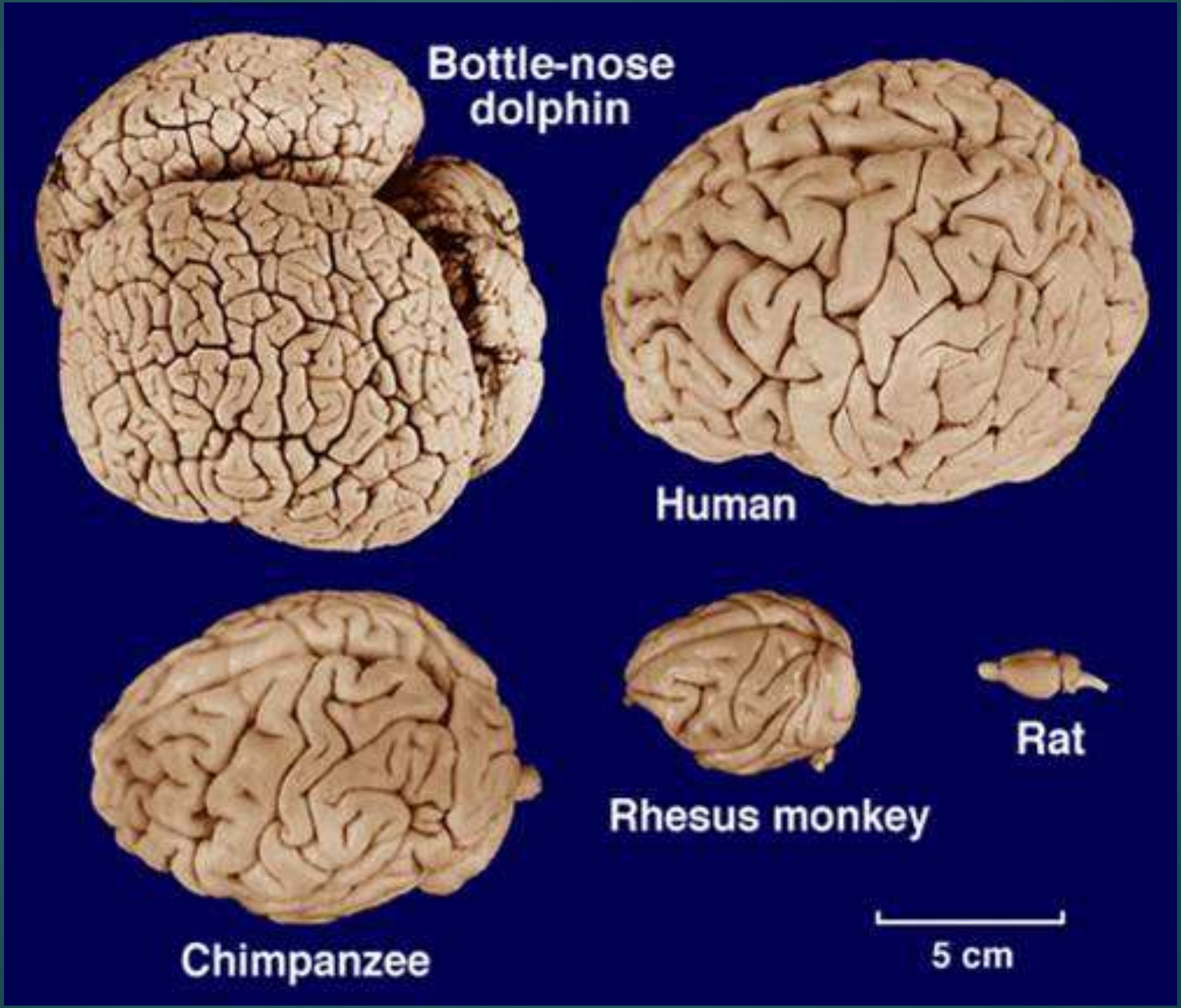


The relationship between brain and body weight in vertebrate groups, plotted in grams on logarithmic scales on which each tick marks a tenfold change. The members of each particular vertebrate group, such as the mammals, fall within a well-defined polygon. The teleosts are a large group of bony fish, distinct from the cartilaginous sharks and rays.

Allman J., 1999

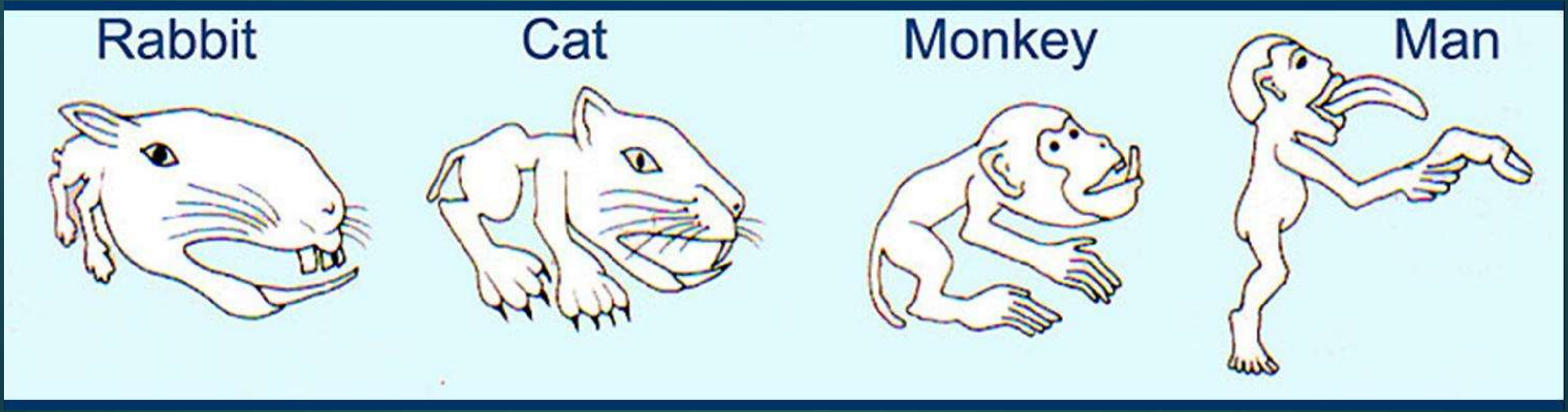


Less to more complex vertebrates

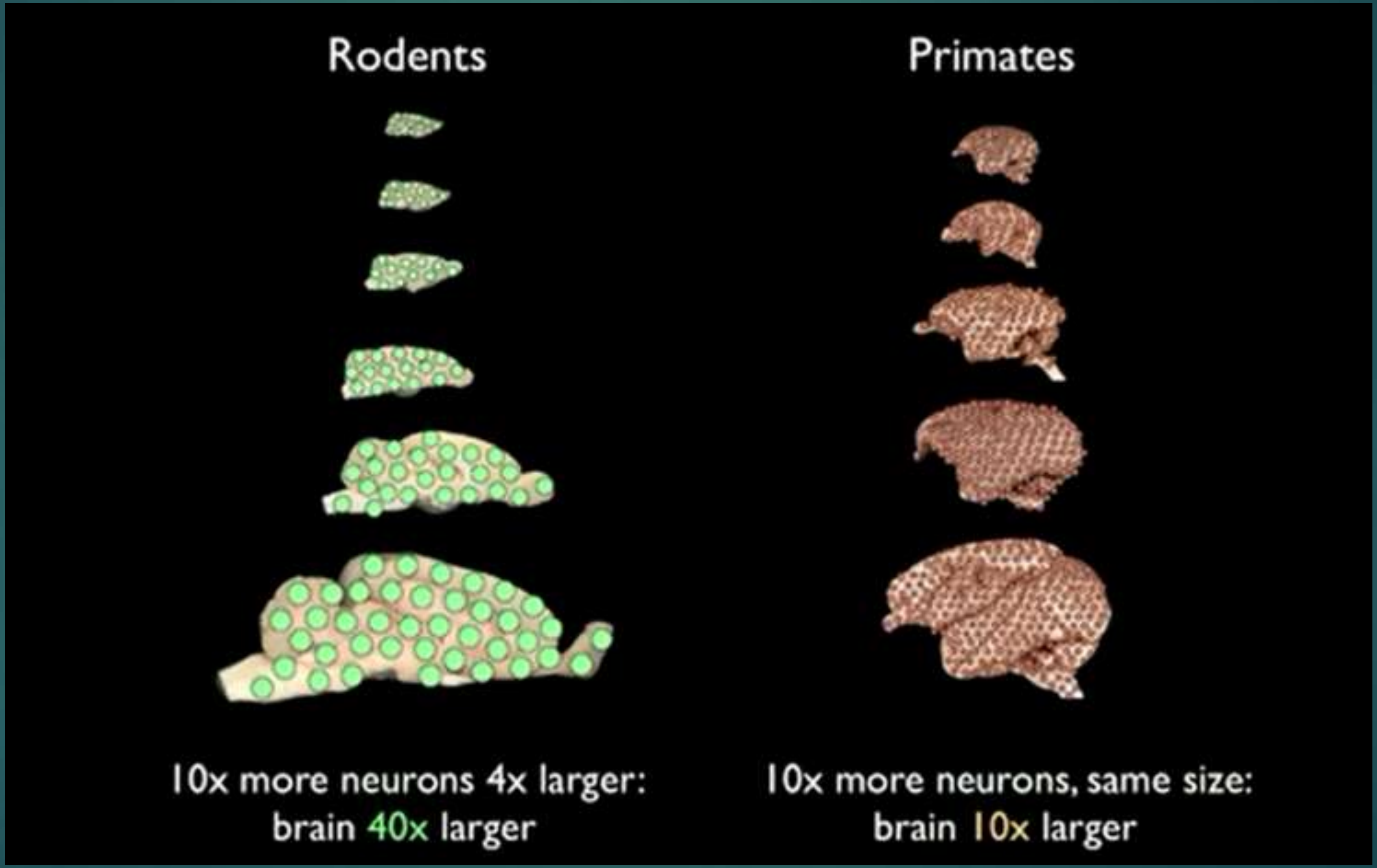


Body parts that are needed to survive have the most brain representation

Changes in representation of the body on the sensory cortex and locomotion



Primate brains always have more neurons than rodent brain of same size

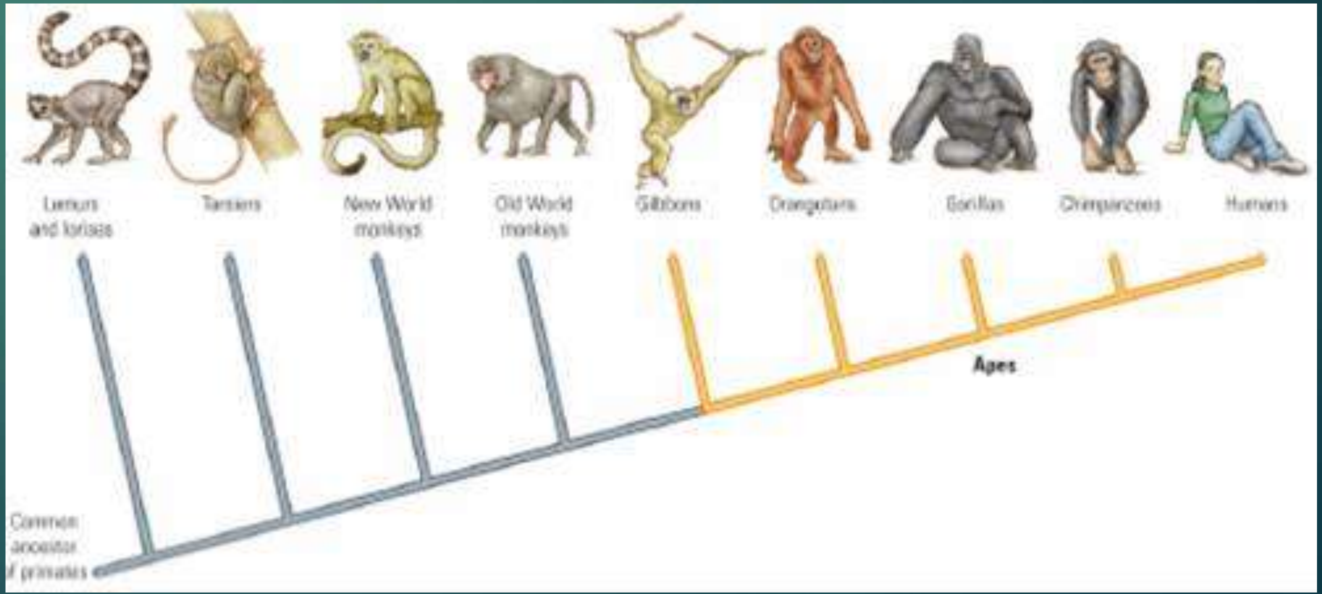


Neurons in rodent brains get larger; but not in primate brains

Chordate → mammals → primates

Features common to primates:

- Excellent color vision
- Eyes in front of face: enhance depth perception
- Females: Usually only one infant per pregnancy; infants require more care
- Larger brains

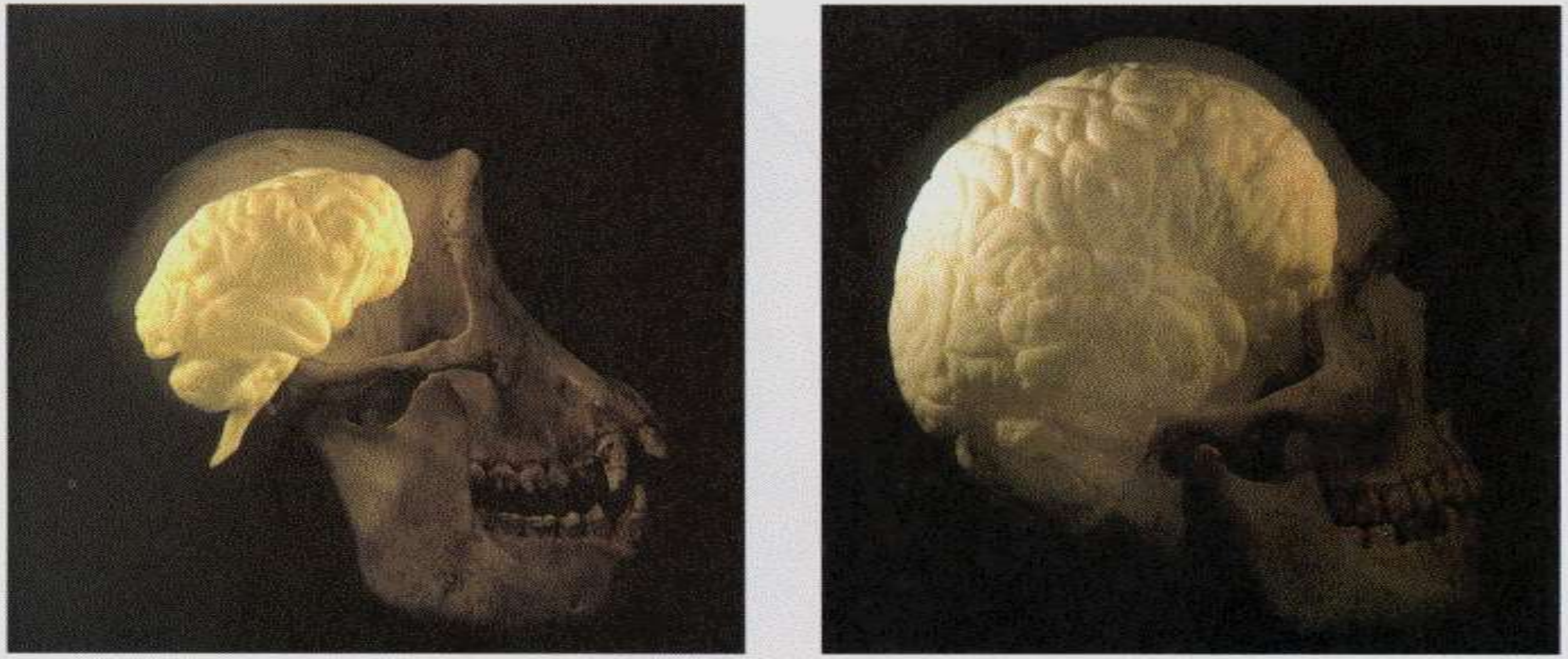


Chimpanzee

400cc

Man

1350cc



98.4% identical DNA!

(30-60 million base pair difference out of 3 billion bp)

Striedter: Brains Evolved (by very general principles)

- Most important principle in brain evolution:
  - Many aspects of brain structure and function are conserved across species, with closely related species tending to have brains that are more similar than those of distant relatives.
- The degree of conservation is highest at the lowest levels of organization (genes)
- Embryonic brains tend to be far more similar than adult brains
- But species differences are real.

George F. Striedter, *Principles of Brain Evolution, 2005*

Brain Evolution Principles

- Brains tend to change internal organization as they vary in size
  - (across all vertebrates, absolute brain size varies by 5 orders of magnitude (20 mg to 2 kg))
- Variation in brain size correlates with variation in
  - diverse structural respects (neuron number, size, density, and connectivity)
  - size of various brain regions relative to one another.

Brain Evolution Principles 2

- These attributes all scale at different rates (relative to absolute brain size) and tend to be interrelated causally.

- Evolutionary changes in absolute brain size by necessity entail a slew of structural changes (and behavior)

- Some principles of brain evolution are rooted in rules of brain development.

Absolute Brain Size & Brain scaling

- Absolute brain size often ignored in favor of relative brain size (which controls for effect of body size on absolute brain size); it is only by the latter that humans have the largest brains.

- 1 - Brain region's size relative to other regions (it's proportional size) tends to change predictably with absolute brain size.

- 2 - As individual brain regions change in size, they tend to change in internal structure.

- 3 - Neuronal connectivity changes predictably with absolute brain size

1 - Regional proportional size tends to change predictably with absolute brain size.

- Dorsal telencephalon (developmentally early cortex & BG) becomes disproportionately large as absolute brain size increases in mammals and birds.

- Each major brain region tends to scale against brain size with a characteristic slope.

- Individual brain regions tend to evolve in concert, not independently.

Late equals large

- Rule of “late equals large”:
  - evolution creates larger brains by “stretching” brain development;
  - brain regions that mature later become larger
  - humans have longest brain developmental period (more synaptogenesis)

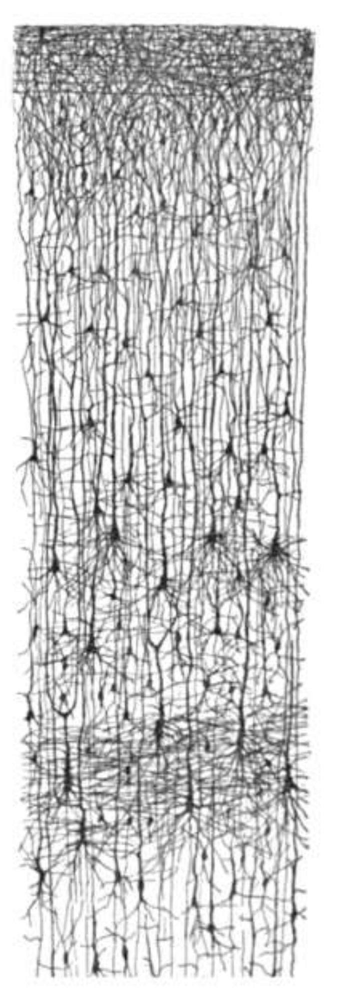
2a - As individual brain regions change in size, they tend to change in internal structure

- Brain regions tend to become more subdivided (based on function).
- Size related proliferation of brain subdivisions: addition of new areas or segregation of old components leads to increased complexity.
- This allows specialization of function in different areas.
- Regions subdivide because the distance over which developmentally important molecules can diffuse or interact is physically limited.

2b - As individual brain regions change in size, they tend to change in internal structure

- Enlarged brain regions tend to become laminar (neurons form sheets rather than nuclei).

- In laminar brain regions, axons and dendrites tend to course parallel or at right angles to the cellular layers suggests that lamination tends to minimize connection lengths, conserving space and energy, which become more limited as neuron number increased.



3 - Neuronal connectivity changes predictably with absolute brain size

- Connection density (proportion of brain's neurons that are directly interconnected) tends to decrease as neurons increase. Neurons are limited in how many other neurons they can innervate.

- Decreasing connection density forces brains to become more modular; distant regions become functionally more independent and diverse.

- Deacon's rule of "large equals well-connected"

- As regions become large, they tend to invade regions that they did not innervate ancestrally, increasing their sphere of influence.

- Larger areas become more important for normal brain function.

Exceptions to principles

- Brain size is not everything.
- There are exceptions to these principles.
- Sometimes brain regions change in size independently of brain size.
- Some regions become simpler even though larger.

Mammalian Brain Evolution

- Mammals have larger brains
- Larger mammals tend to have proportionately larger brains than their smaller relatives (late equals larger).
- Larger mammals tend to have more subdivided areas in their brains.

Brains are conservative: some cortical areas are conserved

- General plan of neocortical organization that has been conserved in all mammals
- Sensory processing, such as primary visual (V1), somatosensory (S1), and auditory (A1) areas.
- These homologous (inherited from common ancestor) areas share:
  - similar patterns of connectivity from both the thalamus and other brain areas,
  - a common architectonic appearance,
  - neurons within these areas have similar properties

Brains are conservative

- Example: Area V1 developed as primary visual area; V1 in blind mole rats is used now only for circadian functions, and not for visual discrimination.

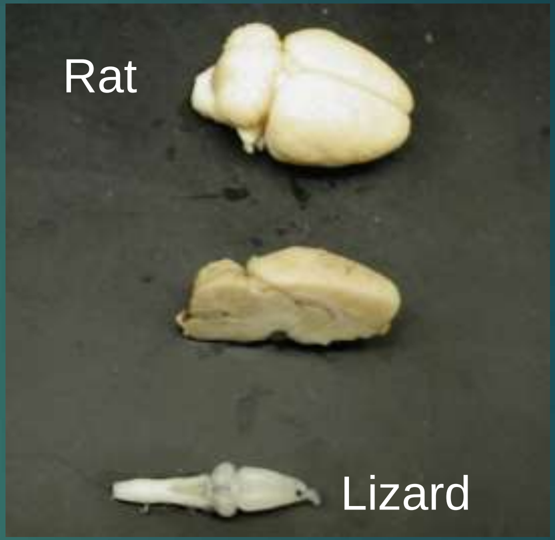
- There are large constraints imposed on evolving nervous systems.

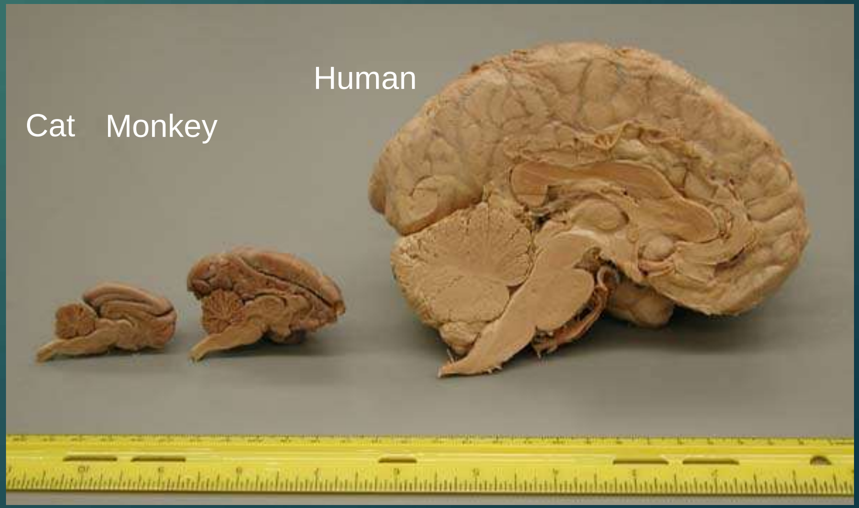
Common components of Mammalian Brain Evolution

- Bones of the inner ear allowing discrimination of higher frequencies.
- Hemoglobin increased availability of oxygen to the brain.
- Specialization of the telencephalon for olfactory input and function.
- Retinal stability via the vestibular system and the cerebellum.
- Insulation of axons by myelin.
- Development of the neocortex in the forebrain.
- Maintenance of constant body temperature (homeostasis): very energy demanding; required increased energy from food and changes in brain, body and behavior.

Cortical Expansion of the forebrain

- **The Forebrain** – evolved in vertebrates as an outgrowth or extension of the brain stem
- In mammals, the "neocortex" is basically an enlargement of the forebrain
- In humans and other primates, the neocortex is so large that it completely covers the brain stem





Primate Order brain capacities

- Agility.
- Dexterity - simple tool making.
- Binocular vision - depth perception.
- Enhanced facial expressiveness.
- Color vision
- Increased brain size relative to body size, especially in neocortex.
- Enhanced parental care.

Possible Characteristics of Our Common Ancestor

- Lived in Africa, perhaps on the edge of the tropical rain forests.
- Was not bipedal, and probably knuckle-walked (like the chimpanzee).
- Had a small body (3 feet) and a relatively small brain (300cc).
- Did not have a large (if any) meat component to its diet.
- Did not use tools to any great extent.
- Had a closed social network of solitary males, females grouped in loose associations; mating would not be monogamous with little male parental investment.
- These are speculative as no fossil remains have been discovered.

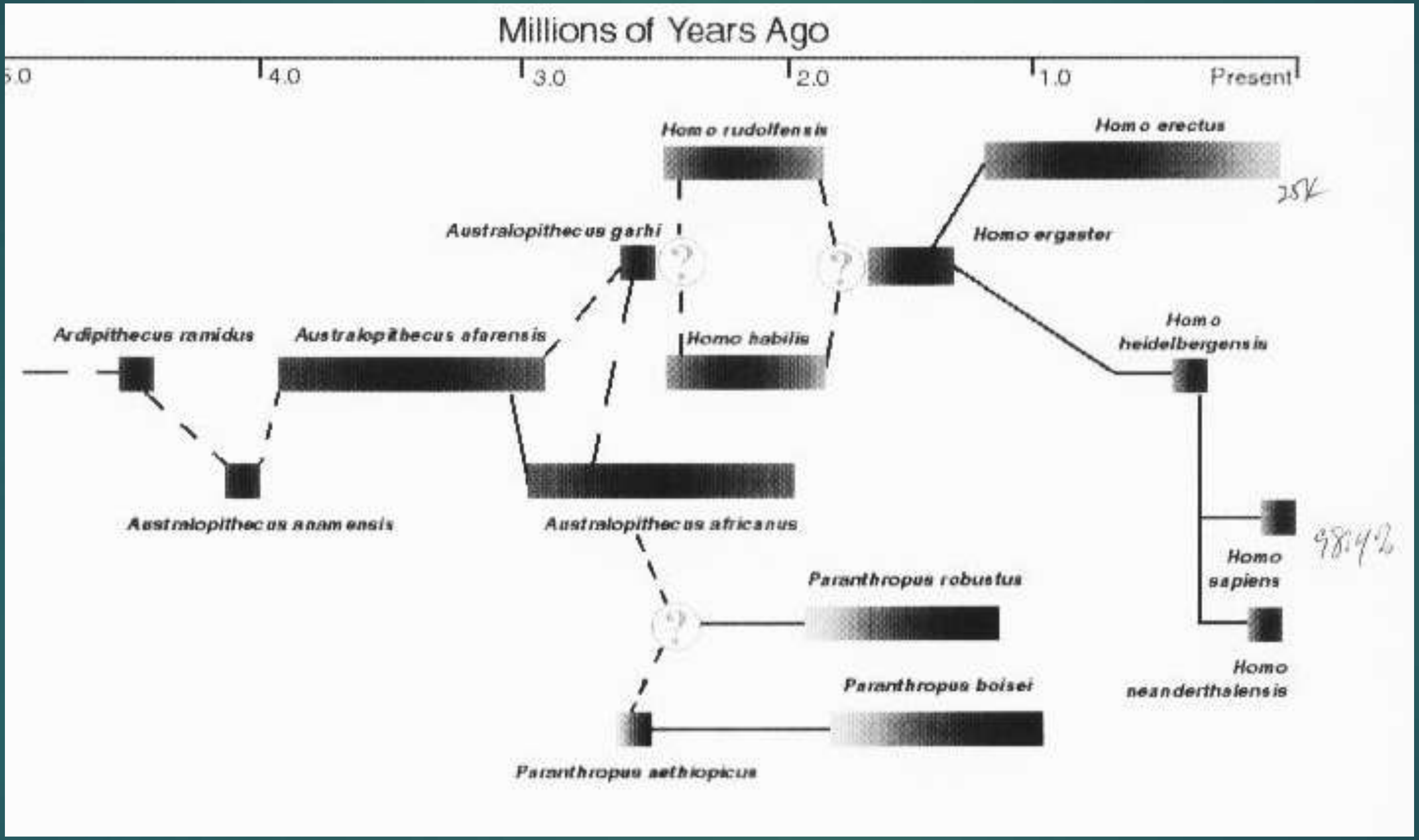
LCA: Last common ancestor had mirror neurons

- In both macaque monkeys and humans, ventral premotor and inferior parietal cortex contain neurons that fire when an individual either performs or observes different goal directed actions

- This 'mirror neuron system' potentially serves as a substrate for understanding others' actions, imitating new skills, and simulating others' intentions.

(Rizzolatti et al. 2002; Arbib, 2005).

Not a straight ascent to modern humans: a bush of experiments, not linear progression; evolution is not teleological

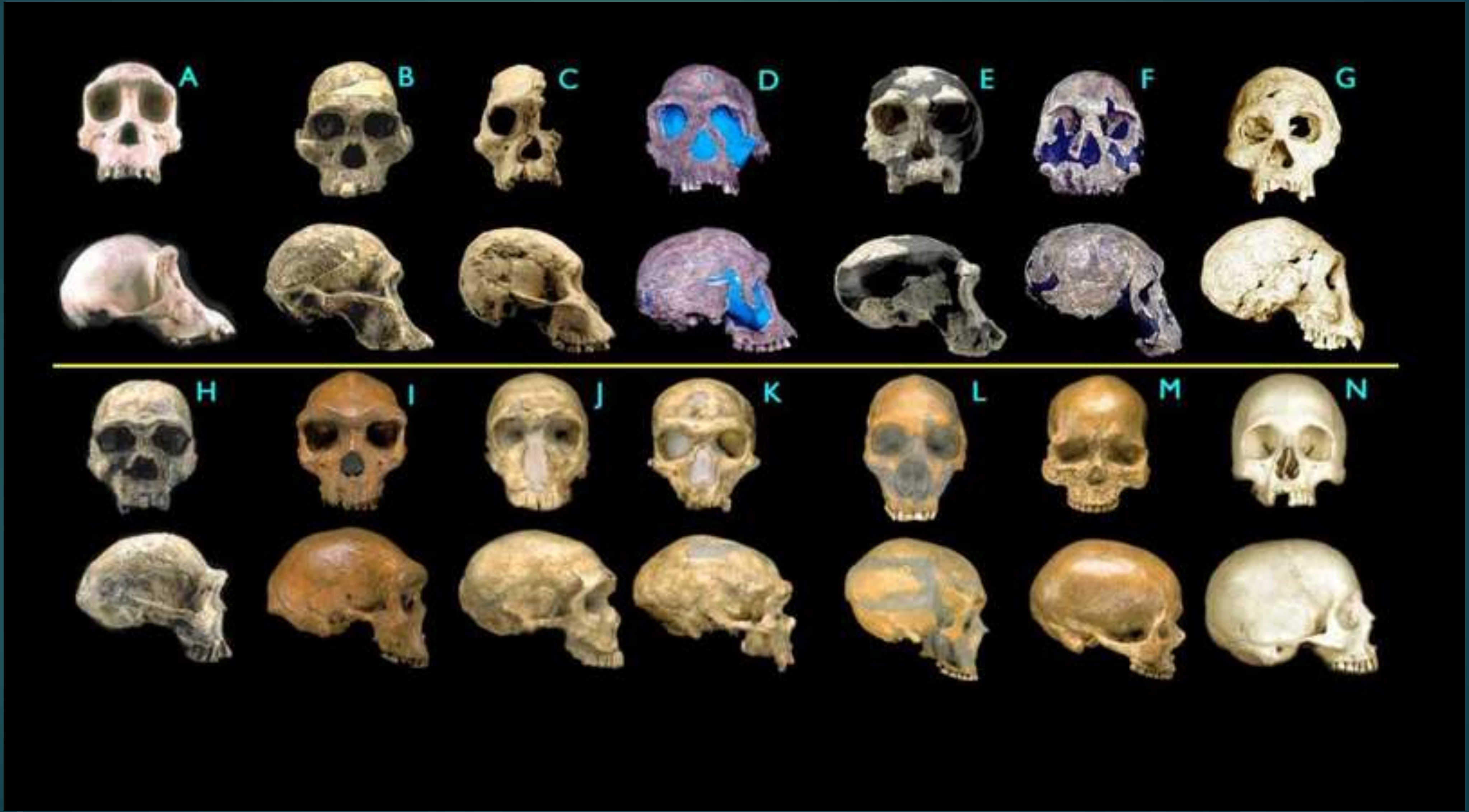


- Coincided with unstable weather (4 ice ages)

...And Then There Was One

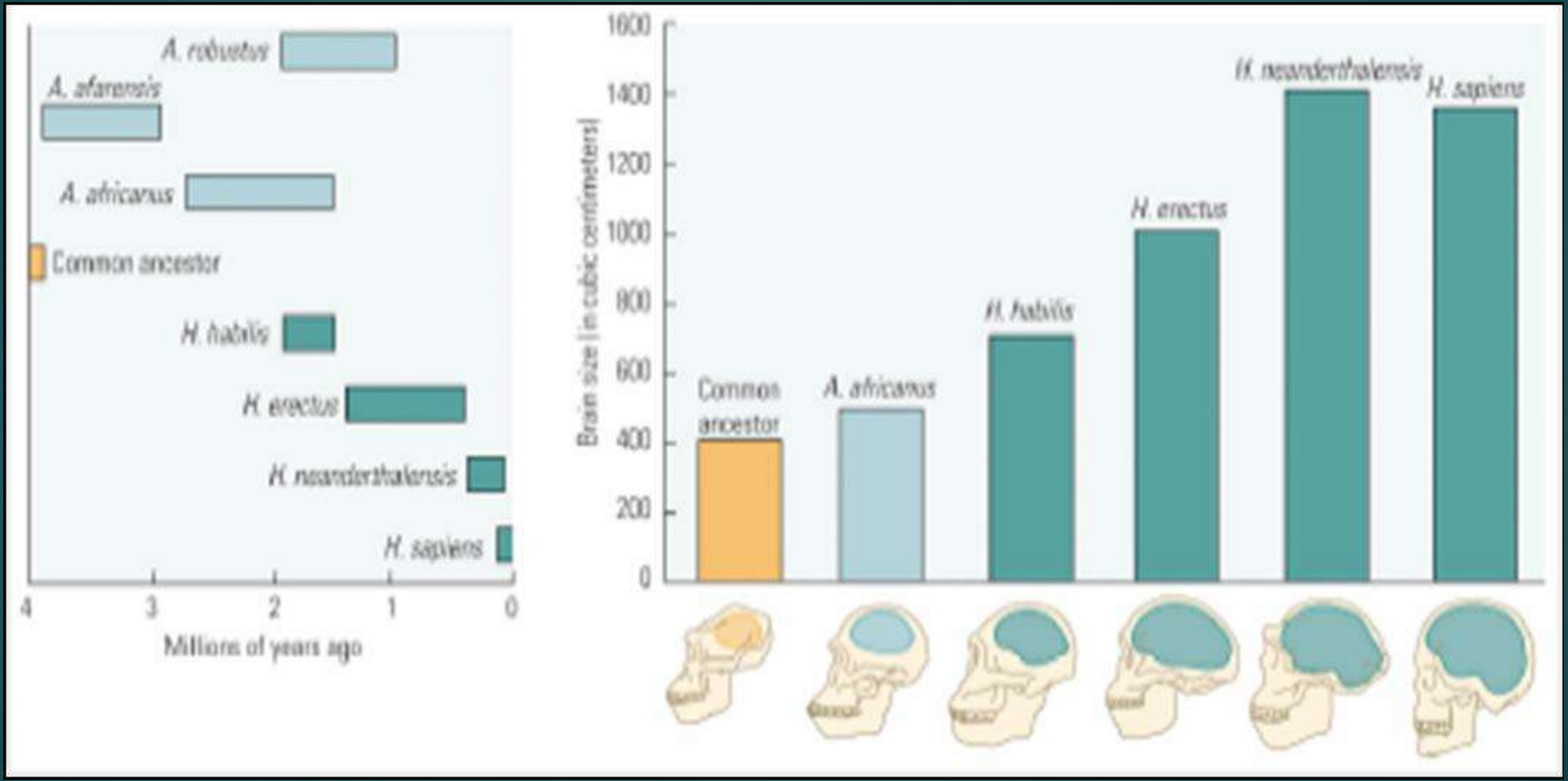
- **23 + Species of Extinct Humans**
- Ardipithecus ramidus
  Australopithecus anamensis
  Australopithecus afarensis
  Australopithecus bahrelghazali
  Australopithecus aethiopicus
  Paranthropus boisei
  Paranthropus robustus
  Australopithecus africanus
  Australopithecus garhi
  Homo rudolfensis
  Homo habilis
  Homo ergaster
  Homo erectus
  Homo antecessor
  Homo heidelbegensis
  Homo neanderthalensis
- Homo sapiens

14 Fossil Hominin Skull Shapes



Homo habilis to Homo sapiens: brains from 300 to 1350cc

Brain size increased in hominid line



Hominid Brain Volume Expansion

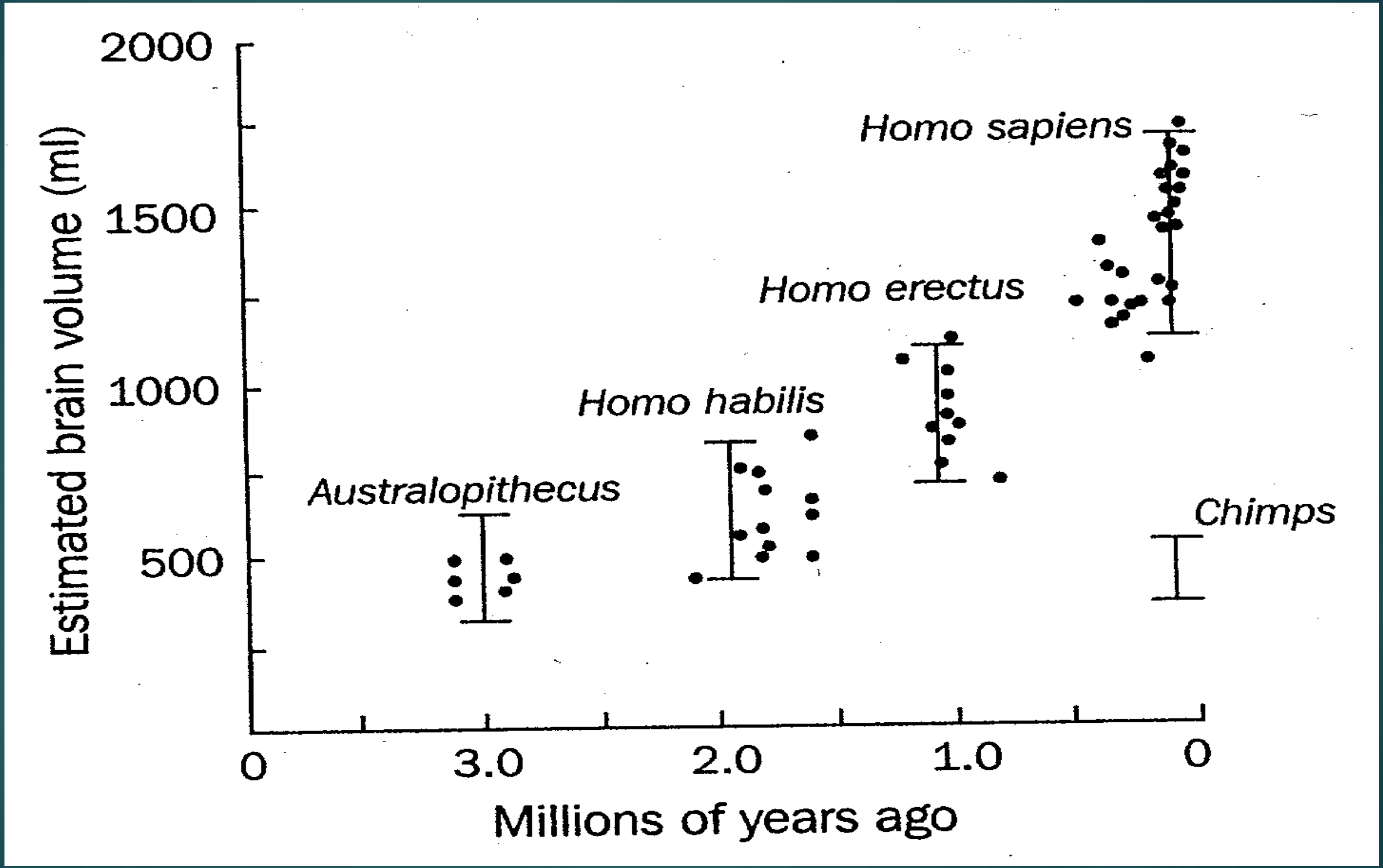


Diagram from Cartwright, 2000, p175.

Brain volume for hominins

Hominin Species	**Millions of Years Ago**	**Average Brain Volume (mL)**
Australopithecus afarensis	3.5	440
Australopithecus africanus	2.5	450
Paranthropus robustus	2.0	520
Paranthropus bosei	1.5	515
Homo rudolfensis	2.0	700
Homo habilis	1.8	575
Homo ergaster	1.8	800
Homo erectus	0.5	1,100
Homo heidelbergensis	0.2	1,250
Homo neanderthalensis	0.05	1,500
Homo sapiens	0.08	1,350

First phase of hominid brain evolution: Australopithecines

- For the **first two thirds of our history**, the size of our ancestors' brains was within the range of those of other apes living today.
- *Australopithecus afarensis (Lucy)* had skulls with internal volumes of between 400 and 550 cc, whereas chimpanzee skulls hold around 400 cc and gorillas between 500 and 700 cc.
- During this time, *Australopithecine* brains started to show subtle changes in structure and shape as compared with apes.
- The neocortex had begun to expand, reorganizing its functions away from visual processing toward more forward regions of the brain.

Next phase: last 2 million years

- The final third of our evolution saw nearly all the action in brain size.
- *Homo habilis*, the first of our genus *Homo* who appeared 1.9 MYA, saw a modest hop in brain size, including an expansion of Broca's area.
- *Homo erectus*, 1.8 MYA, had brains averaging a bit larger than 600 cc.
- From here the species embarked on a slow upward march, reaching more than 1,000 cc by 500,000 years ago.
- *Homo sapiens* had brains within the range of people today, averaging 1,350 cc

Basic history of human brain

- About 7 MY, first hominids became bipedal with brains about 1/3rd of modern size (400cc)
- For 3-4 MY, their brain did not significantly grow, but maybe became larger as proportion of body size. Stone tools appear at 3.3 MYA.
- About 2 MYA, some hominids developed larger brains (650cc)
- 1.5 to 1 MY, brain expanded fairly rapidly, to 2/3rd of modern size (1000cc)
- Language developed somewhere in last 1.5 MY
- In last MY, brain increased to 1,400 cc
- MH appear in Africa 200 TYA.
- Material culture begins only in last 100,000 years
- Hominids got smarter as their brains got bigger

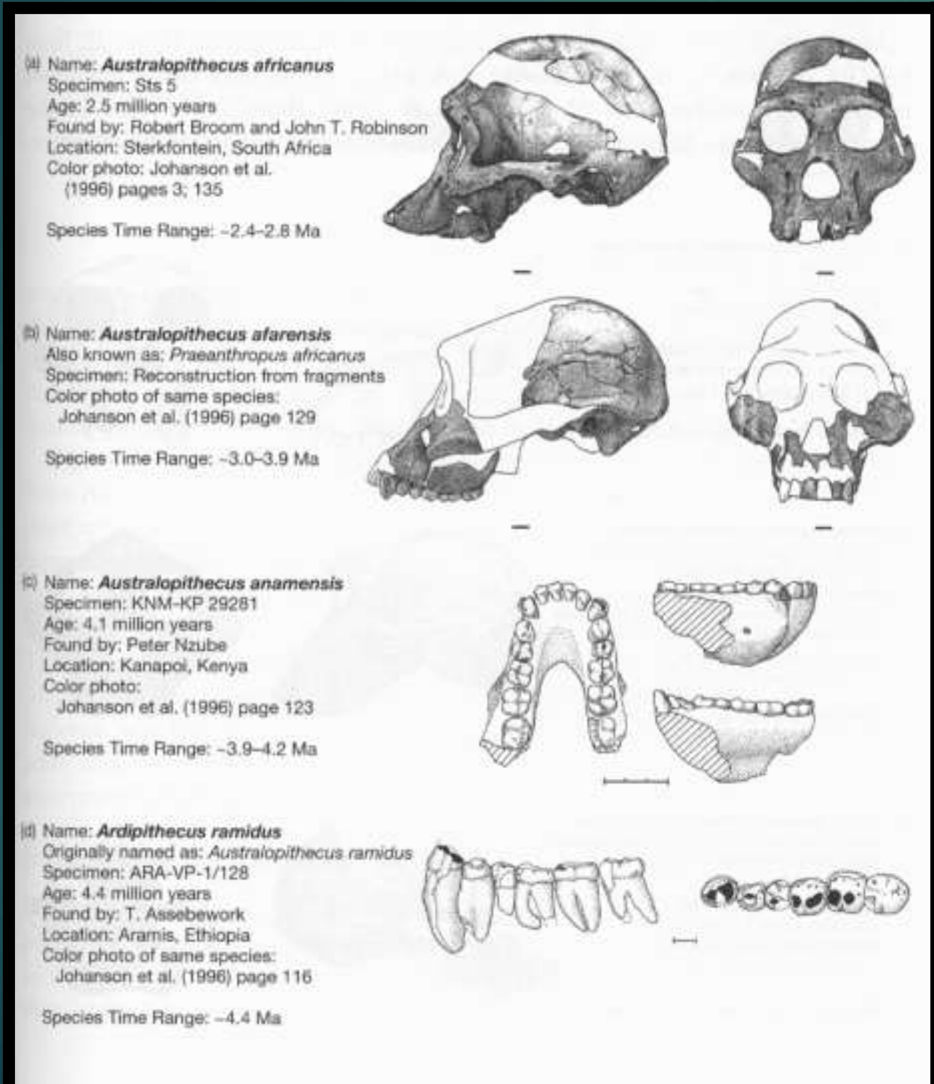
Brain Size & Human Evolution

- For most of hominid evolution, no selective advantage to having larger brain, between 7 to 2 million years ago (australopithecine phase). Species survived for a million years. This period included sociality, tool use, bipedalism.

- Hominids of australopithecine period exhibited an apelike pattern of brain volume stability over a 3 million year period.

- Does not mean there was no brain reorganization producing new cognitive advantages, i.e. stone tool making

Gracile Australopithecines



(a) Name: ***Australopithecus africanus***
Specimen: Sts 5
Age: 2.5 million years
Found by: Robert Broom and John T. Robinson
Location: Sterkfontein, South Africa
Color photo: Johanson et al. (1996) pages 3; 135

Species Time Range: ~2.4–2.8 Ma

(b) Name: ***Australopithecus afarensis***
Also known as: *Praeanthropus africanus*
Specimen: Reconstruction from fragments
Color photo of same species: Johanson et al. (1996) page 129

Species Time Range: ~3.0–3.9 Ma

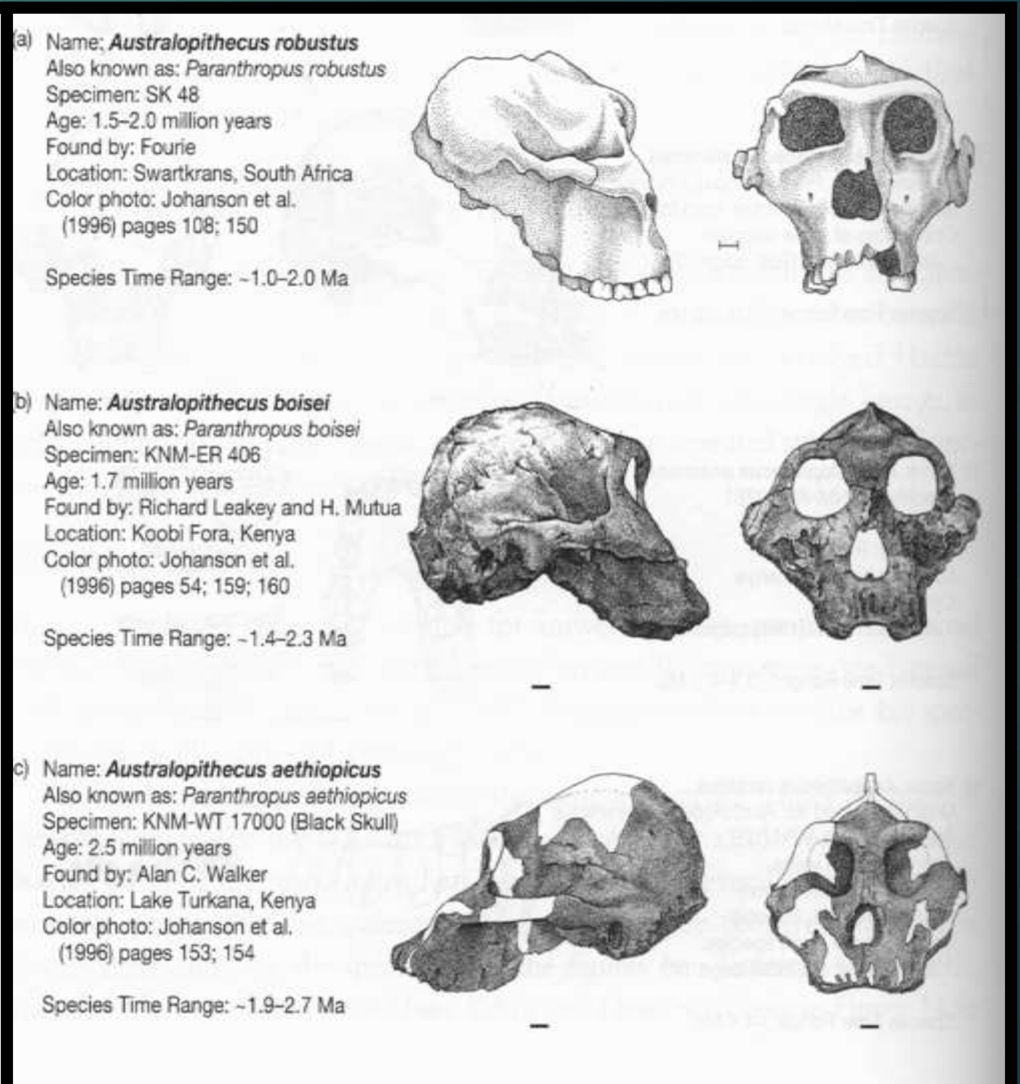
(c) Name: ***Australopithecus anamensis***
Specimen: KNM-KP 29281
Age: 4.1 million years
Found by: Peter Nzube
Location: Kanapoi, Kenya
Color photo: Johanson et al. (1996) page 123

Species Time Range: ~3.9–4.2 Ma

(d) Name: ***Ardipithecus ramidus***
Originally named as: *Australopithecus ramidus*
Specimen: ARA-VP-1/128
Age: 4.4 million years
Found by: T. Assebework
Location: Aramis, Ethiopia
Color photo of same species: Johanson et al. (1996) page 116

Species Time Range: ~4.4 Ma

Robust Australopithecines *Paranthropus*



(a) Name: ***Australopithecus robustus***
Also known as: *Paranthropus robustus*
Specimen: SK 48
Age: 1.5–2.0 million years
Found by: Fourie
Location: Swartkrans, South Africa
Color photo: Johanson et al. (1996) pages 108; 150

Species Time Range: ~1.0–2.0 Ma

(b) Name: ***Australopithecus boisei***
Also known as: *Paranthropus boisei*
Specimen: KNM-ER 406
Age: 1.7 million years
Found by: Richard Leakey and H. Mutua
Location: Koobi Fora, Kenya
Color photo: Johanson et al. (1996) pages 54; 159; 160

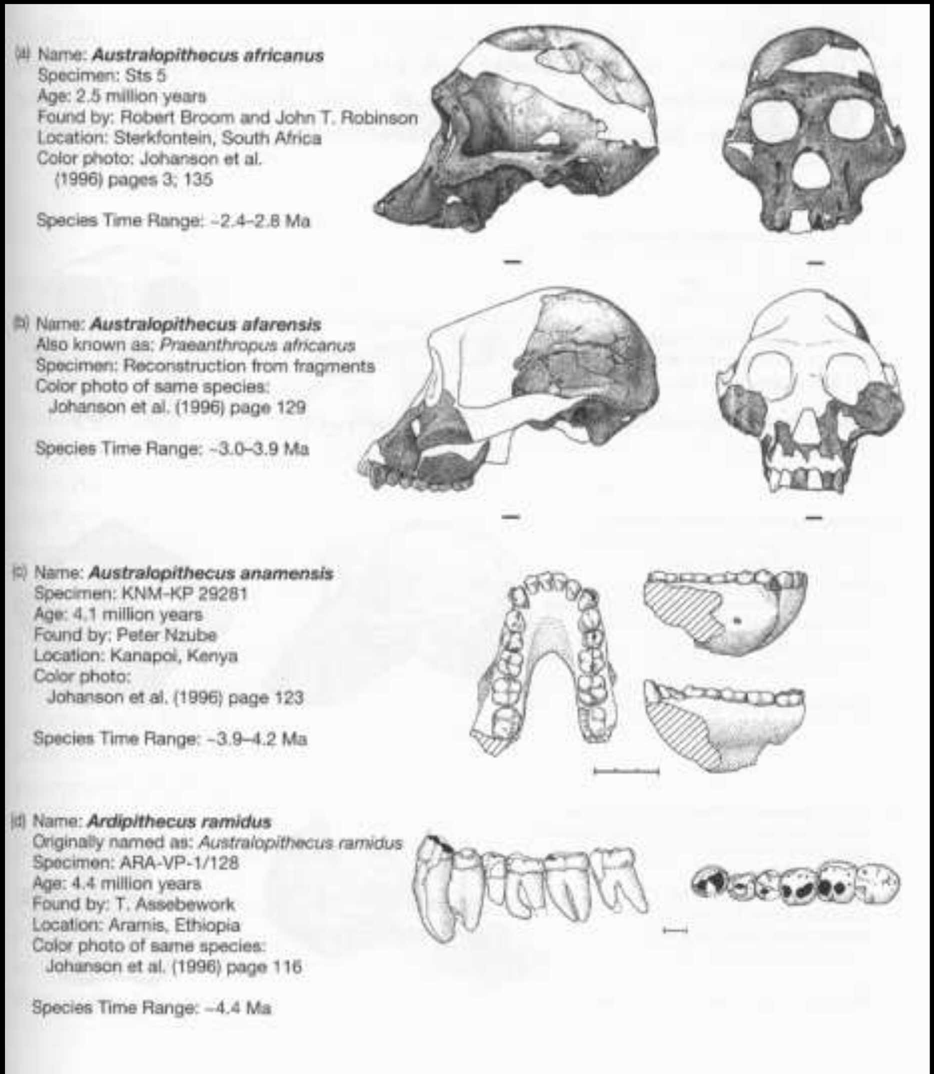
Species Time Range: ~1.4–2.3 Ma

(c) Name: ***Australopithecus aethiopicus***
Also known as: *Paranthropus aethiopicus*
Specimen: KNM-WT 17000 (Black Skull)
Age: 2.5 million years
Found by: Alan C. Walker
Location: Lake Turkana, Kenya
Color photo: Johanson et al. (1996) pages 153; 154

Species Time Range: ~1.9–2.7 Ma

Gracile Australopithecines

Archaic *Homo*



(a) Name: ***Australopithecus africanus***
Specimen: Sts 5
Age: 2.5 million years
Found by: Robert Broom and John T. Robinson
Location: Sterkfontein, South Africa
Color photo: Johanson et al. (1996) pages 3; 135

Species Time Range: ~2.4–2.8 Ma

(b) Name: ***Australopithecus afarensis***
Also known as: *Praeanthropus africanus*
Specimen: Reconstruction from fragments
Color photo of same species: Johanson et al. (1996) page 129

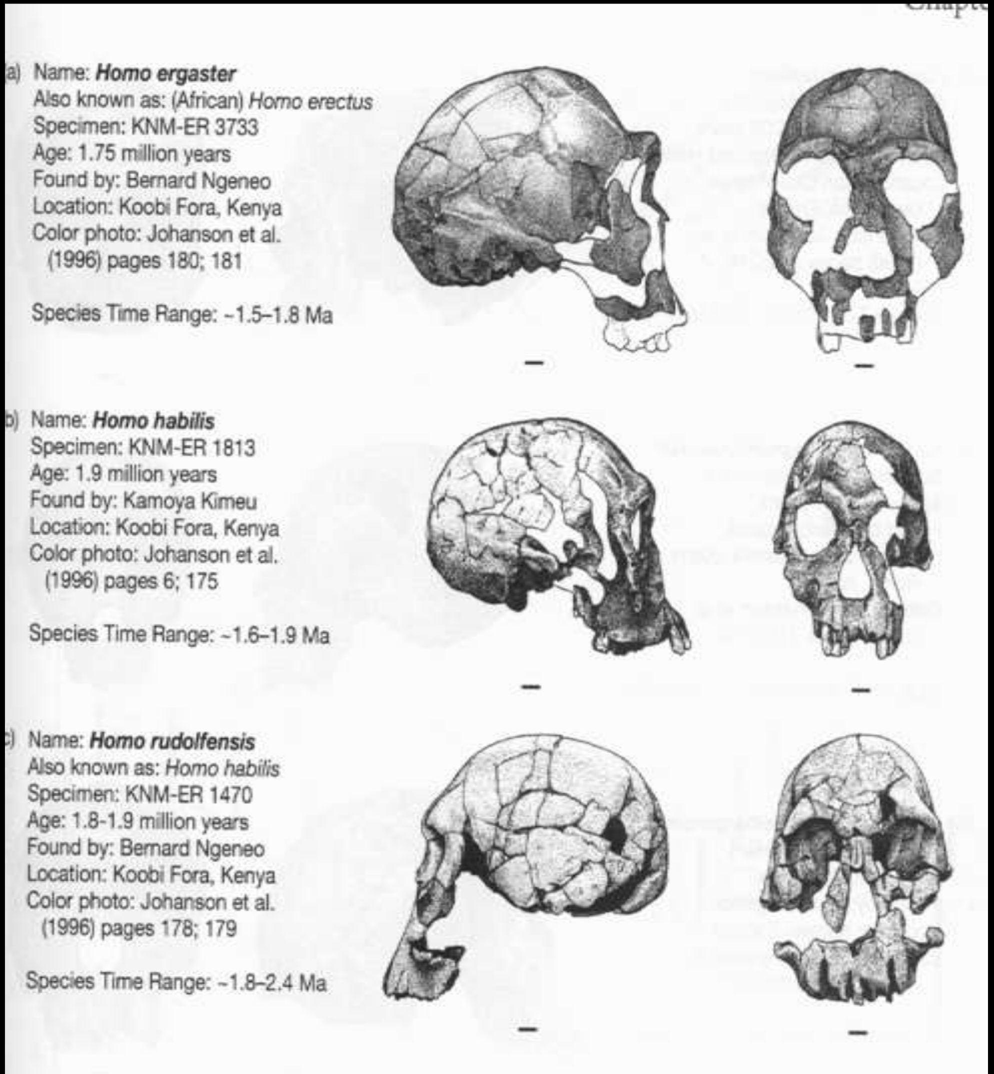
Species Time Range: ~3.0–3.9 Ma

(c) Name: ***Australopithecus anamensis***
Specimen: KNM-KP 29281
Age: 4.1 million years
Found by: Peter Nzube
Location: Kanapoi, Kenya
Color photo: Johanson et al. (1996) page 123

Species Time Range: ~3.9–4.2 Ma

(d) Name: ***Ardipithecus ramidus***
Originally named as: *Australopithecus ramidus*
Specimen: ARA-VP-1/128
Age: 4.4 million years
Found by: T. Assebework
Location: Aramis, Ethiopia
Color photo of same species: Johanson et al. (1996) page 116

Species Time Range: ~4.4 Ma



(a) Name: ***Homo ergaster***
Also known as: (African) *Homo erectus*
Specimen: KNM-ER 3733
Age: 1.75 million years
Found by: Bernard Ngeneo
Location: Koobi Fora, Kenya
Color photo: Johanson et al. (1996) pages 180; 181

Species Time Range: ~1.5–1.8 Ma

(b) Name: ***Homo habilis***
Specimen: KNM-ER 1813
Age: 1.9 million years
Found by: Kamoya Kimeu
Location: Koobi Fora, Kenya
Color photo: Johanson et al. (1996) pages 6; 175

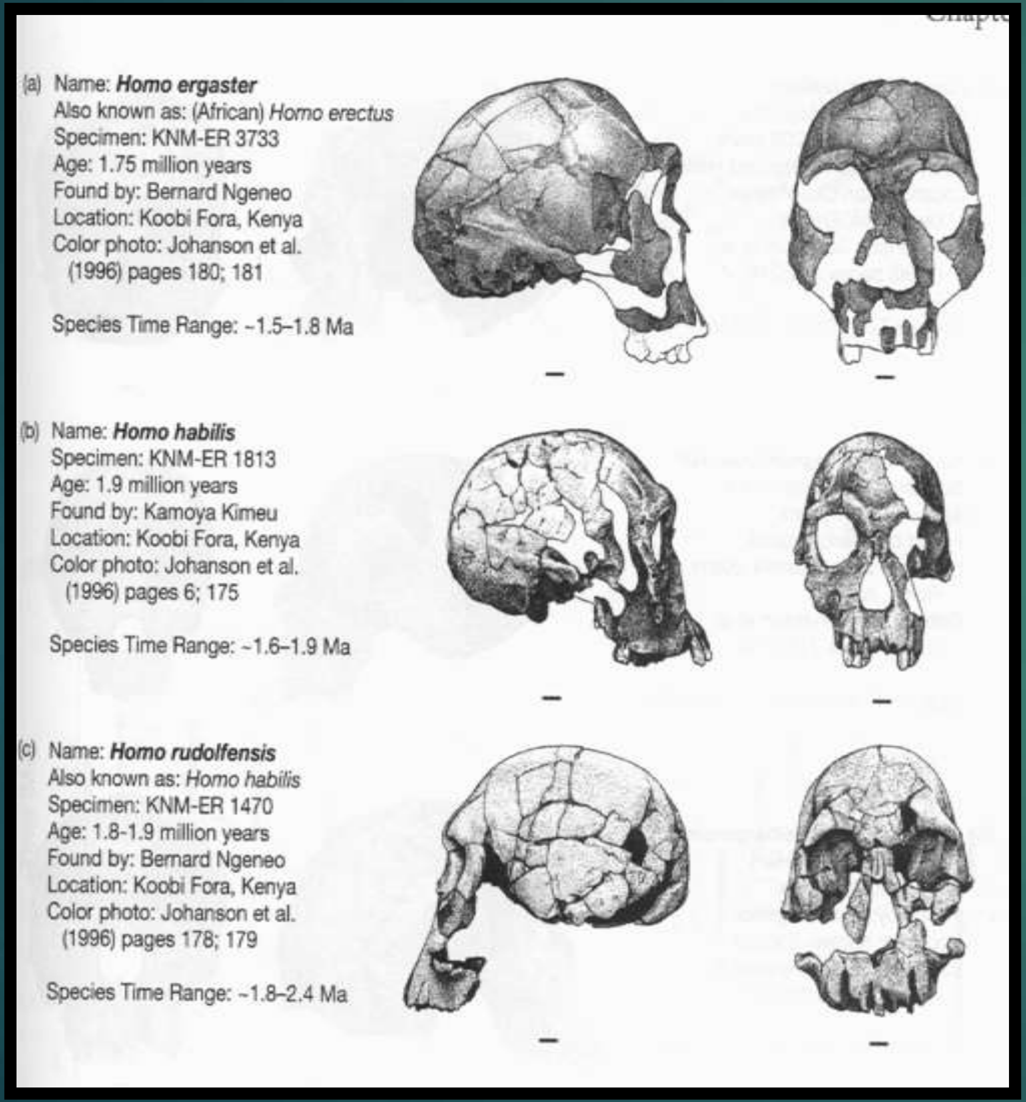
Species Time Range: ~1.6–1.9 Ma

(c) Name: ***Homo rudolfensis***
Also known as: *Homo habilis*
Specimen: KNM-ER 1470
Age: 1.8-1.9 million years
Found by: Bernard Ngeneo
Location: Koobi Fora, Kenya
Color photo: Johanson et al. (1996) pages 178; 179

Species Time Range: ~1.8–2.4 Ma

Archaic *Homo*

Modern *Homo*



(a) Name: **Homo ergaster**
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Age: 1.75 million years
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Location: Koobi Fora, Kenya
Color photo: Johanson et al. (1996) pages 180; 181

Species Time Range: ~1.5–1.8 Ma

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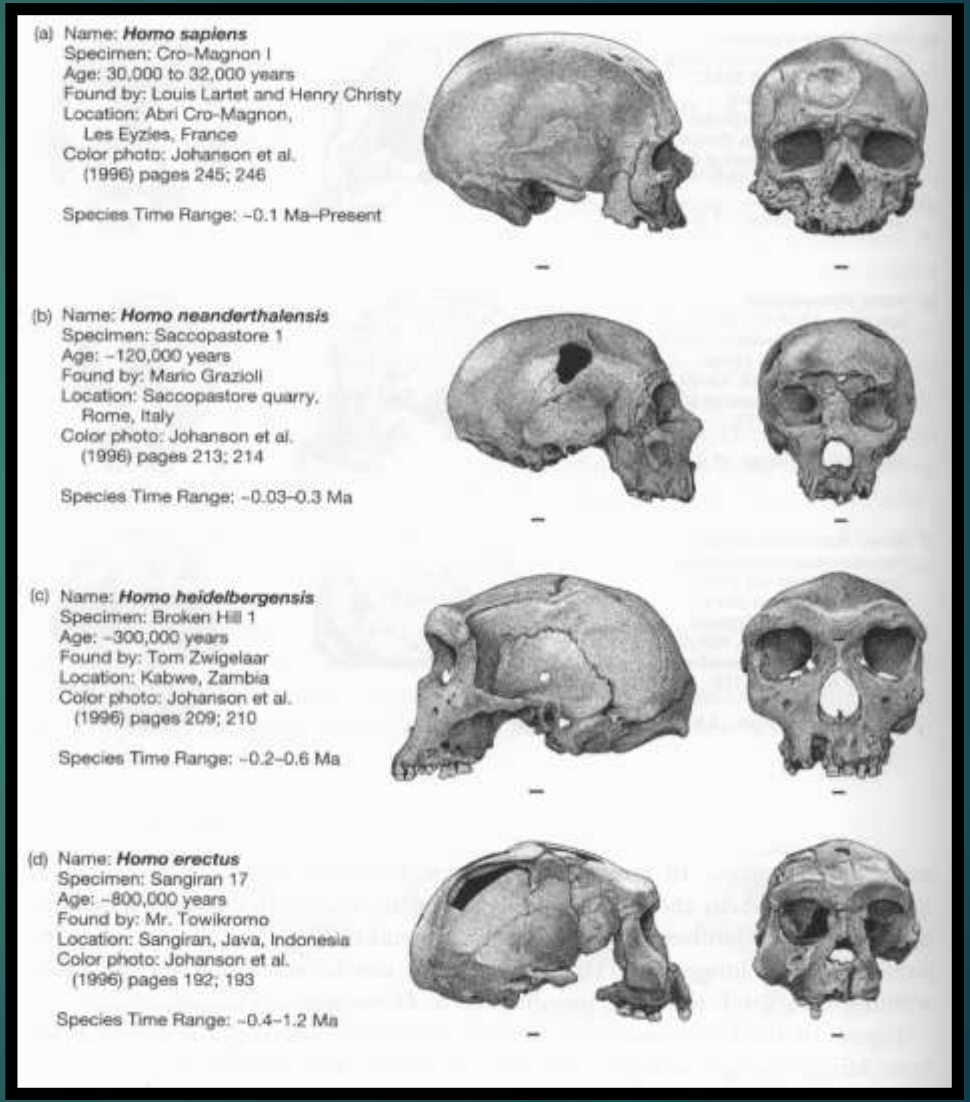
Specimen: KNM-ER 1813
Age: 1.9 million years
Found by: Kamoya Kimeu
Location: Koobi Fora, Kenya
Color photo: Johanson et al. (1996) pages 6; 175

Species Time Range: ~1.6–1.9 Ma

(c) Name: **Homo rudolfensis**
Also known as: *Homo habilis*
Specimen: KNM-ER 1470
Age: 1.8-1.9 million years
Found by: Bernard Ngeneo
Location: Koobi Fora, Kenya
Color photo: Johanson et al. (1996) pages 178; 179

Species Time Range: ~1.8–2.4 Ma



(a) Name: **Homo sapiens**
Specimen: Cro-Magnon I
Age: 30,000 to 32,000 years
Found by: Louis Lartet and Henry Christy
Location: Abri Cro-Magnon, Les Eyzies, France
Color photo: Johanson et al. (1996) pages 245; 246

Species Time Range: ~0.1 Ma–Present

(b) Name: **Homo neanderthalensis**
Specimen: Saccopastore 1
Age: ~120,000 years
Found by: Mario Grazioli
Location: Saccopastore quarry, Rome, Italy
Color photo: Johanson et al. (1996) pages 213; 214

Species Time Range: ~0.03–0.3 Ma

(c) Name: **Homo heidelbergensis**
Specimen: Broken Hill 1
Age: ~300,000 years
Found by: Tom Zwigelaar
Location: Kabwe, Zambia
Color photo: Johanson et al. (1996) pages 209; 210

Species Time Range: ~0.2–0.6 Ma

(d) Name: **Homo erectus**
Specimen: Sangiran 17
Age: ~800,000 years
Found by: Mr. Towikromo
Location: Sangiran, Java, Indonesia
Color photo: Johanson et al. (1996) pages 192; 193

Species Time Range: ~0.4–1.2 Ma

Australopithecus, i.e. Lucy

- ***Australopithecus* lived:** 4.2 to 2.0 MYA
- Lucy, *Australopithecus afarensis* (1974)
- Brain **size:** 310 - 530 cc
- **Intelligence:** used stone tools, probably had some form of language
- **Other:** walked upright (obligate *bipedality)*

Homo habilis (*Australopithecus? habilis*)

- 'Habilis' because of 'handy man' (1960)
- Lived 2.3-1.6 MYA.
  Overlaps Australopithecenes & Paranthropus.
- Ape-like body.
- Skeletal traits variable.
  H. rudolfensis for robust variant.
- 580-750cc. brain.
  Is the big jump with *H. habilis* or with *H. erectus*?
- Used stone tools; no longer the originator.
- *Crocodylus anthropophagus* (Human eating crocodile).

Homo habilis (skull OH 24)

Source: http://www.mnh.si.edu/anthro/humanorigins/ha/a_tree.html

Cranial Capacity in Fossil Hominids

- Expansion in cranial capacity, relative to great apes, was modest from 6 to 2 million years ago; no selective advantage for increased brain size; but functional reorganization?
- Bipedalism and tool making, exploitation of new environments and food sources
- The last 2 million years have been characterized by periods of rapid expansion.
- New Exception: LB1, the “Hobbit”, from Flores, Indonesia: 380 cc, 18 kya

Homo erectus

- ‘Erect man’ (1976).
- 1.8 mya to .1 mya: longest tenure on earth
- Larger body than earlier hominins with modern proportions (savanna populations).
- First great migrator (left Africa for Eurasia); wide range of environments
- Human-like traits: Hunting, use of fire, cooking
- Much variability in cranial capacity in H. erectus (600 to 1070 cc)
- Increase in cc in *H. heidelbergensis (archaic modern)* compared to *H. erectus* may indicate a speciation event

‘Nariokotome Boy’
KNM-WT 15000
Remains found at Lake Turkana
Photo by Kenneth Garrett/National Geographic

Leigh, 1992; Rightmire, 2004

Homo neanderthalensis

- **Neanderthals lived:** 420,000 to 28,500 years ago
- Brain **size:** about 1200-1500 cc
- **Intelligence:** made stone tools, had vocal language
- **Other:** *Homo sapiens Neanderthalis* (Neandertals) lived at the same time as anatomically modern humans, but died out about 30,000 years ago.

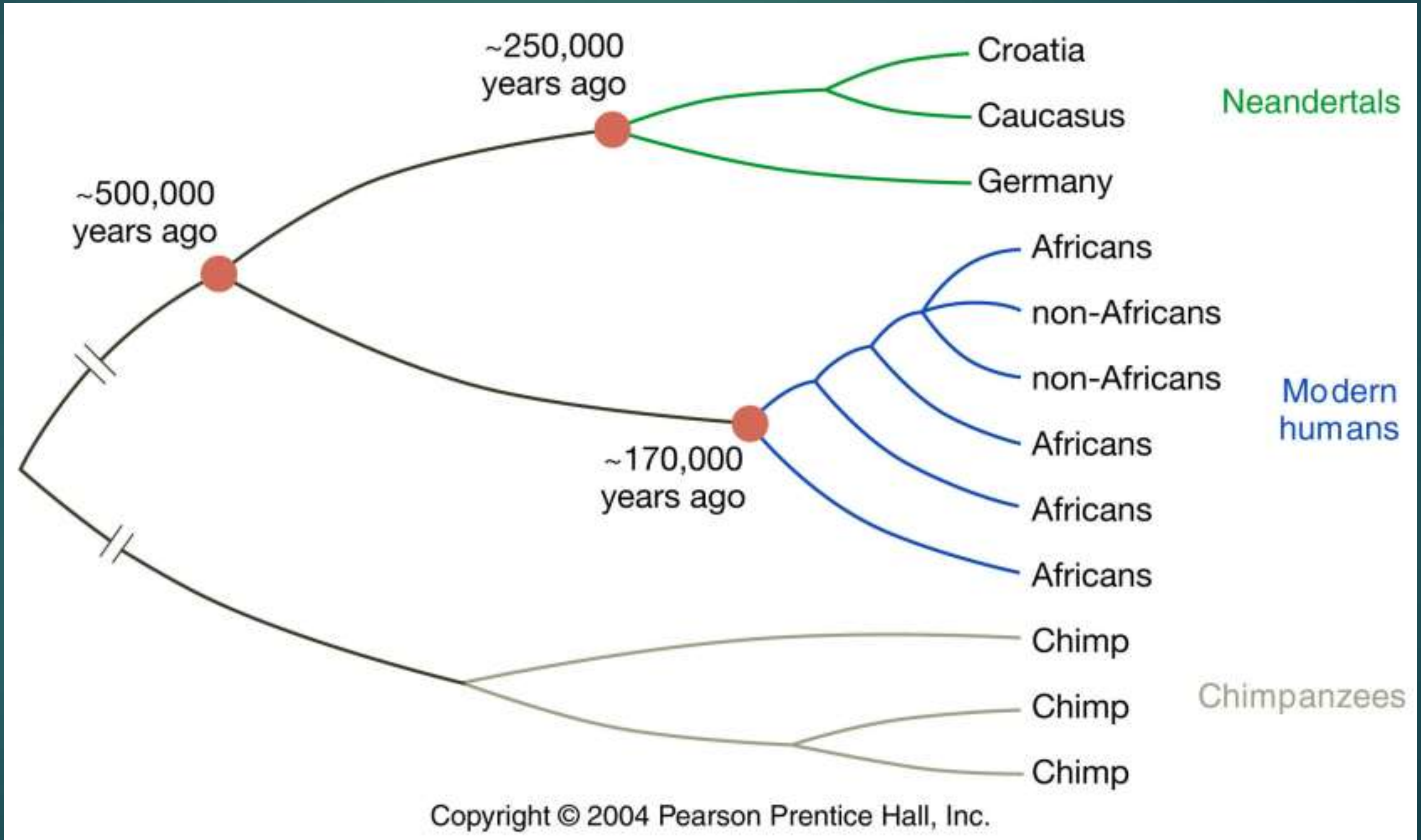
Neandertal

- Less skull globularization:
  - similar in large endocranial capacity to *H. sapiens*,
  - differ in adult & developmental endocranial shape.
  - Show that cranial growth trajectories have influenced shape of modern human brain, independent of size change.

- Neandertals lack early postnatal globularization phase seen in modern humans; results in more elongated cranial shape

- Neandertals had less Parietal-temporal area, bigger Frontal & Occipital

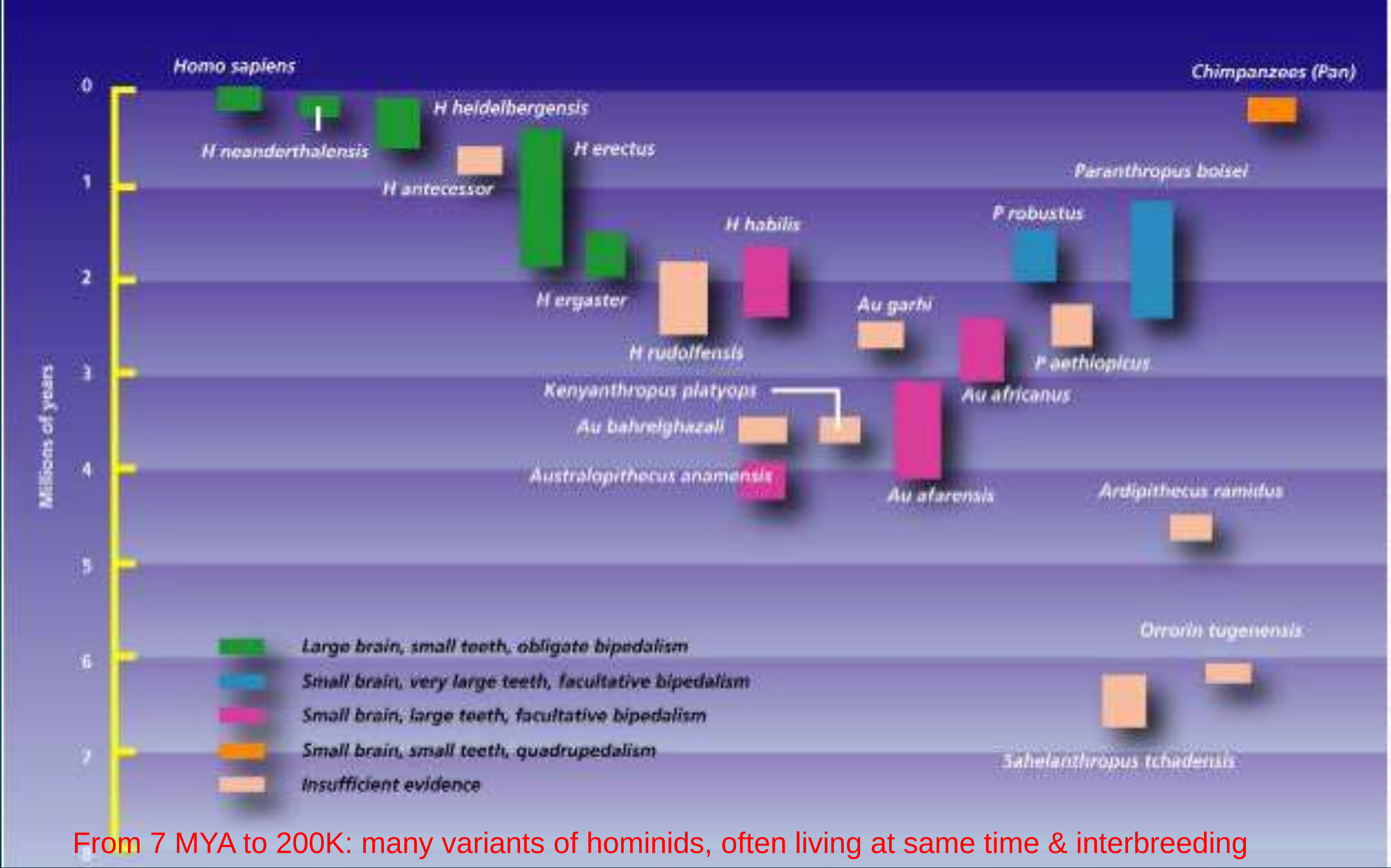
Neanderthals are distinct from *Homo sapiens*



Homo sapiens

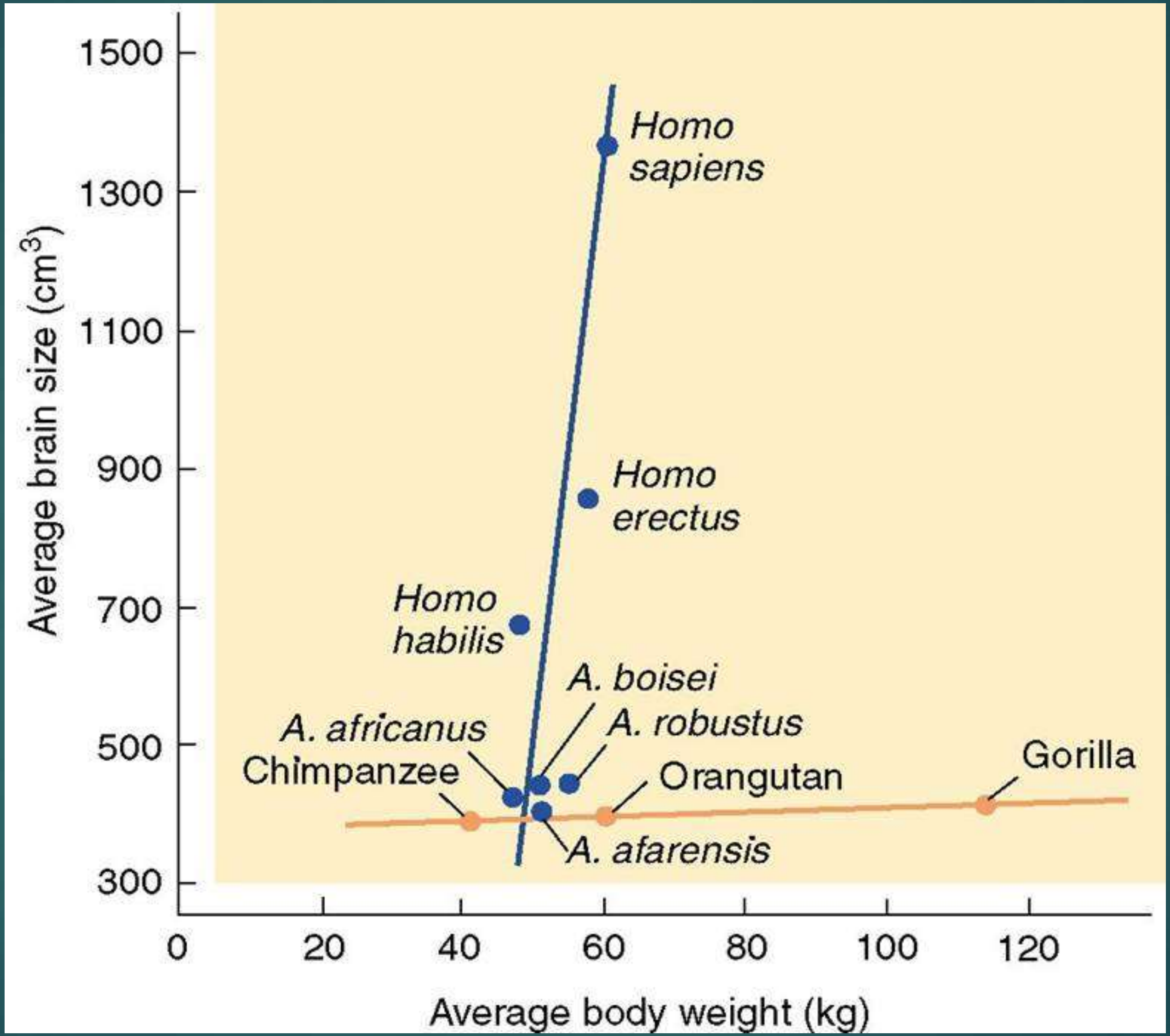
Homo sapiens Neandertal

- **Modern Humans:** 200,000 years ago to the present
- **Brain size:** 1350 cc
- **Intelligence:** made new kinds of tools, had complex language
- **Largest group size:** 150-200
- New geometric morphometrics have shown parietal & cerebellar expansion in modern humans (resulting in globular skull), especially in early postnatal development



From 7 MYA to 200K: many variants of hominids, often living at same time & interbreeding

Once humans started increasing brain size, it happened rapidly



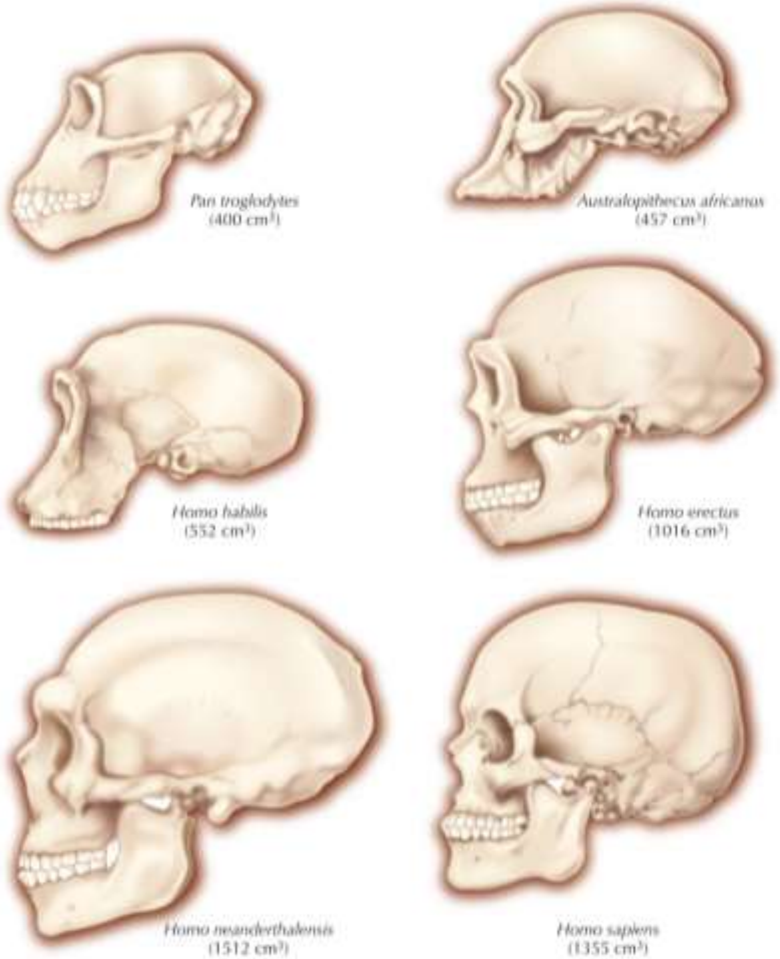


FIGURE 25.11. Series of hominid skulls showing different brain sizes. Notice that *Homo neanderthalensis* had a greater volume that that of modern humans.

Ever larger hominid skull sizes:

Note Neandertal had greater volume than Moderns

Variety of brain changes

- Modern human-specific traits have been described at many different levels of neural organization:
  - gross brain size,
  - relative extent of neocortical areas,
  - asymmetry,
  - developmental patterning,
  - distribution of cell types,
  - histology
  - gene expression.
- Changes in structural modularity and connectivity interact with variation in molecular and neurochemical signaling to determine brain function.

Cytoarchitectural changes: no cortical uniformity

- Changes in processing power of cortical neurons: contents of 1 squared mm of neurons are not uniform across species

- In primates, average number of neurons under 1 squared mm of cortex varies tremendously; total surface area of cortex increases slower than neuron number

- Minicolumns (single-neuron wide vertical arrays through cortical layers):
  - primate comparisons show variability in neuron density, horizontal spacing, amount of neuropil space;
  - in frontal lobe, proportionally (30%) more neuropil (= more processing power) in Broca's area and Area 10

Cytoarchitectural changes

- Fusiform gyrus: humans larger neurons and increased neuropil space, esp. in left hemisphere
- V1: Minicolumns are larger and more variable
- Humans have unique astroglial specializations (have longer processes and increased branching complexity)

Why doesn't everyone have a large brain?

- If large brains enable animals to deal better with changing and unpredictable environments, then why don't all species have large and complex brains?

- In fact animals with large brains are rare, probably due to the costs involved:

  - Extremely energy demanding; compete with other body organs for resources.

  - Long time to mature, which limits the rate at which an individual can reproduce; large-brained infants are heavily dependent upon their parents.

  - More prone to damage and malfunction.

Specializations in *Homo sapiens*

- Gaze-following and joint attention: chimpanzees and humans share many aspects of gaze-following behavior

- Pointing is commonplace in captive chimpanzees and virtually absent in wild chimpanzees; ecological epigenesis

- Complex Theory of Mind: Mirror self-recognition and chimpanzee gaze-following have been widely interpreted to indicate that chimpanzees and other great apes have a ‘theory of mind’ (mental state attribution)

Specializations in *Homo sapiens* 2

- Learning by Imitation: only humans are capable of differentiating between a correct ‘intentional’ response and an incorrect ‘unintentional’ response, and of engaging in counterfactual (past that did not happen) reasoning

- Language: most distinctive feature of human behavior; modality independent; nonhuman animals do not display similar flexibility of modality or of both comprehending and producing hierarchically recursive structures

Large brain size

- The single most obvious neuroanatomical specialization of *Homo sapiens* is large absolute and relative size of the brain.

- All living hominids have large brain sizes in absolute terms and in some measures of relative size.

- Similarly, the LCA is expected to have had a brain mass of approximately 300–400cc.

Large brain size

- Averaging about 1350cc, human brains are approximately three times larger than those of great apes.
- Humans also outrank all other animals in measures of encephalization, the degree to which brain mass exceeds expectations based on allometric scaling for body mass.
- Starting at about 1.8 Ma, beginning with *Homo erectus*, brain expansion in hominins occurred at a much more rapid pace

What’s really different about *Homo sapiens*?

- Bipedality
- Largest brain for body size
- Lateralization of brain
- Advanced theory of mind
- Symbolic ability
- Complexity of technology
- Complexity of language
- Art
- Use complex burial rites

What makes Humans different

- Making tools to make tools
- Cooking and food process: French and California cuisine
- Reading and writing
- Music, dance, visual arts
- Mathematics and science
- Sports, theater

The Intellectual Explosion: 100,000-50,000K.

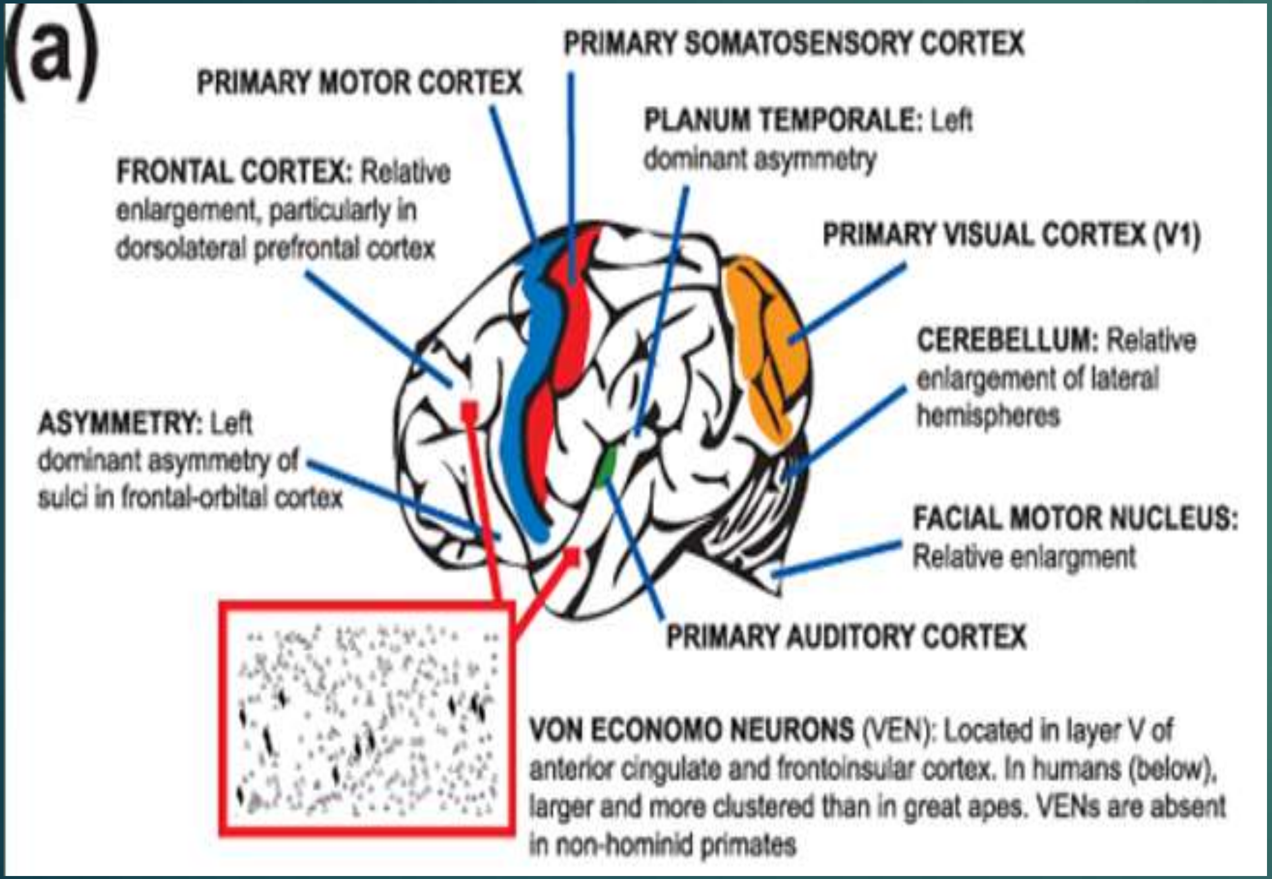
- *Homo sapiens* had large brains but did not show significant creativity or intelligence for 100,000 years. Only between 100,000-35,000 years ago did the following appear:

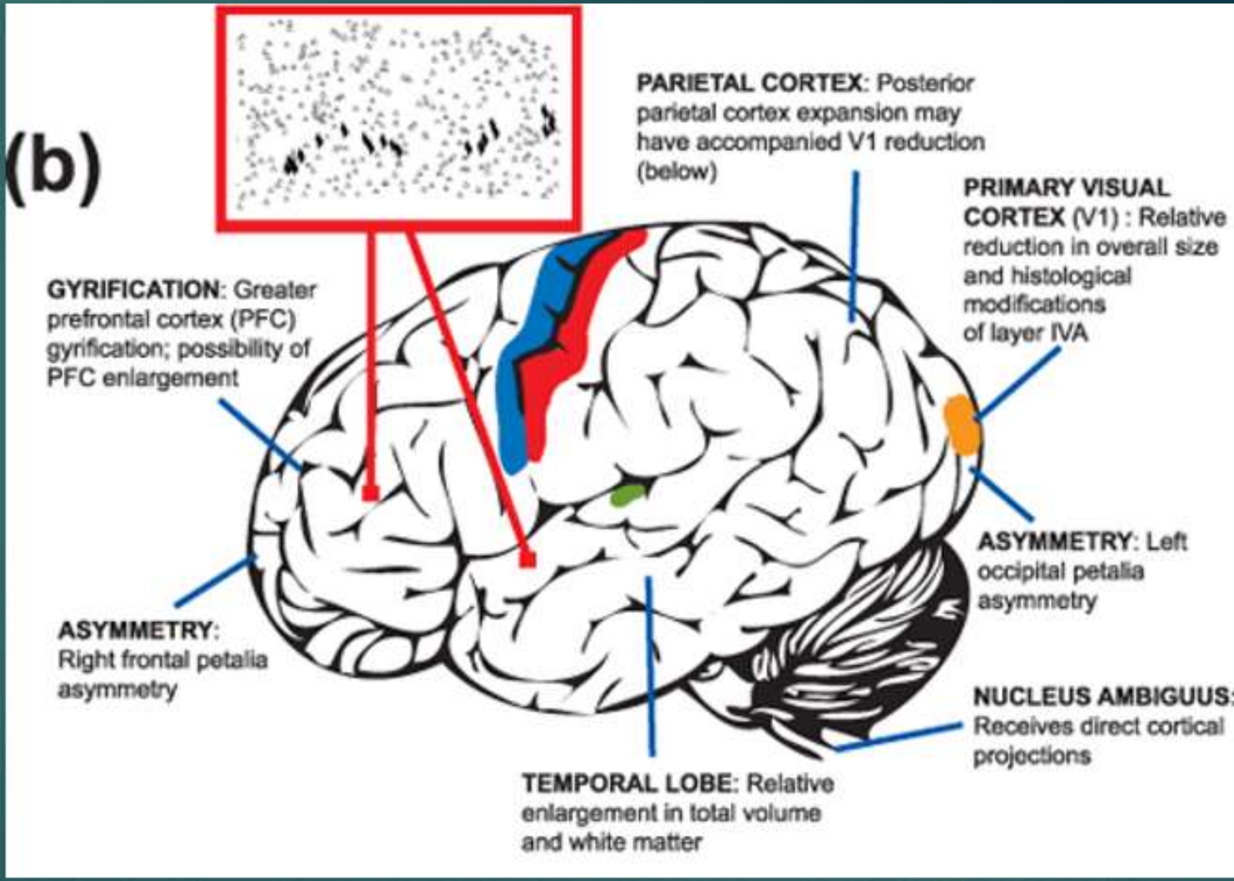
- Advanced culture.
- Sophisticated tools.
- Long-distance transport.
- Social networks.
- Large dwellings.
- Tailored clothing.
- Rituals.
- Art.

A natural history of the human mind: tracing evolutionary changes in brain and cognition in LCA & MHs

LCA

Modern Human





Journal of Anatomy
Volume 212, Issue 4, pages 426-454, 1 APR 2008 DOI: 10.1111/j.1469-7580.2008.00868.x
http://onlinelibrary.wiley.com/doi/10.1111/j.1469-7580.2008.00868.x/full#f1

More Wiring creates problems

- Another cost that goes along with a big brain is the need to reorganize its wiring.
- Issue of speed of processing: As brain size increases, there is increased time to get information from one place to another.
- A solution to this is to do things locally: only connect those parts of the brain that have to be connected, and avoid the need for communication between hemispheres by making different sides of the brain do different things.

Wiring

- Reorganization: A big brain can also be made more efficient by organizing it into more subdivisions, rather like splitting a company into departments

- Overall, because a bigger brain *per se* would not work, brain reorganization and size increase probably occurred in parallel during human brain evolution.

Gyrification: better wiring

- Accompanying enlarged absolute brain size, the LCA probably also had a high degree of cerebral cortical gyrification as compared with other primates.

- The amount of gyral folding in living great apes suggests that there is relatively more associational connectivity between neighboring cortical regions

- Gyri are thought to form due to tension-based mechanisms that bring strongly interconnected regions more closely together, achieving spatially compact wiring

Lateral cerebellum

- Lateral cerebellar hemisphere of hominoids is larger than would be predicted by allometry in monkeys.

- This portion of the cerebellum participates in a variety of functions including planning of complex motor patterns, sensory discrimination, attention shifting, and procedural learning.

- The cerebellar specializations of apes are most likely associated with their suspensory mode of locomotion to allow for feeding on fruits at the tips of branches given a large body size

Prolonged dependency = greater neuroplasticity

- Prolonged development phases have been shown to relate to the evolution of large brain size.
- Extended period of offspring dependency, combined with more slowly maturing neuronal pathways in the LCA, would have provided an opportunity for learning in a social environment to strongly shape neuroplastic changes in the developing brain.

Brain size: developmental cost hypothesis

- Brain size variation in mammals correlates with developmental life histories.
- Larger brains correlate with:
  - Longer gestations,
  - Longer pregnancy & breast feeding
  - Later maturity,
  - Increased longevity.

Brown, 2011

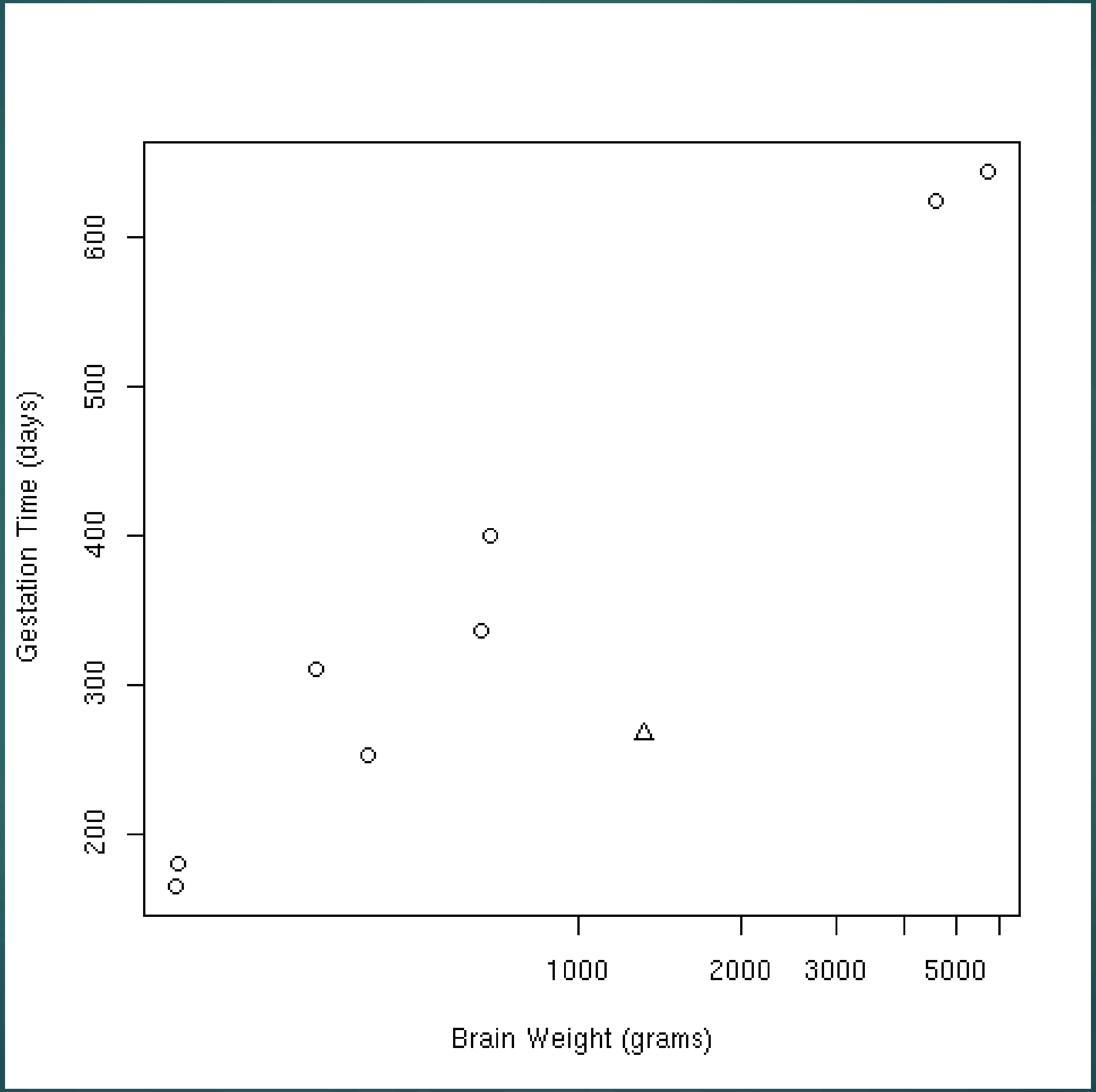
Developmental cost hypothesis 2

- Length of the pregnancy determines brain size at birth and the period of lactation decides brain growth after birth

- Developmental costs (larger brains take longer to grow) and cognitive benefits (large brains enhance survival and increase lifespan).

- Brain growth correlates specifically with duration of the relevant phases of maternal investment (gestation and lactation); mothers with higher BMR fuel faster fetal brain growth

Brain weight increases with gestation time



Large brains need longer dependency; more synaptogenesis

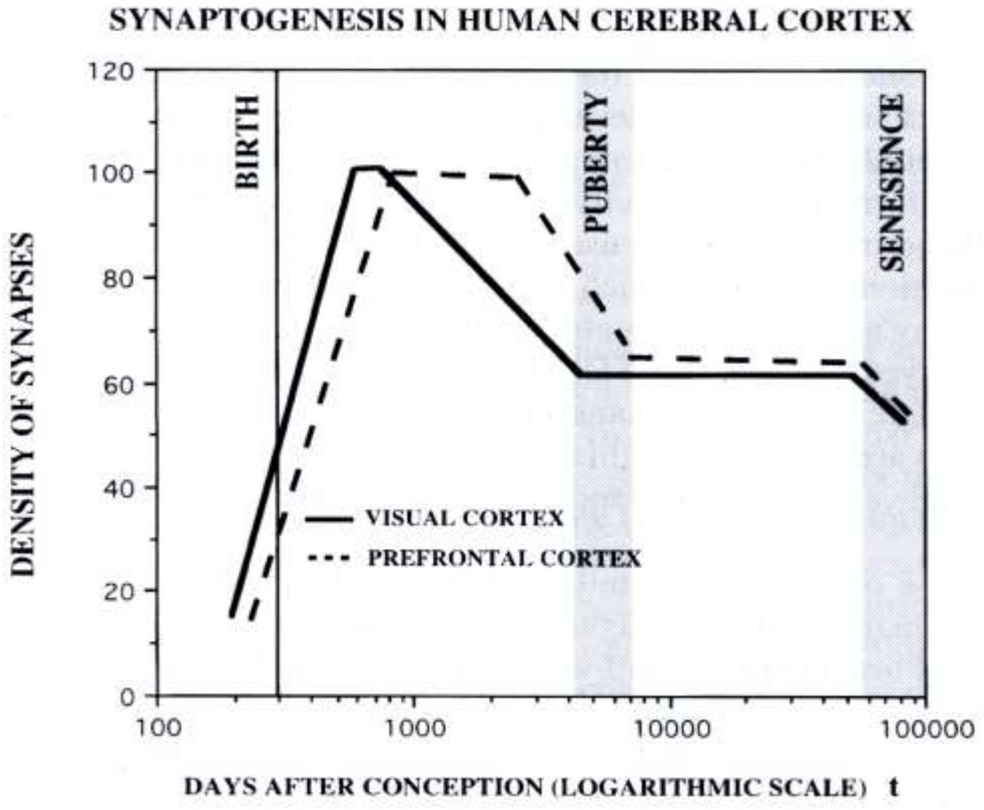
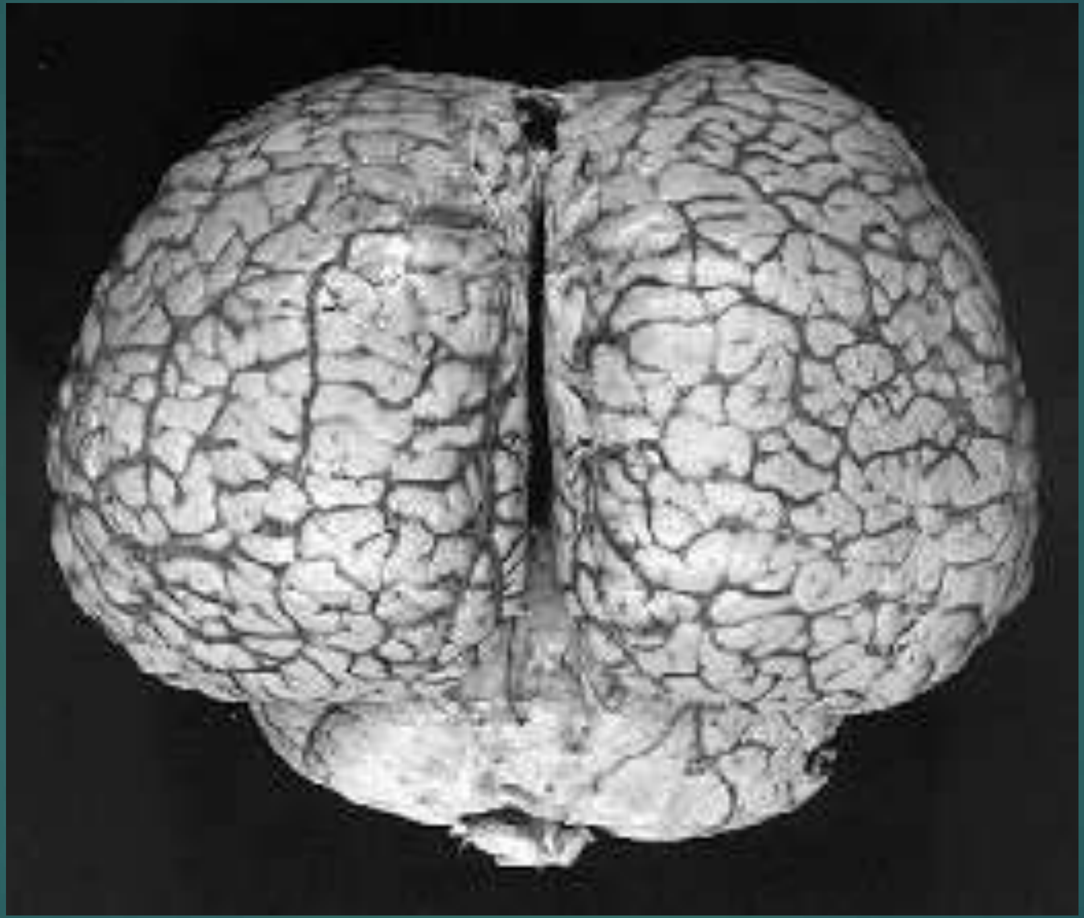


FIGURE 7. Changes in the relative density of synapses in the human cerebral cortex as a function of days after conception. Based on the data of Huttenlocker and Debholkar and reproduced from Bourgeois *et al.* in *Cognitive Neuroscience*, 2nd ed., edited by M.S. Gazzaniga, MIT Press (1999).

Professor Hermon Bumpus & his frozen birds:
First scientific evidence of bigger bodies need bigger brains

- 1898 Prof. Hermon Bumpus, after a severe winter storm, found 136 English sparrows freezing in the snow. He saved half in his lab.
- Birds who survived had longer wing bones, legs, and sternums, and a greater brain capacity (based on mean skull width).
- Principle of larger individuals tend to have larger brains

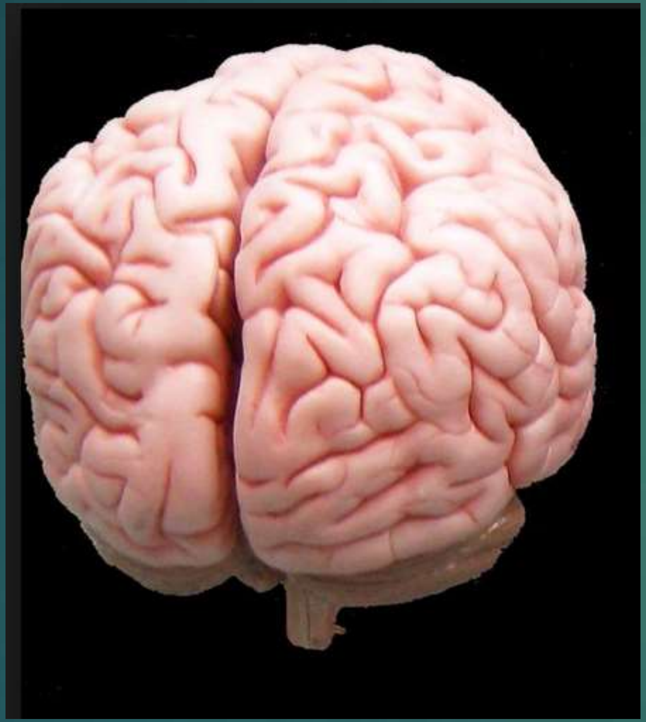
Largest Brain (ave = 17 lbs) on planet is not human.



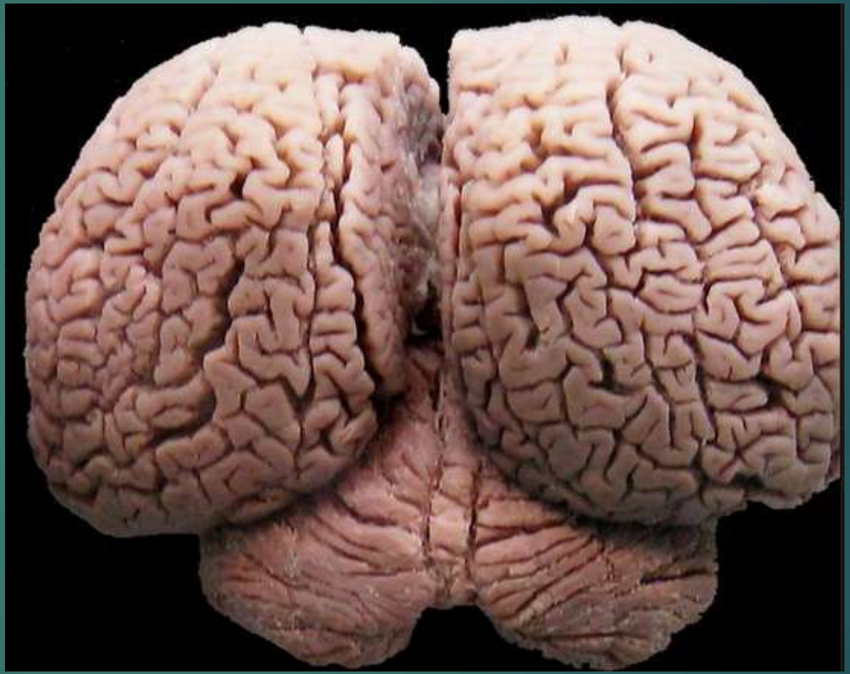
But lower encephalization quotient

Belongs to Sperm Whale

Which is more folded?

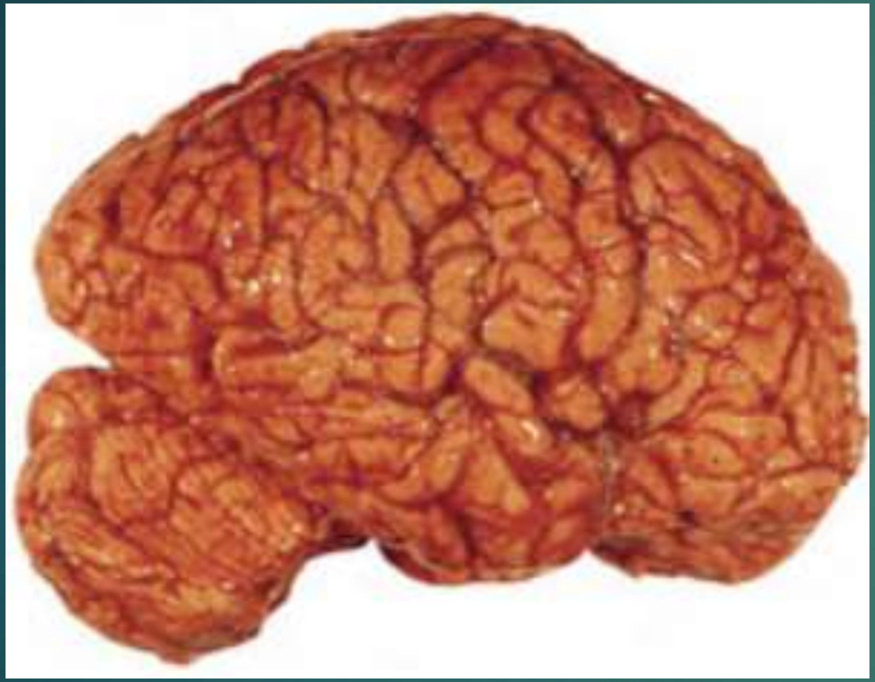


Human

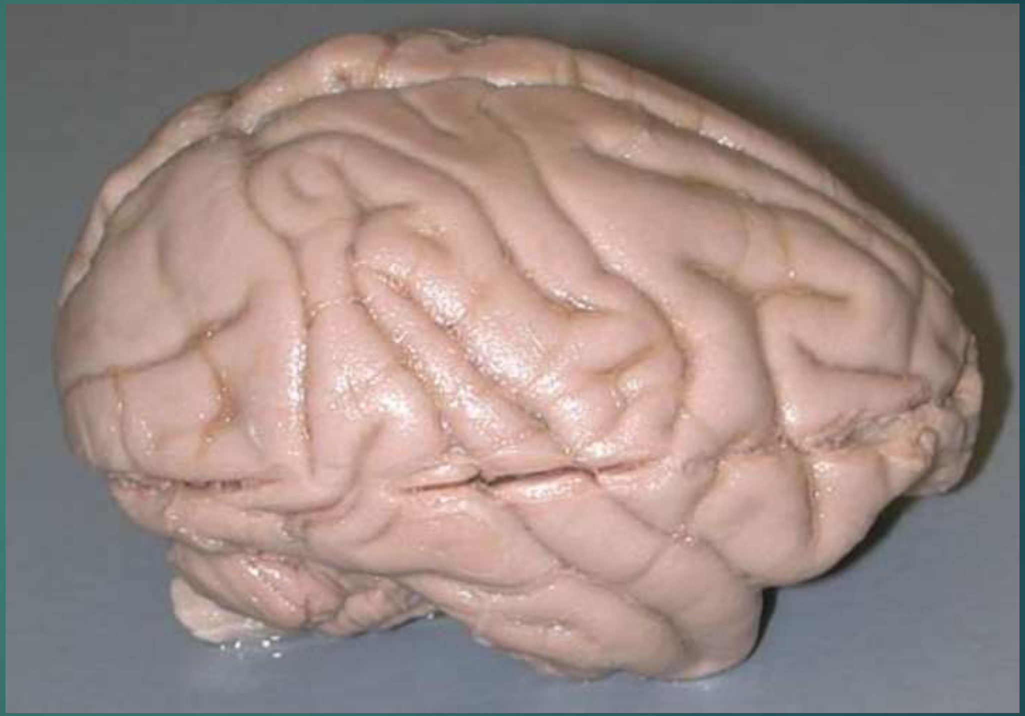


Dolphin

Which is the primate brain?

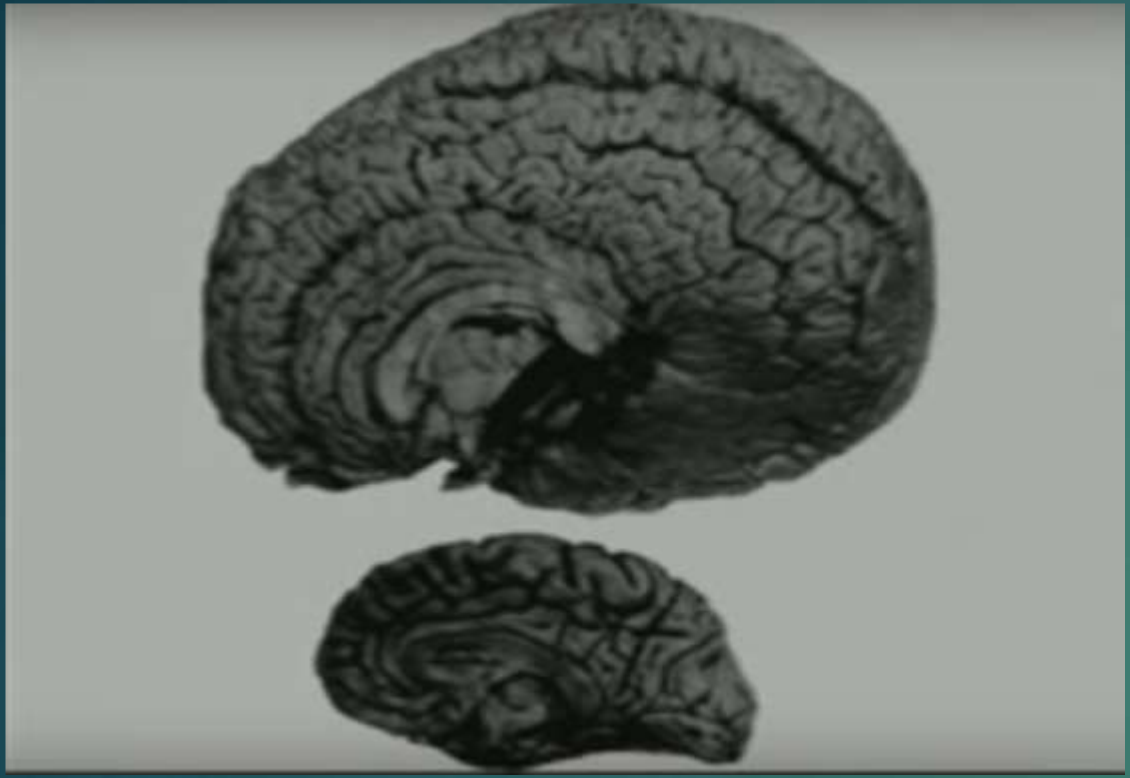


Cow



Baboon

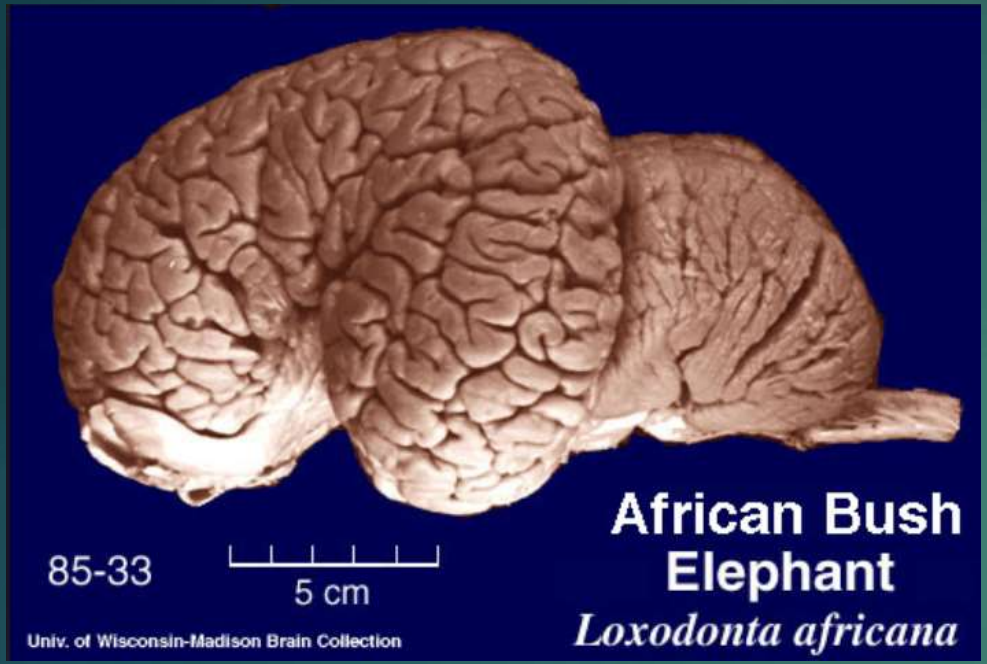
Size is not everything: Killer whale (15 lbs) vs human brain (3 lbs)



Dolphins and whales, for example, exhibit more cortical folds than other mammals for the same cortical surface area

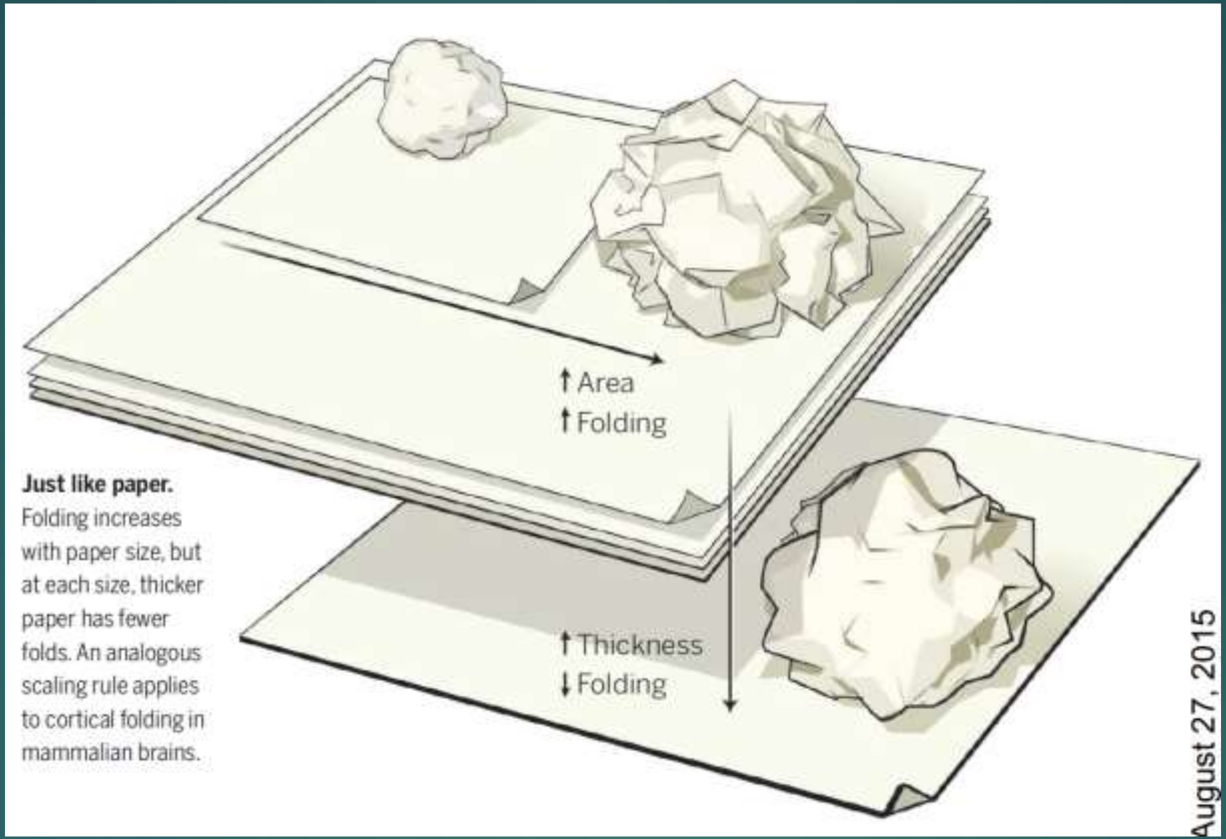
Whale brains are enormously more folded than human brain; <u>folding is response to space requirement, not intelligence.</u>

Cortical folding in the elephant

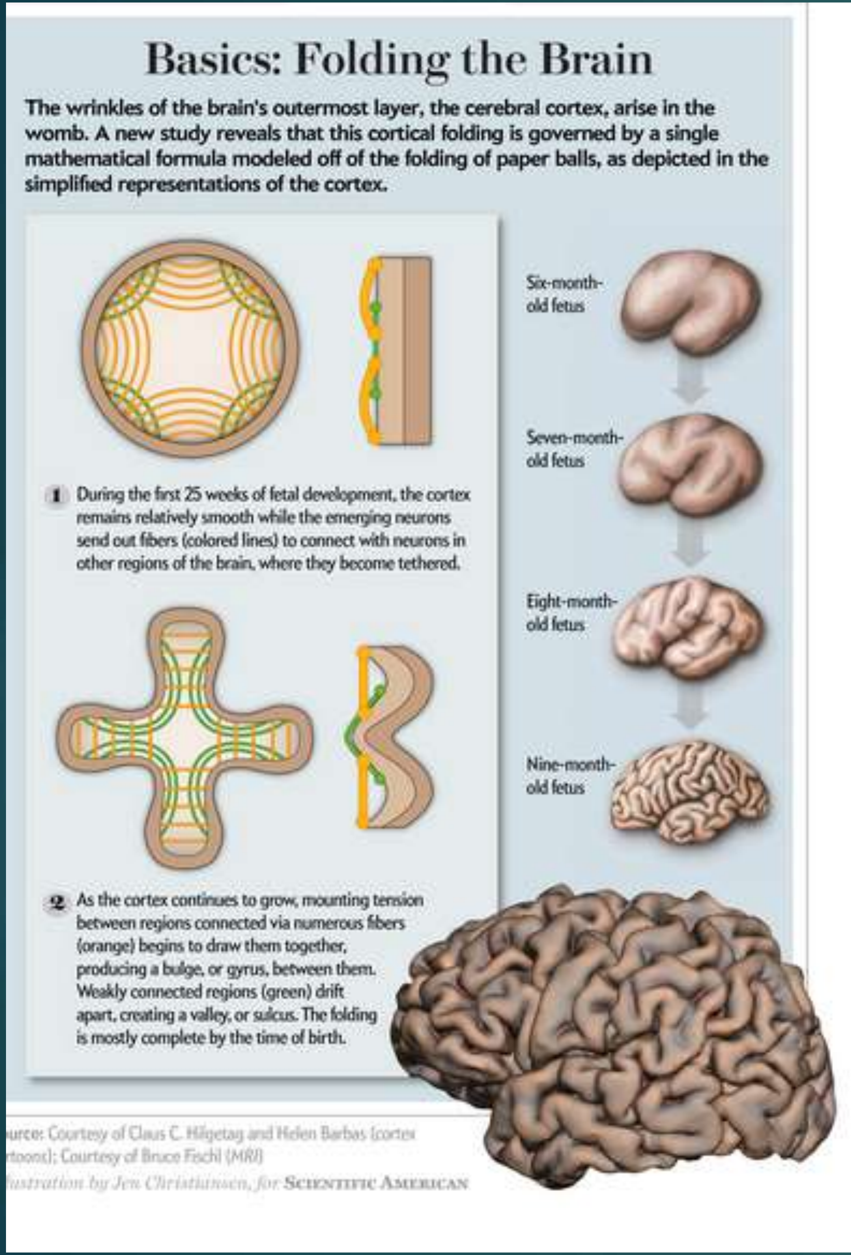


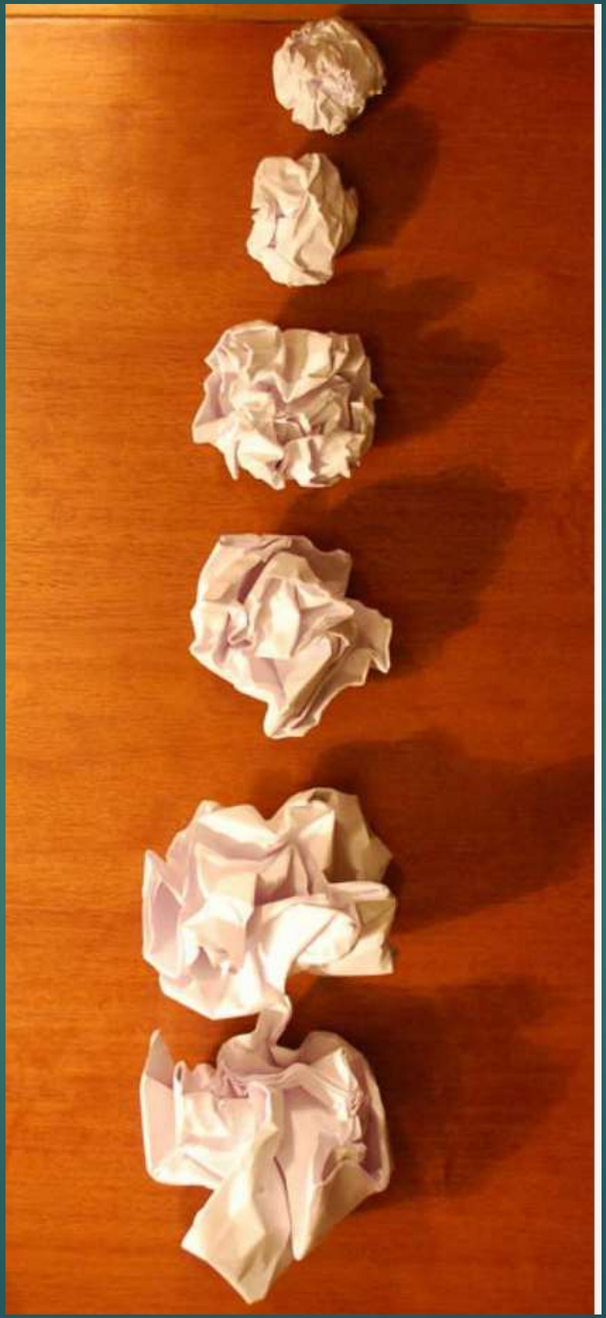
- Humans have 86 B neurons & elephants have 11 B; but elephant brain is 4 times heavier & twice as folded as the human cortex;
- Hippocampus of the African elephant is about 0.7% of the central structures of the brain, comparable to 0.5% for humans and contrasting with 0.1% in Risso dolphins, (*Grampus griseus*) and 0.05% in the bottlenose dolphin, *Tursiops truncatus*

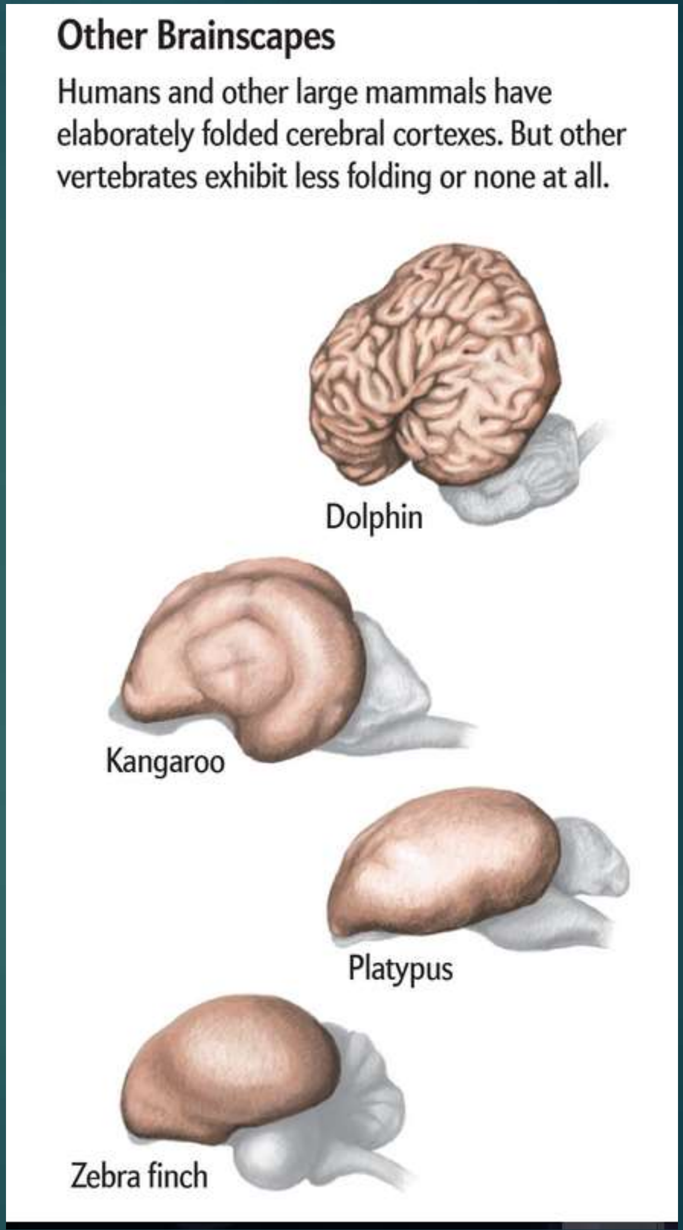
As cortical area ↑, folding ↑; As cortical thickness ↑, folding ↓



<u>Brain folds like paper</u>; thinner, folded cortex means information transfer from one point in the brain to another covers less distance; thicker paper, fewer folds (human lissencephaly); thicker cortices fold less; larger surface area leads to more folding; degree of cortical folding increases with total cortical area (i.e., larger brains tend to be more folded) but increases more rapidly for thinner cortices; crumpled-paper study shows the number of neurons is probably irrelevant in the folding process


Basics: Folding the Brain
The wrinkles of the brain's outermost layer, the cerebral cortex, arise in the womb. A new study reveals that this cortical folding is governed by a single mathematical formula modeled off of the folding of paper balls, as depicted in the simplified representations of the cortex.
Six-month-old fetus
Seven-month-old fetus
Eight-month-old fetus
Nine-month-old fetus
1 During the first 25 weeks of fetal development, the cortex remains relatively smooth while the emerging neurons send out fibers (colored lines) to connect with neurons in other regions of the brain, where they become tethered.
2 As the cortex continues to grow, mounting tension between regions connected via numerous fibers (orange) begins to draw them together, producing a bulge, or gyrus, between them. Weakly connected regions (green) drift apart, creating a valley, or sulcus. The folding is mostly complete by the time of birth.
urce: Courtesy of Claus C. Hilgetag and Helen Barbas (cortex
rtoons); Courtesy of Bruce Fischl (MRI)
Illustration by Jen Christiansen, for Scientific American




Other Brainscapes
Humans and other large mammals have elaborately folded cerebral cortexes. But other vertebrates exhibit less folding or none at all.
Dolphin
Kangaroo
Platypus
Zebra finch

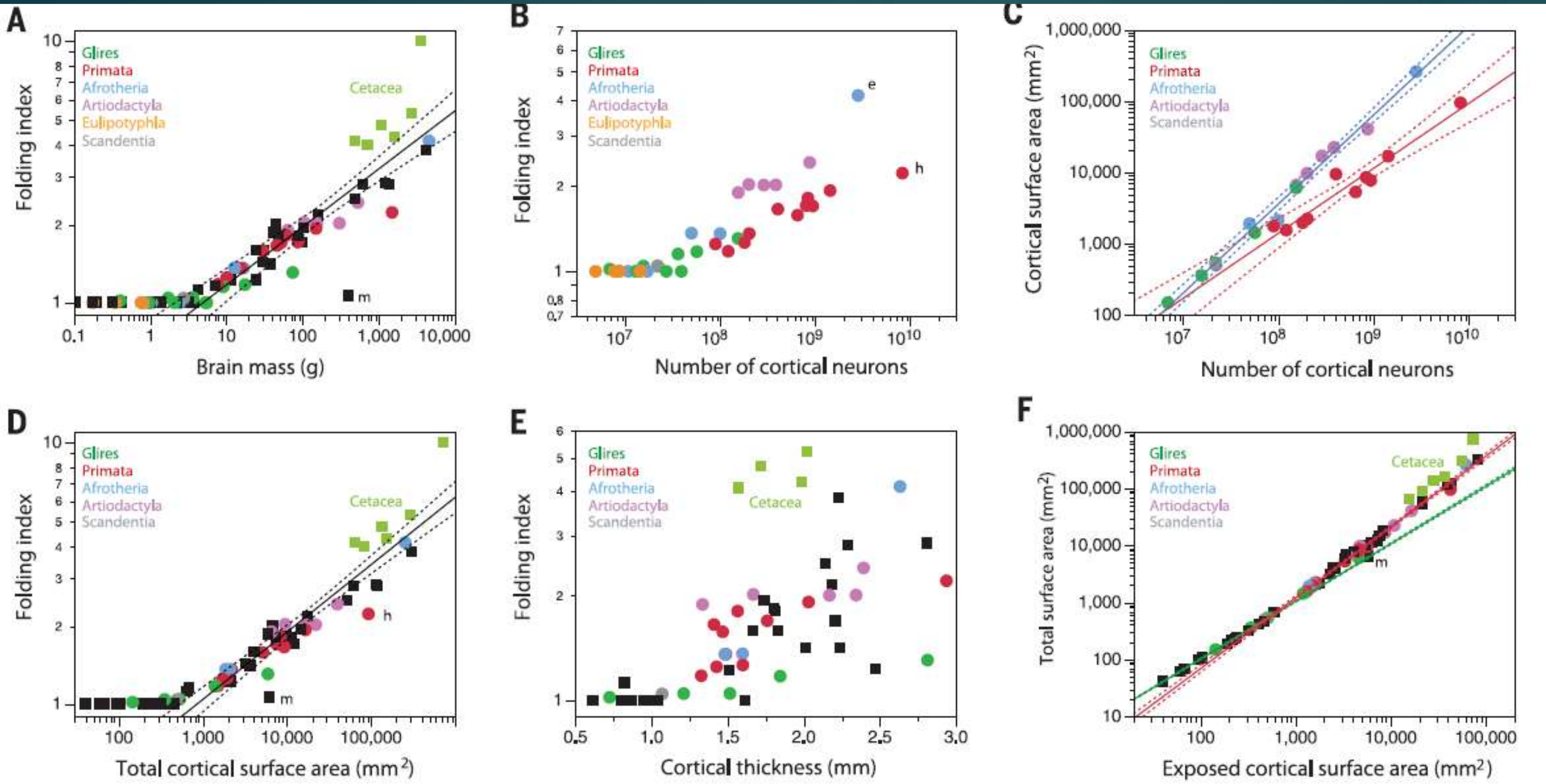


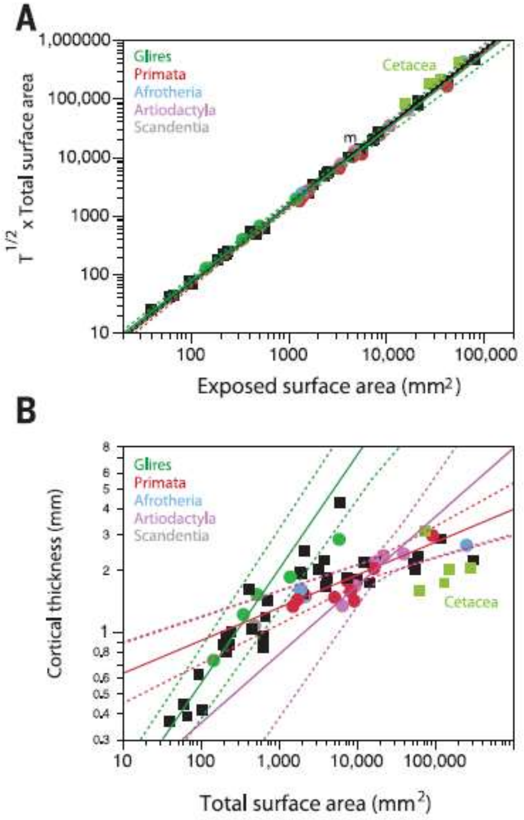
Fig. 1. Scaling of cortical folding index and total cortical surface area. Data points in black are taken from the literature; points in colors are from our own data set, except for cetaceans. (**A** to **E**) Folding index scales across all gyrencephalic species in the combined data sets as power functions of (A) brain mass, with exponent 0.221 ± 0.018 (r^2 = 0.751, P < 0.0001); (B) number of cortical neurons, with exponent 0.168 ± 0.032 (r^2 = 0.573, P < 0.0001; not plotted); (D) total cortical area, with exponent 0.257 ± 0.014 (r^2 = 0.872, P < 0.0001); and (E) average cortical thickness, with a nonsignificant exponent (r^2 = 0.054, P = 0.1430; not plotted). (C) Total cortical surface area of the cerebral cortex scales across primate species with an exponent of 0.911 ± 0.083 (r^2 = 0.938, P < 0.0001) and across nonprimate species with an exponent of 1.248 ± 0.037 (r^2 = 0.989, P < 0.0001). (**F**) Total cortical surface area varies across lissencephalic species as a linear function of the exposed surface area, but as a power function with an exponent of 1.242 ± 0.018 across noncetacean gyrencephalic species (r^2 = 0.992, P < 0.0001). Dashed lines are 95% confidence intervals for the fitted functions.

The average number of neurons per mm2 of cortical surface is highly variable across species;

Cortical expansion and folding is not a direct consequence of increasing numbers of neurons in the cortex.

A. Brain mass x folding
B. Number of neurons x folding
C. Cortical surface area x # of neurons
D. Total cortical surface x folding
E. Cortical thickness x folding
F. Total surface area x exposed cortical surface area

Fig. 3. The degree of folding of the mammalian cerebral cortex is a single function of surface area and thickness across lissencephalic and gyrencephalic species alike, although thickness scales as order-specific functions of cortical surface area. (**A**) The product $T^{1/2}A_G$ varies with $A_E^{1.329\pm0.014}$ (r^2 = 0.996, $P < 0.0001$) across noncetacean gyrencephalic species in the combined data set (red line), with $A_E^{1.325\pm0.009}$ (r^2 = 0.997, $P < 0.0001$, k = 0.157 ± 0.012) across all species (including cetaceans; black line), and with $A_E^{1.292\pm0.027}$ (r^2 = 0.994, $P < 0.0001$) across lissencephalic species alone (green line). Note that the function plotted for lissencephalic species predicts the product $T^{1/2}A_G$ for gyrencephalic species equally well as the functions plotted for gyrencephalic species themselves. (**B**) Cortical thickness varies with cortical surface area $A_G^{0.555\pm0.053}$ (r^2 = 0.887, $P <$ 0.0001) across lissencephalic species in the combined data set (green line), but with $A_G^{0.160\pm0.025}$ (r^2 = 0.703, $P < 0.0001$) across primates (red line), and with $A_G^{0.334\pm0.072}$ (r^2 = 0.879, P = 0.0185) across artiodactyl species (pink line). All fits exclude cetaceans. Dashed lines indicate the 95% confidence intervals for the fitted functions.



Total surface area

Cortical thickness

Gyrification is an intrinsic property of any mammalian cortex; The <u>scaling of cortical folding does not depend on numbers of neurons or how they are distributed in the cortical sheet, but simply on the relative lateral expansion of this sheet relative to its thickness, regardless of how densely neurons are distributed within it.</u> Cortical folding scales universally across clades, species, individuals, and parts of the same cortex implies that the single mechanism based on the physics of minimization of effective free energy of a growing surface subject to inhomogeneous bulk stresses applies across cortical development and evolution.

Cortical folding scales universally with surface area and thickness, not number of neurons

- The folding in the mammalian brain serves to increase the total area of the cortex. no clear relationship between the amount of folding and the number of neurons, the total area of the cortex, or the thickness of the cortex.
- Suzana Herculano-Houzel and Bruno Mota: There is a general correlation between total brain mass and the degree of cortical folding.
- Using data for 62 different species, the duo plotted the area of cortex times the square root of its thickness versus of the exposed area of the brain. All the data points fell on a single universal curve. Cortical folding scales universally with surface area and thickness, not number of neurons. Folding is a function of the product of cortical surface area and the square root of cortical thickness. The cortex simply settles into the configuration of least mechanical energy. Axonal tension is not important.
- Striedter argues that the scaling law describes a pattern in adult brains and doesn't explain how the folding in a developing brain happens. Herculano-Houzel contends that if the scaling relationship holds at all stages of development, then there is no need for another mechanism

An elephant brain = 3,886 cc

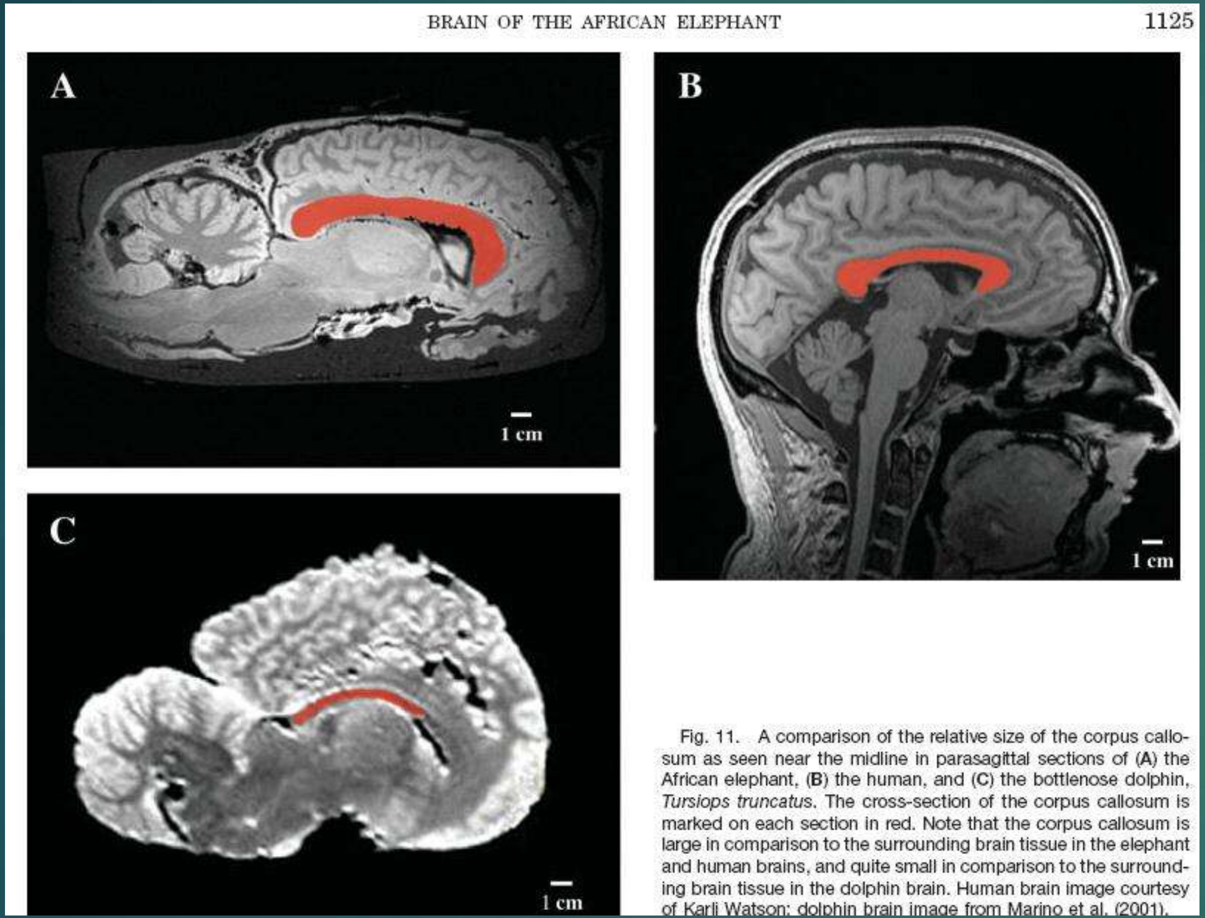
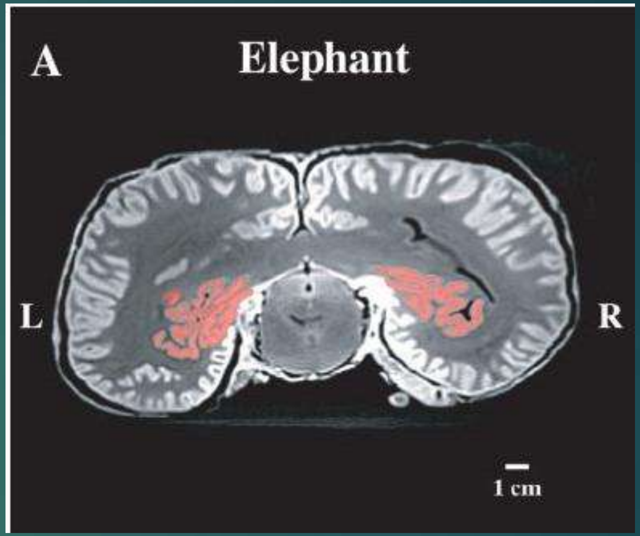


Fig. 11. A comparison of the relative size of the corpus callosum as seen near the midline in parasagittal sections of (**A**) the African elephant, (**B**) the human, and (**C**) the bottlenose dolphin, *Tursiops truncatus*. The cross-section of the corpus callosum is marked on each section in red. Note that the corpus callosum is large in comparison to the surrounding brain tissue in the elephant and human brains, and quite small in comparison to the surrounding brain tissue in the dolphin brain. Human brain image courtesy of Karli Watson; dolphin brain image from Marino et al. (2001).

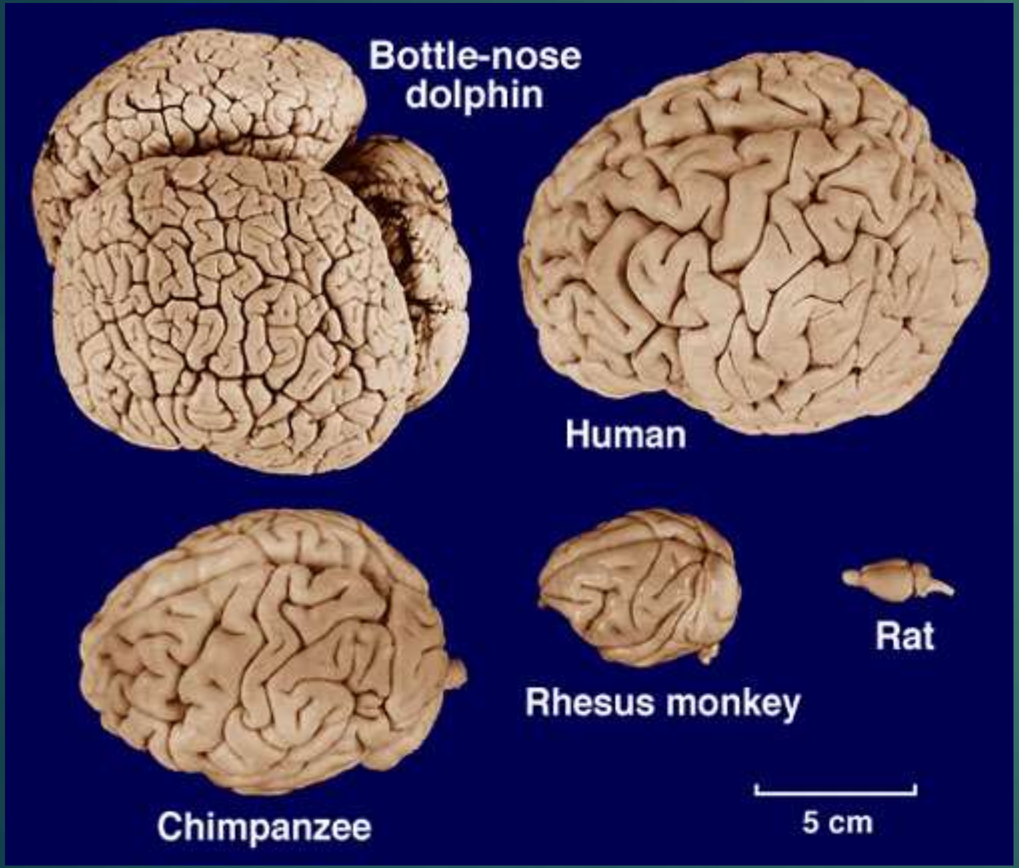


Above is the elephant hippocampus, in pink

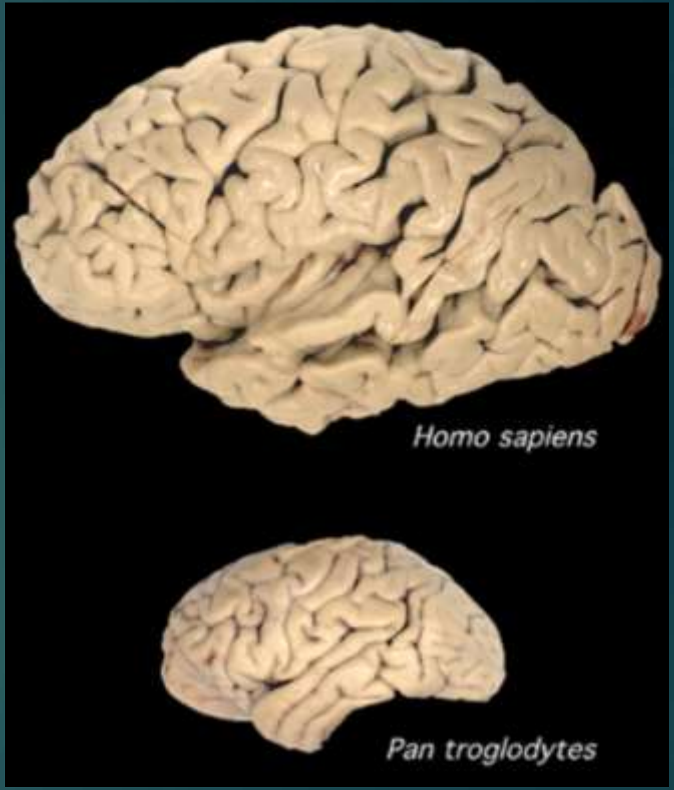
A = elephant; C = bottle nose dolphin

Hakeem, et al. (2005)

Absolute Brain Weight – Does it reflect intelligence?



Species	Adult Brain Weight (grams)
Chimpanzee	450
Human	1,350
Bottlenosed dolphin	1,600
African elephant	6,075
Fin whale	7,200
Sperm Whale	9,200



Relative Brain Weight

Aristotle: *"Of all animals, man has the largest brain in proportion to his size"*

Relative to body size, whales and dolphins have the next biggest brains to us, bigger even than chimpanzees

Species	Brain to Body Weight
Human	2.1 %
Bottlenosed dolphin	1.2 %
Chimpanzee	0.70 %
African elephant	0.50 %
Killer whale	0.10 %
Cow	0.08 %
Sperm Whale	0.02 %

Brain Size

Table 1. Brain weight, encephalization quotient and number of cortical neurons in selected mammals

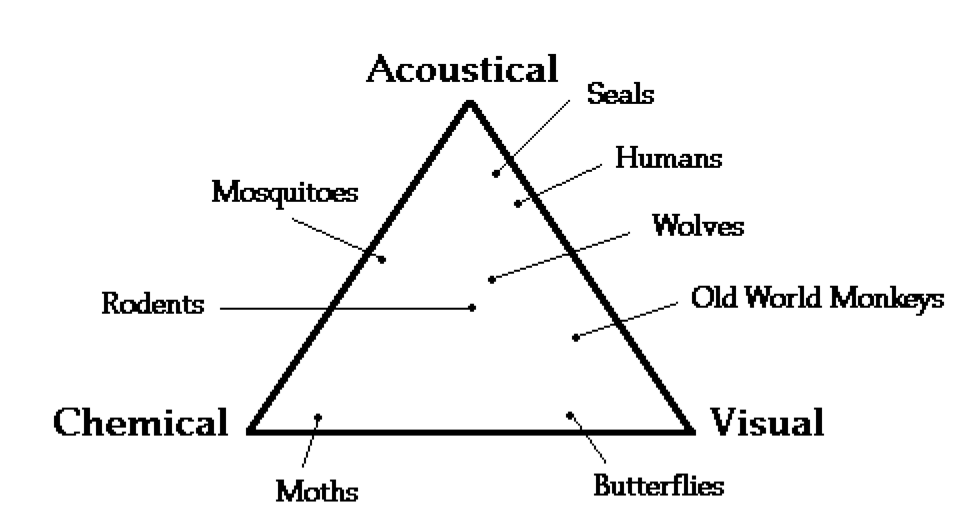
Animal taxa	Brain weight (in g)[a]	Encephalization quotient[b,c]	Number of cortical neurons (in millions)[d]
Whales	2600–9000	1.8	
False killer whale	3650		10 500
African elephant	4200	1.3	11 000
Man	1250–1450[e]	7.4–7.8	11 500
Bottlenose dolphin	1350	5.3	5800
Walrus	1130	1.2	
Camel	762	1.2	
Ox	490	0.5	
Horse	510	0.9	1200
Gorilla	430[e]–570	1.5–1.8	4300
Chimpanzee	330–430[e]	2.2–2.5	6200
Lion	260	0.6	
Sheep	140	0.8	
Old world monkeys	41–122	1.7–2.7	
Rhesus monkey	88	2.1	480
Gibbon	88–105	1.9–2.7	
Capuchin monkeys	26–80	2.4–4.8	
White-fronted capuchin	57	4.8	610
Dog	64	1.2	160
Fox	53	1.6	
Cat	25	1.0	300
Squirrel monkey	23	2.3	480
Rabbit	11	0.4	
Marmoset	7	1.7	
Opossum	7.6	0.2	27
Squirrel	7	1.1	
Hedgehog	3.3	0.3	24
Rat	2	0.4	15
Mouse	0.3	0.5	4

Mammals: Smell, Sight, or Sound Brains

% volume	Rat	Human
Cortex	**31**	**77**
Midbrain	13	8
Brainstem	7	2
Cerebellum	10	10
Spinal cord	**35**	**2**

Number of olfactory receptor cells

- Human 40 Million
- Rabbit 100 M
- Dog 1000 M



Number of Brain Cells: 170 Billion:
First Official Count in 2009 by Suzana Herculano-Houzel

- Adult male human brain contains on average 170 billion cells:
  - 86 ± 8 billion neurons
  - 85 ± 10 billion glial cells.

- Cerebral cortex: 16 billion cells
  - 19% of all neurons in the brain

  - 82% of total brain mass.
  - 61 billion glia; 16 billion neurons = 4 to 1

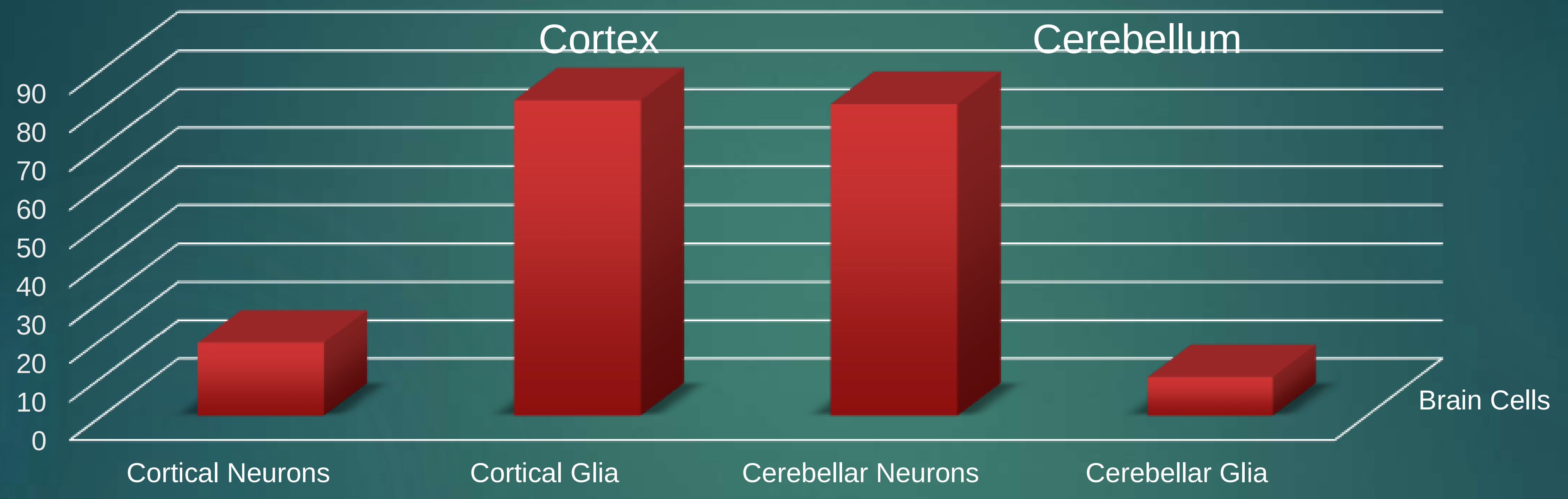
F. Azevedo et al., J. *Comp. Neurol*. 513:532–541, 2009

Number of Brain Cells 2

- Cerebellum: 69 billion cells:
  - 81% of all neurons
  - 10% of brain mass
  - 60 billion neurons; 16 billion glial cells: 4 neurons to 1 glia
- Brainstem: 8% of mass, but 0.7 B neurons (9%)

Cortical Brain Cells: 170 Billion

Brain Cells



19% 81% 81% 19%

Adult male human brain contains on average:

86 ± 8 billion neurons

85 ± 10 billion glial cells.

Cortex: 4 to 1 glia to neuron; Cerebellum: 4 to 1 neurons to glia

Number of Brain Cells 3

- Glial cells are 50% of all brain cells.

- Gray: 6 billion neurons and 9 billion glia;
- White: 1.3 billion neurons and 20 billion glia

- Baboon brain: only 14 B neurons

- Human brain is a linearly scaled-up primate brain, with just the expected number of neurons for a primate brain of its size,

Elephant IQ: 257 billion neurons; 97.5% in the cerebellum.

- Elephants have large complex brains, exhibit complex social behavior, show a facility with tools, and are generally thought to be highly intelligent.
- Cognitive studies have demonstrated that elephants are capable of:
  - visual symbol discrimination
  - long term memory,
  - means-end recognition,
  - relative quantity judgment,
  - mirror self-recognition,
  - tool use and manufacture (branches to swat flies or scratch; move box)
  - an understanding of cooperation.

Homology

- Brains vary tremendously.
- Homologous features observed in different species are thought to be shared by inheritance from a common ancestor.
- Mammalian large brained lineage tend to have more gyrified brains with greater number of distinct cortical areas.
- Highly gyrified brains of dolphins & humans are due to convergent evolution.

Brain regions

- Cerebellum present in all vertebrates; is ancient.
- Cortex increases with brain size
- Increase in association vs primary sensory areas is a defining characteristic of human brain development

Brain weight during human lifespan

Average brain weights (BW)

AGE	BW - Male (grams)	BW - Female (grams)
Newborn	380	360
1 year	970	940
2 years	1,120	1,040
3 years	1,270	1,090
10-12 years	1,440	1,260
19-21 years	1,450	1,310
56-60 years	1,370	1,250
81-85 years	1,310	1,170

(Data from Dekaban, A.S. and Sadowsky, D., Changes in brain weights during the span of human life: relation of brain weights to body heights and body weights, *Ann. Neurology*, 4:345-356, 1978)

Cerebellar Size

- Among primates, positive correlation between cerebellum size (but not brain size) and the amount of social play a species engages in.
- Combination of motor skills, behavioral flexibility, and decision making required for interactive play may have favored increased cerebellar size.
- Social play is also correlated with size of amygdala and hypothalamus.
- Hominid species have relatively smaller cerebellar sizes than great apes.

Cerebellum

- Spatial positioning of the cerebellum is different among the human species:
  - modern humans: positioned under the temporal areas,
  - *Homo erectus* almost under the occipital lobes,
  - Neanderthals under the parietal lobes.
- The cerebellar structures co-evolved together with the cerebral cortical areas.
- Anne Weaver (2005) proposed that the cerebellum underwent a volumetric increase in Neanderthals and anatomically modern humans.

Larger neocortex

- Trend for larger-brained mammals to be more gyrified (folding), allowing for an increase in brain size.

- Primates possess relatively more neocortex for a given brain volume (chimp brain is 120 x larger than hedgehog or galago and has 76% neocortex).

- Human neocortex is about 80%, compromising 95% of total cortical area

Association Areas

- Relative increase in heteromodal association vs. primary association has been a defining characteristic of human brain evolution.
- All major lobes contain both primary and association areas

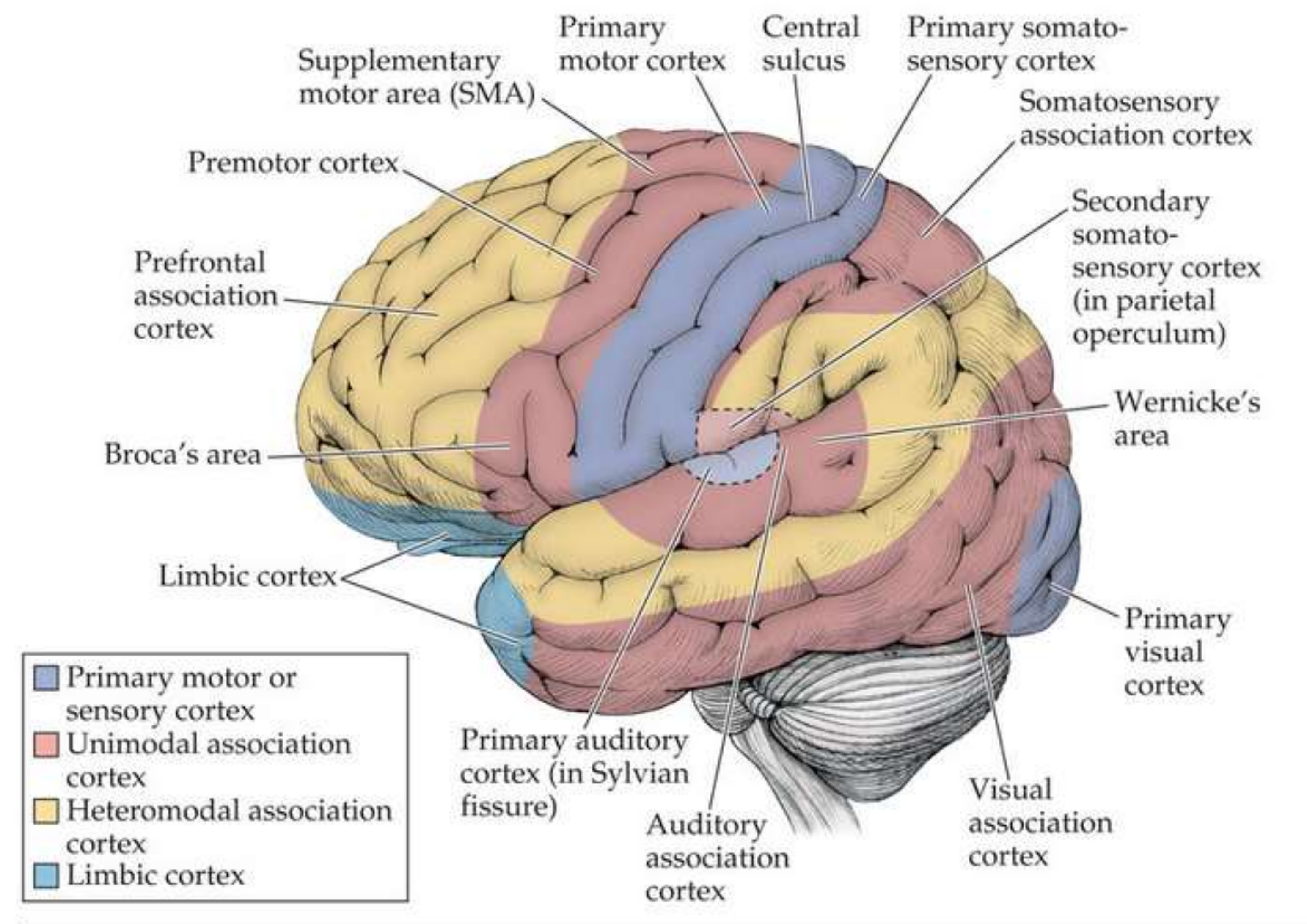


Figure 2.25 Association Cortex Lateral view of left hemisphere showing main areas of primary sensory and motor cortex,

Primary = direct perception; Unimodal Association = single perceptual processing

Heteromodal association = multisensory, multimodal, higher cognitive processing

Brodmann’s Areas

- 47 cortical areas in human brain
- Brodmann areas can be identified as homologous units across primate species.

Thalamus & language

- Thalamic nuclei not universally conserved
- Compared to apes, human pulvinar-lateral posterior nuclei is about as big as would be expected, but different parts of pulvinar nuclei have changed at different rates.
- Human anterior thalamus (part of vocalization pathway, present in songbirds and humans) is not present in mammals.
- This may imply evolution of specializations of the thalamus not seen in apes, possibly related to language vocalization or consciousness.

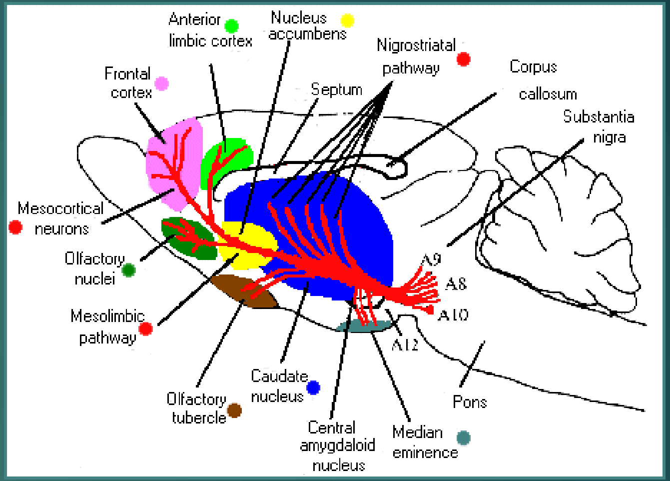
White Matter

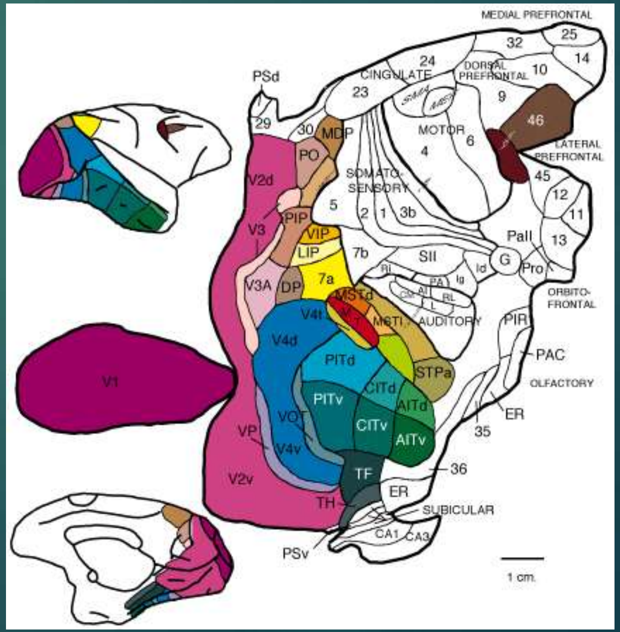
- Synaptogenesis (& subsequent white matter growth) occurs at different rates in humans, compared to more uniform rate in monkeys.

- White matter growth in prefrontal regions, which is developmentally delayed, is more extensive in humans than other primates.

Model animal paradigm: rat vs. macaque

- In the study of the mammalian cortex, the rat has served as the model of choice (Google hits = 1,160,000)
- However, the monkey, esp. the macaque, has been a more specific model for the human cerebral cortex.
- PubMed article search for “macaque brain”: 14,265 hits
- 20 M year separation





Comparative Mammalian Brain Collections Online

- Brain Museum: www.brainmuseum.org
- Whole Brain Atlas: www.med.Harvard.edu/AANLIB/home.html
- Human Brain Atlas: www.msu.edu~brains/brains/human/index.html

- Brains vary by overall size, shape, and relative sizes of cerebrum and cerebellum.
- Some are smooth; some are wrinkled

Brain Size

Brain Size

- Size is the most fundamental issue in the study of human brain evolution.

- In part is an artifact of the paleontological record, which preserves information about brain volume but little else.

Darwin, *The Descent of Man:* Bigger is better

- “As the various mental faculties gradually developed themselves the brain would almost certainly become larger. No one, I presume, doubts that the large proportion which the size of man’s brain bears to his body, compared to the same proportion in the gorilla or the orang, is closely connected with his higher mental powers…On the other hand, no one supposes that the intellect of any two animals or of any two men can be accurately gauged by the cubic centimeters of their skulls.”

Bigger is Better

- Hypothesis that bigger is better
- Has been historically used in frankly racist/sexist ways.
- Function: size of brain in some way reflects cognitive function
- Physiology: brain size is related to overall body size, not necessarily linearly (Cuvier: "…the small animals have proportionally larger brains"); human brains are both larger and proportionally larger than a gorilla brain
- Phylogeny: comparison to other primates

The cerebral rubicons: different opinions

- Increased brain size is a hallmark of the genus *Homo*

- Sir Arthur Keith (1947): the cerebral rubicon of 750cc that would demarcate brains of genus *Homo*
- Ralph Holloway(1968): not just size but functional reorganization

- Anatomist Wilfred LeGros Clark (1978) described *Homo sapiens as* "a species of the genus *Homo* characterized by a mean cranial capacity of 1350 cc"
- Allen: if there is a rubicon, it emerges at around 600 cc, in H. habilis (although robustus survived for 1 million years)

Dmanisi *Homo erectus*

- Georgia, 1.7 M, 600 cc
- Increased intelligence was not prerequisite for migration
- And how about Homo floresiensis? Did he leave Africa early?
- 2 miles a generation got them from Africa to China in 200 KY

Holloway: 4 major brain reorganizations in hominid evolution

Four major reorganizational changes during hominid brain evolution:

- (1) reduction of the relative volume of primary visual striate cortex area, with a concomitant relative increase in the volume of posterior parietal cortex, which in humans contains Wernicke's area;

- (2) reorganization of the frontal lobe, mainly involving the third inferior frontal convolution, which in humans (Broca's area);

-Holloway, R. 1996. "Evolution of the human brain".

Brain reorganization

- (3) the development of strong cerebral asymmetries of a torsional pattern consistent with human right-handedness (larger left-occipital and right-frontal in conjunction);
- (4) refinements in cortical organization to a modern human pattern. (inferred; no direct palaeoneurological evidence for it.)

Other Rubicons

- With new discovery of 3.3 million year old stone tools, brains in the 450 cc range could produce technology and survive million years

- First appearance of symbolic art (perforated shell beads), 100 kya after emergence of Homo sapiens

- First appearance of complex language

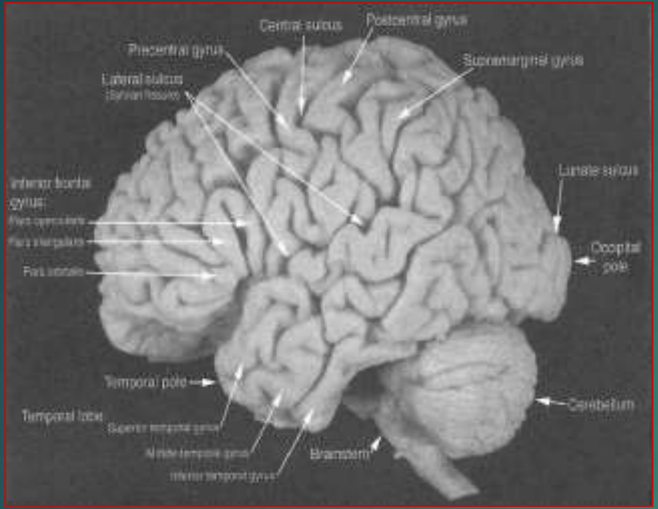
Problem with endocasts

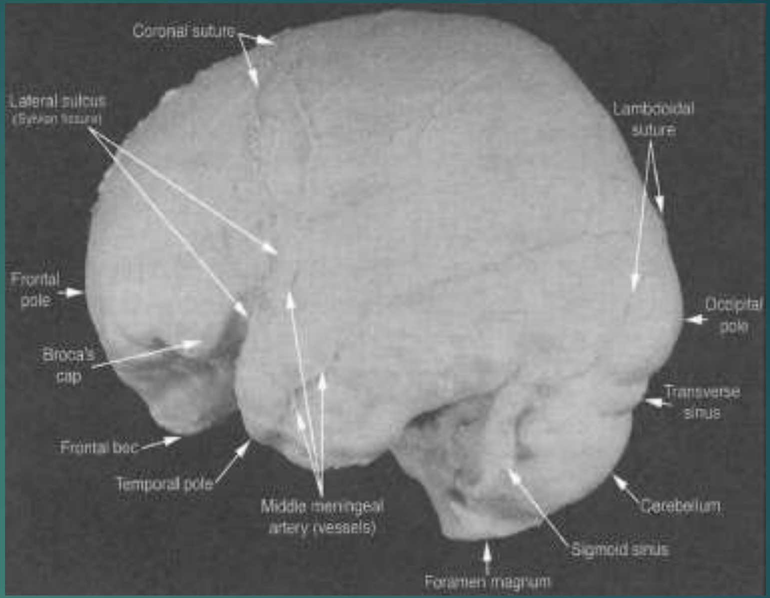
- Paleoneurology is study of endocasts.
- Major limits:
  - In many fish, amphibians, and reptiles, the brain does not fill more than about half of the endocranial space; estimation of brain size from endocasts can be inaccurate
  - In birds and mammals, extent of brain fill varies with body size
  - Endocasts reveal only surface features of the brain

Evidence from Endocasts (fossilized brains)

- Paleoneurologists focus on several types of evidence from endocasts:
  - 1. Changes in shape of the brain
  - 2. Overall brain size differences
  - 3. Locations of specific surface features of brain anatomy
    - Imprints of cerebral vasculature
    - External convolutional morphology of well preserved gyri and sulci location

Endocasts





- Asymmetries in overall shape:
  - Enlarged left occipital lobe & Expanded right frontal lobe

- Locations of specific surface features:
  - Lunate sulcus marks boundary between
    - Parietal lobes
    - Occipital lobes
  - Expanded parietal lobes in hominids

Cranial capacity is measured from inside of cranium

- Nonbrain proportion of total cranial capacity is substantial
- Current decline in brain volume between ages of 30 to 80 of 20 percent are typical
- Cranial capacity of a fossil specimen is traditionally measured by water displacement of the endocast.
- Current determination of cranial capacities involves CT scanning

Brain Size

- Brain size is the most commonly used measure of brain difference in evolutionary science.
  - Animals with large brains exhibit more complex behaviors than those with small brains
  - Brain size is easy to measure using brain weights, imaging techniques, and endocranial volume.

- Brain size in vertebrates is correlated to body size.
  - Meeting the demands of a larger body requires a larger brain

Allometry: disproportionate growth of a part of an organism as the organism changes in size

- To compare the brain sizes of two animals, you must also know their body size.
  - It is difficult to compare fossils of terrestrial vertebrates for two reasons:
    - Lack of tissue – muscles, organs, brain, etc.
    - Finding complete skeletons is rare
  - Paleontologists must calculate body size relative to living organisms

Allometry 2

- Allometric relationships further complicate brain measurements.
  - Body size increases faster than brain size
  - Smaller organisms have larger relative brain sizes

Cranial Capacity in endocasts

- Cranial capacity from endocast is a proxy for brain size
- Limited by number of available fossils
- Only a small amount of information on brain structure can be gleaned from endocasts; intracranial volume is 14% greater than total brain volume
- Relationship between external cranial size and brain volume is weak; Only a modest correlation between head circumference and brain volume by MRI
- Correlation between brain volume and IQ test performance is about .40

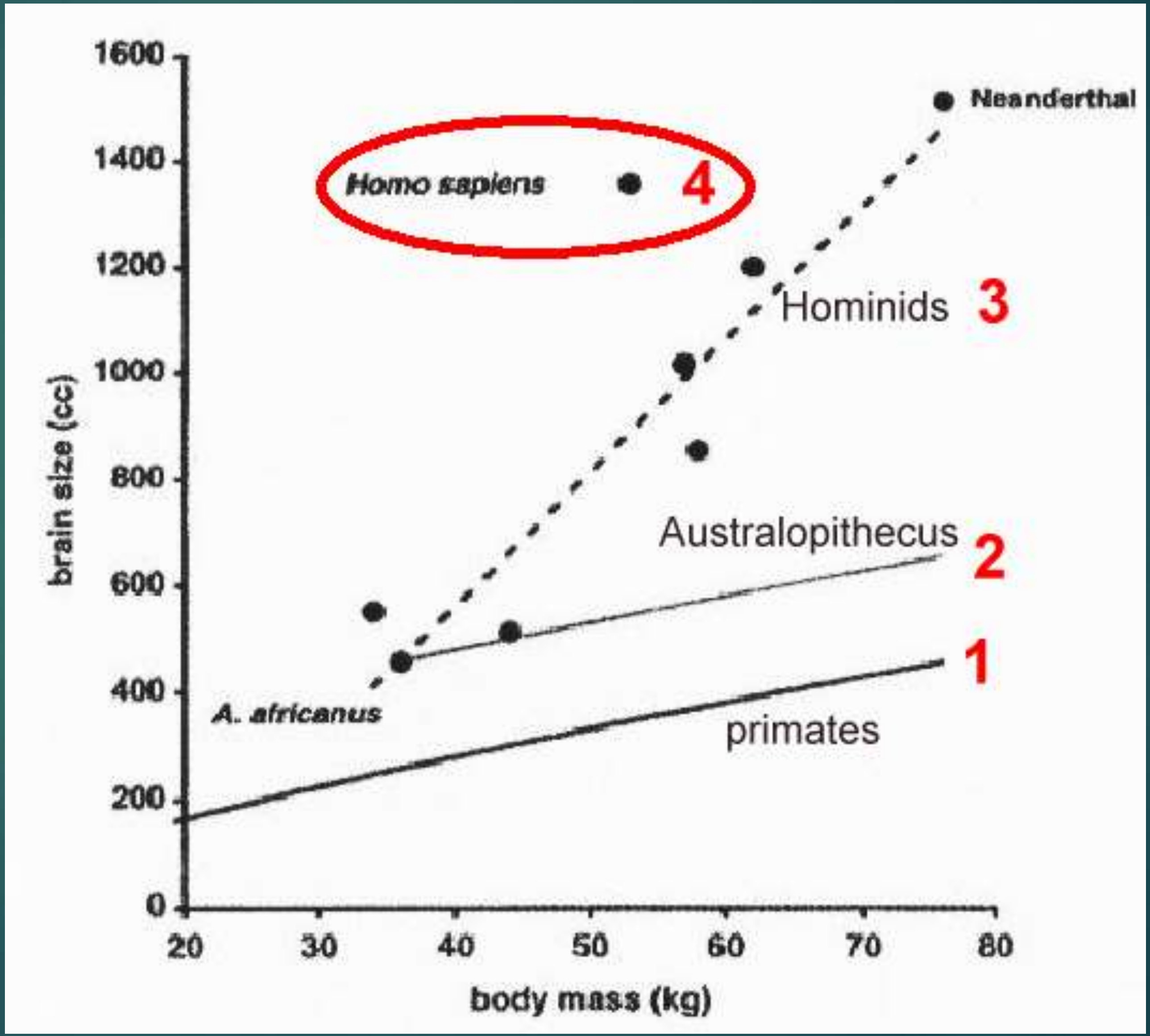
Hominid cranial capacity

(Allen, based on Martin 1983)

	CC	EQ	MYA	
Chimpanzee	390			
Gorilla	440/540			
Sahelanthropus tchadensis:	400			
A. afarensis	*446*	*4.9*	*3.5*	
A. garhi	*450*			
A. africanus	*461*	*5.2*		
A. robustus & boisei	*503*	*5.3*		
H. habilis	*610*	*7.1*	*1.8*	
H. rudolfensis	*789*	*7.4*		
H. ergaster	*801*	*6.3*	*1.5*	
H. erectus	*951 (727-1200)*	*7.3*		*Major jump in size*
H. heidelbergensis	*1263*	*8.6*	*600kya*	
H. neanderthalensis	*1450*	*10.6*	*250 kya*	
H. sapiens sapiens	*1350*	*9.6*	*200 kya*	*Globularization: Parietal bulging*

Four leaps in braininess

1. To Primate
2. To Australopithecus
3. To Hominid
4. To Homo sapiens



Slogans of primate brain development

- From lower to higher (brainstem to neocortex)
- Overproduction, then 50% pruning of neurons and synapses
- Use it or lose it! Neuroplasticity depends on environmental experience
- Learning is embodied in new synapses.
- Early "plasticity" of the CNS (but always some!)
- Myelination speeds information flow.
- Species brain differences reflect differential regional growth rates, differential apoptosis, and environmental feedback directed pruning and reorganization.

Human uniqueness

- The human brain is uniquely large
- It is also functionally lateralized in a way which differs from chimpanzees
- It is metabolically enhanced (Cacares et al., 2003)
- It may include different genetic components (Allman et al., 2005)
- It may be organized uniquely, e.g. large frontal lobes (Deacon, 1997)
- Humans: 86 billion neurons; 16 billion in cortex (cortically the most of any primate)
- Correct number of neurons for a primate brain for human body size

Encephalization

Encephalization = estimate of intelligence?

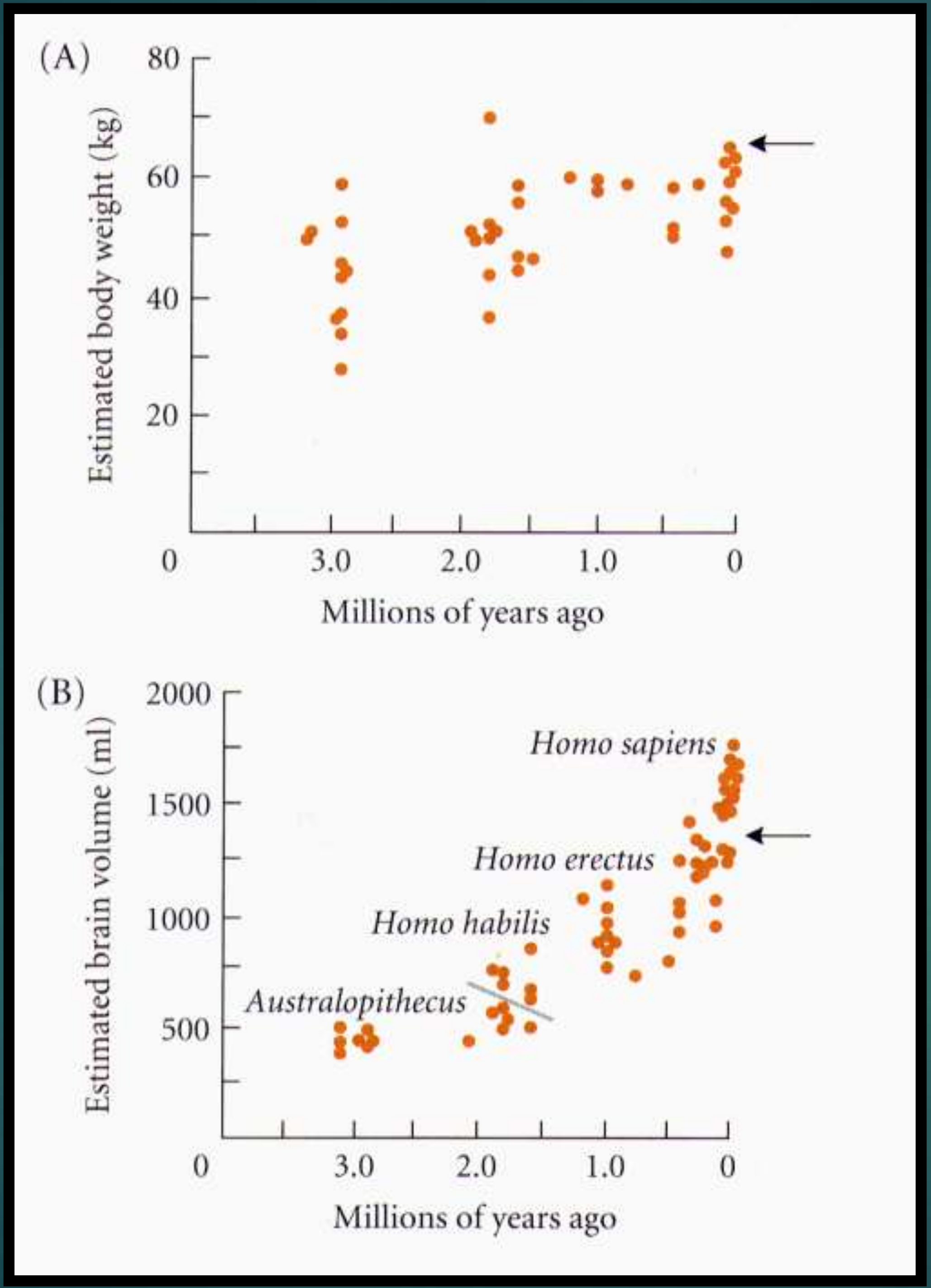
- A first most obvious manner of comparison would be the ratio of body weight to brain weight.
- Cuvier's fraction E/S: E=brain weight and S= body weight
- Brain weight in vertebrates does not in general appear to increase linearly with body weight, so that heavy vertebrates have proportionally smaller brains than light vertebrates, and many small mammals have, in terms of these simple ratios, relatively larger brains than that of humans.
- Brain size increases with body size in an exponential rate.
- Higher primates are generally more "encephalized" than lower primates relative to mammals as a whole and that smaller mammals and rodents are below average.

Encephalization Quotient (EQ)

Human	**7.4**
Dolphin	**5.6**
Killer whale	**2.9**
Chimpanzee	**2.5**
Rhesus Monkey	**2.1**
Elephant	**1.9**
Whale	**1.8**
Dog	**1.2**
Cat	**1.0**
Horse	**0.9**
Sheep	**0.8**
Mouse	**0.5**
Rabbit	**0.4**

Anatomical estimate of species' intelligence based on brain/body size and not behavior

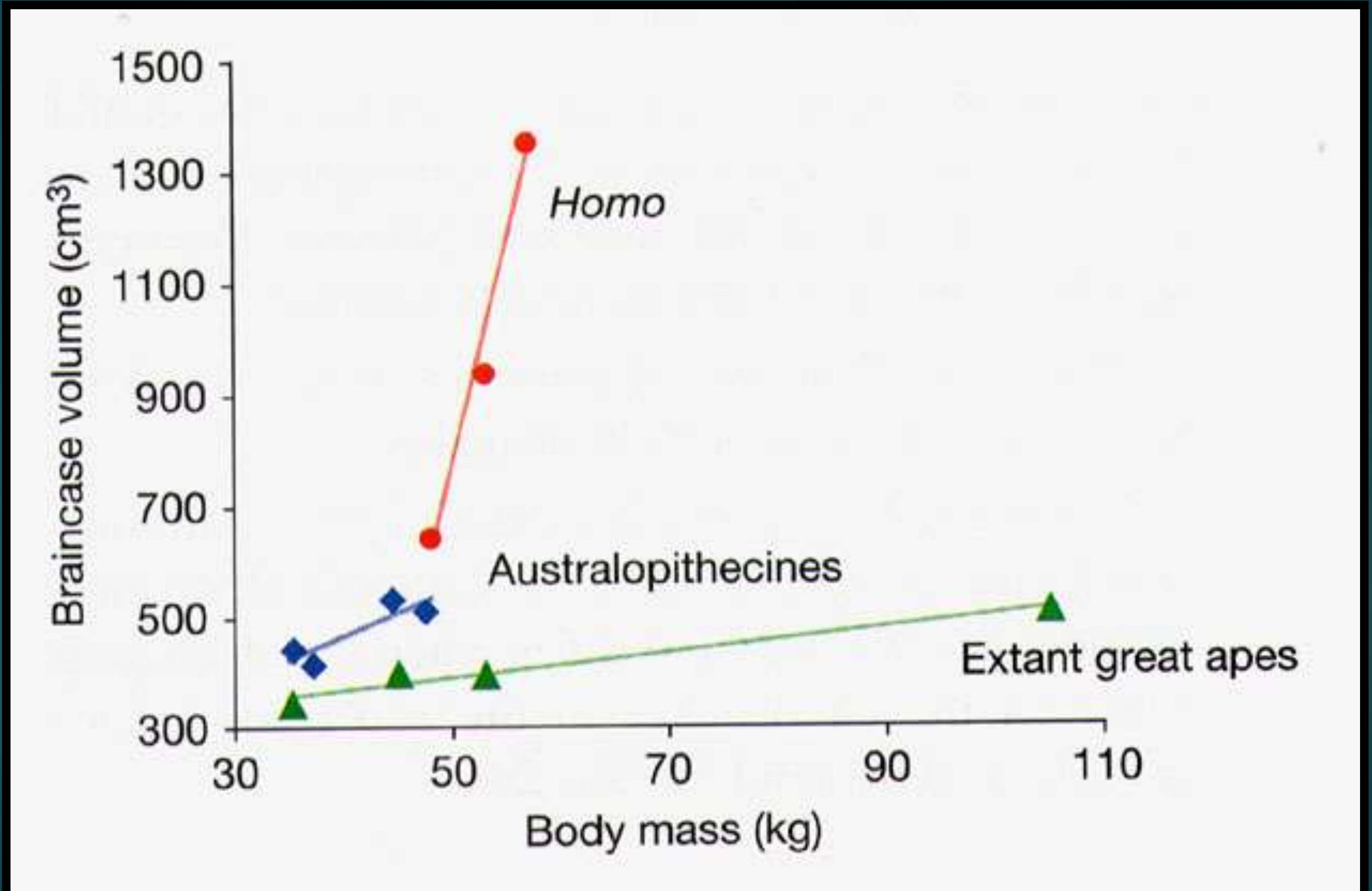
EQ = ratio of brain weight of animal to brain weight of "typical" animal of same body weight



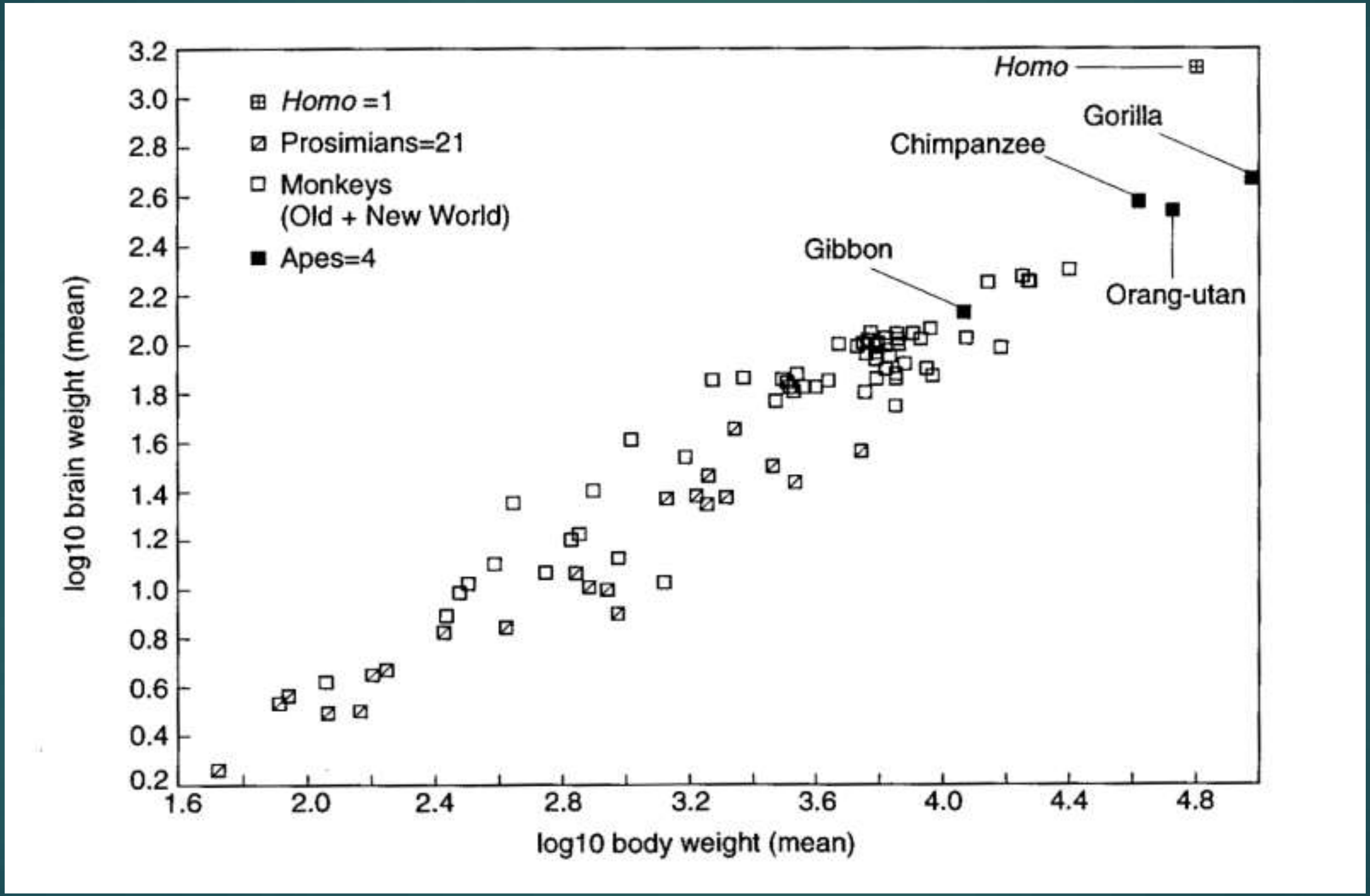
Slight Increase In Body Size

Much Greater Increase In Brain Volume

Braincase Volume and Body Mass

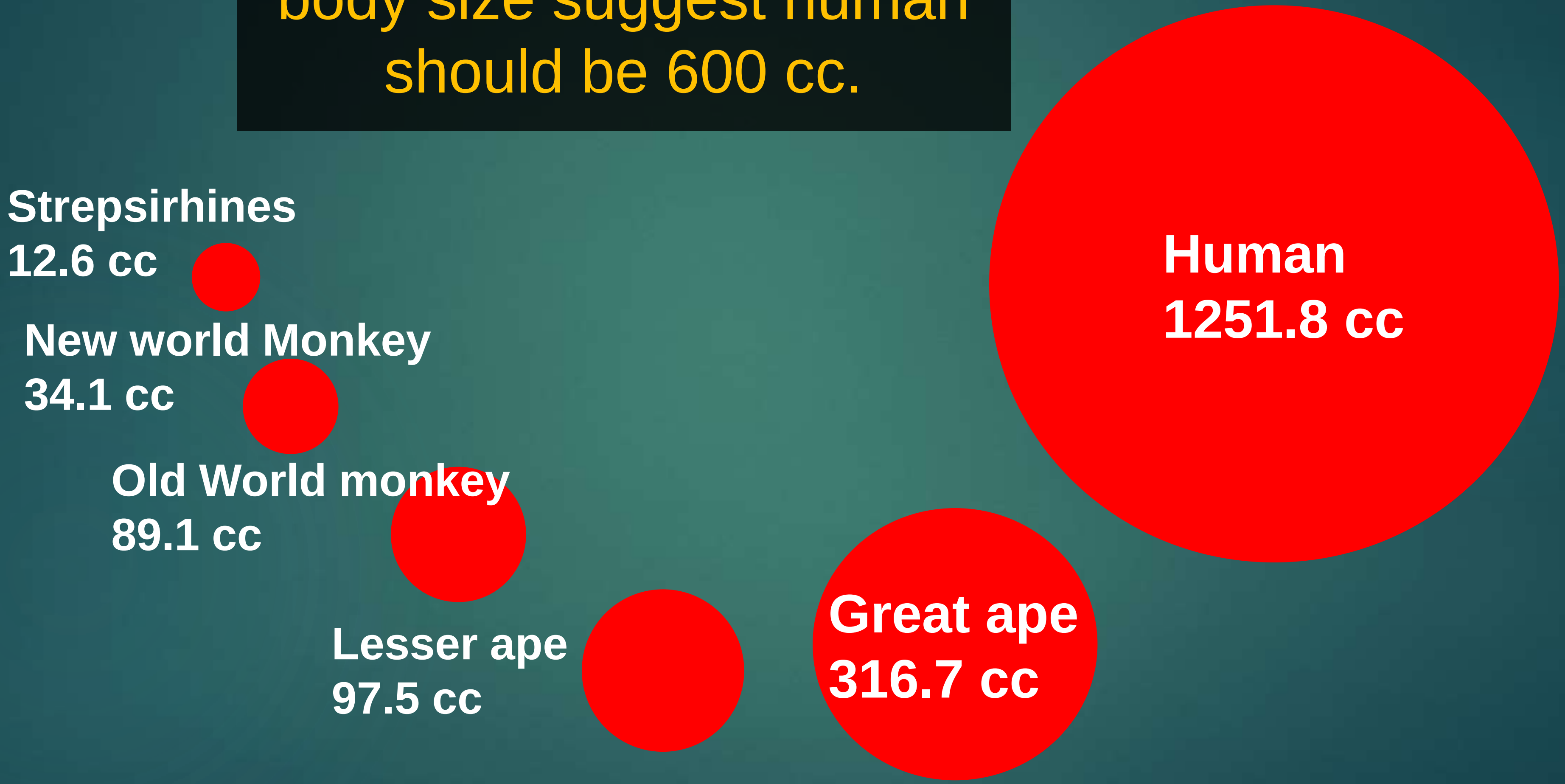


Brain weight to body weight ratio



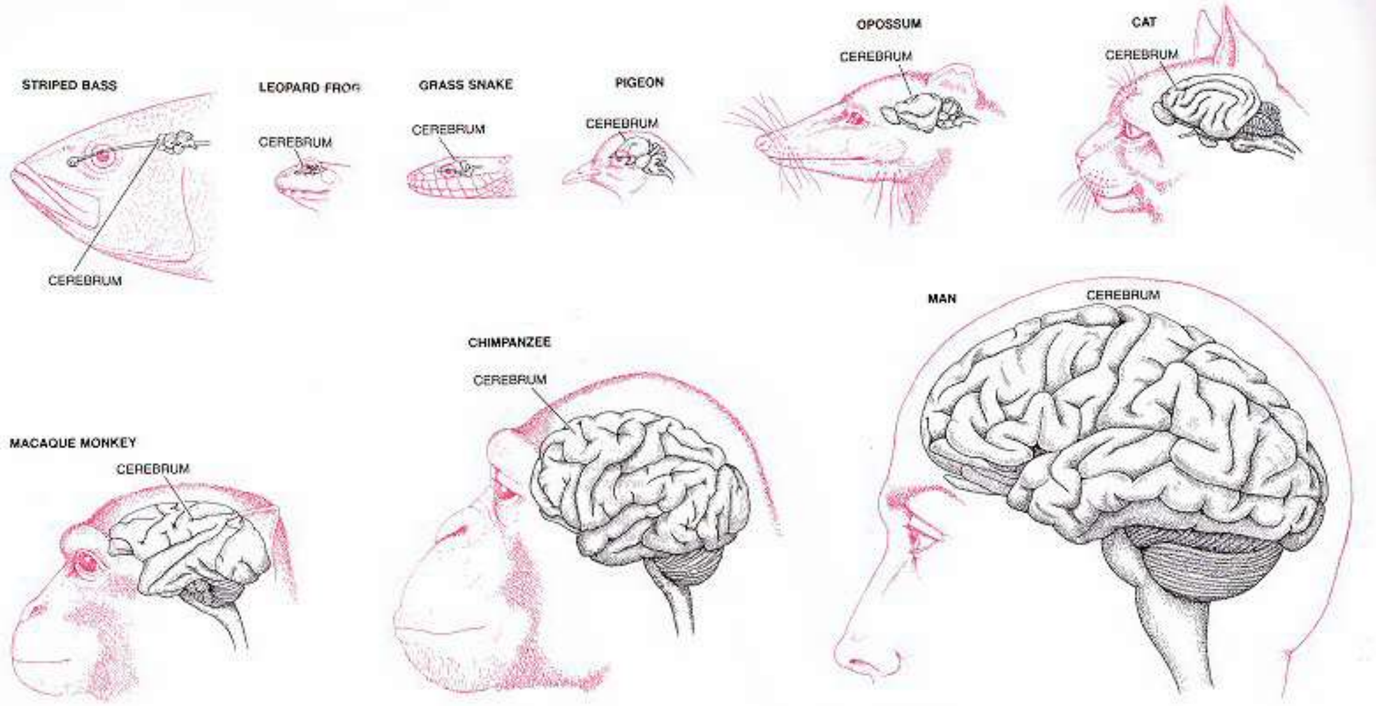
Relative brain sizes

Most formulae based on body size suggest human should be 600 cc.



Source: James K. Rilling. 2006. Human and NonHuman Primate Brains: Are They Allometrically Scaled Versions of the Same Design? *Evolutionary Anthropology* 15: 65-77.

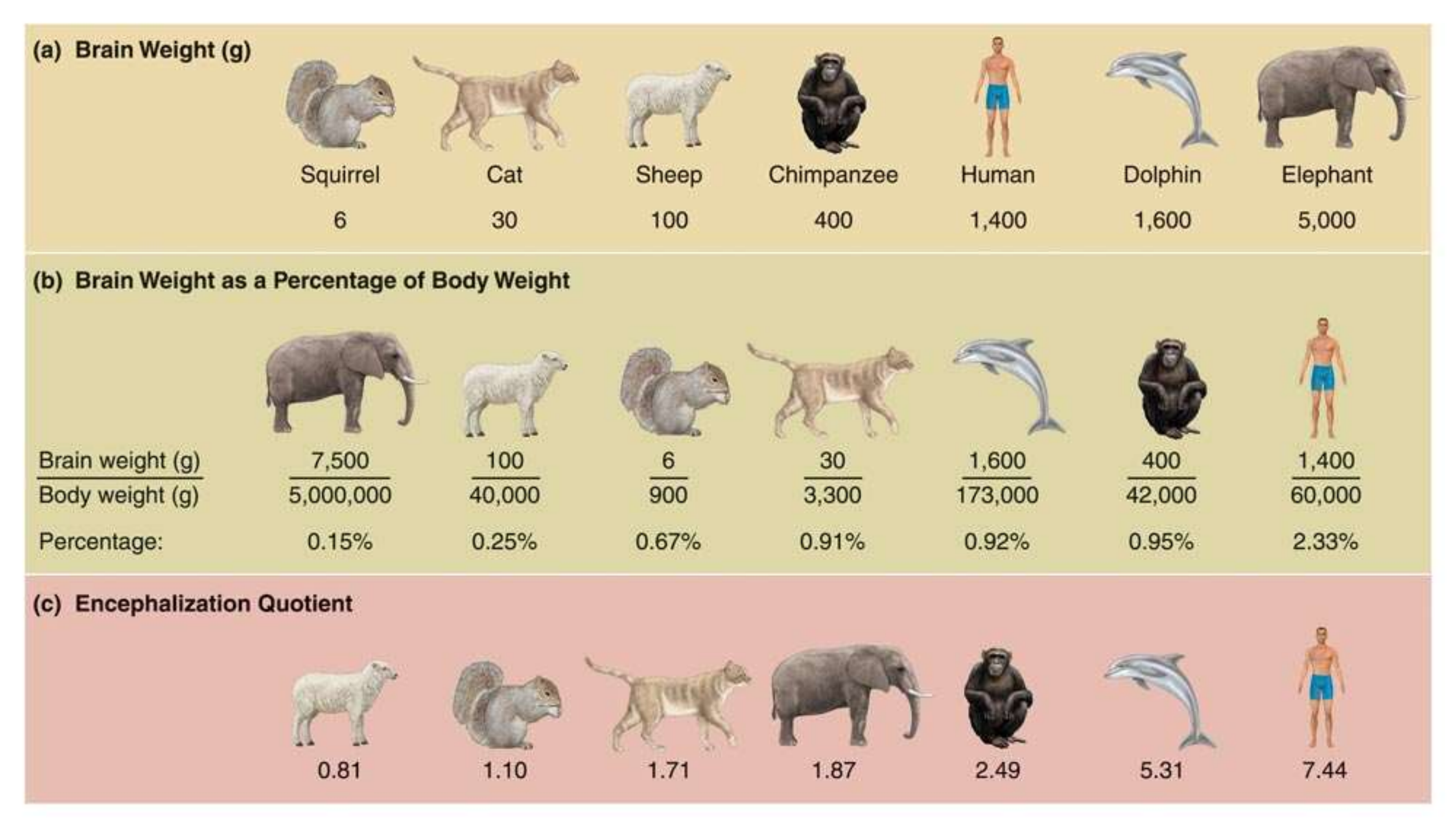
Encephalization: Increase in brain size during evolution of a SPECIES, with no concomitant increase in body size



PROGRESSIVE INCREASE in the size of the cerebrum in vertabrates is evident in the drawings above, which show a representative selection of vertebrate brains, all drawn to the same scale. In vertebrates lower than mammals the cerebrum is small. In carnivores, and particularly in primates, it increases drammatically in both size and complexity.

Source: "the Brain," a SCIENTIFIC AMERICAN BOOK. San Francisco:W.H.Freeman, 1979, pp. 4-5.

Comparative Intelligence: EQ



EQ is the actual brain size compared to the brain size necessary to operate body

Encephalization: $E = bP^a$

Brain size relative to body size

- Larger mammals tend to have larger brains
- Large proportion of the variance in brain size among mammals is explained by body size: 90% of variance in brain size attributed to body size variation
- Larger body required larger brain for somatic maintenance
- ~10% of variance unrelated to body size can be attributed to “encephalization”
- Extra neurons beyond those needed for somatic maintenance should lead to greater intelligence
- EQ also is measure of metabolic rate

EQ equation

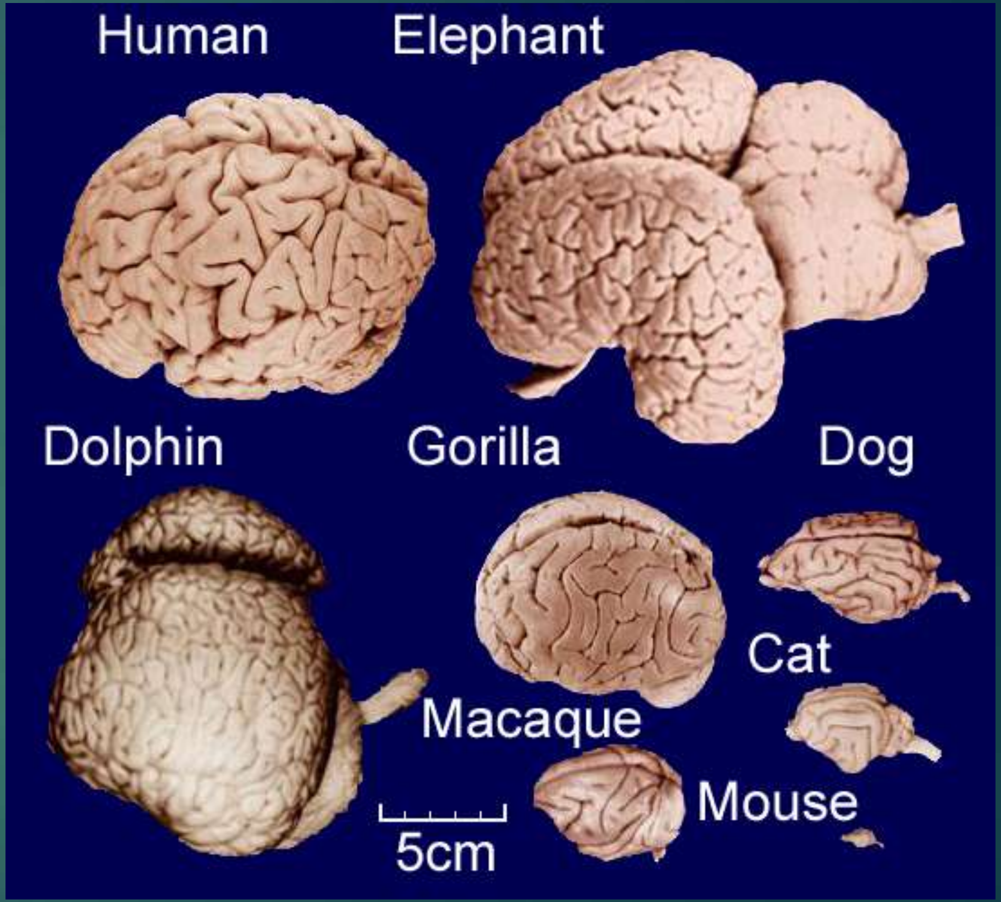
- There is a direct and predictable relationship between brain size and body size.
  - It can be described mathematically or graphically
    - $Y = kX^a$
      - Y = Brain weight
      - X = Body weight
      - k = “Scaling” constant
      - a = Exponent describes the slope of regression line
      - EQ = relationship to this regression line: if higher, smarter

- Or $E = bP^a$: E (brain wgt) = b (allometric parameter (k above)) P (body wgt) a (allometric - slope of regression line);
- Given species’ relationship to this line determines its EQ; EQ is ratio of actual brain size of a species to its expected brain size as predicted by the allometric equation

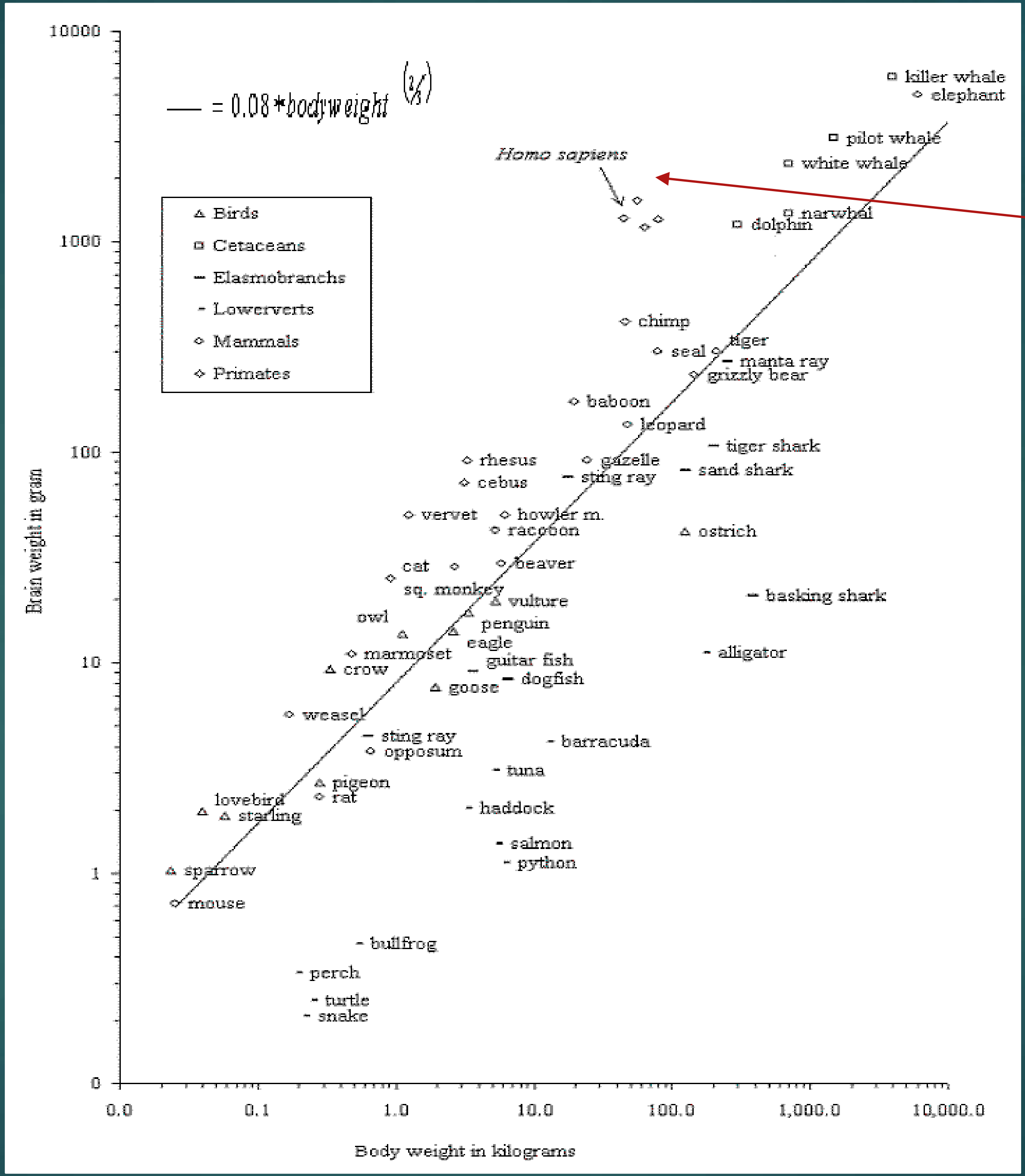
Issues with Encephalization Quotients

- “Encephalization" -- covers up changes in relative organization and interconnectivity.

- Primates, elephants, and cetaceans all display an increase in encephalization

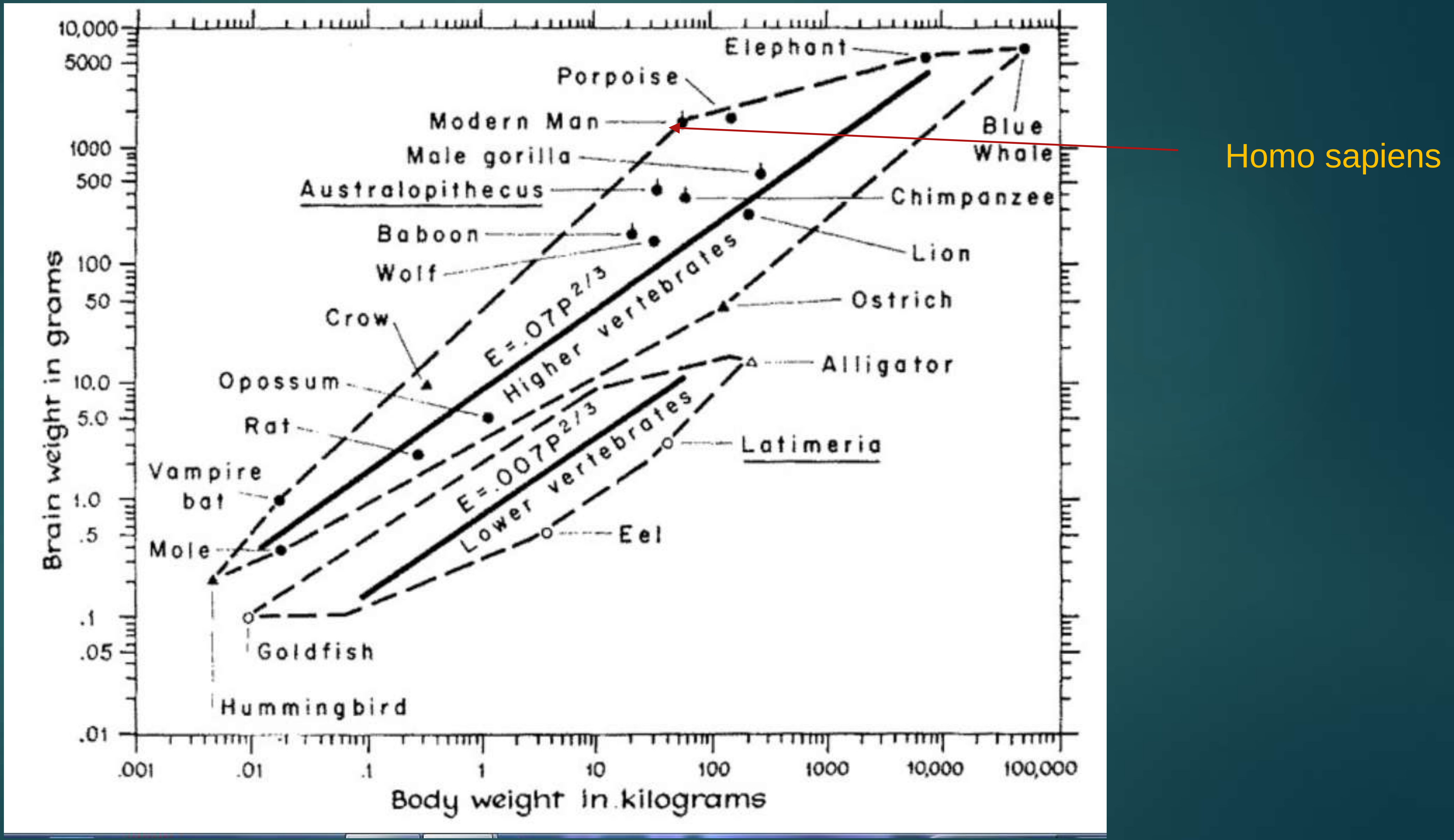


Position above regression line determines higher EQ

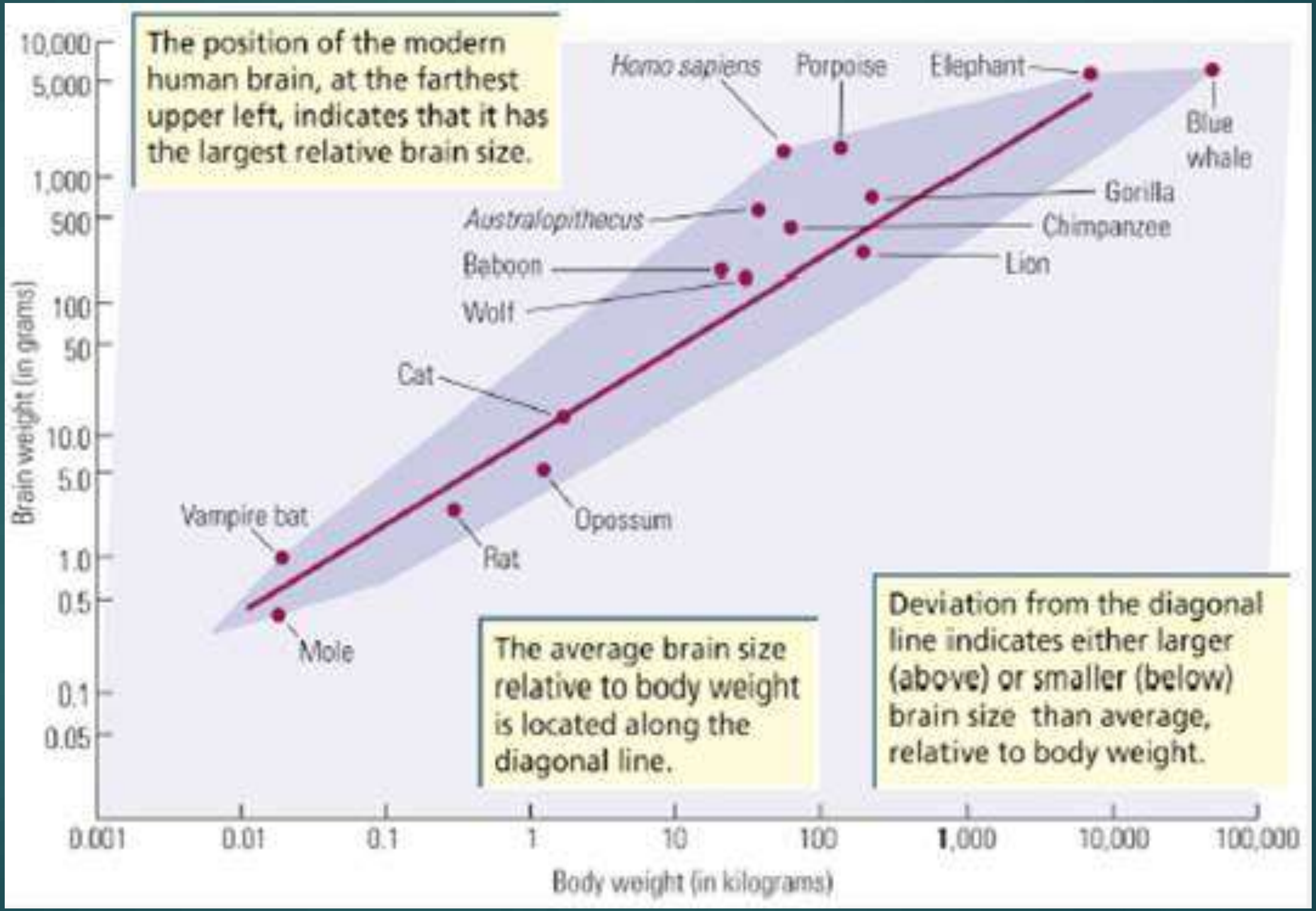


Homo sapiens

EQ: Body weight vs. Brain weight

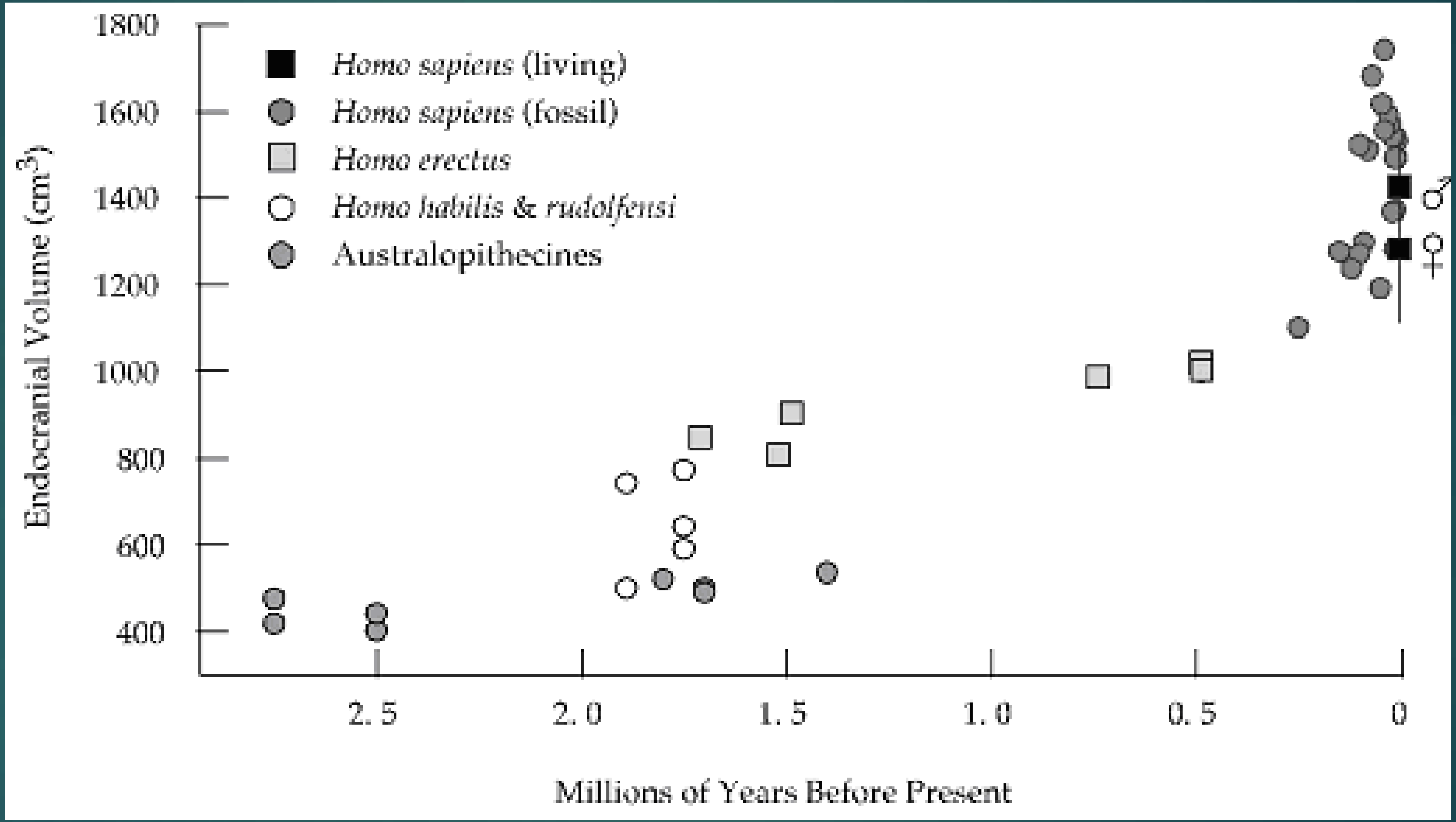


EQ: above line = smarter (larger extra brain); below line = less so



Brain volume evolution: Homo sapiens have decreased a little

Striedter brain size



Fossil

Living
H. sapiens

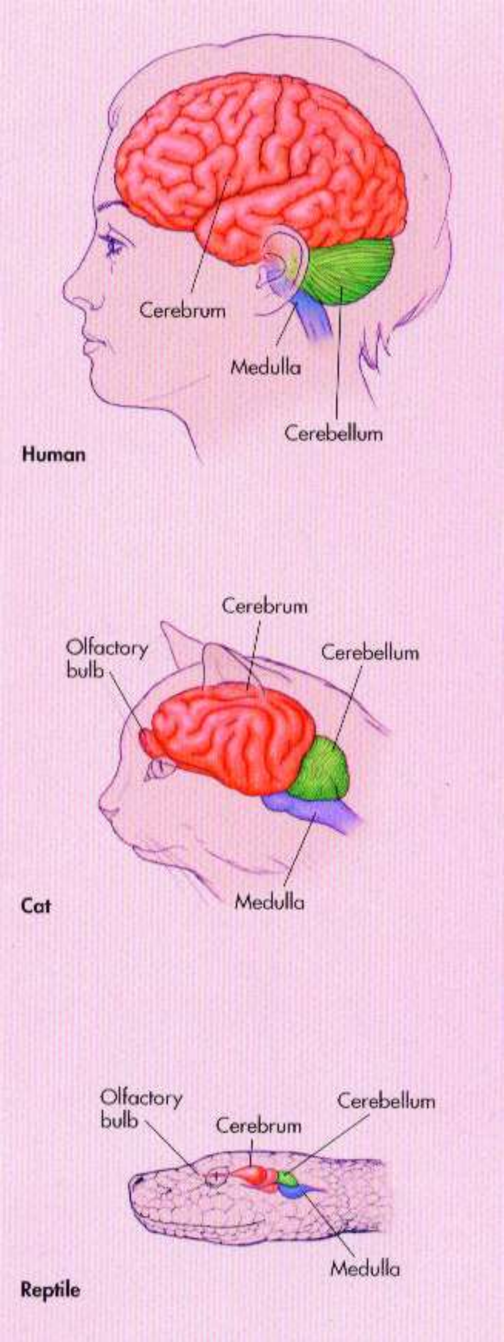
In Striedter, G. F. (2006). Precis of *Principles of brain evolution*.

EQs: indicator of hominid brain jumps

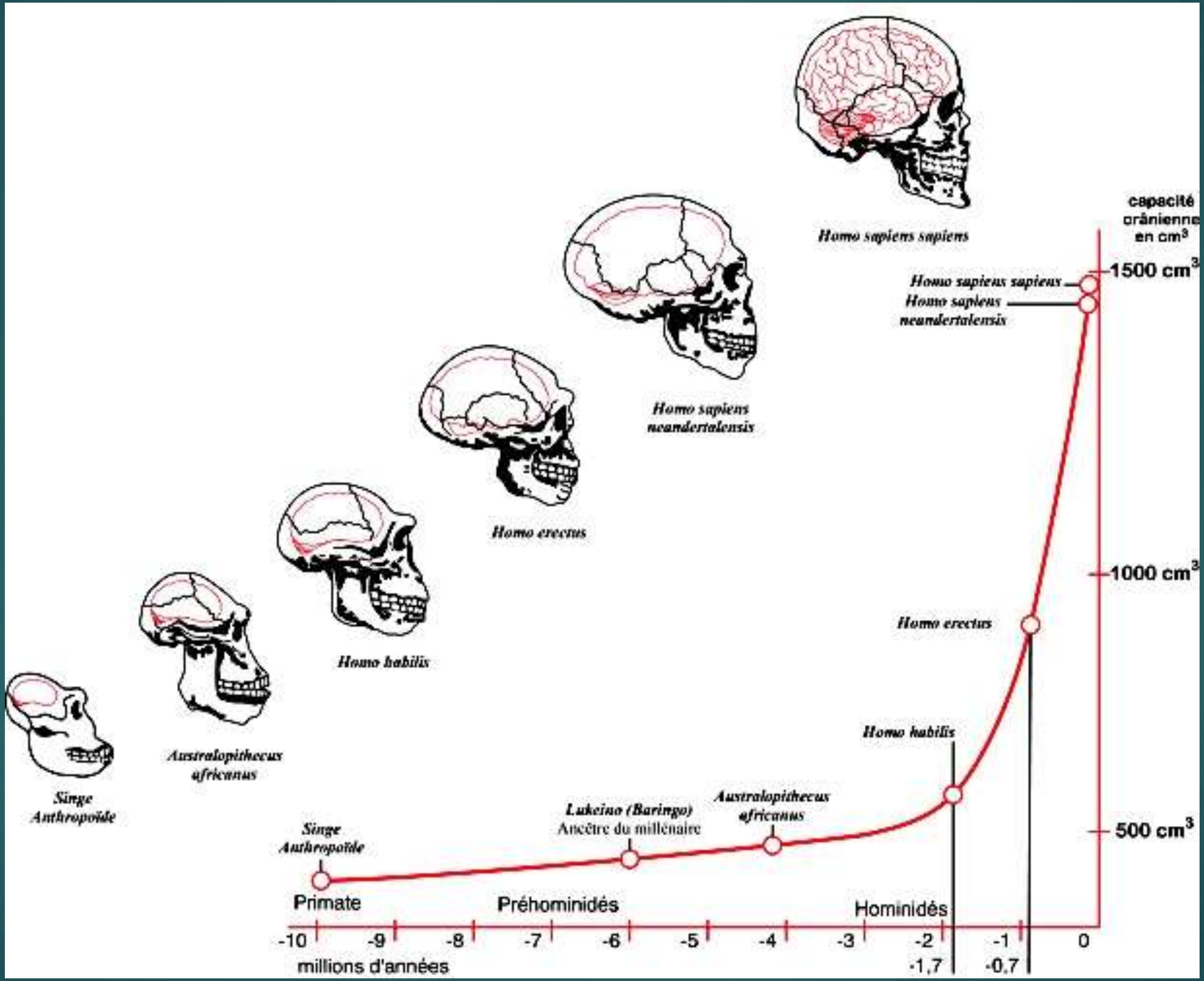
- Anthropoid primates have higher EQs than prosimians;
- Frugivous bats more than insectivorous bats;
- Dolphins & toothed whales more than other mammals
- Substantial increase in EQ is seen in early *Homo*; but no substantial subsequent increases in cc in *H. erectus* (modest cc increase in context of increased body size)
- Substantial increase in EQ with *H. heidelbergensis* and *H. sapiens*
- Neandertals had higher EQ than modern humans due to higher body mass

Factors that increase Encephalization

- Increase in absolute, & especially relative, brain size
  - Cortex enlarged compared to lower brain structures
- Rise of importance of biophysical senses (vision) compared to chemical senses (smell)
- More brain tissue for sensory functions compared to motor functions
- Increase in associative areas



Encephalization among hominins: Homo sapiens has highest EQ



Numbers of neurons: Humans, Cetaceans, vs Elephants

- Humans have the largest number of cortical neurons (86 bn) but are closely followed by large cetaceans and elephants.

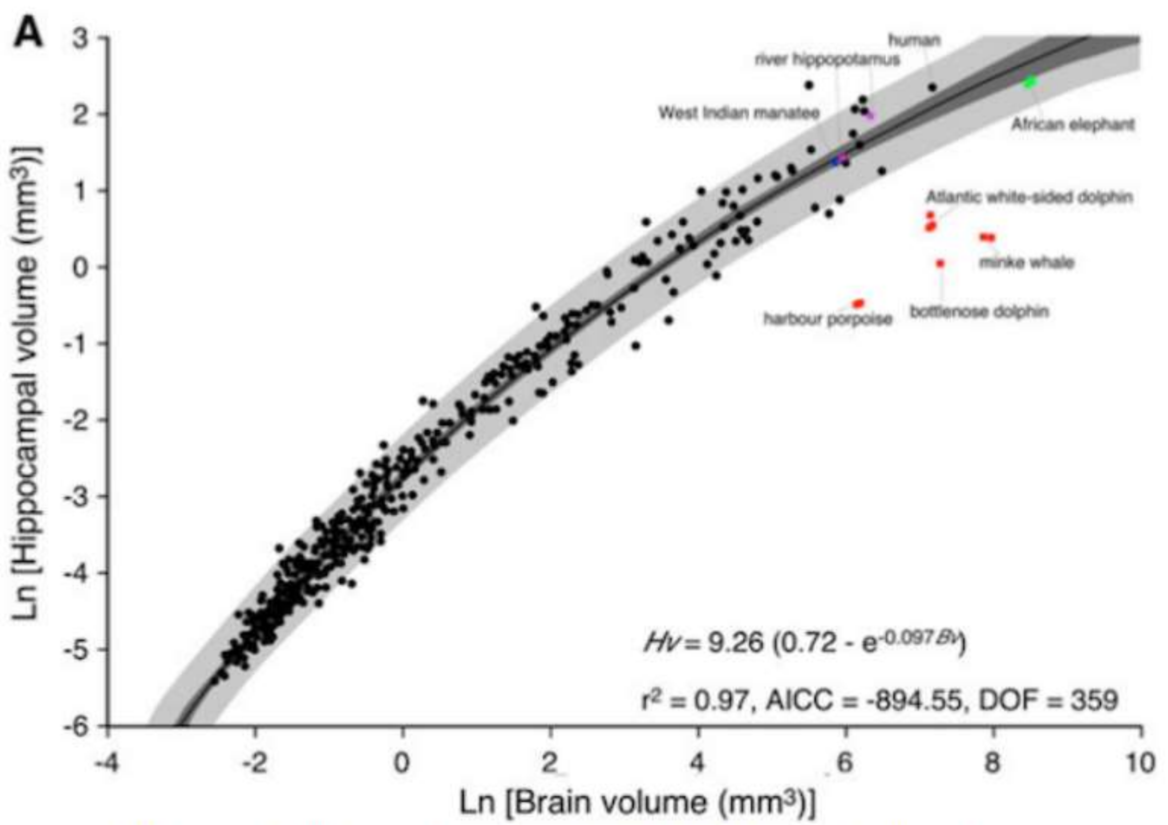
- Human cortex is much smaller in surface area than that of these animals, it is twice as thick and has a much higher cell density

- Neurons in the human cortex have 10,0000 synapses on average resulting in a total of about 10 trillion synapses.

Number of neurons

- An important parameter for information processing capacity (IPC) is conduction velocity of cortical fibers.
- It is mostly determined by the diameter of myelinated fibers. Myelinated cortical fibers are particularly thick in primates (higher conduction velocity) and relatively thin in elephants and cetaceans

Dolphins have unusually small hippocampus & no neurogenesis



Log-log plot of hippocampal volume versus total brain volume, for 375 species of mammals from a wide variety of groups. Used with permission from Patzke et al, 2013.

Only 8 percent to 20 percent of what would be expected on the basis of total brain size;

Lack neurogenesis

May be related to the lack of postnatal sleep; only conscious breathing; sleep 1 hemisphere at time

Capable of recall vocal call of another dolphin after decades.

Unclear if they have episodic memory or cognitive maps.

Patzke N, et al,, 2015

Dolphins practice infanticide

Birthing a large brain

- Issue of delivering a large headed baby through the birth canal: an evolutionary equilibrium between neonatal brain size and maternal pelvis size
- Human infant has a brain that is about 30% of size of an adult brain (400cc; relatively same as chimpanzee; Neandertal, 400cc; H. erectus, 300cc))
- At 2 years, 1100cc (but more synapses than both parents); 2-14 years, 1350cc (25% increase)
- Bipedal effects on pelvis: thicker bones, more bowl-like shape; requires rotation through birth canal

Highest correlations with brain volume are found for Gray Matter Volume

Total Brain Volume | Gray Matter Volume | White Matter Volume

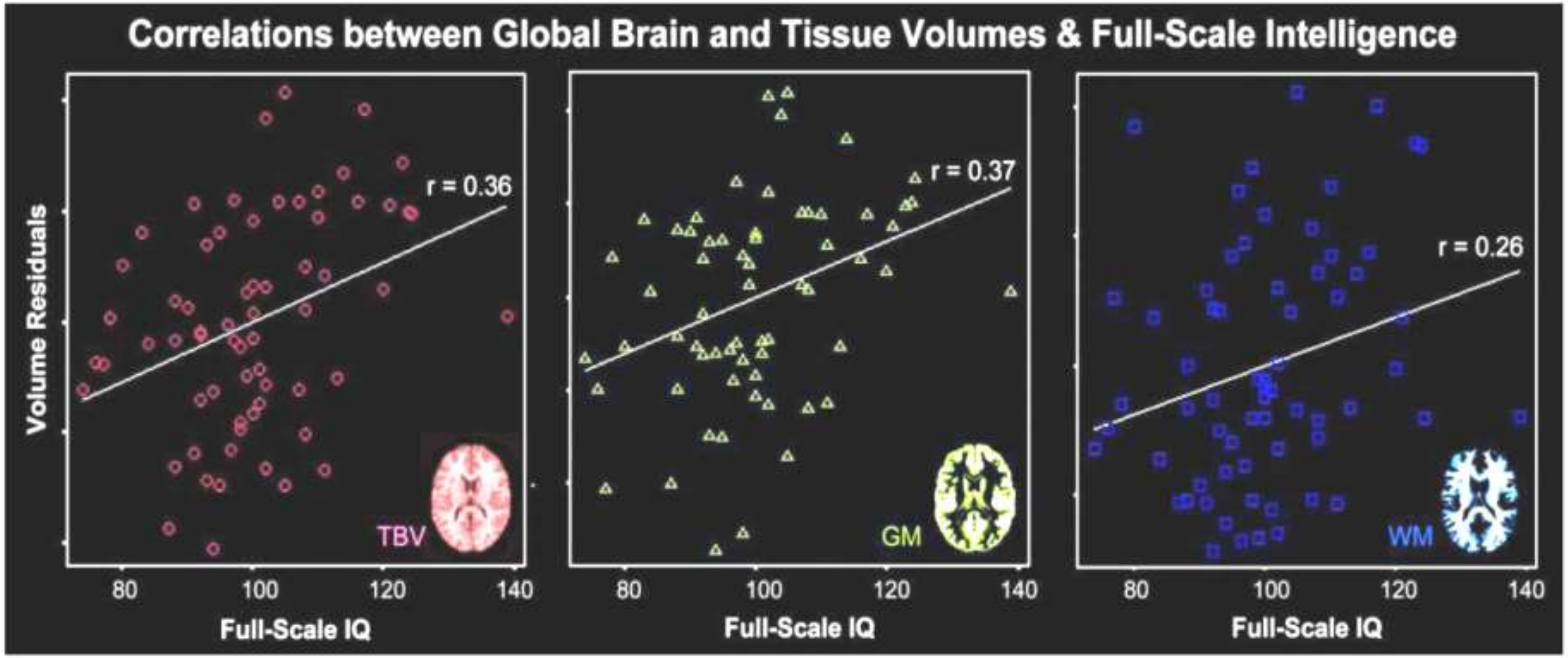


Fig. 1. Correlations between global volumes and full-scale intelligence in a sample of 65 healthy subjects, after removing the partial effects of sex and age (Narr et al., 2007). Illustrated are the intelligence-specific relationships with the residuals of total brain volume (TBV), gray matter volume (GM), and white matter volume (WM).

Reference: Luders et al. (2008), Intelligence

Brain size, IQ, & Cognitive Reserve

- What is the relationship between brain size and cognitive measures.
- Studies have reported correlations that range from 0 to 0.6, with most correlations 0.3 or 0.4
- Rushton and Ankney (2009) in a literature review write that in 28 samples using MRI, the mean brain size/*g* correlation was 0.40 (N = 1,389).
- In 59 samples using external head size measures it was 0.20 (N = 63,405).

Brain size and IQ

- In 6 studies that corrected for that different IQ subtests measure *g* unequally well, the mean correlation was .63.

- Some studies have found the whole brain to be important for *g* while others have found the frontal lobes to be particularly important.

- Two studies found correlations of .48 and .56 between brain size and the number of neurons in the cerebral cortex.

- Scottish Lothian study: IQ at age 11 correlates .50 with IQ at age 77; better brain to begin with predicts less NCD; other 50% is Cognitive Reserve factors

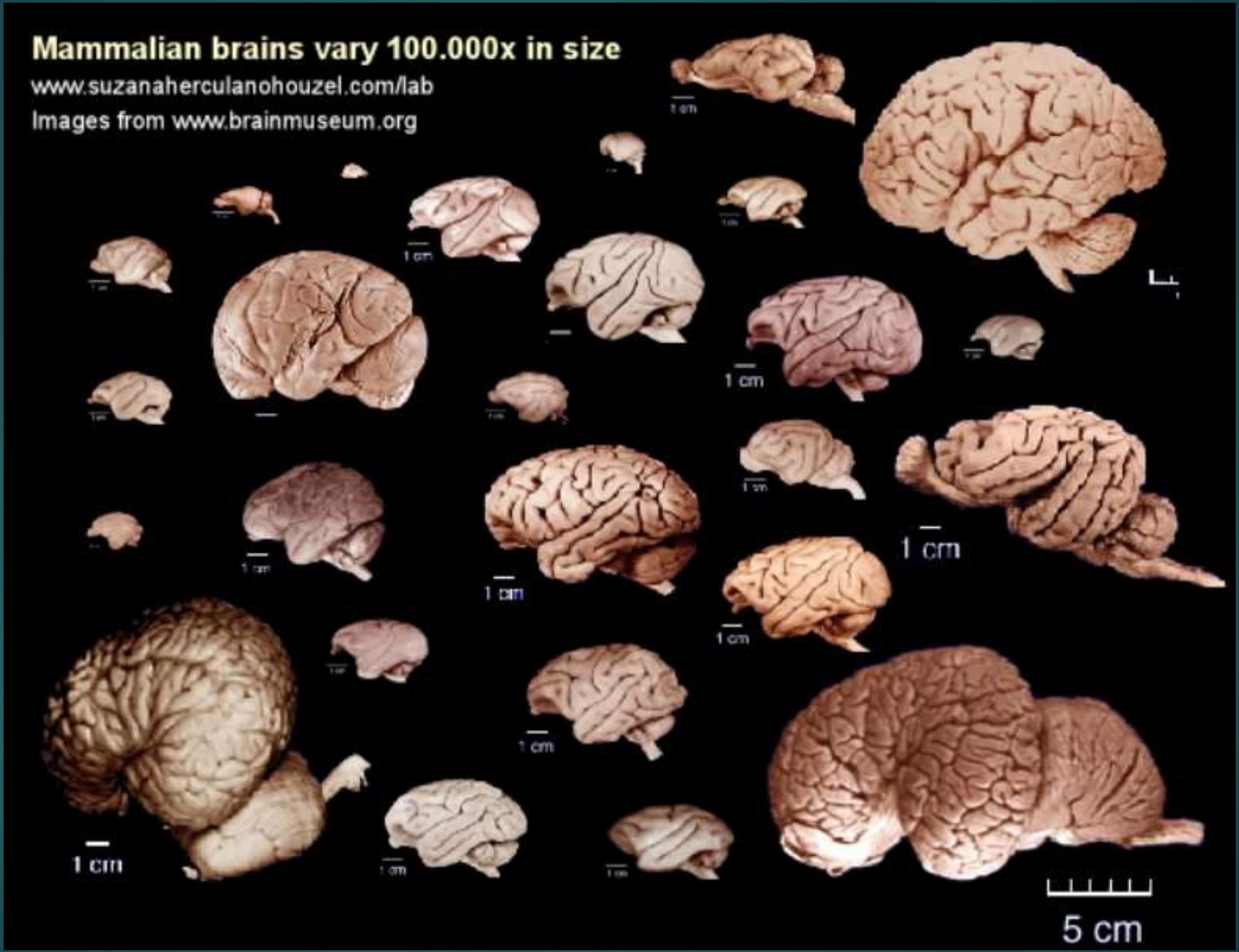
Brain weight: other variables

- Rushton (2004) argued that the theory was supported by relationships between brain weight and several other variables among 234 mammalian species:
  - longevity (r = .70),
  - gestation time (.72),
  - birth weight (.44),
  - litter size (-.43),
  - age at first mating (.63),
  - duration of breast feeding (.62),
  - body weight (.44),
  - body length (.54).
- Looking 21 primate species, brain size still correlated .80 to .90 with life span, length of gestation, age of weaning, age of eruption of first molar, age at complete dentition, age at sexual maturity, inter-birth interval, and body weight.

Some <u>classically accepted "facts about human brain</u>: human brain is literally extraordinary

- 86 B neurons, 86 glia in the brain (old idea = 10- to 50-fold more glial cells)
- The largest-than-expected for its body among primates and mammals; 5-7 x larger than expected
- Costs more energy: 2% mass, 20% energy cost
- The most developed cortex (relative size); the largest compared with brain size

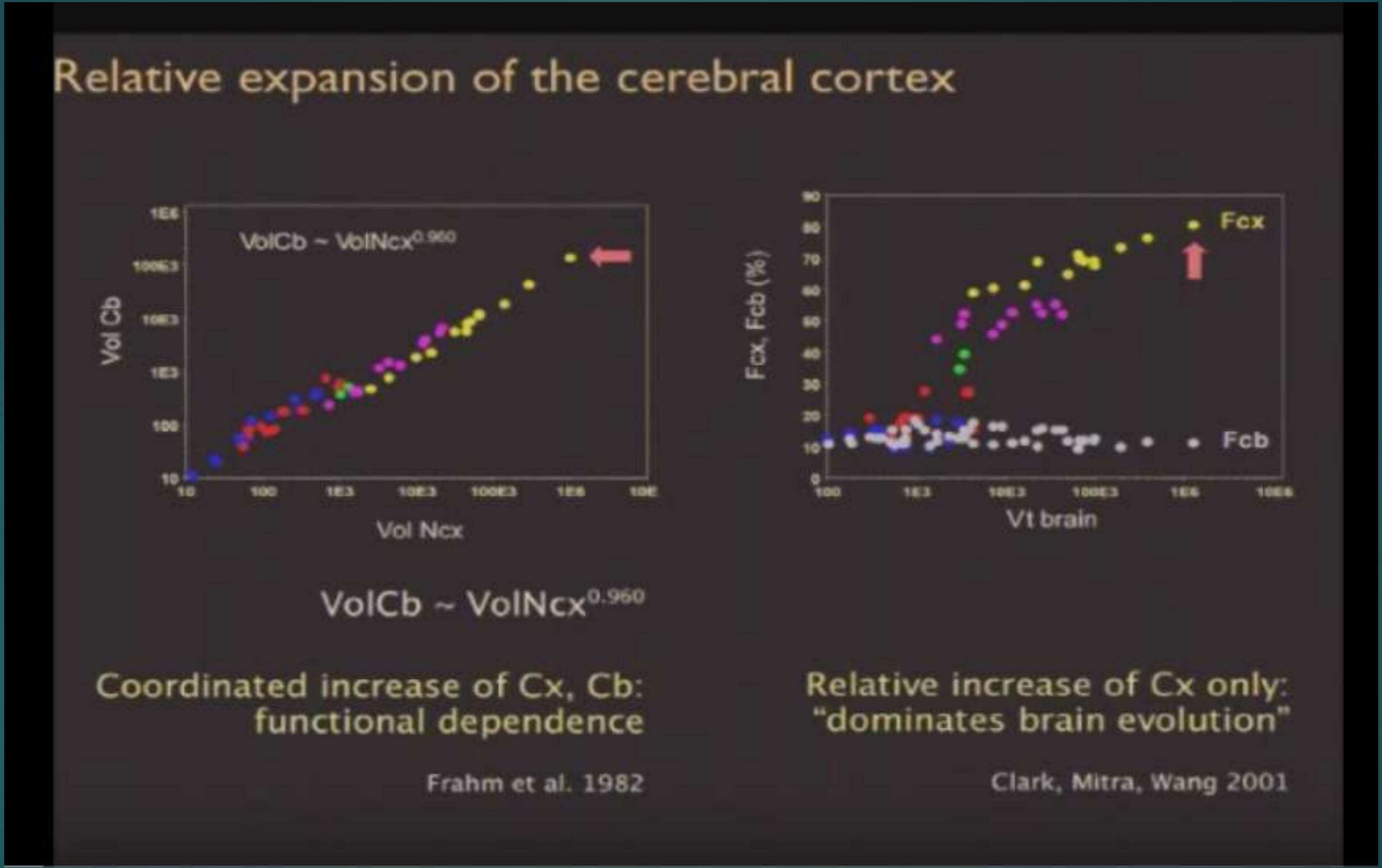
Suzana Herculano-Houzel, 2013


Mammalian brains vary 100.000x in size
www.suzanaherculanohouzel.com/lab
Images from www.brainmuseum.org
1 cm
1 cm
1 cm
1 cm
1 cm
1 cm
1 cm
1 cm
5 cm

Historical view of Brain Scaling in Mammals

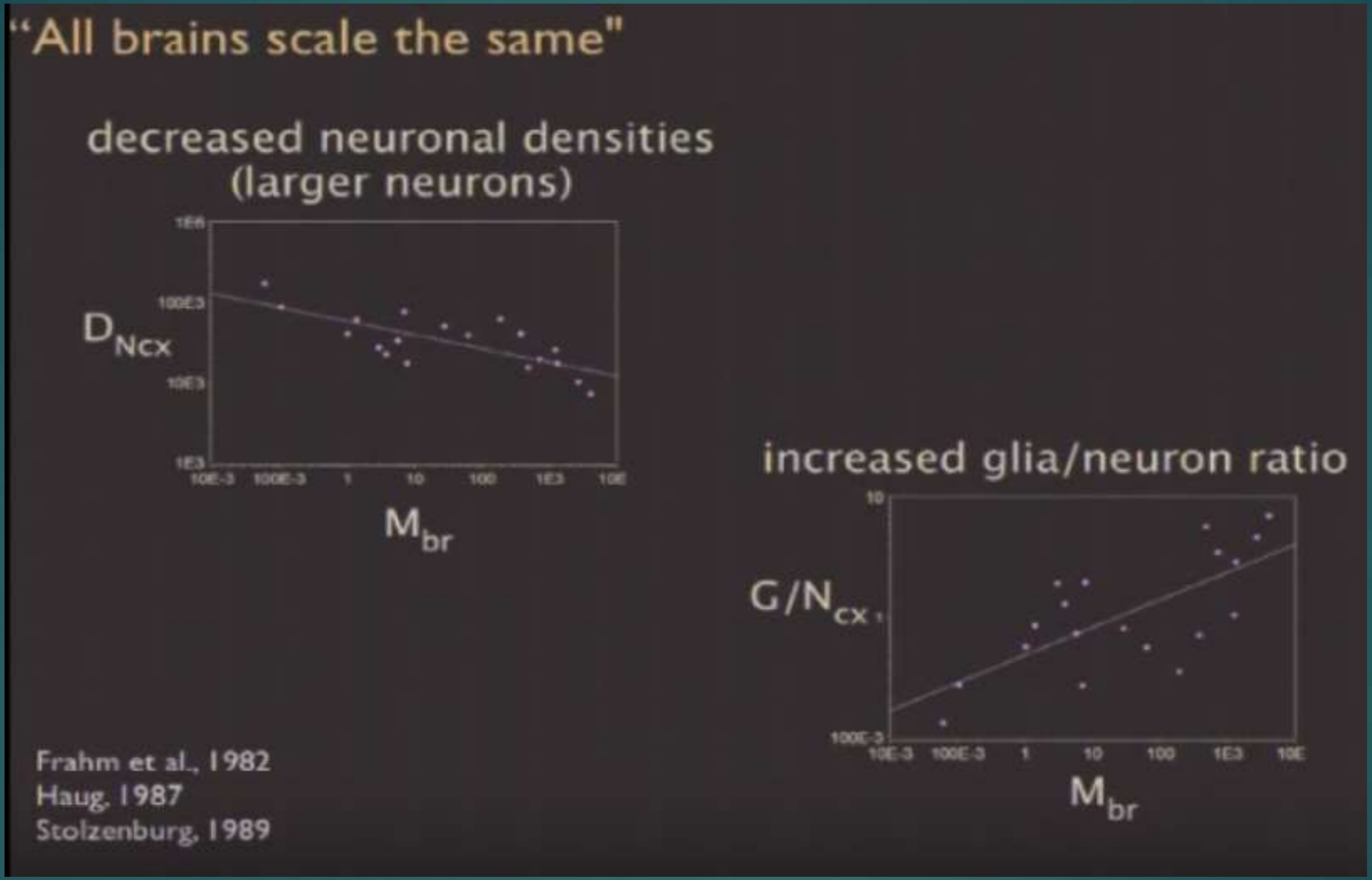
- Brain scaling in mammalian evolution has tacitly been considered a homogeneous phenomenon in terms of:
  - numbers of neurons,
  - neuronal density,
  - ratio between glial and neuronal cells,
  - with brains of different sizes viewed as similarly scaled-up or scaled-down versions of a shared basic plan.
- According to this traditional view, larger brains would have:
  - more neurons,
  - smaller neuronal densities (and, hence, larger neurons),
  - larger glia/neuron ratios than smaller brains.
  - a cerebellum that maintains its relative size constant
  - a cerebral cortex that becomes relatively larger to the point that brain evolution is often equated with cerebral cortical expansion.

Old consensus on relative size of cortex



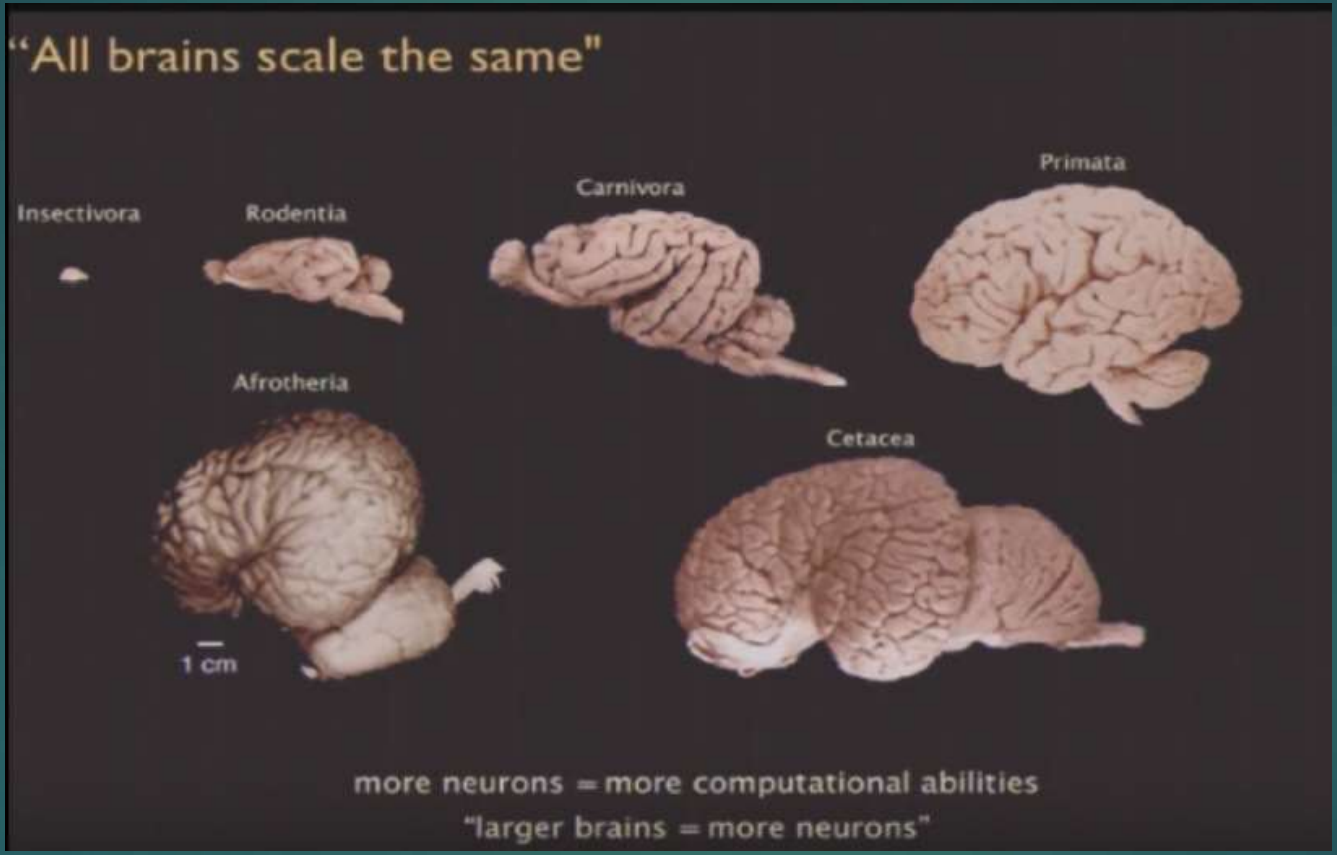
The larger the brain, the larger the cortex in percent size; cortex increases linearly with cerebellum. Human cortex's relative increase dominates all others. (dots are 1 species)

Old consensus: All brains scale the same



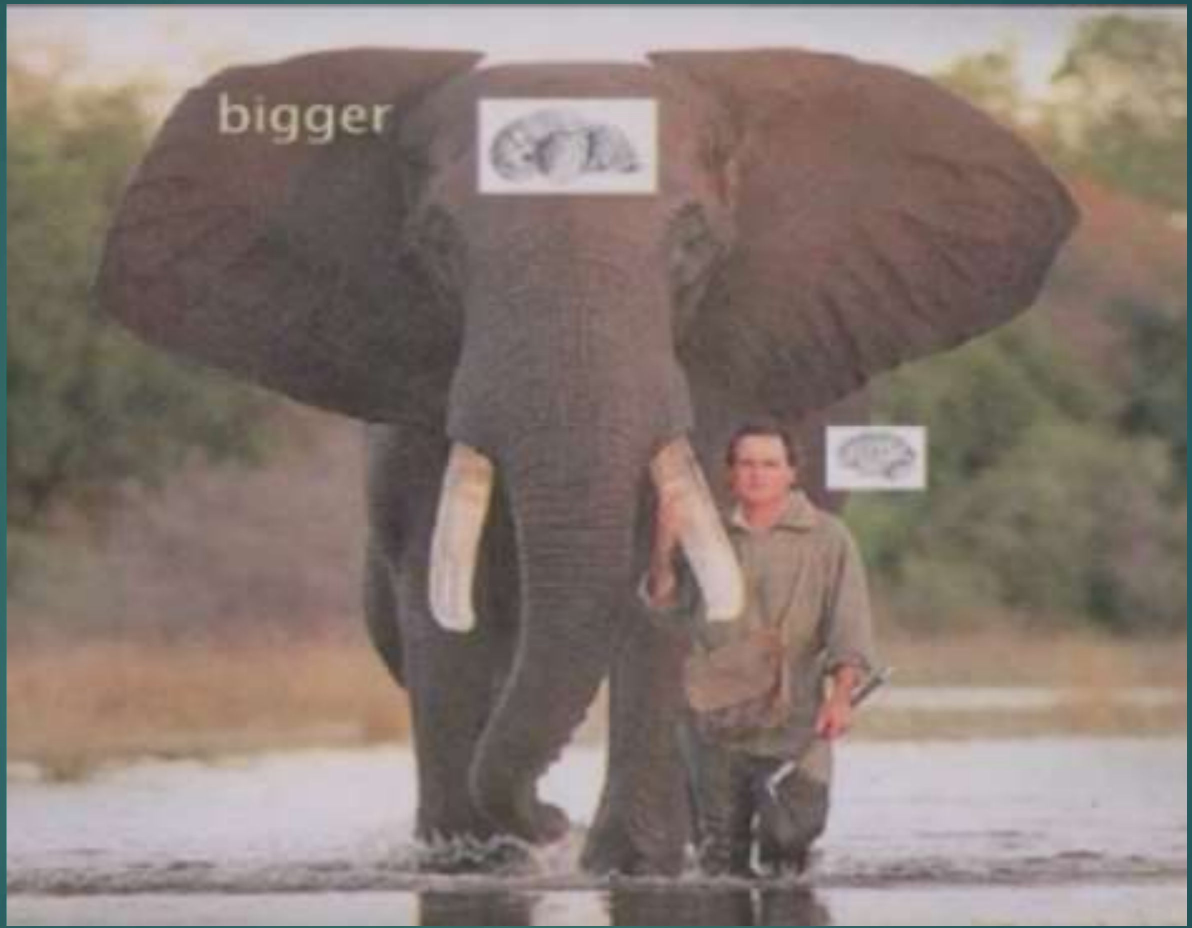
Larger brains have lower neuronal densities because they have larger neurons and ratio of glia to neurons also increases.

Old consensus: All brains scale the same: big brains are larger versions of smaller brains



Larger brains = more neurons; more neurons = more computational abilities

Size cannot be all

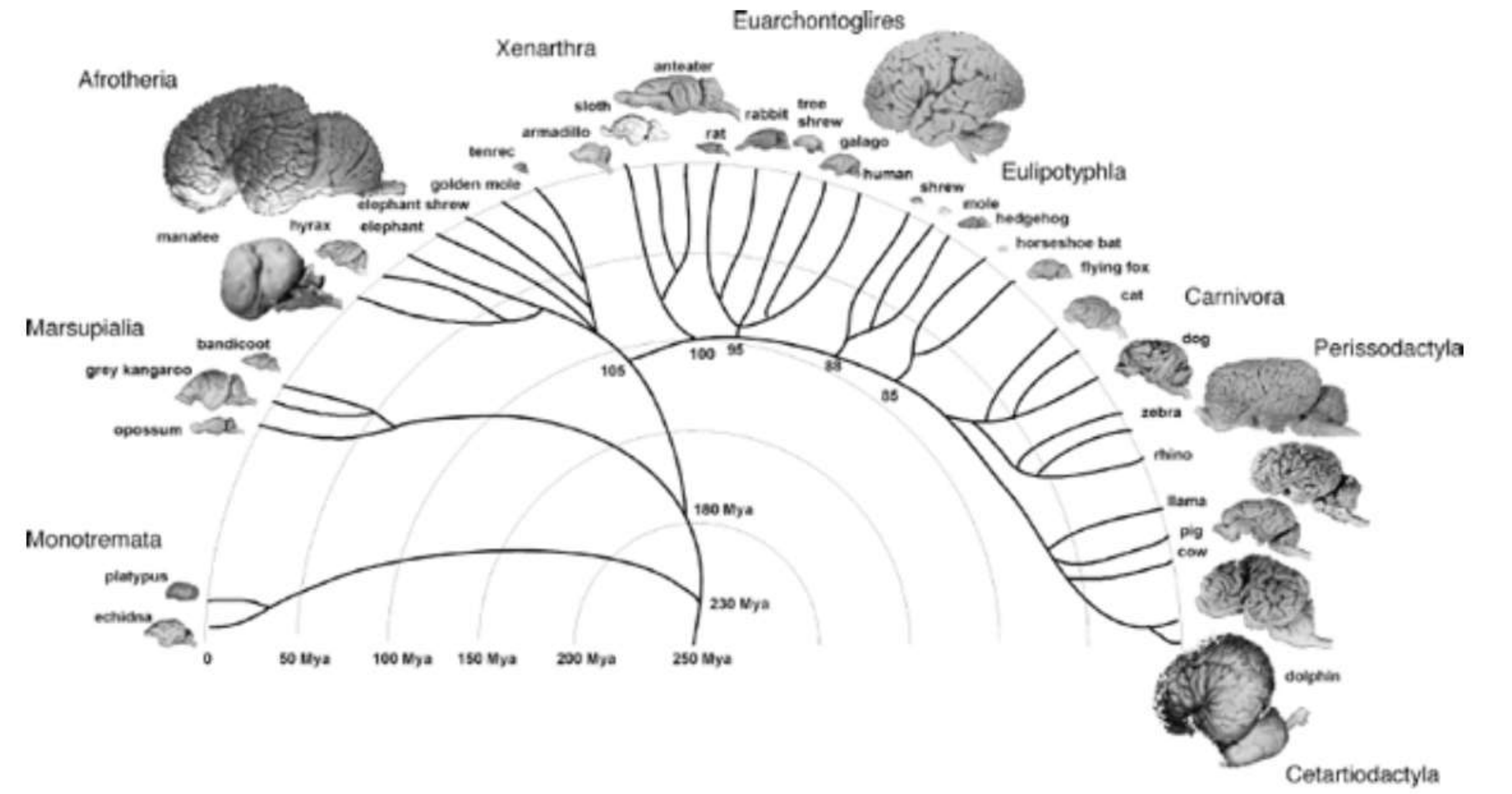


Two 400 gram brains

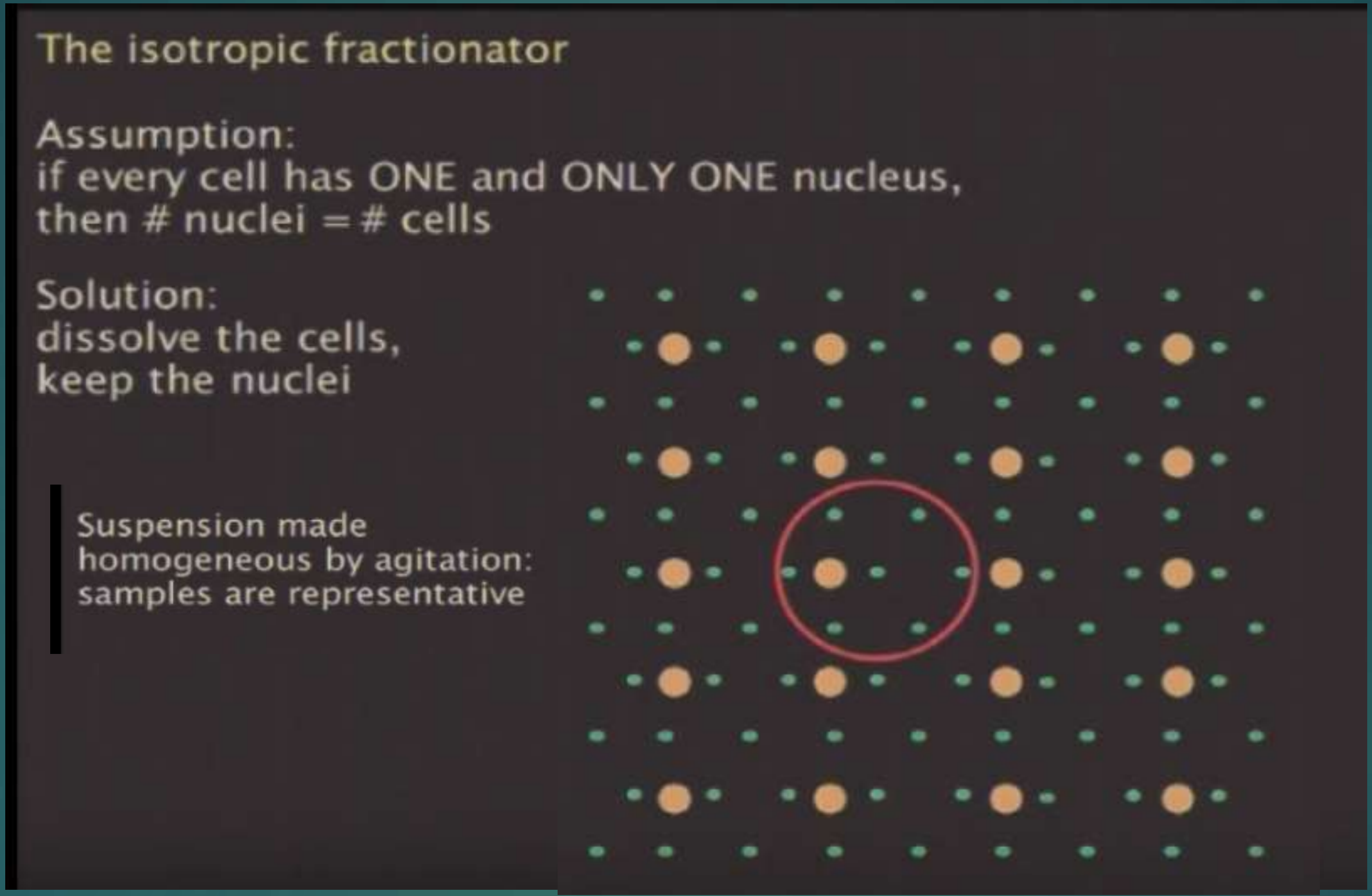
Elephant brain is 4 x larger than ours

But ours:
Relatively larger cortex
More encephalized
Matures later

Large brains evolved several times independently in mammals

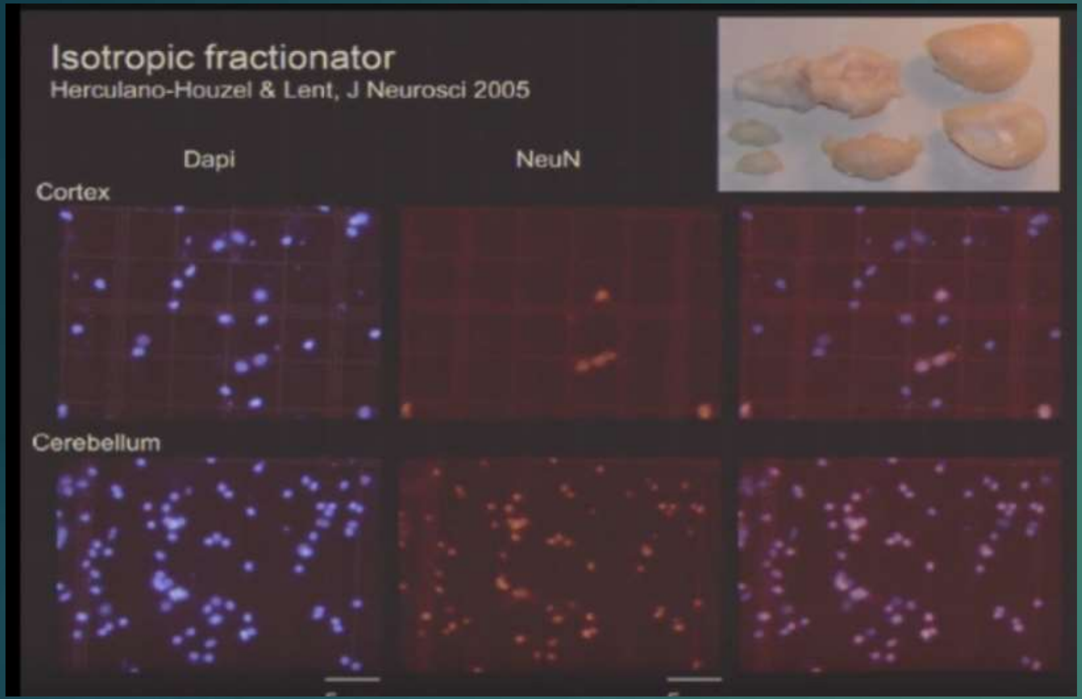


Isotropic Fractionator Method: Turn brain into soup

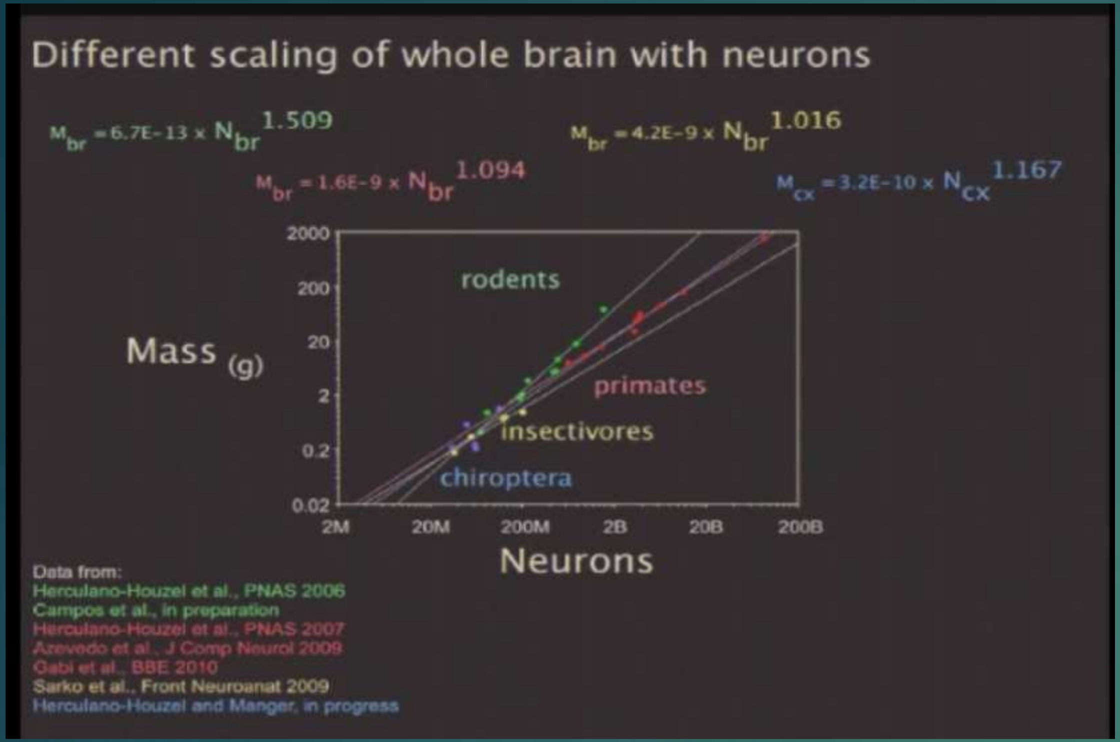


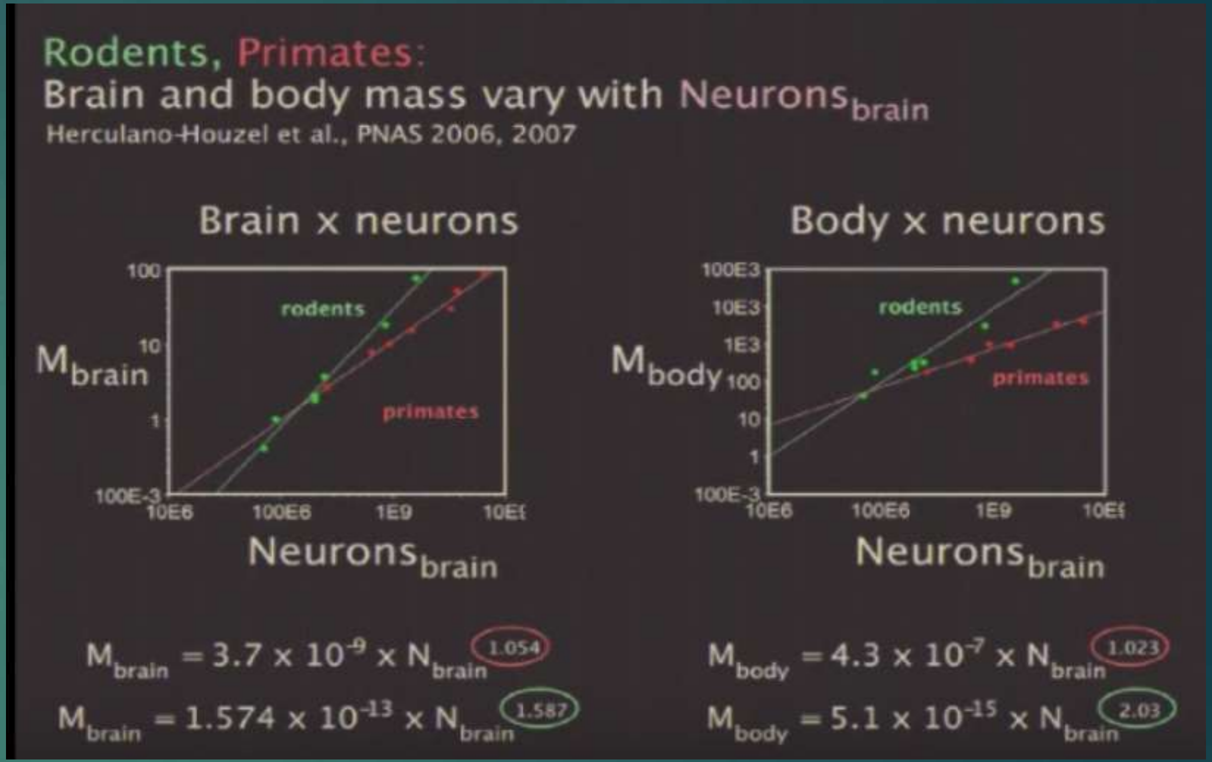
In 2009, Suzana Herculano-Houzel & team rounded up the brains of four recently deceased men, brought them to a laboratory, and liquefied them, using a novel technique called "isotropic fractionation.“ They dissolved each fixed brain into a homogenous mixture of "brain soup" (via detergent that leaves nuclei), took samples from the soups, measured the number of neurons in each sample, and then scaled up to find the neuronal content of each brain bisqué.

Can then stain and count; and do many species for comparison



Mass of whole brain vs number of neurons





Not a homogeneous distribution; differences are enormous

Rodents: larger brains made up of larger number of neurons; Brain that gains 10 x more neurons, becomes 45 x larger (scale = 1.6); inflationary way to add neurons; size of neuron increases; and gain body mass much faster than they gain neurons

Larger primate brains have more neurons, but if it gains 10 x more neurons, becomes 10x large (scale = 1)

Suzana Herculano-Houzel

- Human brain is not extraordinary in its cellular composition compared to other primate brains – but it is remarkable in its enormous absolute number of neurons, which could not have been achieved without a major change in the diet of our ancestors.
- Such a change was provided by the invention of cooking, which she proposes to have been a major watershed in human brain evolution, allowing the rapid evolutionary expansion of the human brain.

Large brain and diet

- Humans are the primates with the largest brain and number of neurons, but not the largest body mass.
- Why are great apes, the largest primates, not also those endowed with the largest brains?
- Energetic cost of the brain is a linear function of its numbers of neurons.
- Metabolic limitations that result from the number of hours available for feeding and the low caloric yield of raw foods impose a tradeoff between body size and number of brain neurons, which explains the small brain size of great apes compared with their large body size.

Karina Fonseca-Azevedo and Suzana Herculano-Houzel, 2012

Brain and diet

- This limitation was probably overcome in *Homo erectus* with the shift to a cooked diet.

- Absent the requirement to spend most available hours of the day feeding, the combination of newly freed time and a large number of brain neurons affordable on a cooked diet may thus have been a major positive driving force to the rapid increased in brain size in human evolution.

Human Brain in Numbers: A Linearly Scaled-up Primate Brain

- Contrary to the traditional notion of shared brain scaling:
  - Both the cerebral cortex and the cerebellum scale in size as clade-specific functions of their numbers of neurons.
  - As a consequence, neuronal density and the glia/neuron ratio do not scale universally with structure mass
  - Most importantly, mammalian brains of a similar size can hold very different numbers of neurons.
  - Remarkably, the increased relative size of the cerebral cortex in larger brains does not reflect an increased relative concentration of neurons in the structure.
  - Instead, the cerebral cortex and cerebellum appear to gain neurons coordinately across mammalian species.

Suzana Herculano-Houzel

New idea of brain scaling

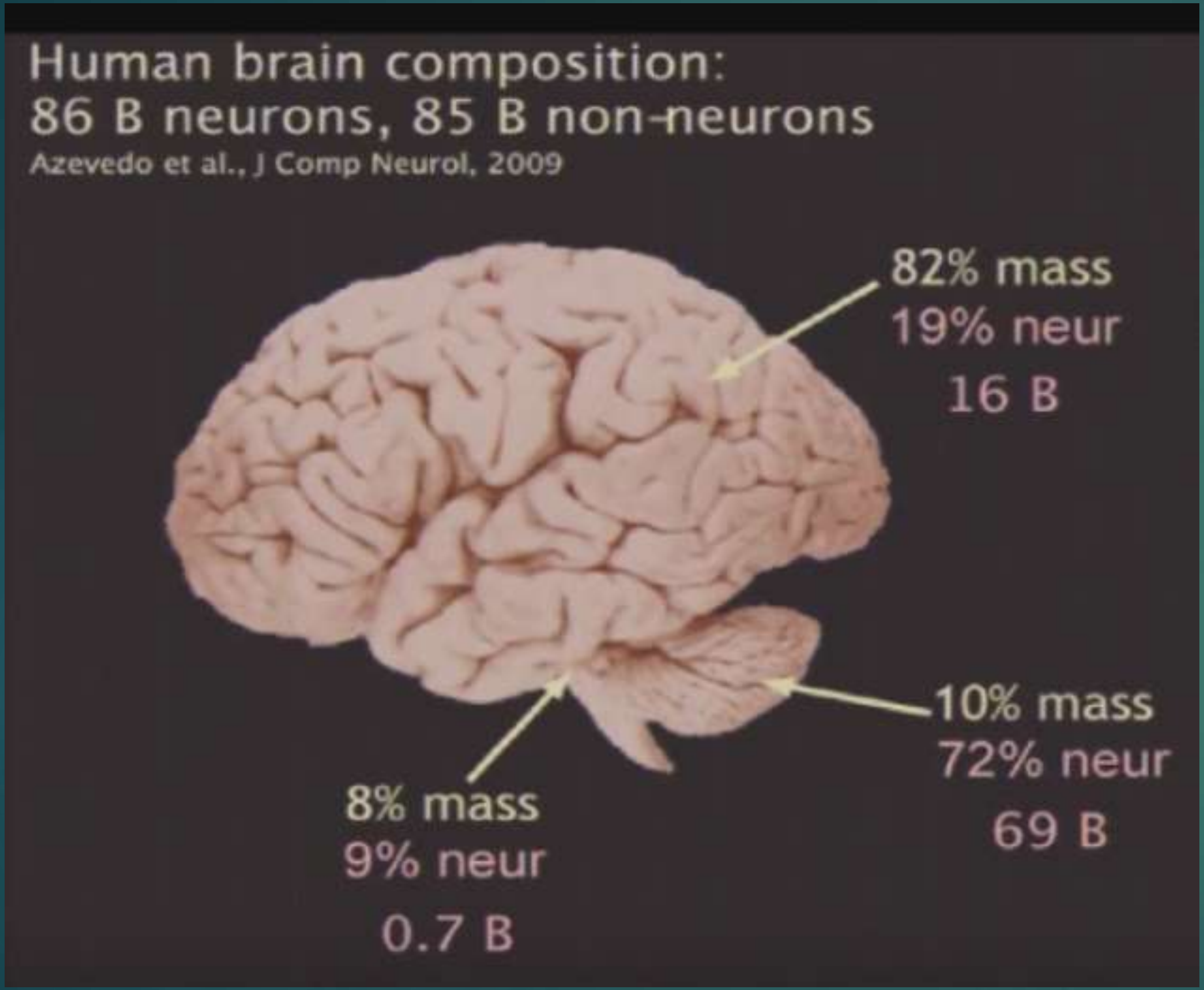
- Brain scaling in evolution should no longer be
  - equated with an increasing dominance of the cerebral cortex
  - but rather with the concerted addition of neurons to both the cerebral cortex and the cerebellum.
- Strikingly, all brains appear to gain nonneuronal cells in a similar fashion, with relatively constant nonneuronal cell densities.

Suzana Herculano-Houzel

Number of neurons count

- As a result, while brain size:
  - can no longer be considered a proxy for the number of brain neurons across mammalian brains in general,
  - It is actually a very good proxy for the number of nonneuronal cells in the brain.

Our brain: 171 billion cells – 85 Billion neurons



85 B neurons, 85 B glial cells

Cortex: 82% of mass of brain, but only 16 B neurons (19% of neurons)

Cerebellum: 10% of mass, but 69 B neurons (72%)

Brainstem: 8% of mass, but 0.7 B neurons (9%)

Human brain is not exceptional – but has absolute largest number of neurons

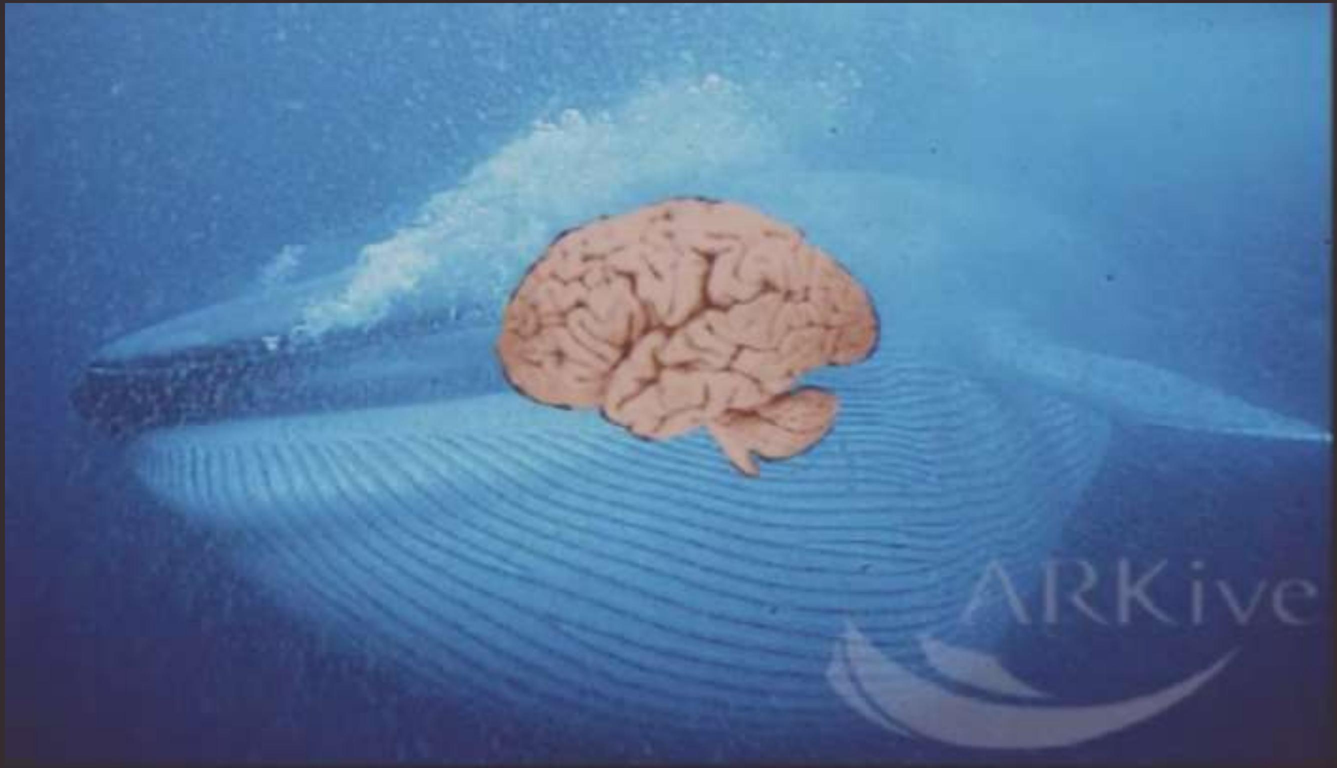
- Human brain is not exceptional in its cellular composition; contains as many neuronal and non-neuronal cells as would be expected of a primate brain of its size.

- Additionally, the so-called overdeveloped human cerebral cortex holds only 19% of all brain neurons, a fraction that is similar to that found in other mammals.

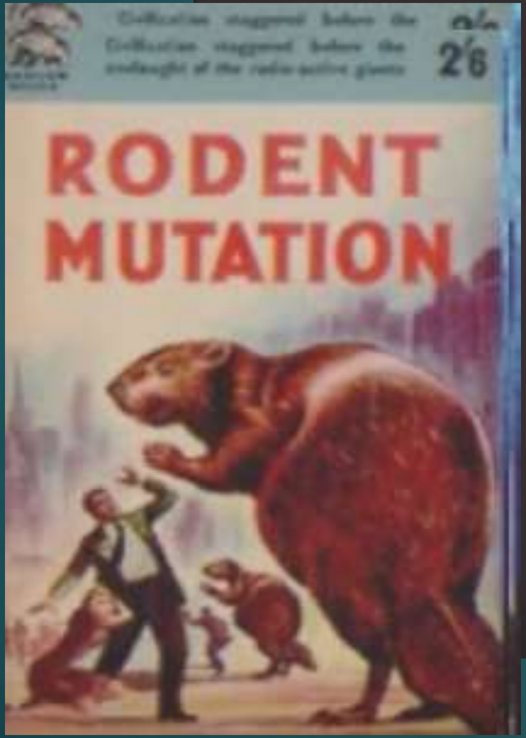
Not exceptional

- In regard to absolute numbers of neurons, however, the human brain does have two advantages compared to other mammalian brains:
  - compared to rodents, and probably to whales and elephants as well, it is built according to the very economical, space-saving scaling rules that apply to other primates;
  - among economically built primate brains, it is the largest, hence containing the most neurons.

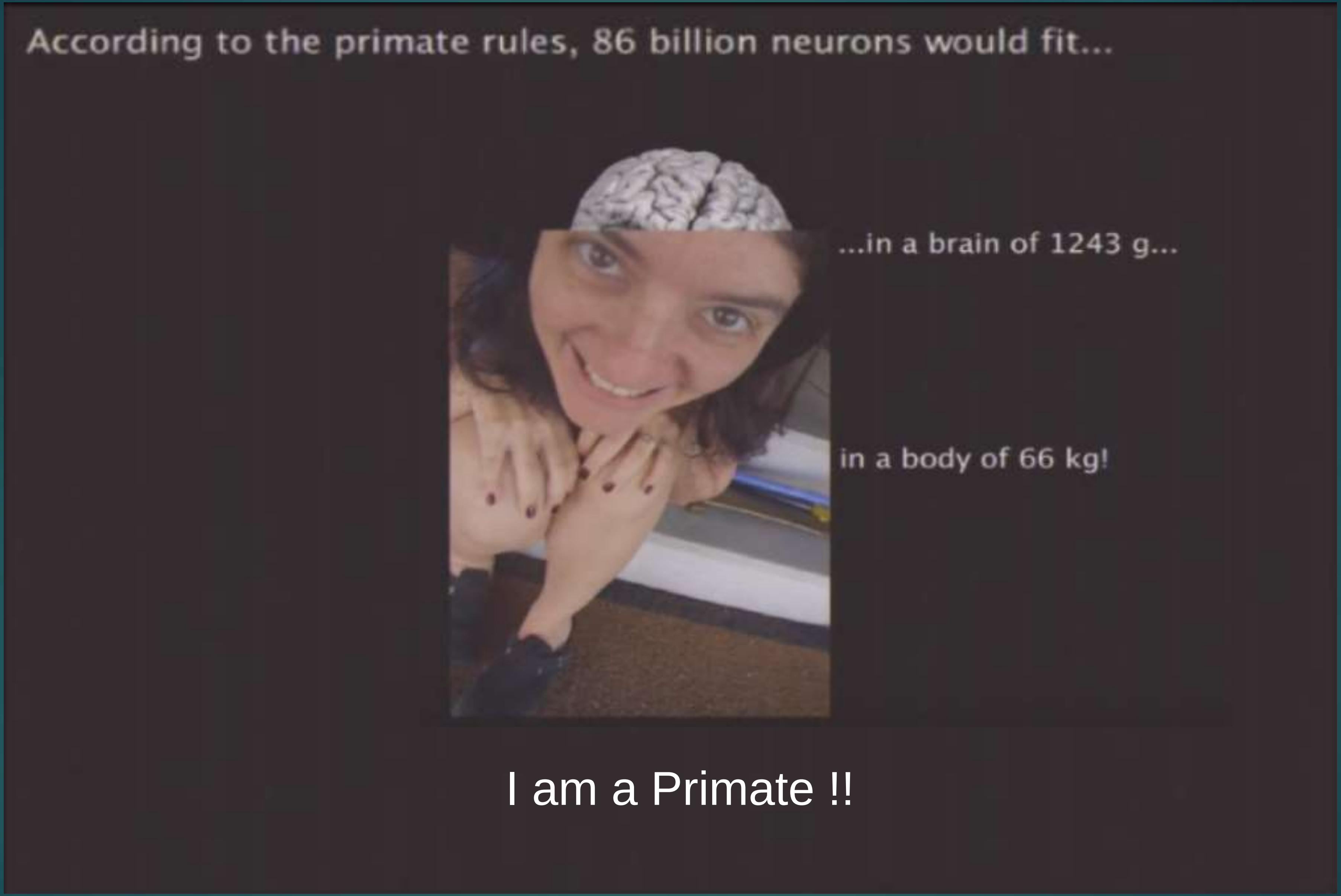
- These findings argue in favor of a view of cognitive abilities that is centered on absolute numbers of neurons, rather than on body size or encephalization, and call for a re-examination of these concepts



= 80 lb child

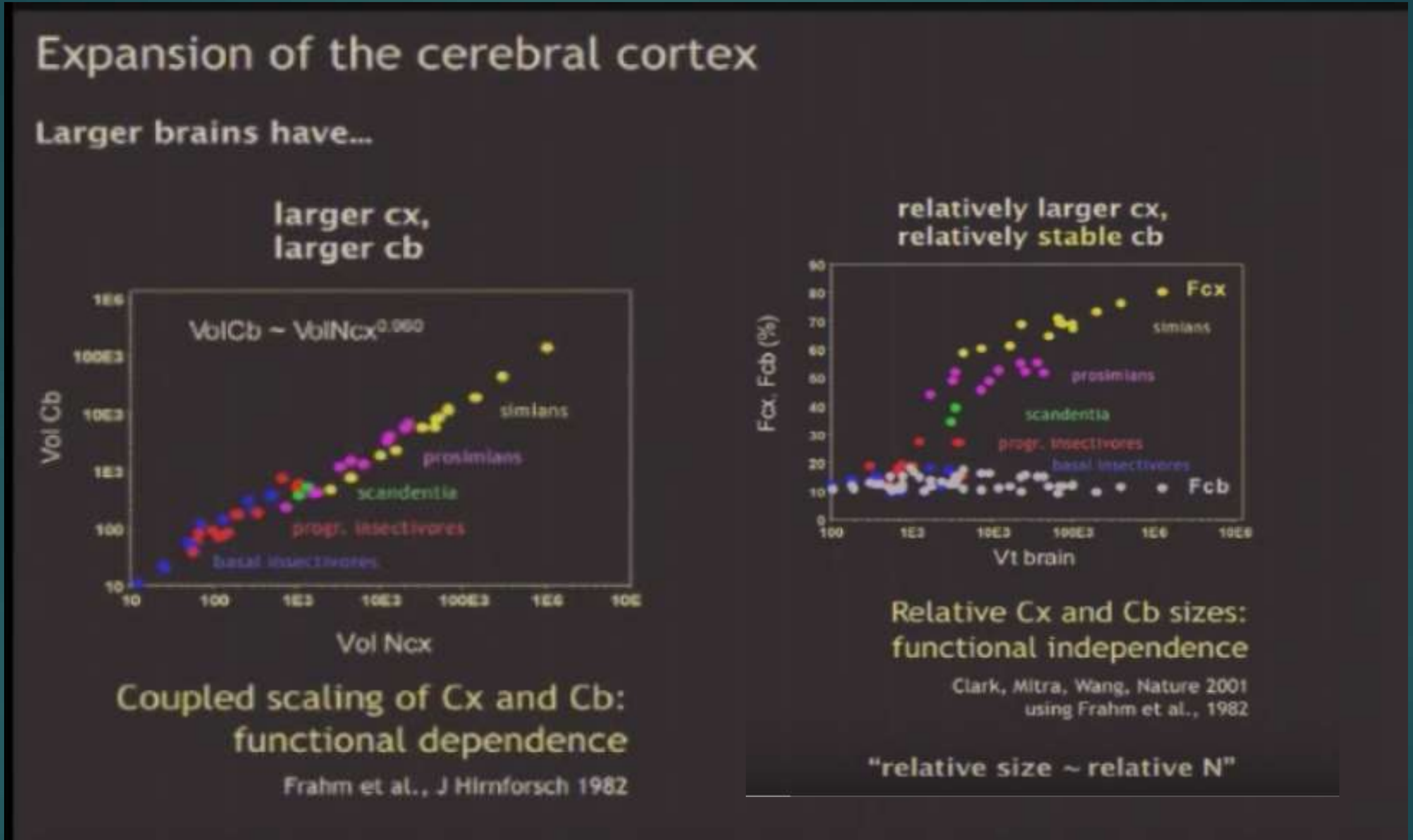


Such a rodent would have to live underwater



Human brain is built exactly like a primate brain when it comes to number of neurons;
A scaled up primate brain.

Relative expansion of cortex

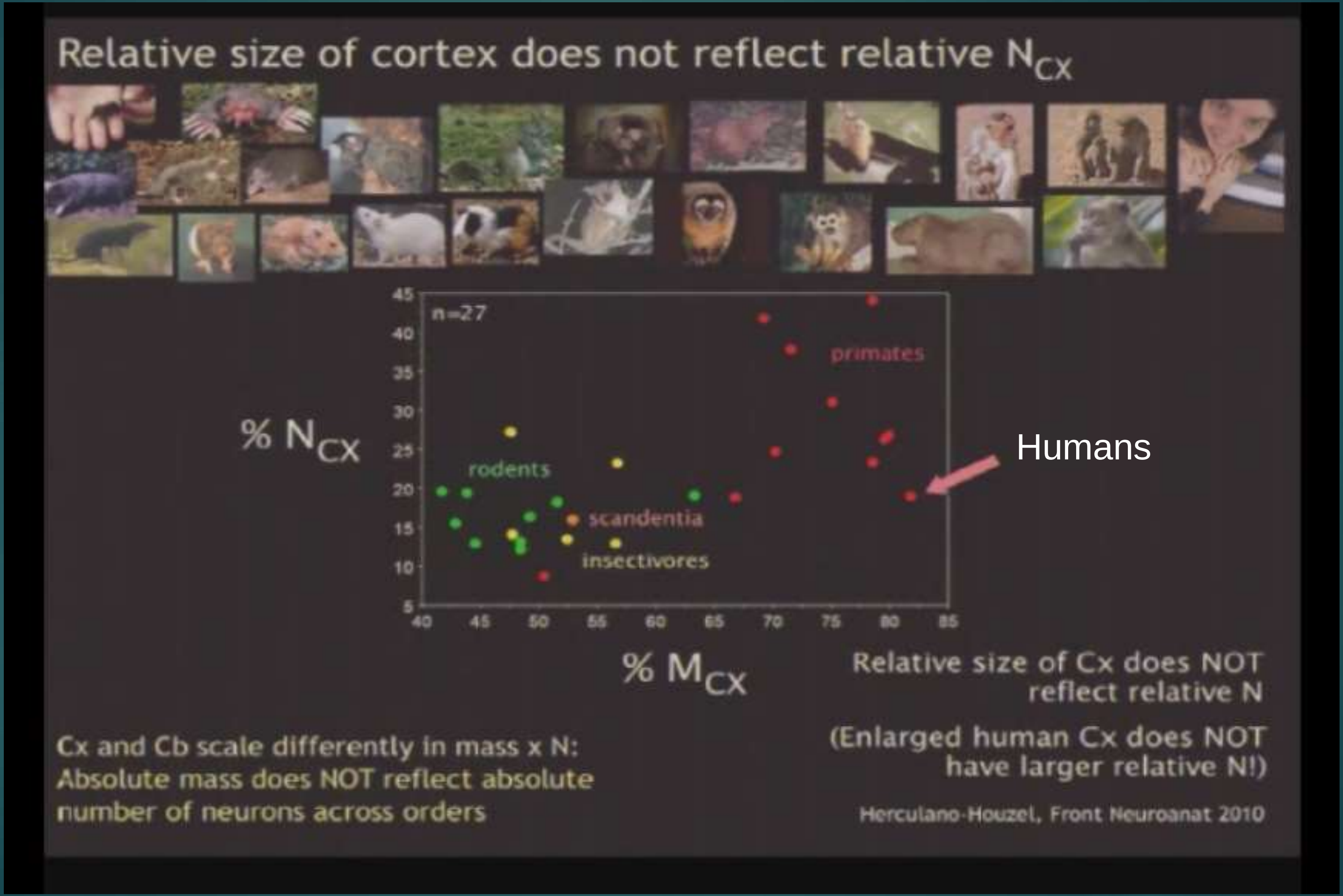


Absolute size – absolute N

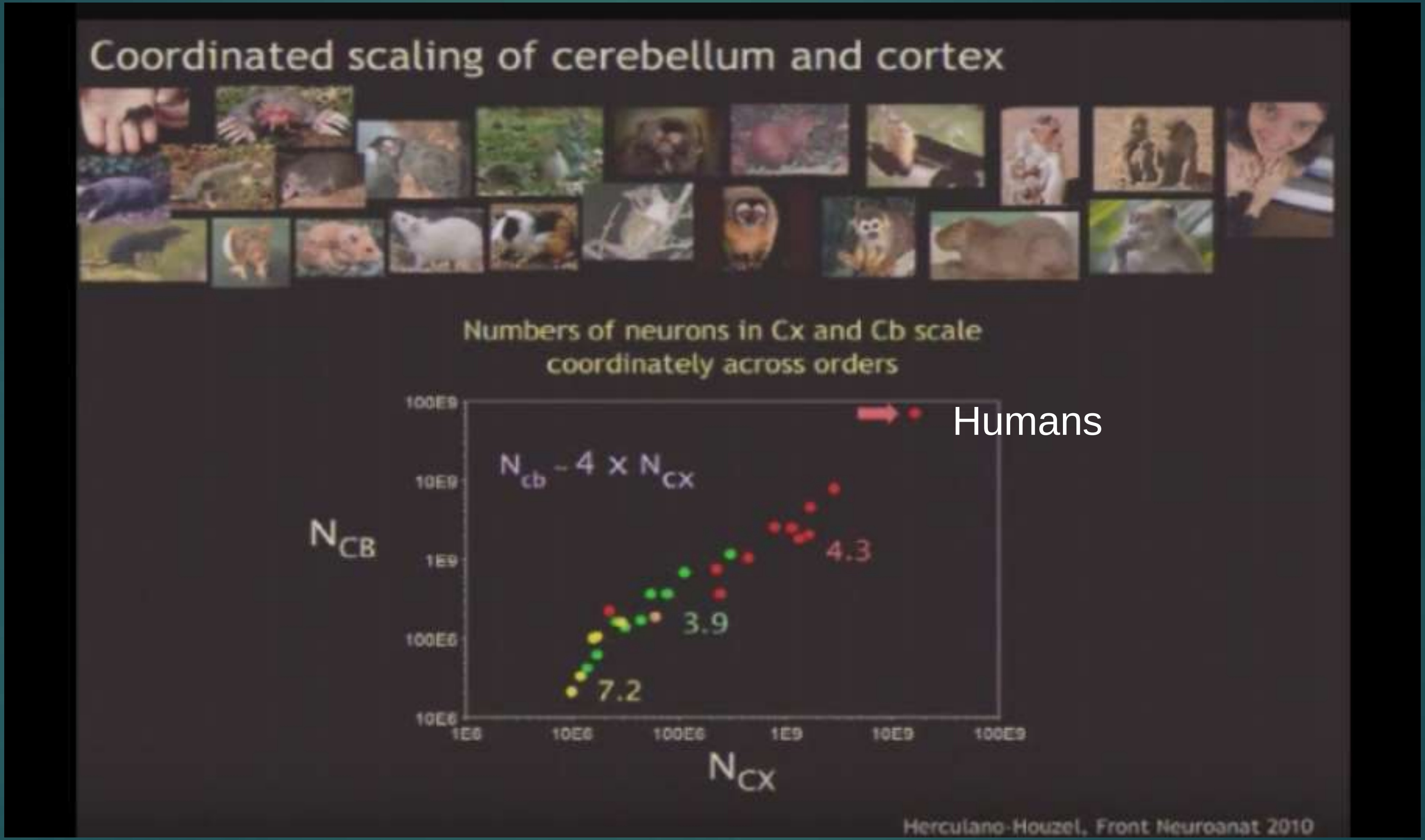
Relative size – relative N

Does relatively larger cortex, have relatively more brain neurons?

Answer: No. Size of cortex does not reflect number of neurons

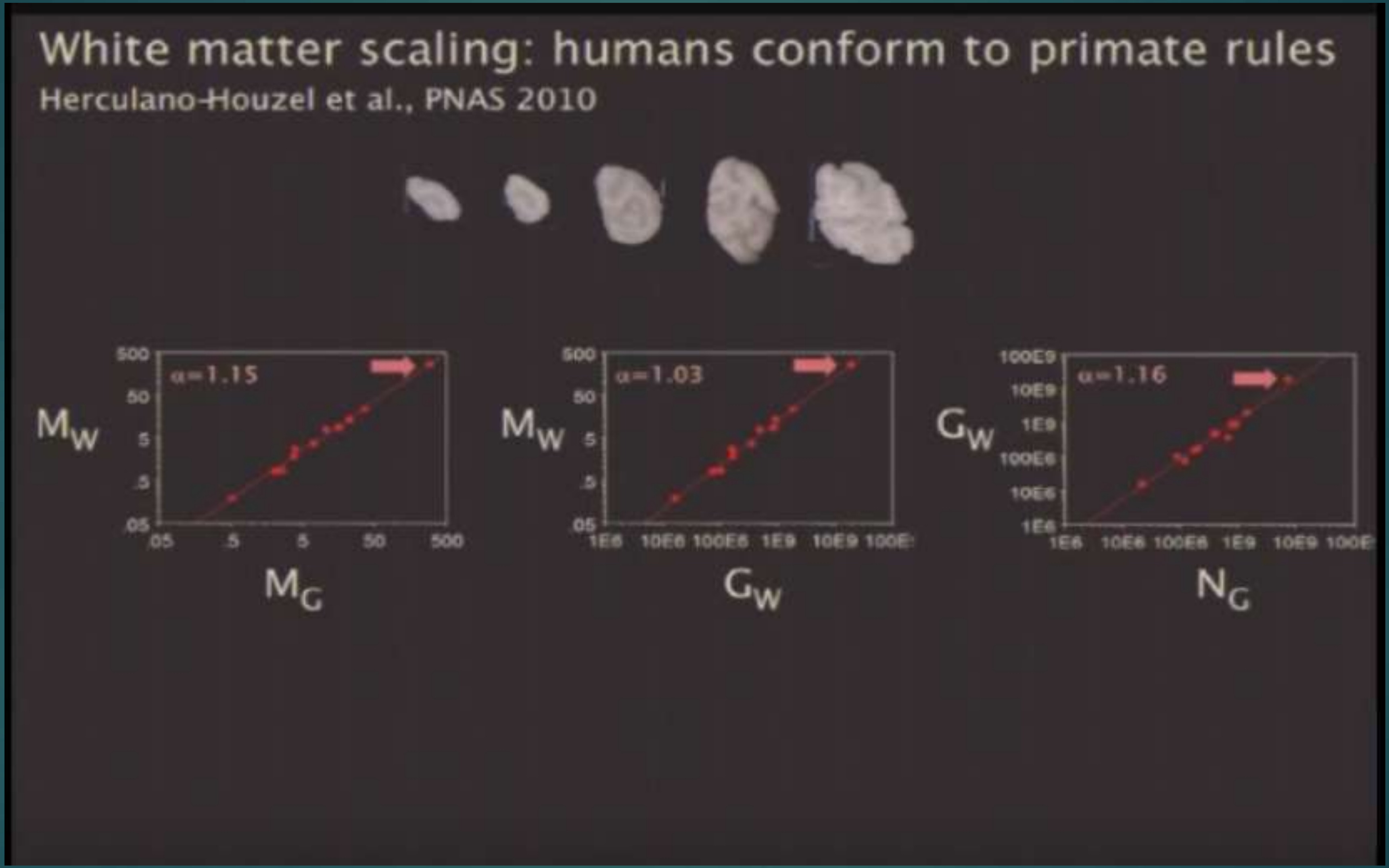


Number of neurons in cortex and cerebellum scale together in 28 species



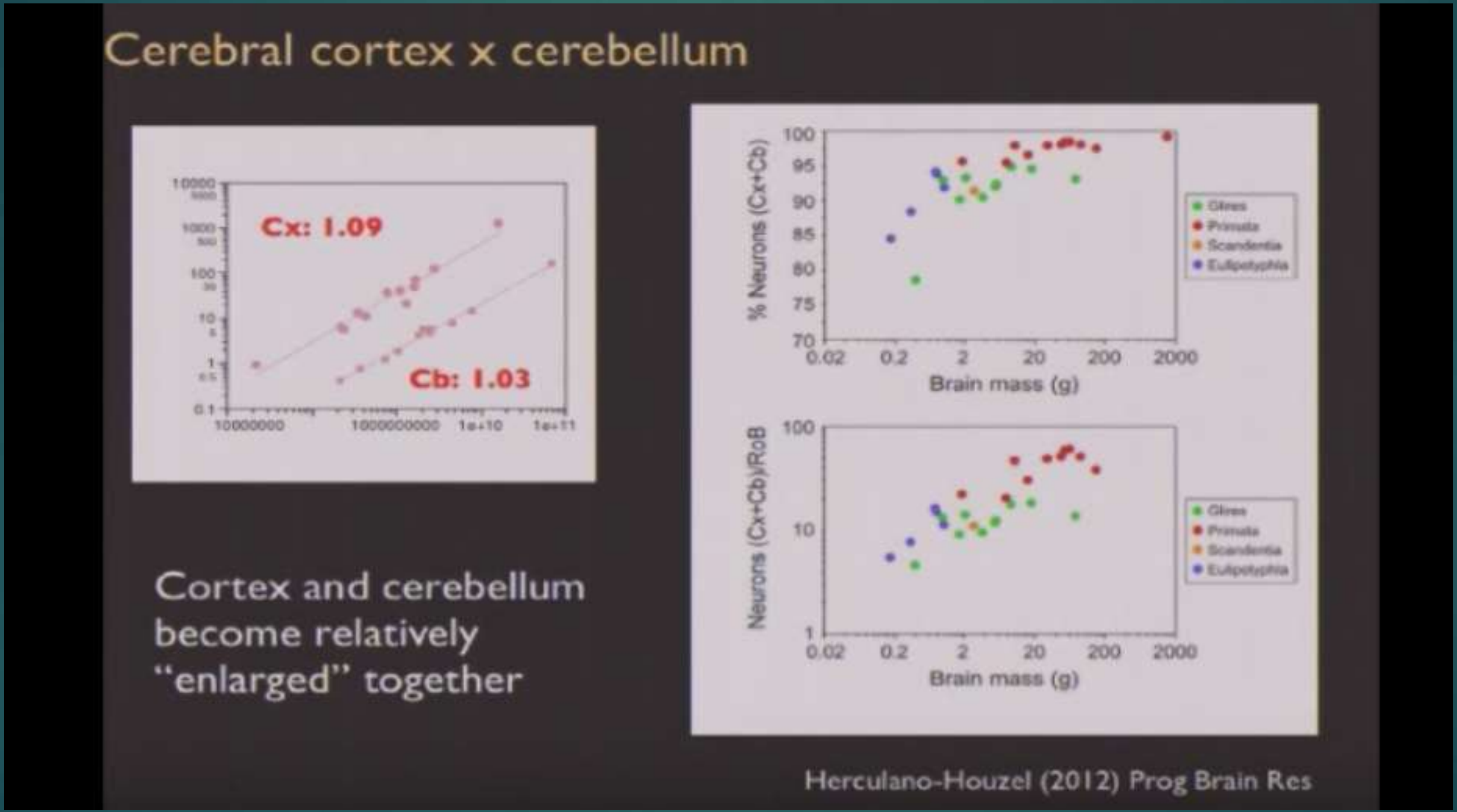
Linear relationship: 4 more neurons added to cerebellum for each neuron added to cortex

Why relative expansion of cerebral cortex?



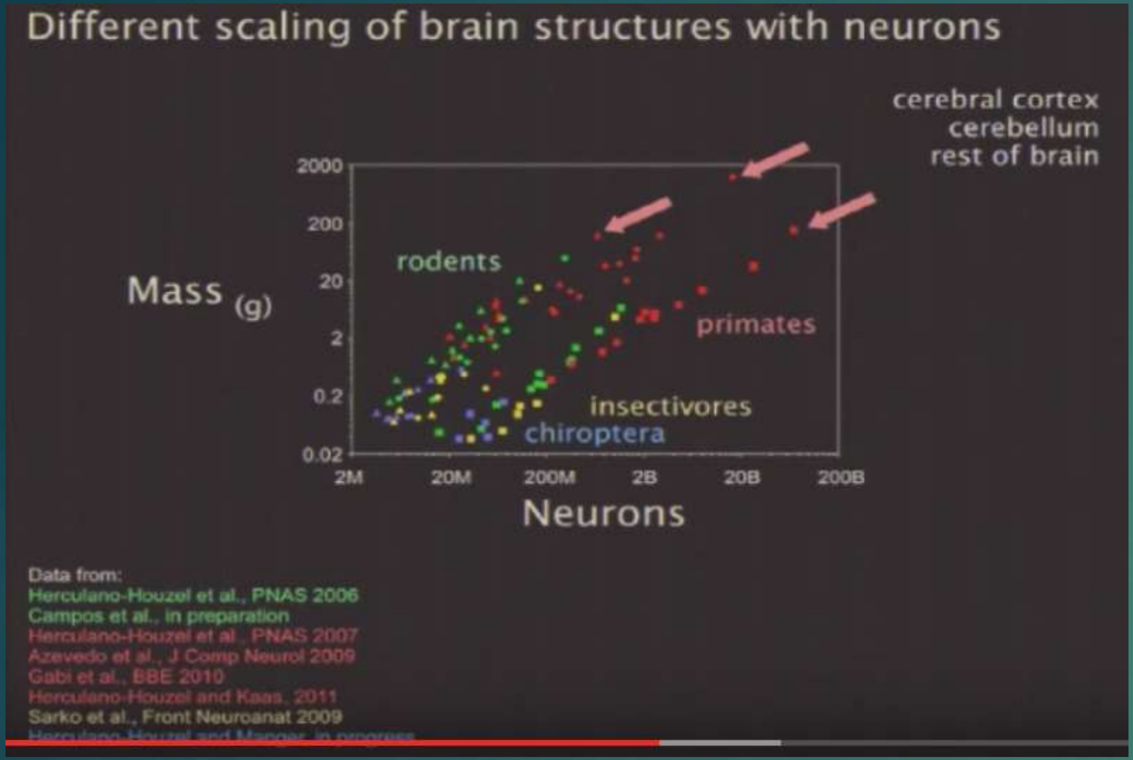
White matter & glial cells increase in volume faster than grey matter

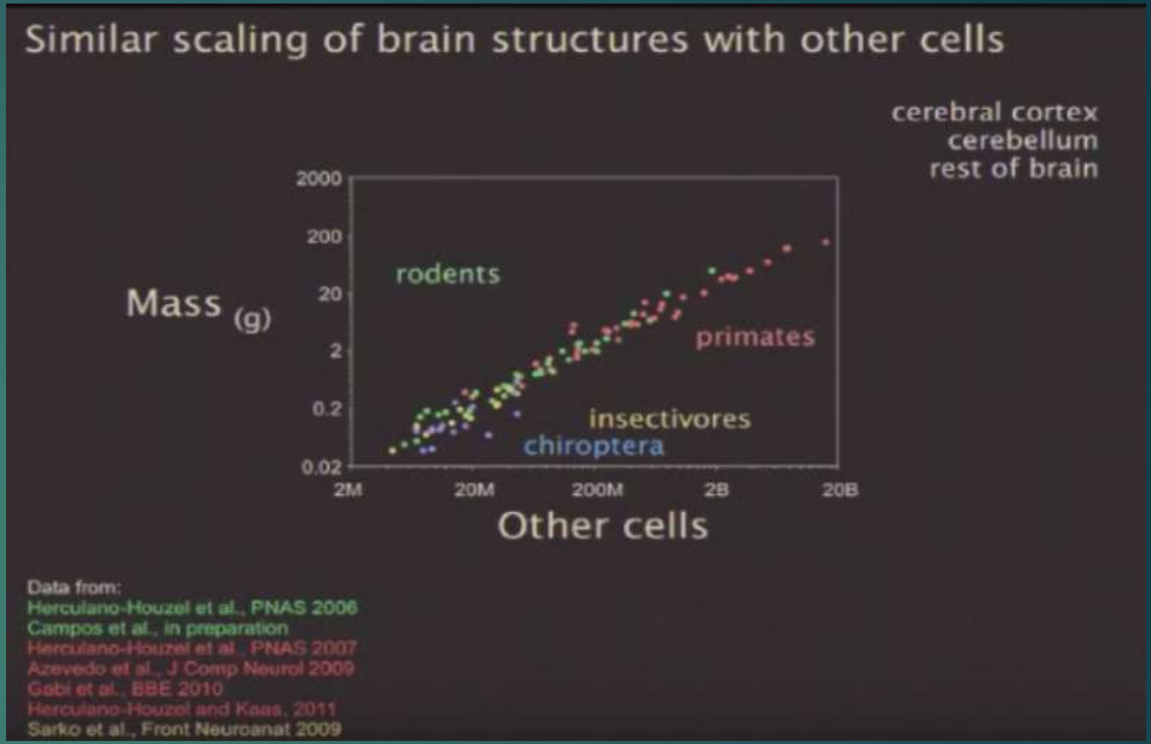
Cortex & cerebellum enlarge together in primates



More neurons than just for somatic maintenance.

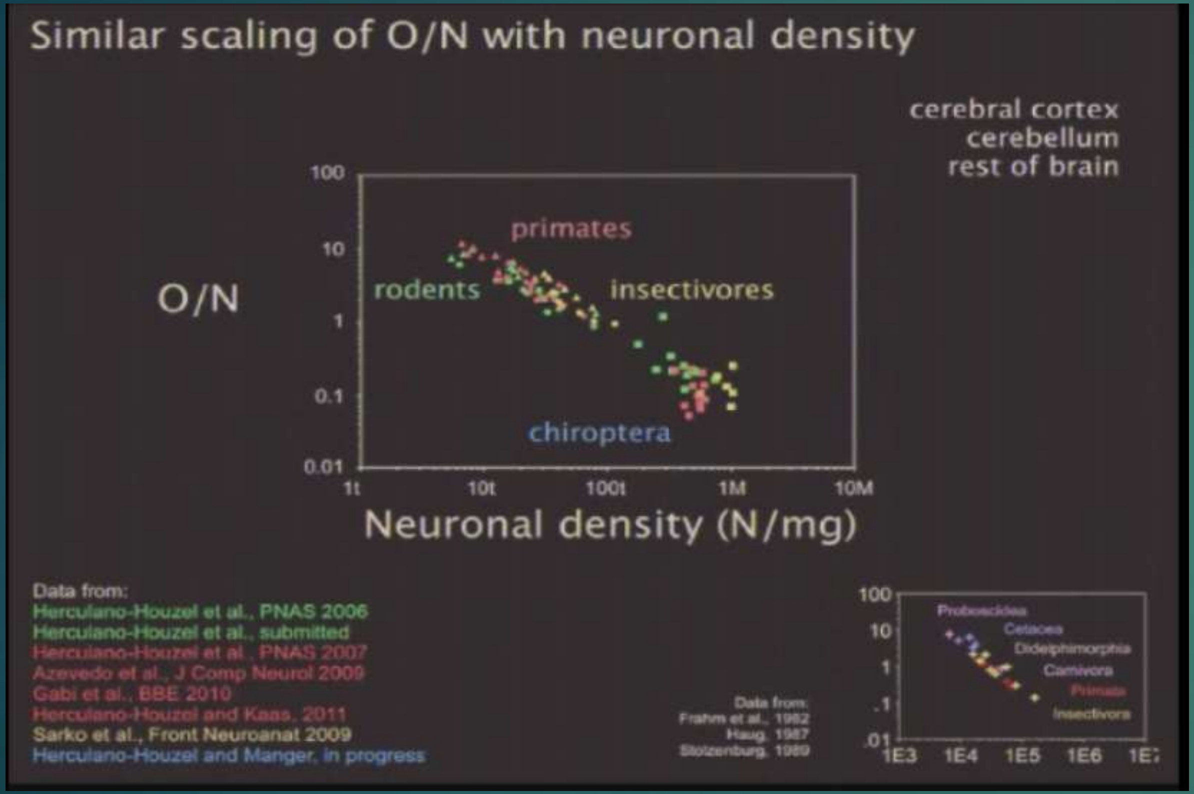
Non-neuronal cells

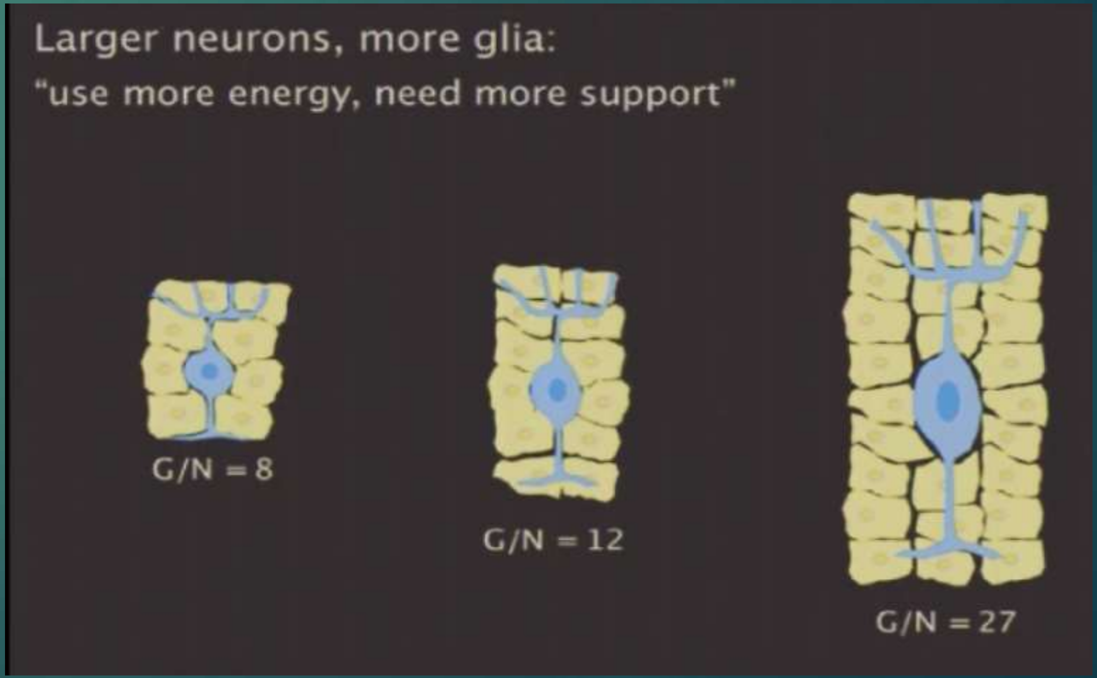




<u>Neurons scale differently than glial cells in cortex</u>;
In glial/neuron ratio, no constant relation between them & size of structure
<u>Larger the neuronal density, smaller the glial/neuron ratio (larger the neuron, more glial cells)</u>

Consensus: Larger neurons, more glia because of higher activity





New data: glucose per minute per neuron

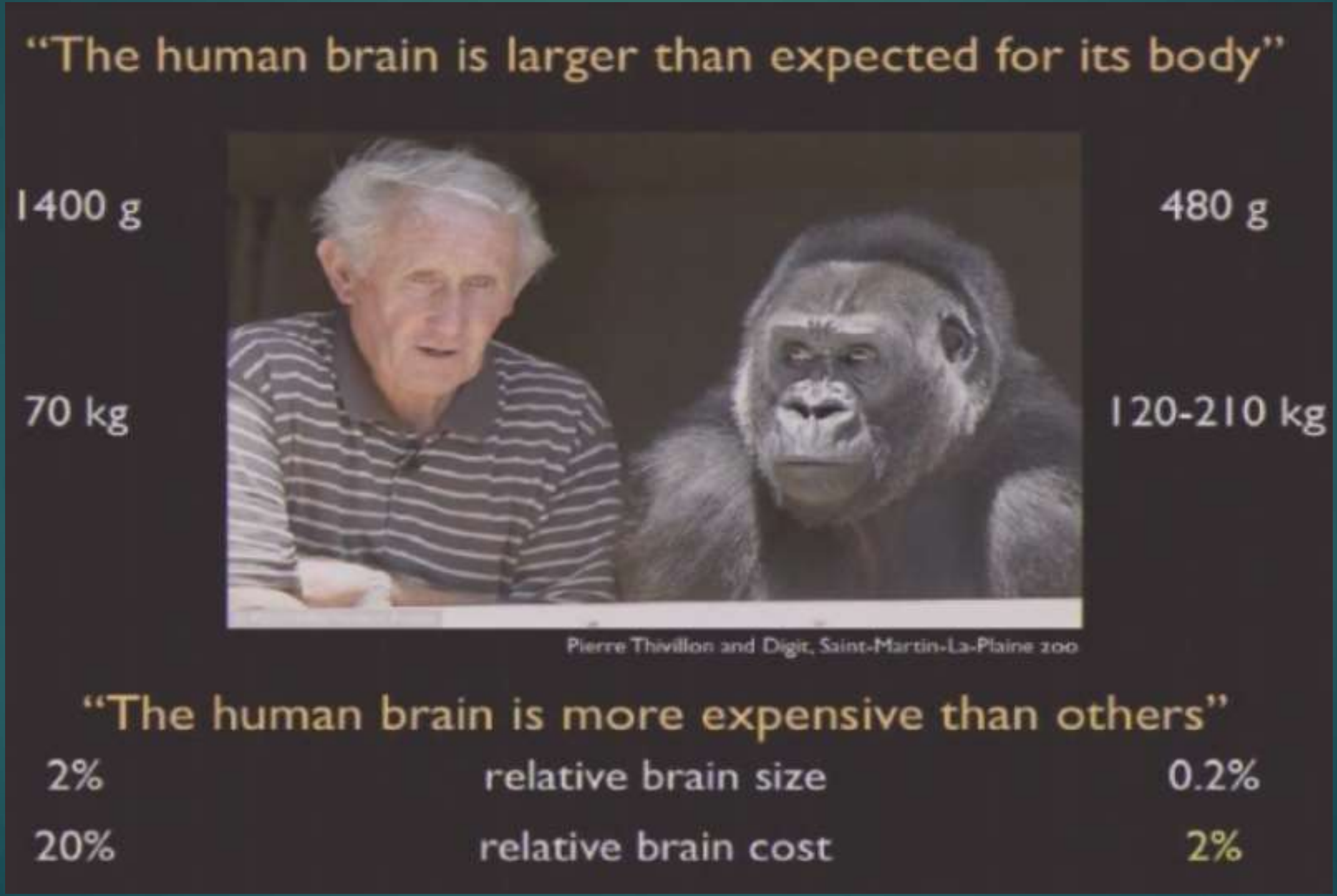
How does metabolic cost scale with number of neurons?

Herculano-Houzel (2011) PLoS One

	whole brain	whole brain	whole brain	whole brain
	Glu µmol/g.min	Glu µmol/min	Neurons	Glu µmol/neuron.min
mouse	0.89	0.32	70.89 M	5.20 E-9
rat	0.68	1.52	200.13 M	6.10 E-9
squirrel	0.60	3.88	472.44 M	7.05 E-9
monkey	0.36	35.98	6.38 B	4.93 E-9
baboon	0.44	60.40	10.91 B	6.00 E-9
human	0.31	428.55	86.06 B	5.44 E-9
	Karbowski, 2007	Karbowski, 2007	our data	our data

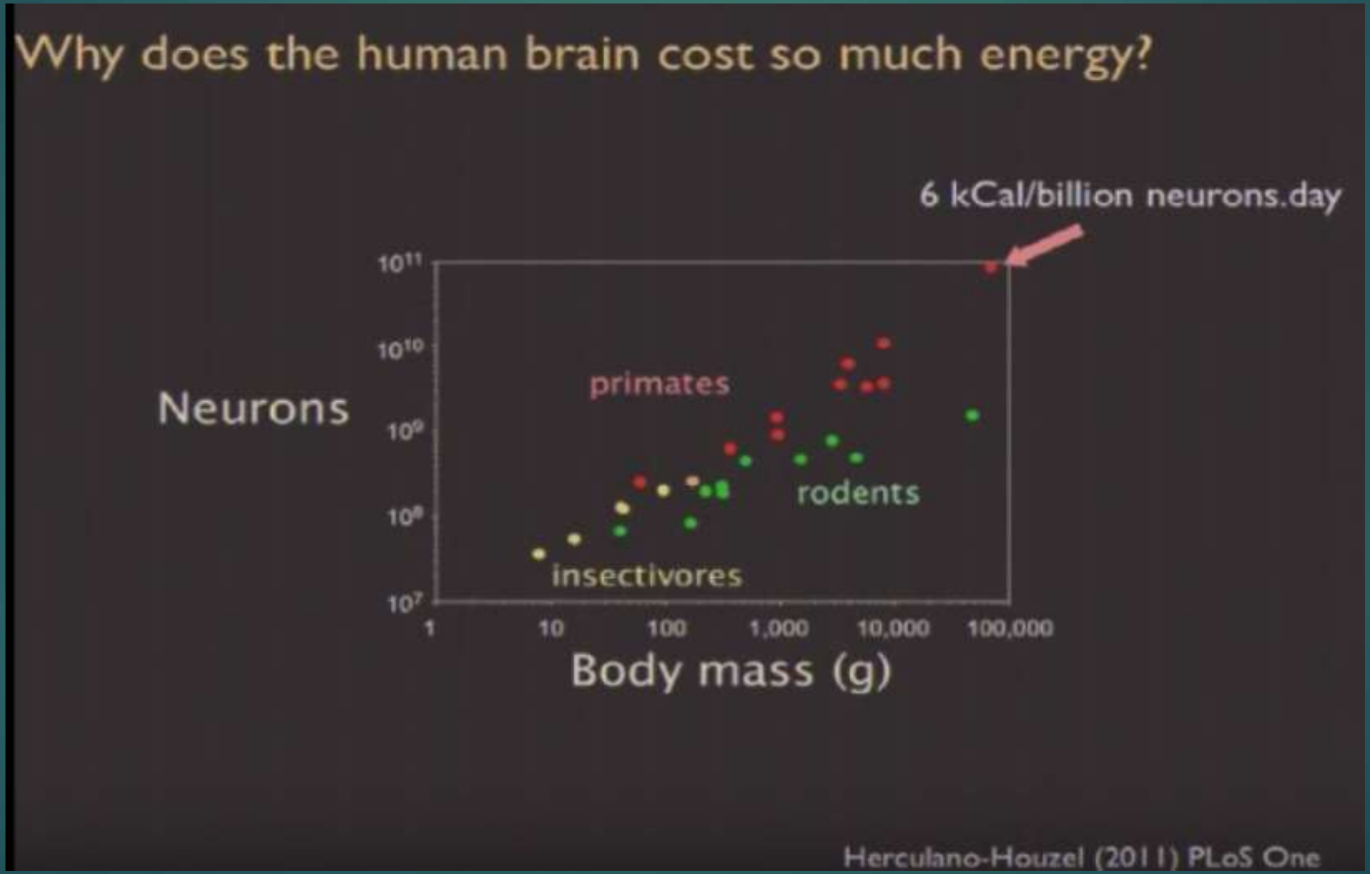
New numbers: glucose utilization is same across species; glucose/neuron does not scale; but <u>total glucose/minute use</u> scales with number of neurons
Larger brains use more energy, but metabolic cost per neuron does not change

Is the brain larger than expected for its body and more metabolically expensive?



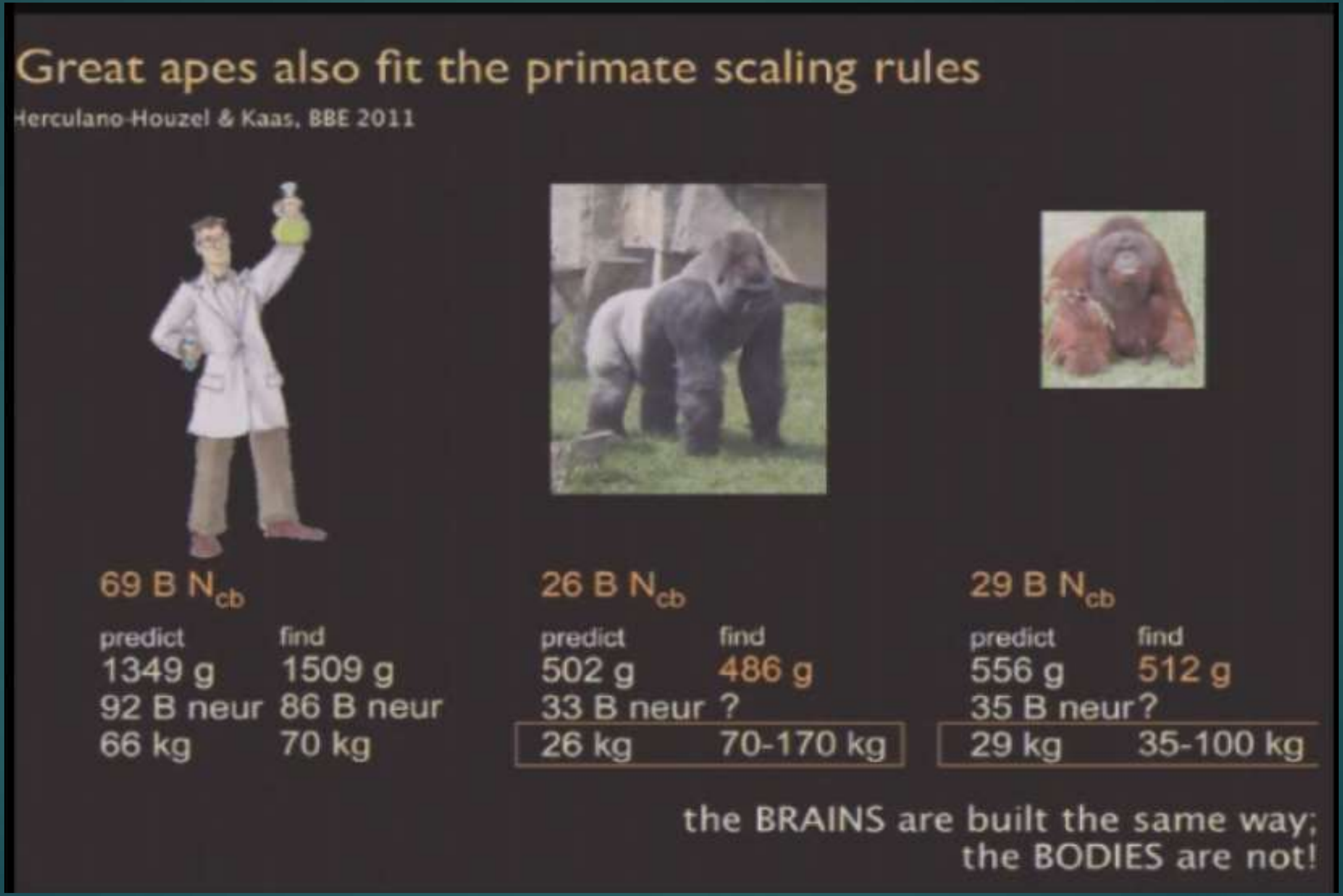
Answer: need 6 kilo calories per billion neurons per day

- Amount of energy a brain costs is a simple linear function of how many neurons it has regardless of its size and of its body size.

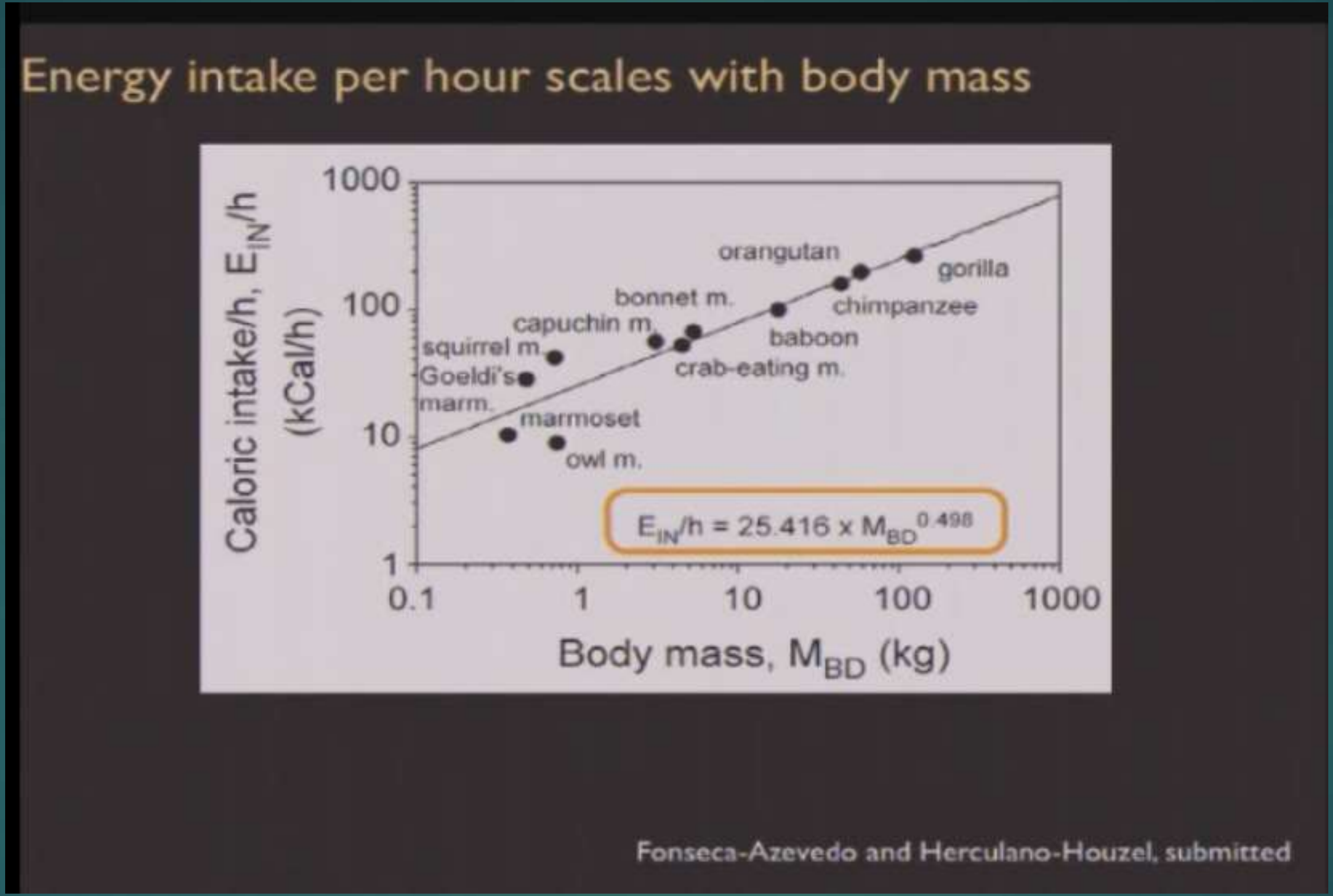


Just because it has an enormous number of neurons!

Why doesn't largest primate have largest brain? Brains are built same way, but bodies are not. Cannot have both

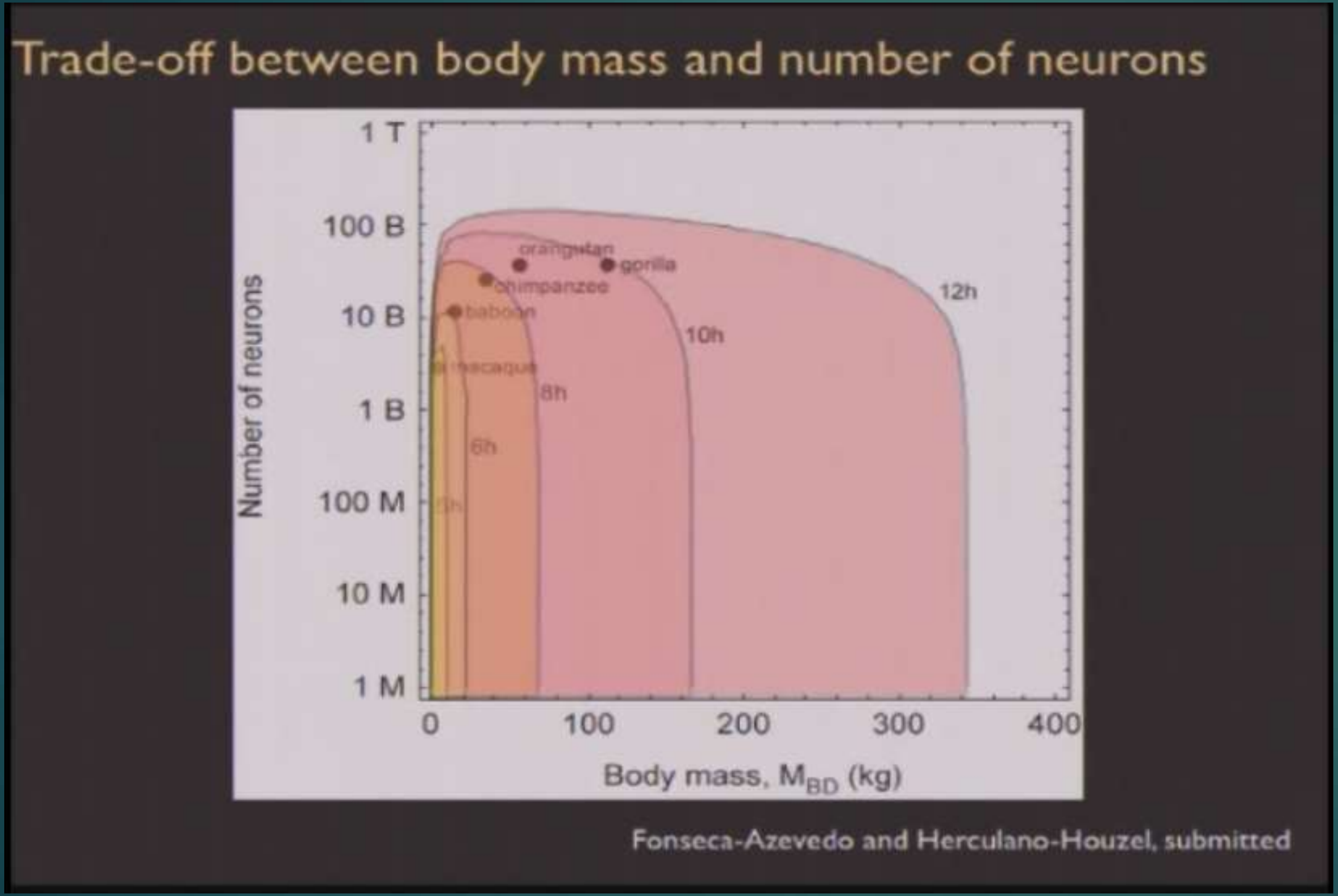


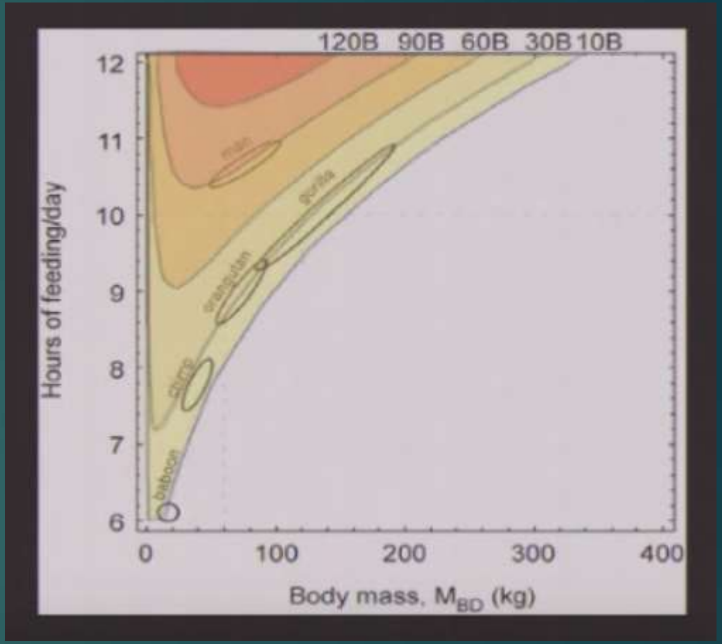
Are number of neurons and body size metabolically constrained?



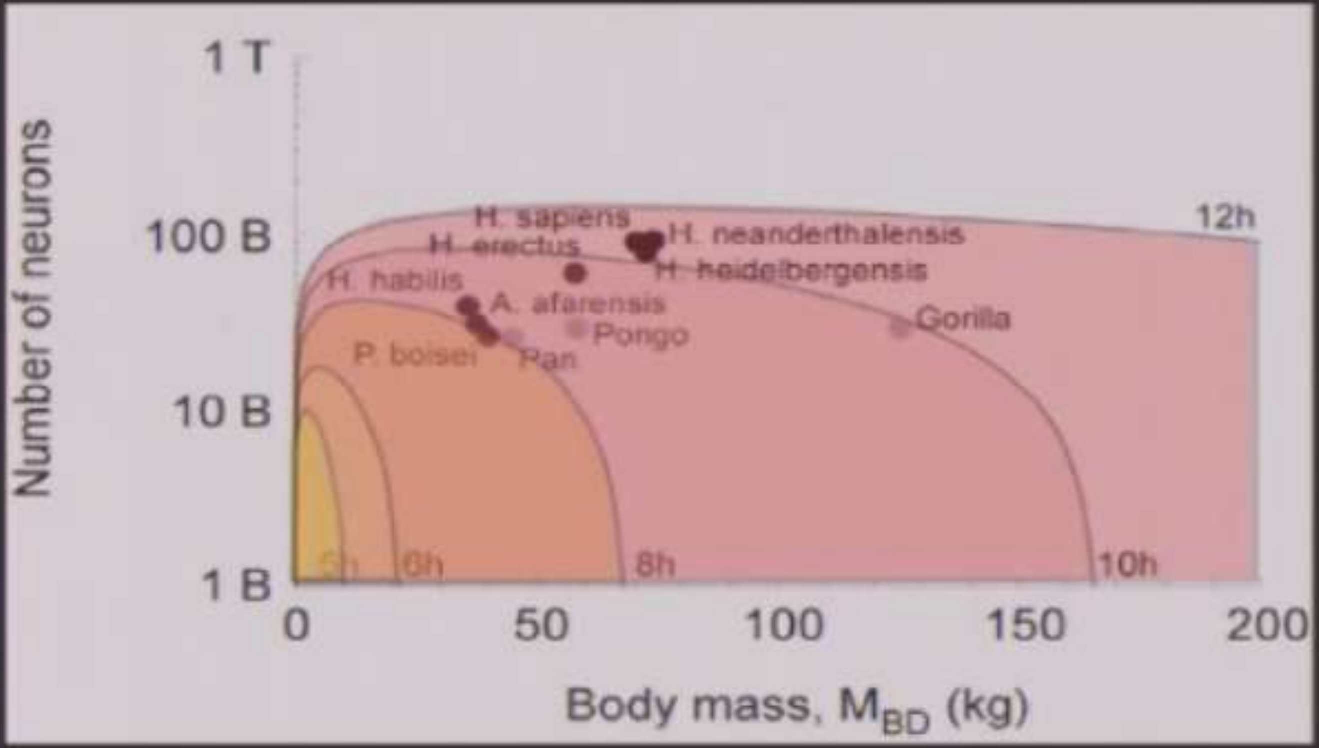
Energy intake per hour scales with body mass:
Larger animals take in more calories per hour at a rate of square root of body mass
Upper limit of primate body mass = 344 kg (max of 12 hours of eating)

Trade off between body mass and # of neurons





Daily feeding time was a limiting factor in human evolution



How did *Homo* overcome it? Cooking !

Fonseca-Azevedo and Herculano-Houzel, submitted

All hominids under 10 hour per day feeding time

Her conclusions

- Order-specific addition of neurons:
  - In different species, neurons added in different manners;
  - brain size varies as different functions of number of neurons across mammalian orders
- Conserved addition of glial cells for 90 million years

Brain size is not determent of anything; it is a consequence of conserved (glial)/unique (neuron) program of adding neurons to brain structures

Size is a misleading parameter; should be looking at number of neurons.

Human brain: Remarkable, yet not extraordinary

- The human brain…
- Has the number of neurons expected for a primate of its brain size.
- Gained neurons coordinately in the cortex and cerebellum
- And faster than in subcortical and brainstem structures: a mechanism for added complexity & flexibility

It costs a lot of energy because it has a lot of neurons

- In that sense, costs just what would be expected
- On a raw diet, can only be afforded by giving up body mass & eating full-time (a major liability)
- But on a cooked diet, can be afforded in much less time spent feeding: free time to put those neurons to good use.

Old idea of 100 billion brain cells?

- According to neuroscientist Herculano-Houzel, it's because there was no direct estimate of total neuron quantity in the human brain

- 86 billion neurons and just as many nonneuronal cells, the human brain is a scaled-up primate brain in its cellular composition and metabolic cost, with a relatively enlarged cerebral cortex that does not have a relatively larger number of brain neurons yet is remarkable in its cognitive abilities and metabolism simply because of its extremely large number of neurons.

Relative brain size

- Humans also do not rank first, or even close to first, in relative brain size (expressed as a percentage of body mass), in absolute size of the cerebral cortex, or in gyrification.
- At best, we rank first in the relative size of the cerebral cortex expressed as a percentage of brain mass, but not by far.
- Although the human cerebral cortex is the largest among mammals in its relative size, at 76-84% of the entire brain mass or volume, other animals, primate and nonprimate, are not far behind:
- The cerebral cortex represents 73% of the entire brain mass in the chimpanzee, 75% in the horse, and 73% in the short-finned whale.

Old idea of EQ

- A largely accepted alternative explanation for our cognitive superiority over other mammals has been our extraordinary brain size compared with our body size, that is, our large encephalization quotient (Jerison, 1973).
- Compared with the trend for brain mass to increase together with body mass across mammalian species in a fashion that can be described mathematically by a power law (von Bonin, 1937), the human species appears to be an outlier, with a brain that is about sevenfold larger than expected from its body mass compared with mammals as a whole (Jerison, 1977), or threefold larger than expected compared with other primates (Jerison, 1985), although how we came to be that way has not been well accounted for in the literature.

EQ

- An “excess brain mass,” relative to the brain mass necessary to operate the body, would endow the behavior of more encephalized animals with more complexity and flexibility (Jerison, 1985).
- The most encephalized species should also be the most cognitively able, and that species, finally, was our own.

EQ vs number of neurons

- However, the notion that higher encephalization correlates with improved cognitive abilities has recently been disputed in favor of absolute numbers of cortical neurons and connections (Roth and Dicke, 2005), or simply absolute brain size (Deaner et al., 2007).

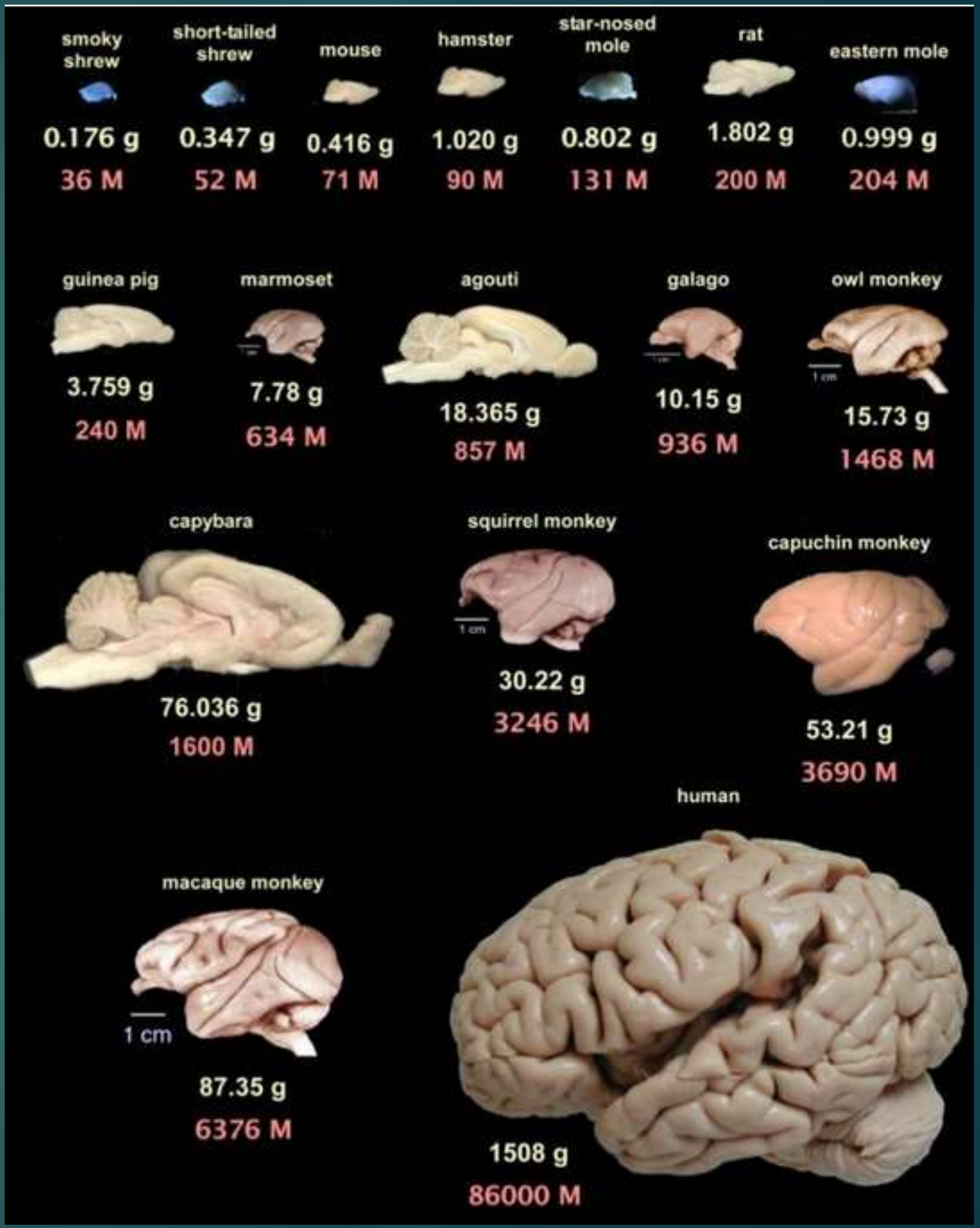
- If encephalization were the main determinant of cognitive abilities, small-brained animals with very large encephalization quotients, such as capuchin monkeys, should be more cognitively able than large-brained but less encephalized animals, such as the gorilla (Marino, 1998).

- However, the former animals with a smaller brain are outranked by the latter in cognitive performance (Deaner et al., 2007).

A bigger brain contains more neurons than a smaller brain?

The encephalization quotient is inherently flawed, for one very important reason: a bigger brain does not necessarily contain more neurons than a smaller brain.

Relative brain size cannot be used as a reliable measure of neuron quantity across orders. By extension, it really drives home the point that brain size, body size, and the relationship between the two, are insufficient benchmarks for assessing cognitive abilities, and that such assessments could instead focus more attention on the total number of *neurons*.



Not exceptional

- Our brains are, to some extent, pretty unexceptional. They may contain 86-billion neurons, but that is *precisely* the number that you would expect to find (based on the scaling rules of primates) for a brain of its size

Not all brains are made the same: Neuronal scaling rules - Neuronal density is not constant

- Most studies have assumed that neuronal *density* —i.e. the number of neurons relative to the mass of an animals brain — was more or less constant across various mammalian orders.
- But Herculano-Houzel found that brains of different mammals follow different "scaling rules":
  - Primate brains were found to increase at the same rate that they gained neurons; if you compared a gram of brain matter from a large primate against a gram of brain matter from a smaller one, you could expect to find the same number of neurons.
  - 10-fold increase in the number of neurons in a primate brain results in an increase in brain size of only 11-fold.

Neuronal scaling rules

- Rodent brains, on the other hand increase in size *faster* than they gained neurons. As a result, larger rodents tended to have fewer neurons per gram of brain matter than smaller rodents.
  - A 10-fold increase in the number of neurons in a rodent brain results in a 35-fold larger brain.
- Insectivores increased in size faster than they gained neurons (like a rodent), and linearly (like a primate).
- The primate brain appears to be built using the most economical, space-saving scaling rules.

Mosaic brain organization

- Mosaic brain organization is a fact. It describes the independent scaling of different parts of the brain across species in evolution, as opposed to every brain part scaling in line with every other part
- Mosaic scaling in evolution is seen for example in the enormous size that some structures exhibit in some species but not others, relative to the rest of the brain:
  - the common squirrel has an enormous superior colliculus, involved in visual processing, that other rodents of a similar brain size do not have;
  - moles and shrews, who rely heavily on olfaction, have even more neurons in the olfactory bulb than in the cerebral cortex – something that is quite different from rodents of a similar brain size

- Mosaic brain evolution means that the numbers of neurons allocated to different brain structures can vary independently across said structures.
- Mosaic brain evolution also refers to the possibility of one system (for instance, vision) expanding faster than another system (say, audition).

Mosaic evolution

- Apparent expansion of the cerebral cortex in mammalian evolution, varying from less than 40% of brain size in the smallest mammals to over 80% in humans and other even larger brains, is NOT the result of an expansion in numbers of neurons in the cortex:
  - regardless of the relative size of the cortex across different species, it has about 20% of all brain neurons – even in the human brain.
  - That’s another example of how apparent mosaic evolution (of one structure taking over the others) can actually not be mosaic evolution. It all depends on the precise variable examined.

Mosaic evolution

- The relationship between the particular size of a brain structure and its number of neurons is constant and shared across primate species.
- This does not at all imply or require that all brain areas have the same ratios of numbers of neurons *relative to one another*, which is what mosaic evolution states: given brain regions can become relatively enlarged or reduced compared to others, and still maintain the same relationship between their number of neurons and mass as seen across species.

Elephant: Most neurons in cerebellum

- Elephant brain as a whole has 3 times the number of neurons of the human brain, 257 billion neurons against an average 86 billion in ours, BUT 98% of those neurons are located in the elephant cerebellum.
- While other mammals (humans included) have about 4 neurons in the cerebellum to every neuron in the cerebral cortex, the elephant has 45 neurons in the cerebellum to every neuron in the cerebral cortex.
- All we can do for now is to speculate on the reason for this extraordinary number of neurons in the elephant cerebellum, and the most likely candidates right now is to me the fine sensorimotor control of the trunk, a 200-pound appendage that has amazingly fine sensory and motor capabilities, which are known to involve the cerebellum.
- The cerebral cortex, which is twice the size of ours, has only one third of the neurons in an average human cerebral cortex. Taken together, these results suggest that the limiting factor to cognitive abilities is not the number of neurons in the whole brain, but in the cerebral cortex (

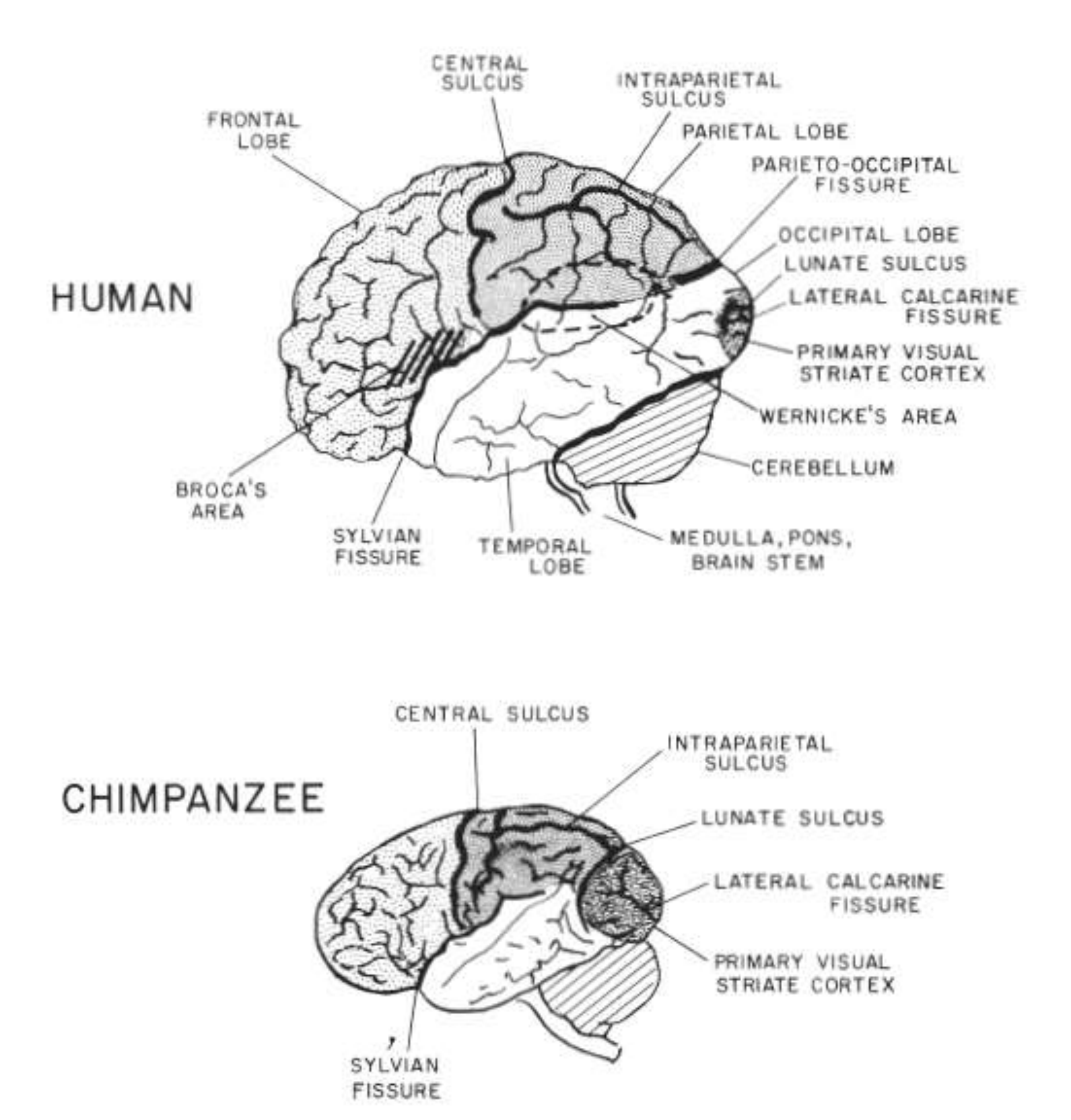
Glia

- It is a widespread notion that the proportion of glial to neuronal cells in the brain increases with brain size, to the point that glial cells represent "about 90% of all cells in the human brain."
- This notion, however, is wrong on both counts: neither does the glia/neuron ratio increase uniformly with brain size, nor do glial cells represent the majority of cells in the human brain.
- Glia/neuron ratio does not increase with brain size, but rather, and in surprisingly uniform fashion, with decreasing neuronal density due to increasing average neuronal cell size, across brain structures and species.
- Variations in the glia/neuron ratio are proposed to be related not to the supposed larger metabolic cost of larger neurons (given that this cost is not found to vary with neuronal density), but simply to the large variation in neuronal sizes across brain structures and species in the face of less overall variation in glial cell sizes.
- The emerging evidence that the glia/neuron ratio varies uniformly across the different brain structures of mammalian species that diverged as early as 90 million years ago in evolution highlights how fundamental for brain function must be the interaction between glial cells and neurons.

GLIA 2014;62:1377–1391

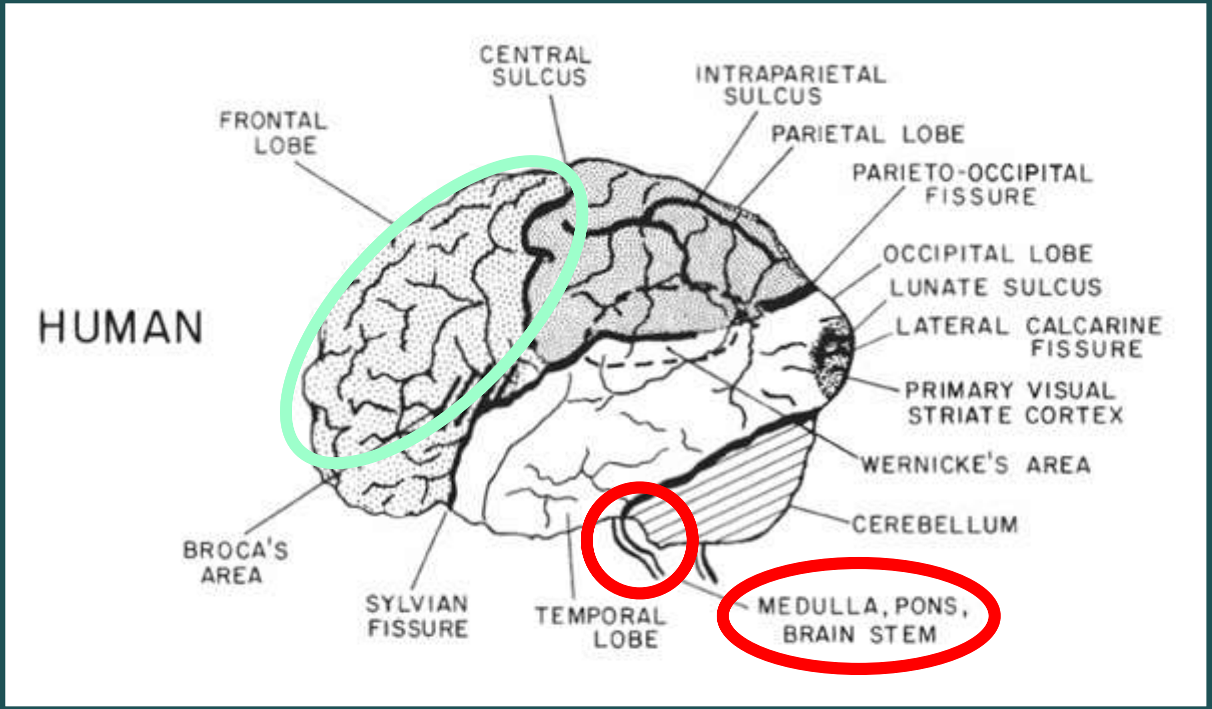
Brain

Although the human brain is 3 to 4 times heavier than the chimpanzee brain, there is considerable similarity between the 2 species in convolutional details.



Tattersall, Delson, van Couvering (1988)
Encyclopedia of human evolution and prehistory.

Neocortex - Medulla



Medulla

Primitive part of the brain that controls basic body function such as respiration and heart rate.

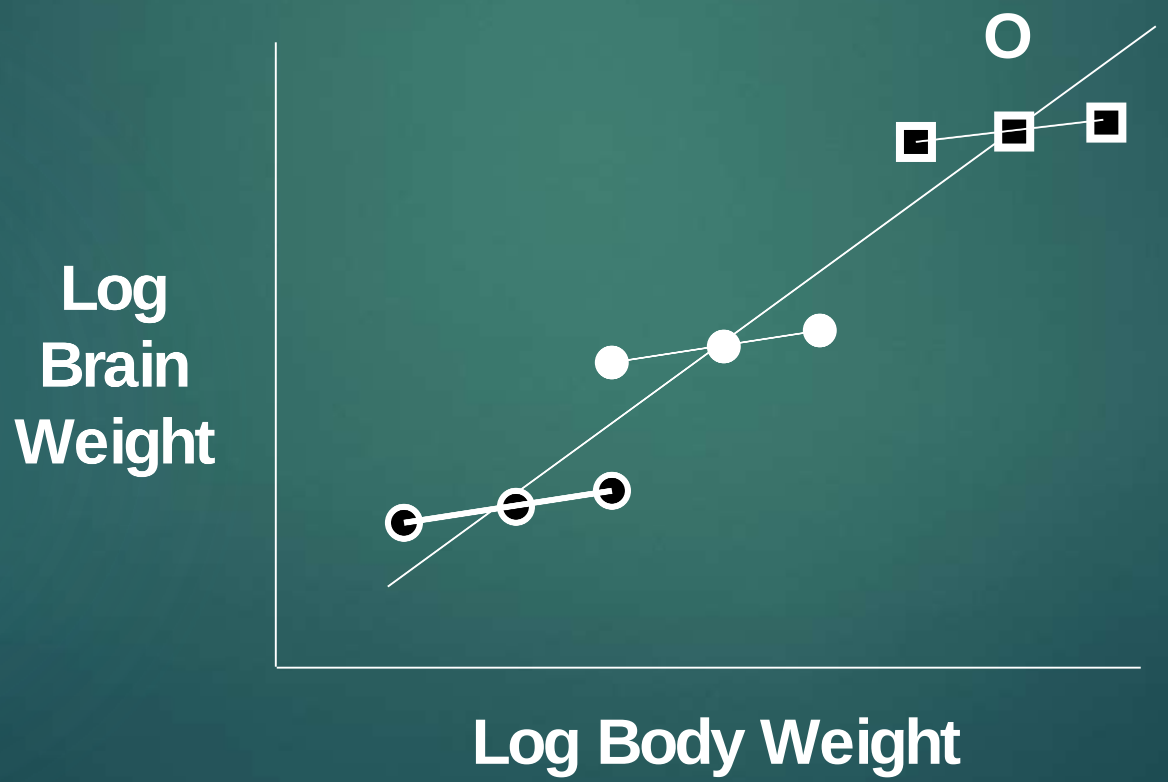
- Insectivorous mammals: neocortex same size than medulla
- Prosimians: neocortex 10x larger
- Monkeys/Apes: neocortex 20-50x larger
- Humans: neocortex 105x larger

Strier (2003) Primate Behavioral Ecology

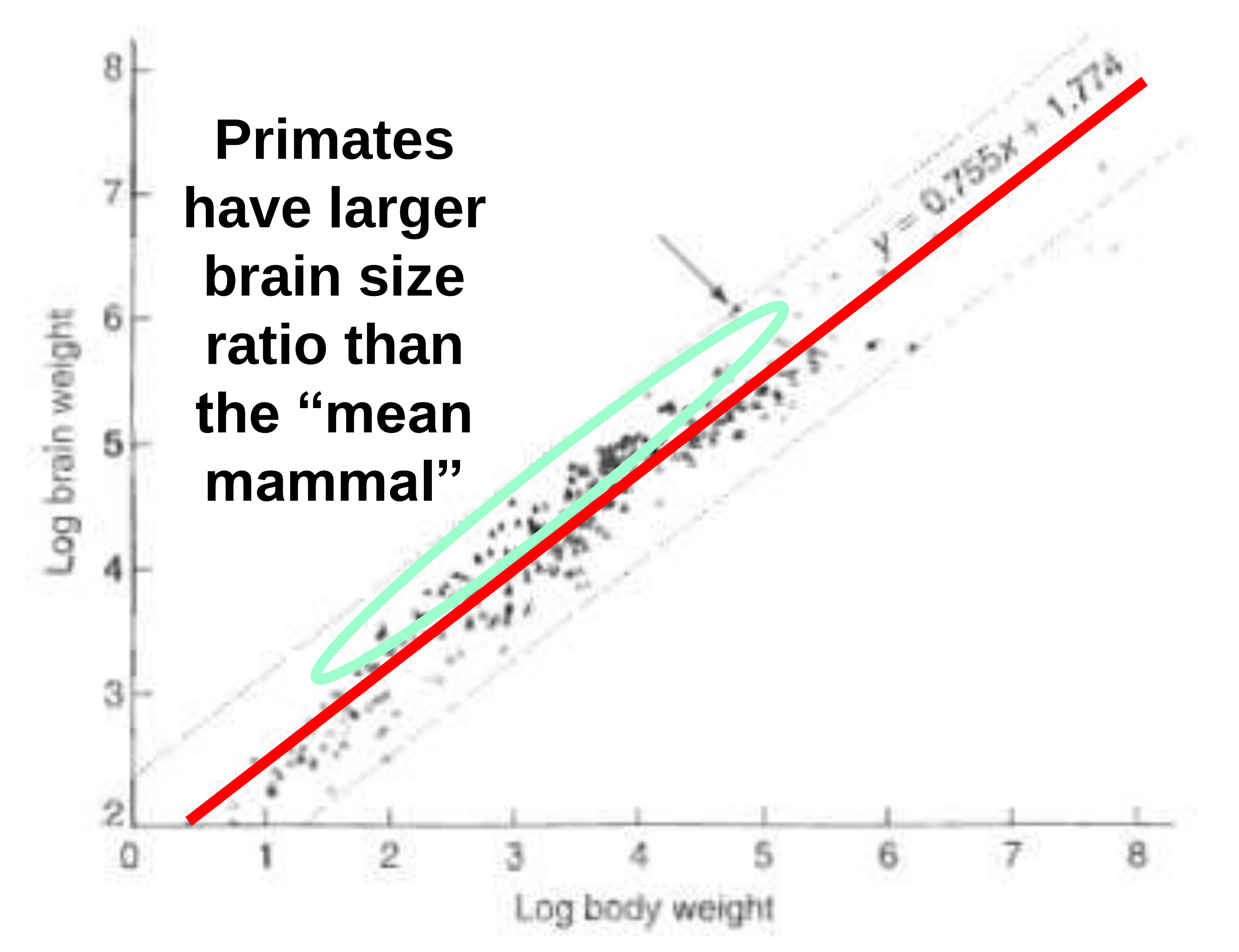
Measuring relative brain size

1. Brain Weight as a function of Body Weight
2. EQ = Encephalization Quotient

   = Observed / Expected brain size



Brain size



Allometric relationship between brain and body weight for 309 extant placental mammals.

Next to humans? Dolphins!

Strier (2003) Primate Behavioral Ecology

Social intelligence, innovation, and enhanced brain size in primates

Simon M. Reader and Kevin N. Laland, 2002

Despite considerable current interest in the evolution of intelligence, the intuitively appealing notion that brain volume and “intelligence” are linked remains untested.

Study: ecologically relevant measures of cognitive ability, the reported incidence of behavioral innovation, social learning, and tool use, to show that brain size and cognitive capacity are indeed correlated.

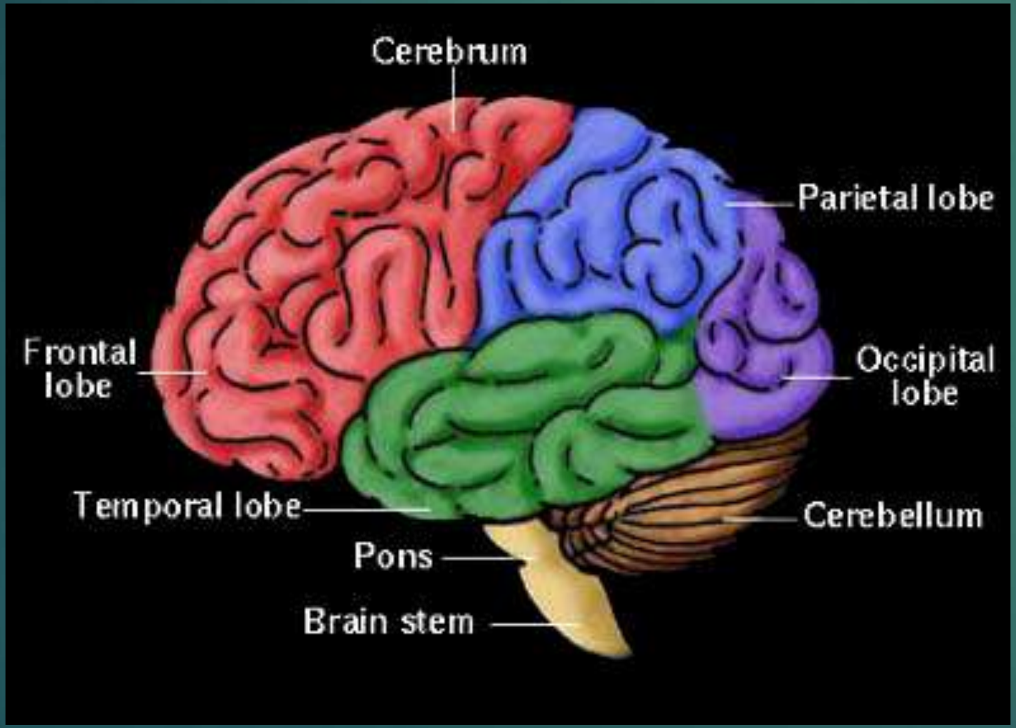
A comparative analysis of 533 instances of innovation, 445 observations of social learning, and 607 episodes of tool use established that social learning, innovation, and tool use frequencies are positively correlated with species' relative and absolute “executive” brain volumes, after controlling for phylogeny and research effort. Moreover, innovation and social learning frequencies covary across species

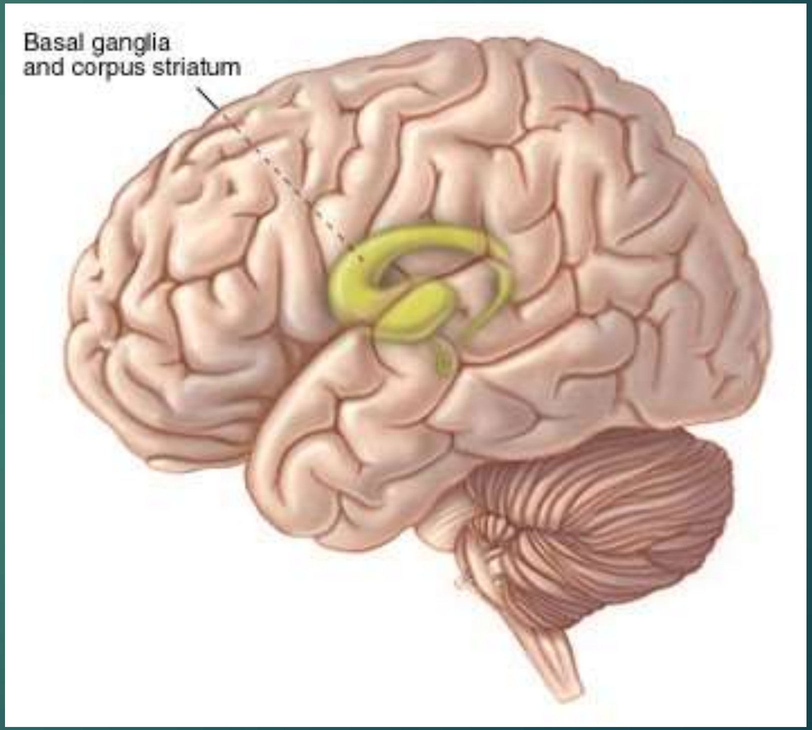
These findings provide an empirical link between behavioral innovation, social learning capacities, and brain size in mammals.
The ability to learn from others, invent new behaviors, and use tools may have played pivotal roles in primate brain evolution.

Correlates of larger brains

Executive Brain Ratio=

(Neocortex + striatum) / (Brain stem)





Reader & Laland 2002

Correlates of larger brains

Executive Brain Ratio=

(Neocortex + striatum) / (Brain stem)

1. Behavioral innovation
2. Social learning
3. Tool-use

Reader & Laland 2002

Correlates of larger brains

Significance of the Executive Brain Ratio?

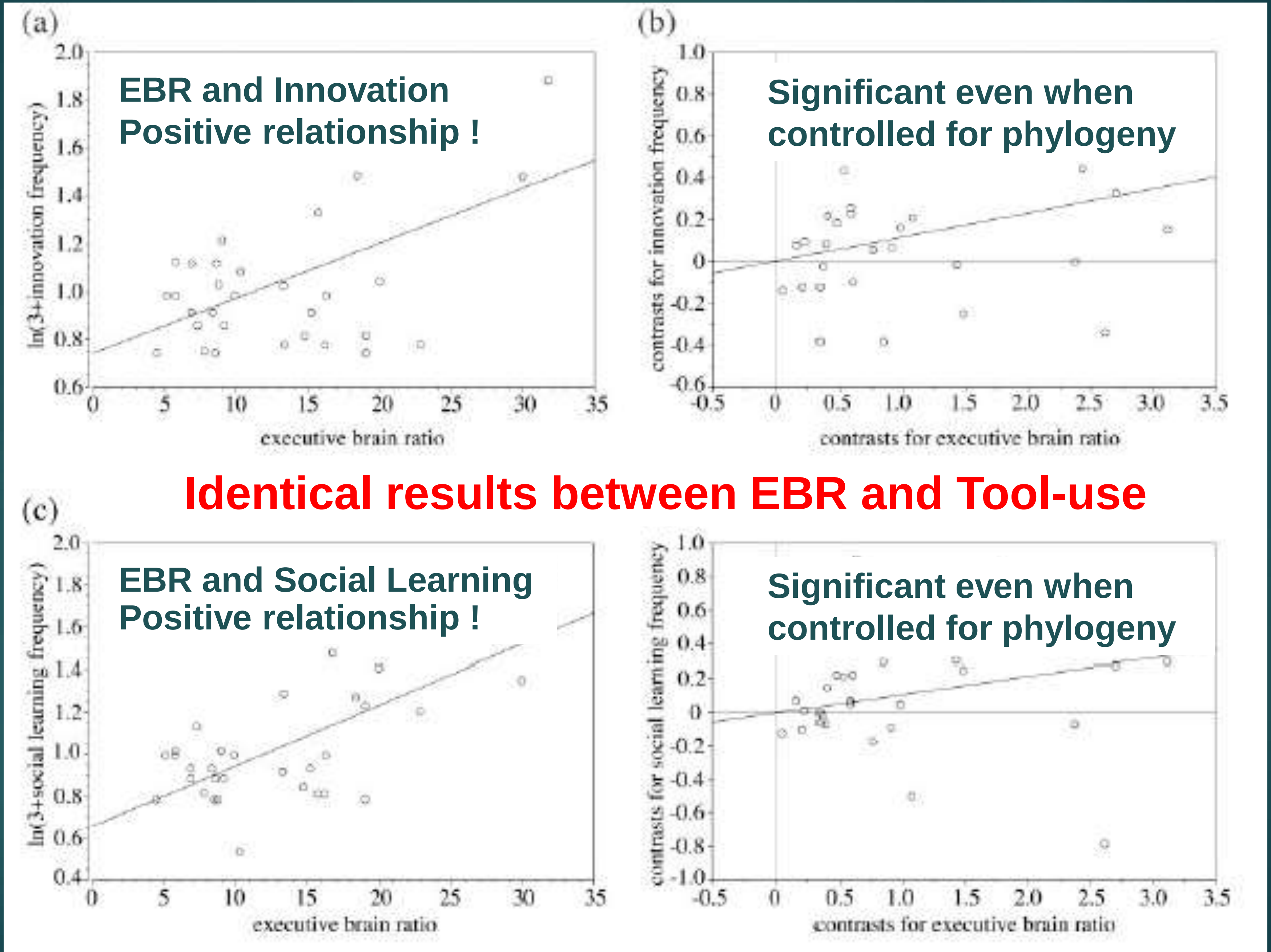
Members of large-brained primates

- innovate more often
- learn from others more often
- use tools more frequently

than small-brained primates

May have played critical roles in primate brain evolution

Reader & Laland 2002



Lineages
are not
independent

Correlates of larger brains : PLAY

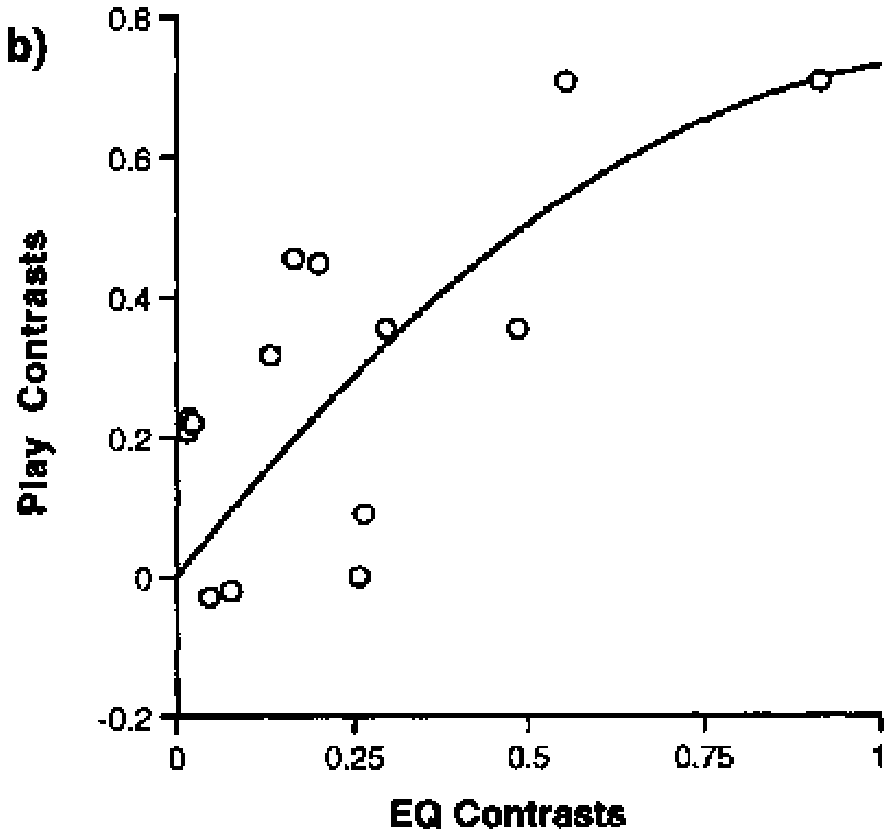


Figure 2. Scatter plots showing the relationship between brain size (i.e., encephalization quotient or EQ) and play among mammalian orders using raw scores (a) and independent contrasts (b). The line of best fit for both (a) and (b) was derived from a polynomial model, as the scores were not transformed to logarithmic values.

Larger-brained mammals play more than smaller-brained

This is true between different orders of mammals

But not within the Orders of Primates or Rodents

15 mammalian orders

Iwaniuk et al 2001 JCP

Mosaic Brain Evolution:
Brain reorganization

Specializations of the human brain

- Larger representations of the hands
- Neocortical specializations for speech (Broca’s & Wernicke’s)
- Extreme hemispheric specialization
- Reduction of visual area
- Expanded parietal and prefrontal cortex

Humans have larger brains

- Brain size has increased over evolutionary time in several mammalian lineages, especially in primates.
- Scaled to body size, cranial capacity in the hominin lineage has increased even more dramatically than is typical of other primates, indicating that brain size has expanded in hominins significantly more than expected based only on body size increase
- Modern human brain mass (~1350 g) is about 3 times larger than in great apes.
- While cranial capacity displays clear evidence of enlargement in the hominin fossil record, the issue of when brain reorganization occurred is more difficult to determine.
- Brain reorganization = changes in structures of the brain that account for differences in function and behavior that are independent of variation in brain size.

Jerison, 1973,1979; Shultz & Dunbar 2010; Hawks et al., 2000; Holloway 2008

Concerted vs mosaic brain evolution

- Concerted brain evolution: changes in brain structure that occur in a coordinated manner throughout the entire brain due to constraints on neural development
- Mosaic evolution is the ability for specific systems or regions to change independently of one another
- One hypothesis: size of brain regions in mammals enlarge predictably based on absolute brain size, due to conserved order of neural development in mammals, which is correlated with relative enlargement of different brain regions as brain size increased; modifications of individual regions is most easily achieved by changing the duration of the entire brain's schedule of neurogenesis
- But examples of certain systems within the brain of particular species that have shown to increase in size independently of changes in overall brain size, i.e. neocortical volume of primates is larger than that in insectivores; 5 x larger

Concerted vs mosaic brain evolution 2

- These results indicate that neocortical enlargement in primates is associated with adaptation toward different ecological niche
- Evidence also of an adaptive shift in primates toward a diurnal niche and increased reliance on vision; size of areas associated with vision are negatively correlated with size of olfaction areas.
- Evidence of brain reorganization in primates indicates that constraints may have resulted in overall concerted evolution among most brain structures, but this did not preclude system-specific changes.
- <u>Did brain reorganization happen prior to major brain expansion</u> or whether these changes were linked to allometric effects of cortical enlargement (i.e. debate over lunate sulcus; indication of location of parietal areas vs visual areas

Concerted vs mosaic brain evolution 3

- Modern human visual cortex is significantly reduced; position of lunate sulcus provides reasonable approximation of primary visual cortex size; lunate in fossil apes is more anterior than in modern humans; A more posterior positioned lunate sulcus in an endocast would signal a shift in cortical reorganization toward a more modern human-like pattern of parietal expansion and occipital reduction

- *A. africanus* lunate sulcus: Falk – more anterior, apelike; Holloway – more posterior, humanlike; Falk – reorganization of brain did not occur before expansion; Holloway – reorganization happened before expansion

- *A. sediba* (~2 mya): cortical reorganization before expansion – orbitofrontal region is more similar to later *Homo*.
- *H. floresiensis*: more posterior lunate, & frontal and temporal lobes similar to *H. erectus,* yet cranial size of 417 cc.

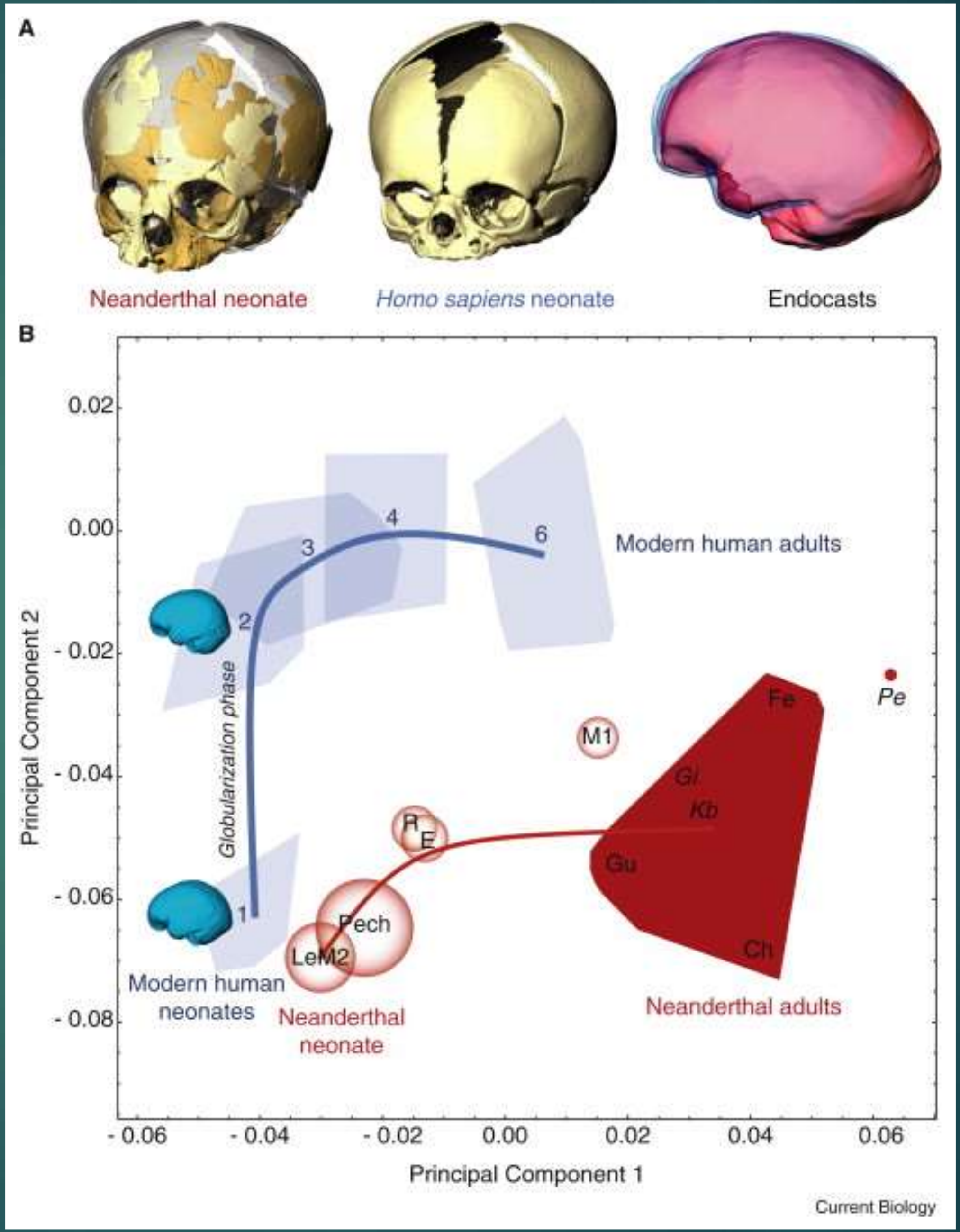
Concerted vs mosaic brain evolution 4

- Evidence of changes occurring in mosaic fashion without a change in overall brain size:
  - *H. sapiens vs. neandertalensis:* marked differences in relative lobe sizes despite similar overall size; differ in both adult & developmental endocranial shape
  - Neandertals - larger frontal and occipital lobes, smaller parietal-temporal lobes than humans; lack early postnatal globularization phase – develop more elongated skull shape
  - Modern humans – parietal and cerebellar expansion (globularization); undergo pronounced expansion during early postnatal development (not seen in chimps or Neandertals)
  - Cranial growth trajectories have influenced shape of the human brain independently of changes in overall brain size

Gunz et al., 2010, 2012)

Neanderthal and modern human brains grow differently.

MH globularization happens in 1st 2 years of development.



Both size increase and reorganization

- Conclusion: brain reorganization has occurred in parallel with brain size expansion in hominin evolution

The Evolution of Brains from Early Mammals to Humans. Jon H Kaas

- The large size and complex organization of the human brain makes it unique among primate brains. In particular, the neocortex constitutes about 80% of the brain, and this cortex is subdivided into a large number of functionally specialized regions, the cortical areas.

- Early mammals were small, with small brains, an emphasis on olfaction, and little neocortex.

- Neocortex was transformed from the single layer of output pyramidal neurons of the dorsal cortex of earlier ancestors to the six layers of all present-day mammals.

How did human brain evolve?

- Answers from:
  - comparative studies of the brains of present-day mammals and other vertebrates in conjunction with
  - information about brain sizes and shapes from the fossil record,
  - studies of brain development,
  - and principles derived from studies of scaling and optimal design.

Brain evolution in mammals & primates

- The small neocortex was divided into 20-25 cortical areas, including primary and some of the secondary sensory areas that characterize neocortex in nearly all mammals today.

- Early placental mammals had a corpus callosum connecting the neocortex of the two hemispheres, a primary motor area, M1, and perhaps one or more premotor areas.

- Neocortex was greatly expanded, and included an array of cortical areas that characterize neocortex of all living primates

Brain evolution

- Specializations of the visual system included new visual areas that contributed to
  - a dorsal stream of visuomotor processing in a greatly enlarged region of posterior parietal cortex and
  - an expanded motor system and the addition of a ventral premotor area.

- Higher visual areas in a large temporal lobe facilitated object recognition, and frontal cortex, included granular prefrontal cortex.

- Auditory cortex included the primary and secondary auditory areas that characterize prosimian and anthropoid primates today.
- As anthropoids emerged as diurnal primates, the visual system specialized for detailed foveal vision. Other adaptations included an expansion of prefrontal cortex and insular cortex.

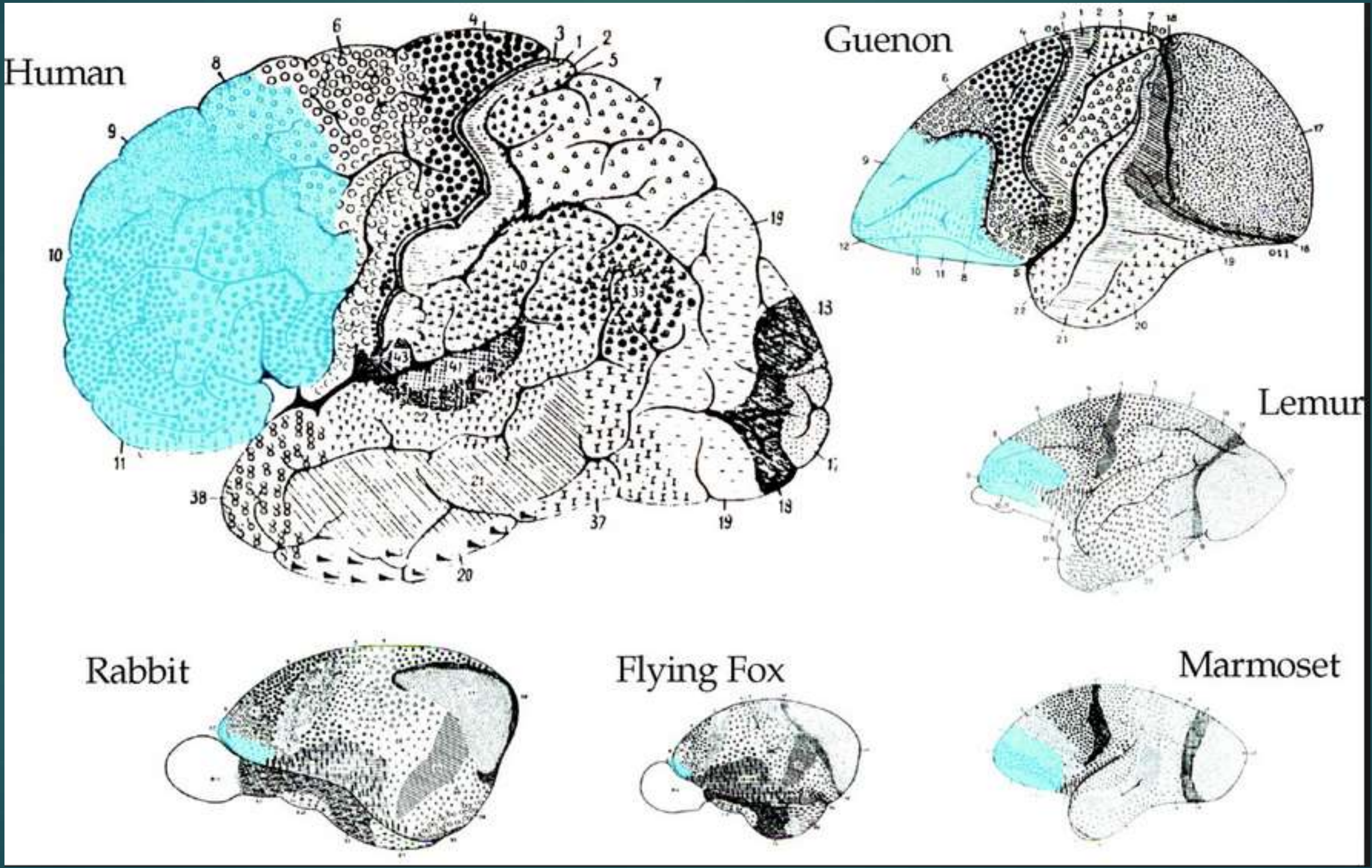
Brain Evolution

- The human and chimpanzee-bonobo lineages diverged some 6-8 million years ago with brains that were about one-third the size of modern humans.
- Over the last two million years, the brains of our more recent ancestors increased greatly in size, especially in the prefrontal, posterior parietal, lateral temporal, and insular regions.
- Specialization of the two cerebral hemispheres for related, but different functions became pronounced, and language and other impressive cognitive abilities emerged.

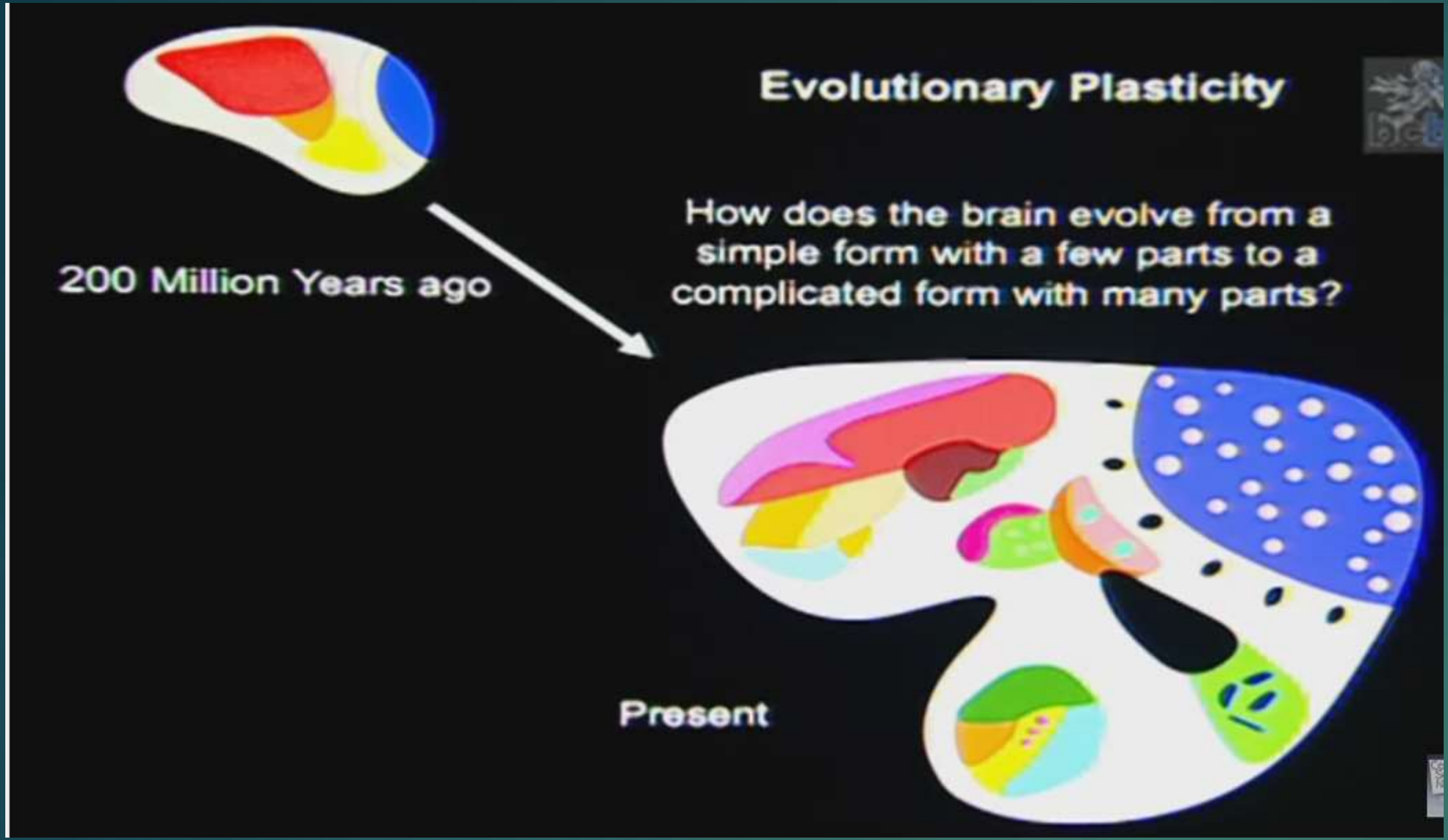
Brain evolution: functional specializations

- Posterior parietal cortex was greatly expanded with sensorimotor modules for reaching, grasping, and personal defense.
- Motor cortex had become more specialized for hand use, and the functions of primary motor cortex were enhanced by the addition and development of premotor and cingulate motor areas.
- Cortical architecture became more varied, and cortical neuron populations became denser overall than in nonprimate ancestors.
- Primary visual cortex had the densest population of neurons, and this became more pronounced in the anthropoid radiation.
- Within the primate clade, considerable variability in cortical size, numbers of areas, and architecture evolved.

Evolution of the brain: 10 to 250 cortical regions



Brodmann, 1909



Can Compare:

1 Architecture

2 Functional organization

3 Connectivity

4 Development

5 Cellular composition

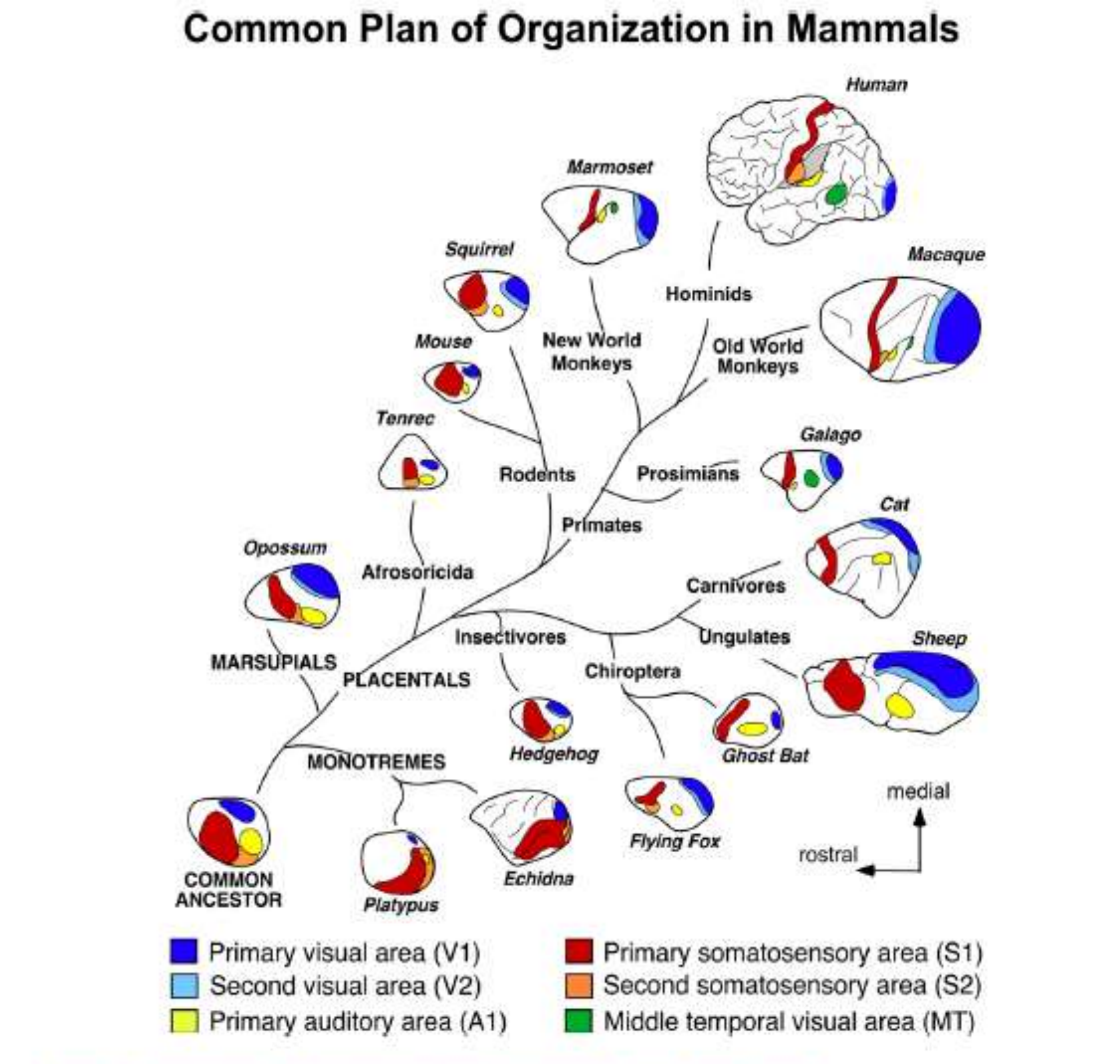


Figure 1. A Phylogenetic Tree Illustrating the Relationship between Major Groups of Mammals
Common cortical fields have been identified in all species examined. The genes involved in specifying these areas in development were likely inherited from the common ancestor of all mammals. Modified from Krubitzer and Kahn, 2003.

Phylogenetic Tree

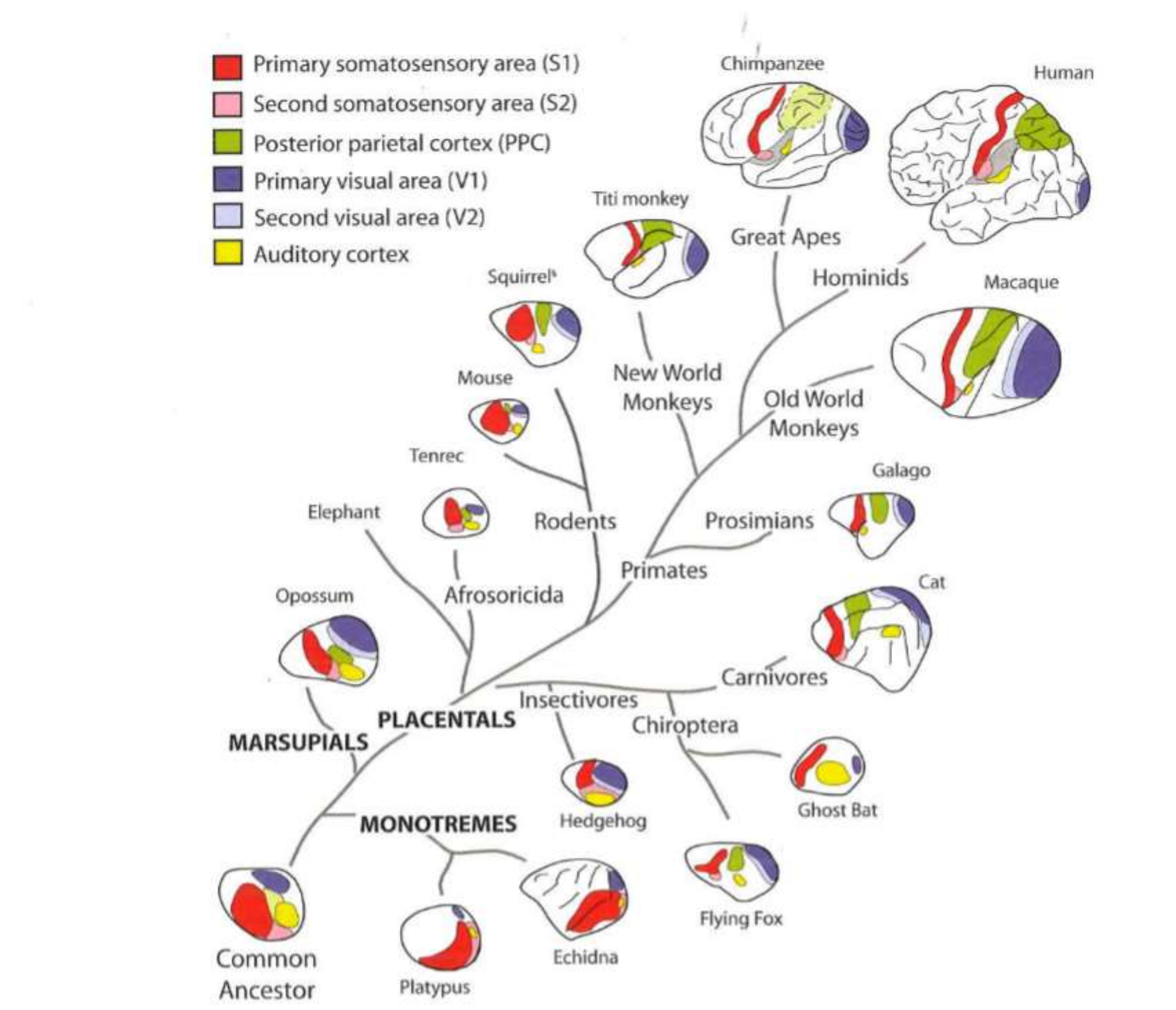
Conserved common cortical areas have been identified in all species examined.

Genes involved in specifying these areas in development were likely inherited from the common ancestor of all mammals

All have V1, S1, geniculate pathways, even in absence of use (blind mole rat (V1 for circadian rhythms).

The Magnificent Compromise: Cortical Field Evolution in Mammals, Leah Krubitzer. Neuron 56: 201-208, 2007

Parietal lobe evolution

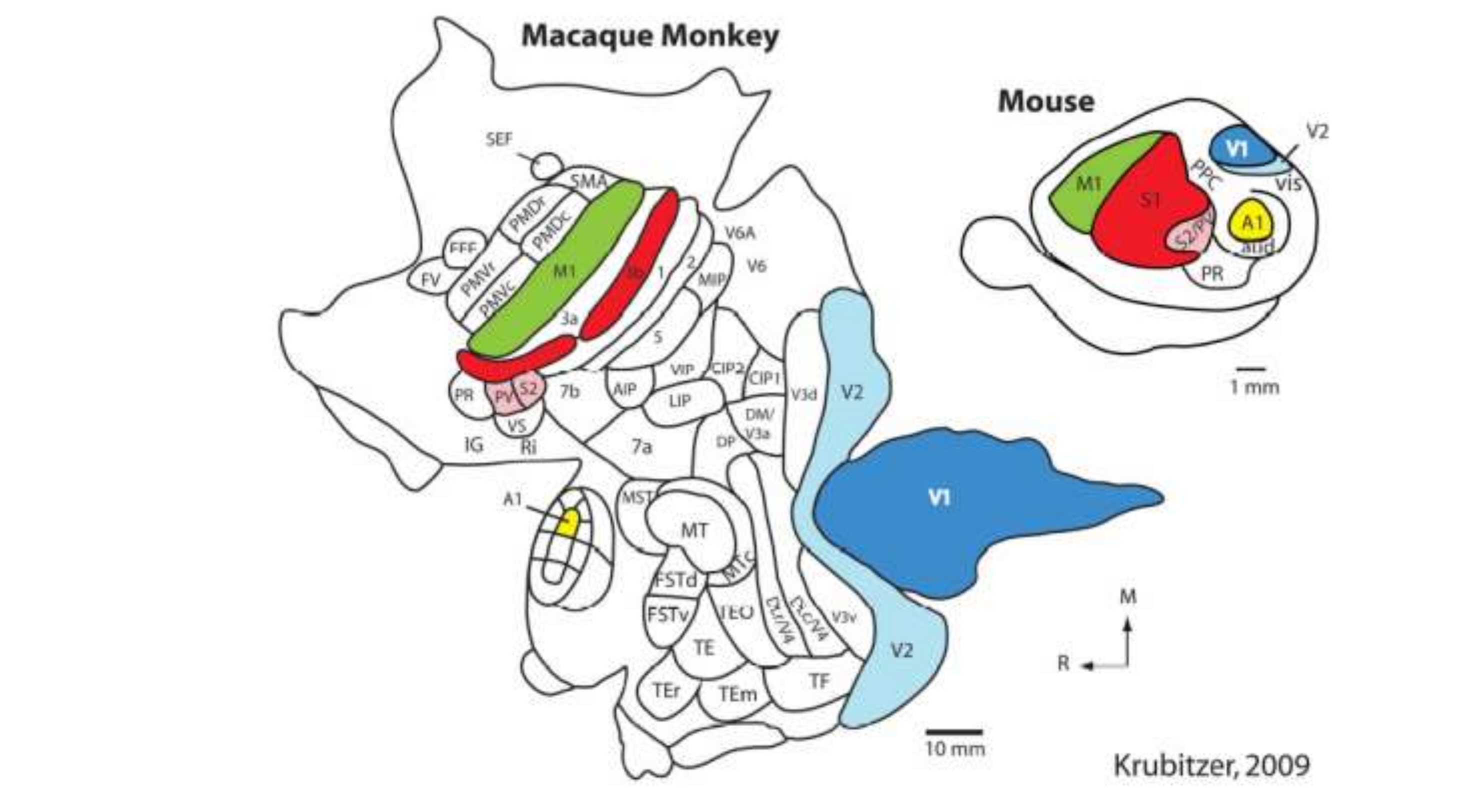


6 Conserved sensory areas

Parietal lobe expansion in humans

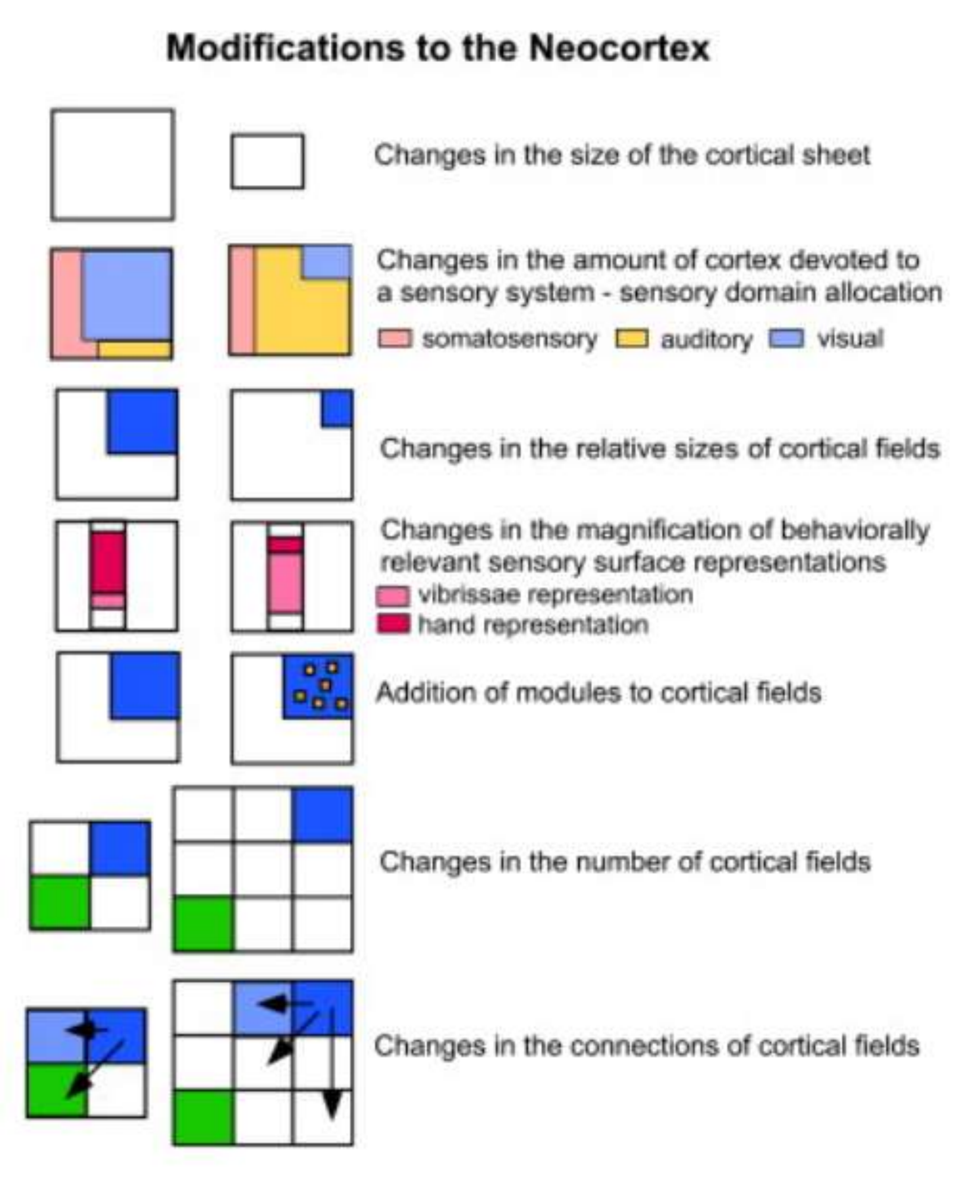
Human: 250-300 separate brain regions

Not all brains are same: cortical changes in evolution



Changes in size of cortex, location of functional modules (V1, S1, etc.), size of modules

- Areas developmentally driven by genes: intrinsically mediated aspects of cortical organization – cortex size, region size, internal organization, connectivity
- Always V1, S1, etc.
- Size of area: Epigenetic effects of environmental experience; activity dependent



Types of Evolutionary Brain Changes

Entire Brain Size change

Sensory system distribution (S1, A1, V1)

Relative size of specific brain areas

Size of sensory representation (i.e. hand)

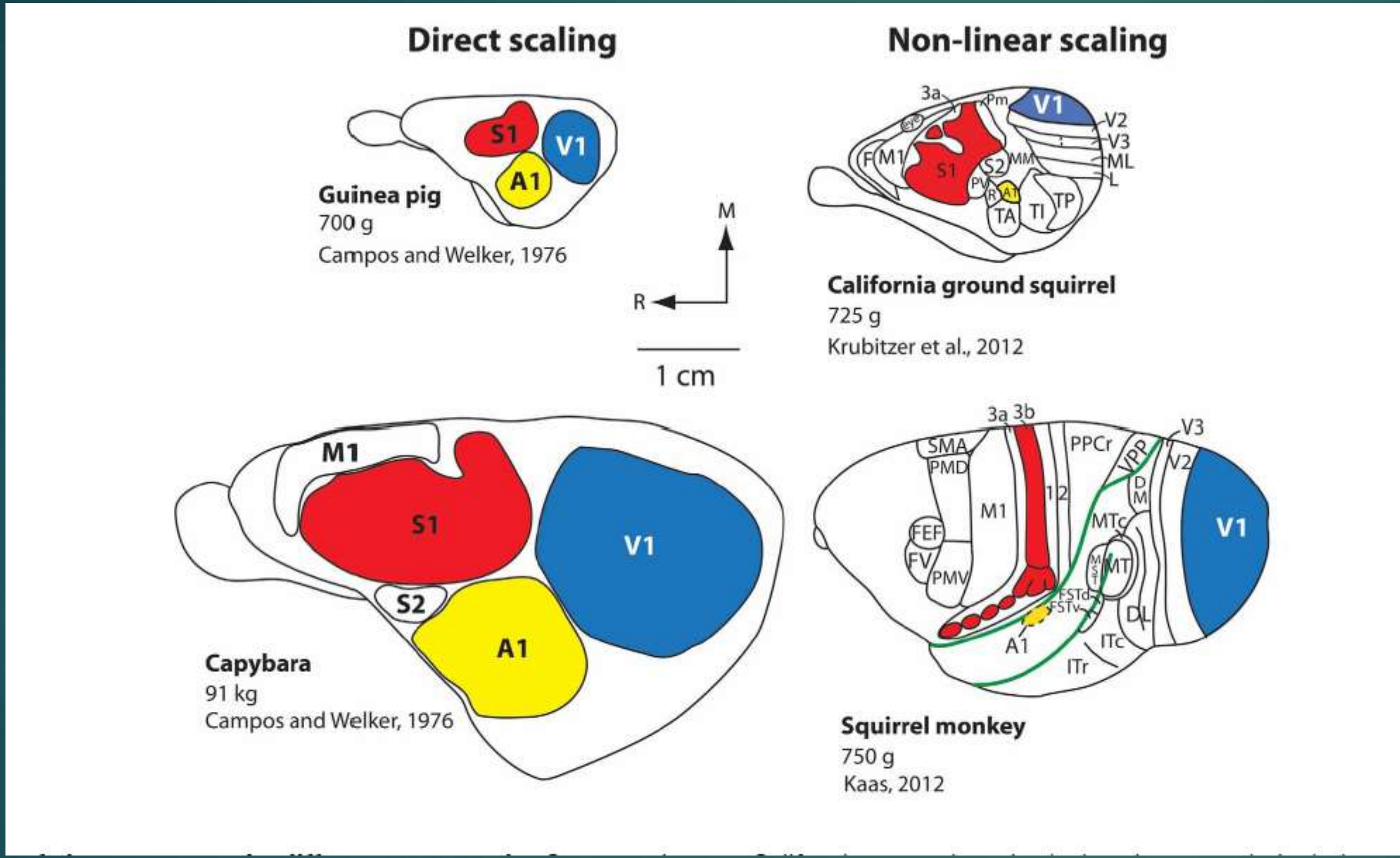
New modules within brain areas

Number of brain areas

Connections between brain areas

Leah Krubitzer, *Neuron*, 2007

How has the neocortex increased in size?

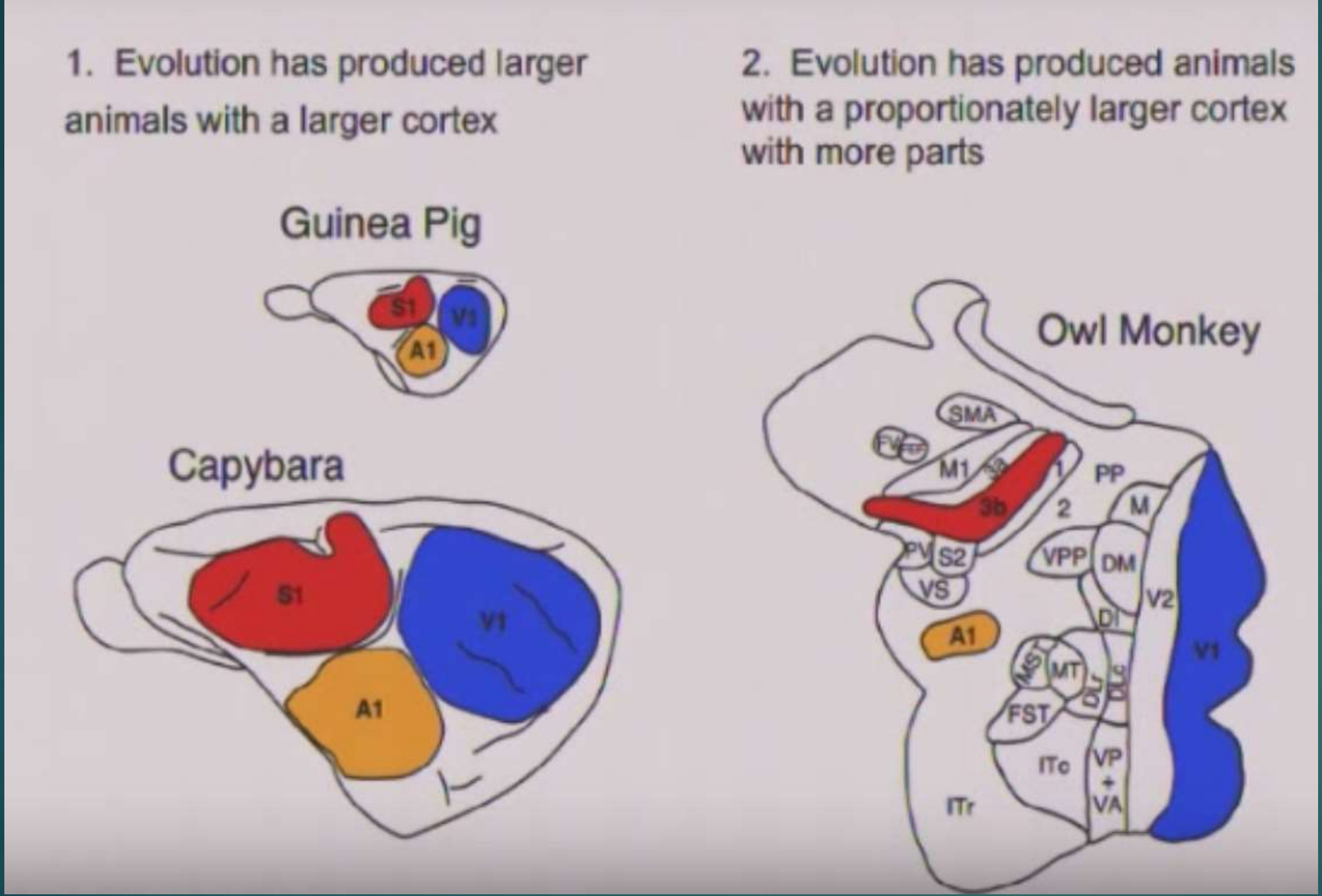


Larger body

Method 1 (direct scaling): <u>larger body, larger brain</u>

Method 2 (non-linear scaling): <u>Proportionally larger brain with more parts (regional anatomic variations)</u>

How the cortex has increased in size

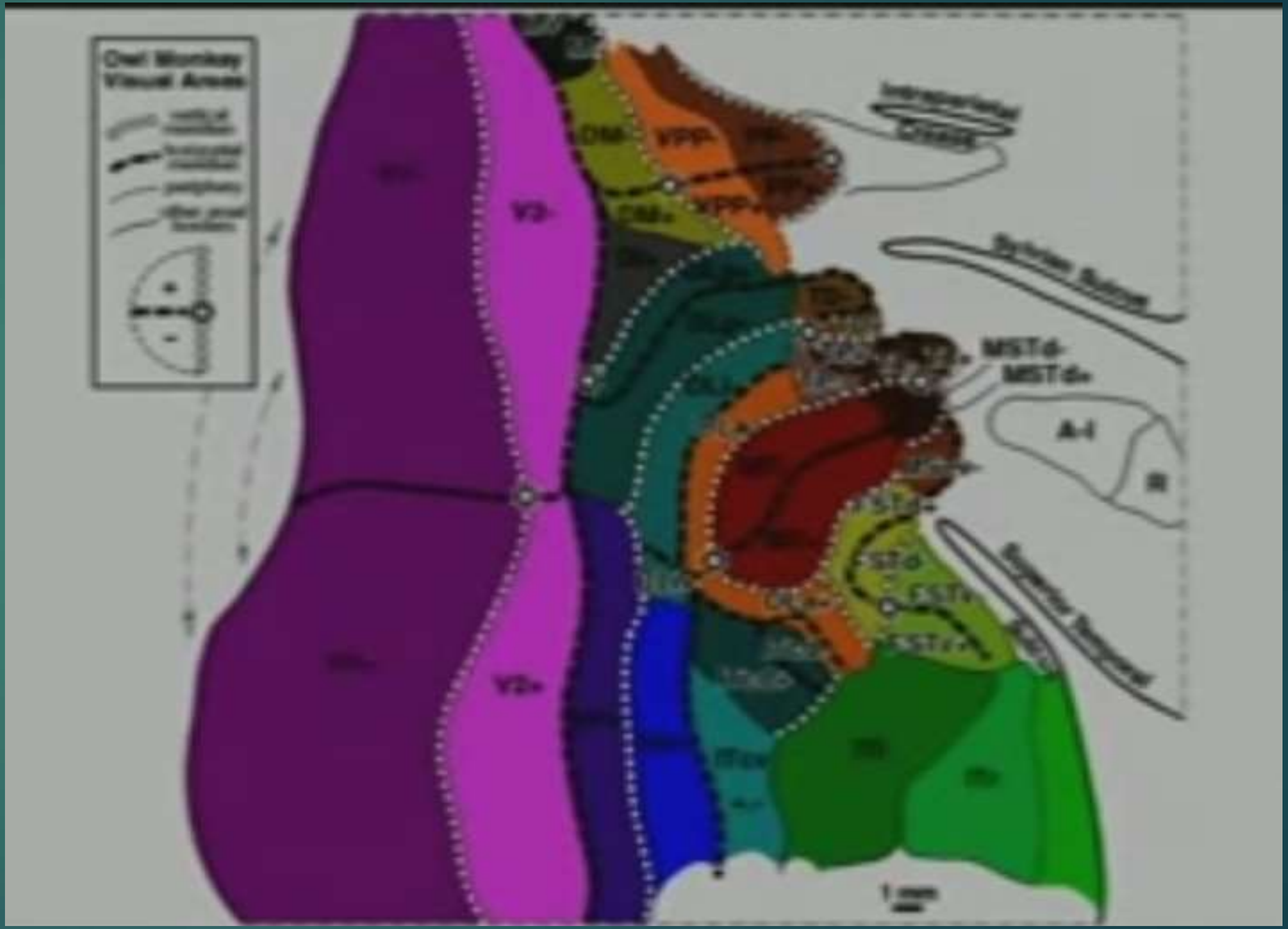


Scaling up of cortical fields

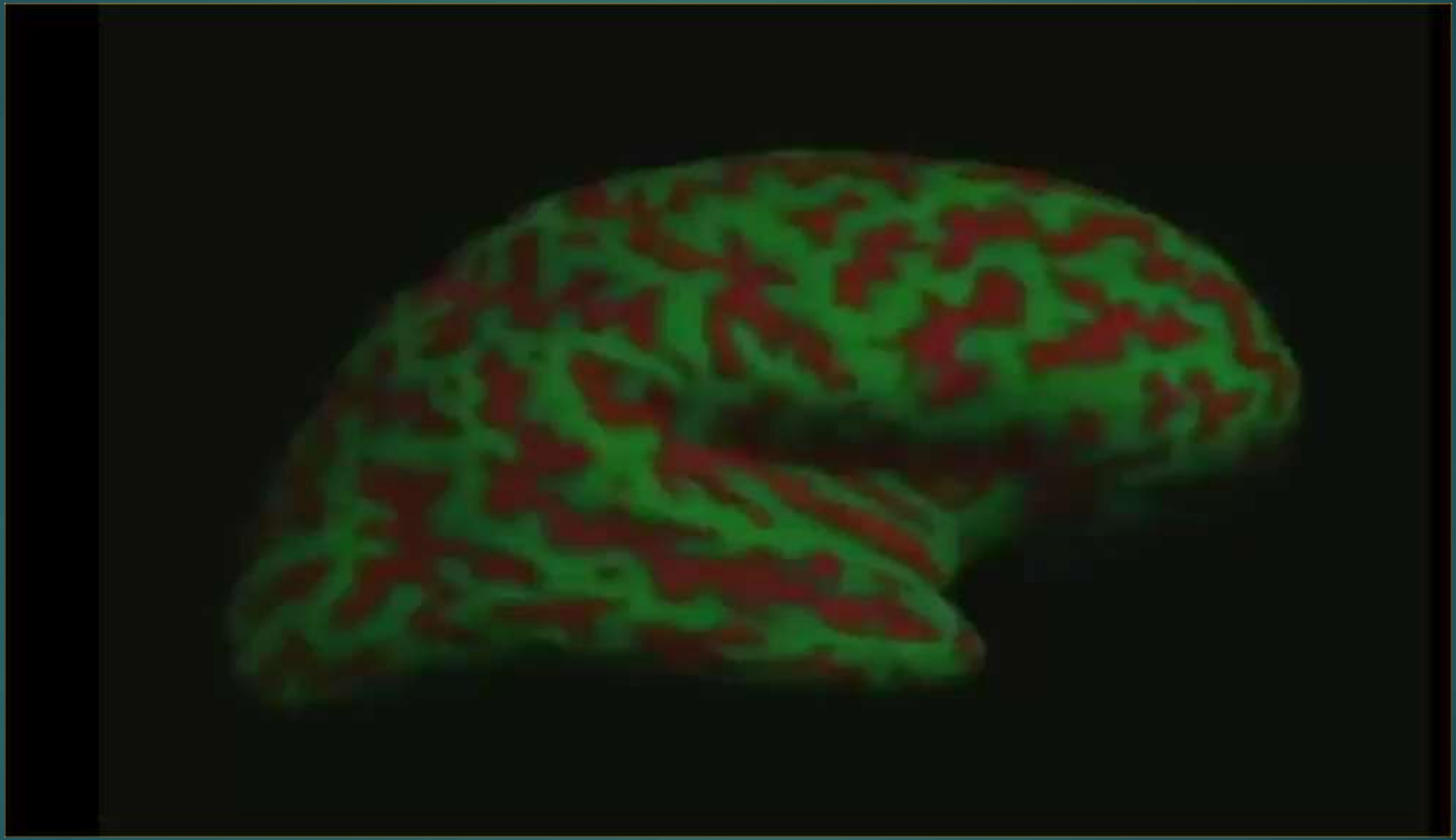
Addition of cortical fields

Premise:
<u>Natural variation of these cortical organizational features within a population, must ultimately lead to speciation</u>

Owl Monkey: 30 Visual areas = 50% of cortex

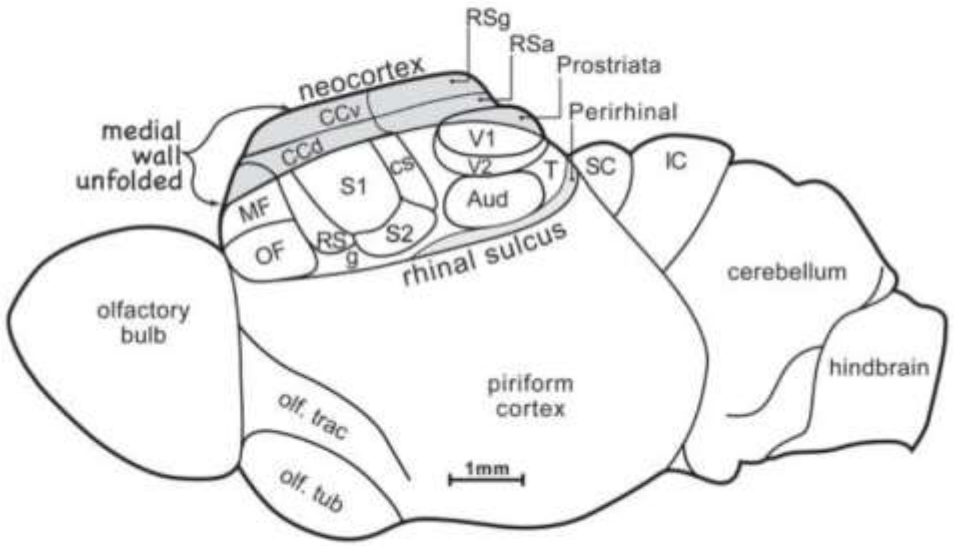


Flattening a human brain by computer



Martin Sereno

Proposed organization of neocortex in early mammals



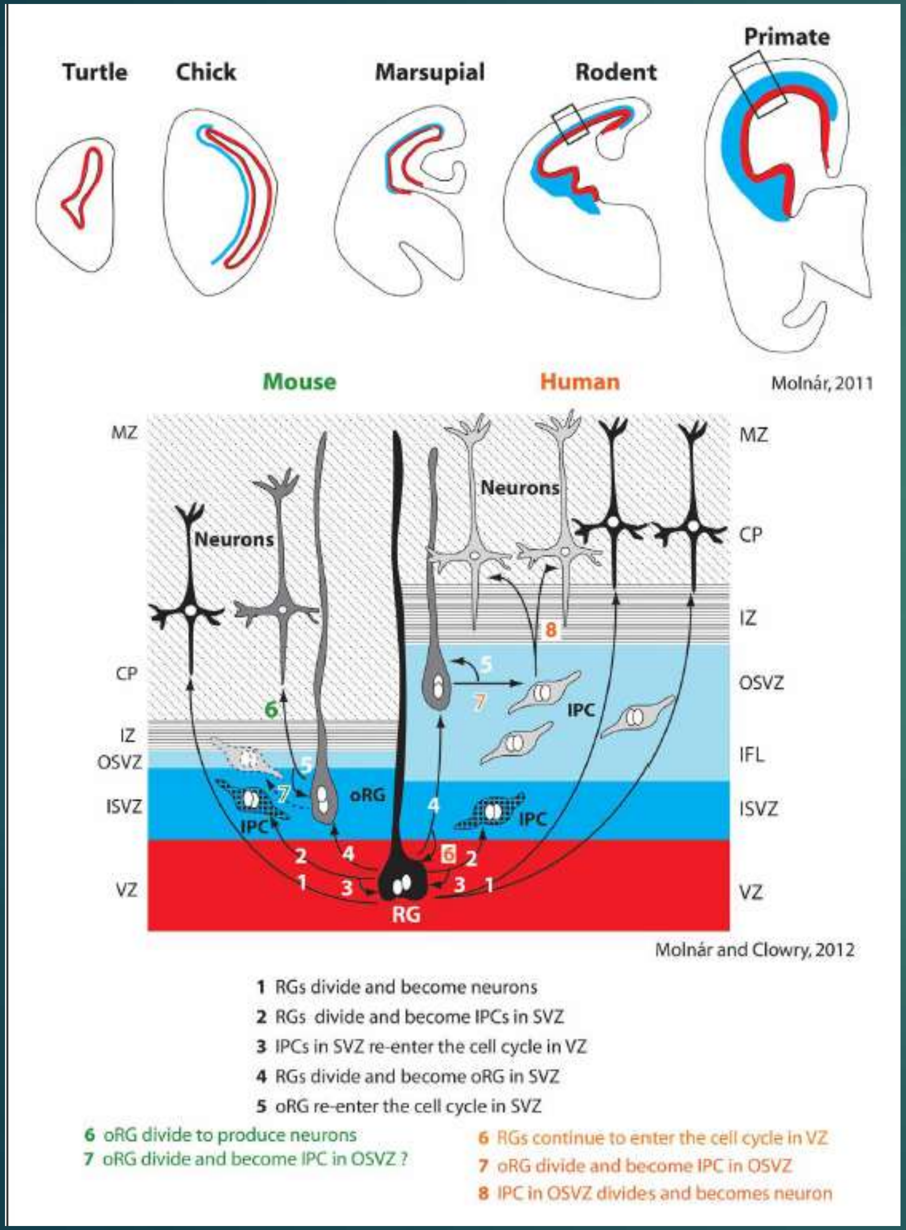
The proposed organization of neocortex in early mammals

The proportion of the forebrain devoted to the neocortex of early mammals was small compared to that in most subsequent mammals, and there were few cortical areas. Neocortex included orbital frontal (OF) and medial frontal (MF) areas, primary somatosensory cortex (S1) bordered by secondary, dorsal, and caudal somatosensory areas (S2, RS, CS), possibly a gustatory area (g), and primary, secondary, and temporal visual areas (V1, V2, T), auditory cortex of one or more divisions (Aud), ventral and dorsal cingulate areas (CCv, CCd), and retrosplenial granular and agranular areas (RSg, RSa) as well as an area prostriata, a visual area. The superior colliculus (SC) and inferior colliculus (IC) of the midbrain were not covered by neocortex or cerebellum, and the olfactory bulb and piriform cortex were proportionately large.

Forebrain (neocortex) relatively small; large olfactory bulb & piriform cortex (olfaction)

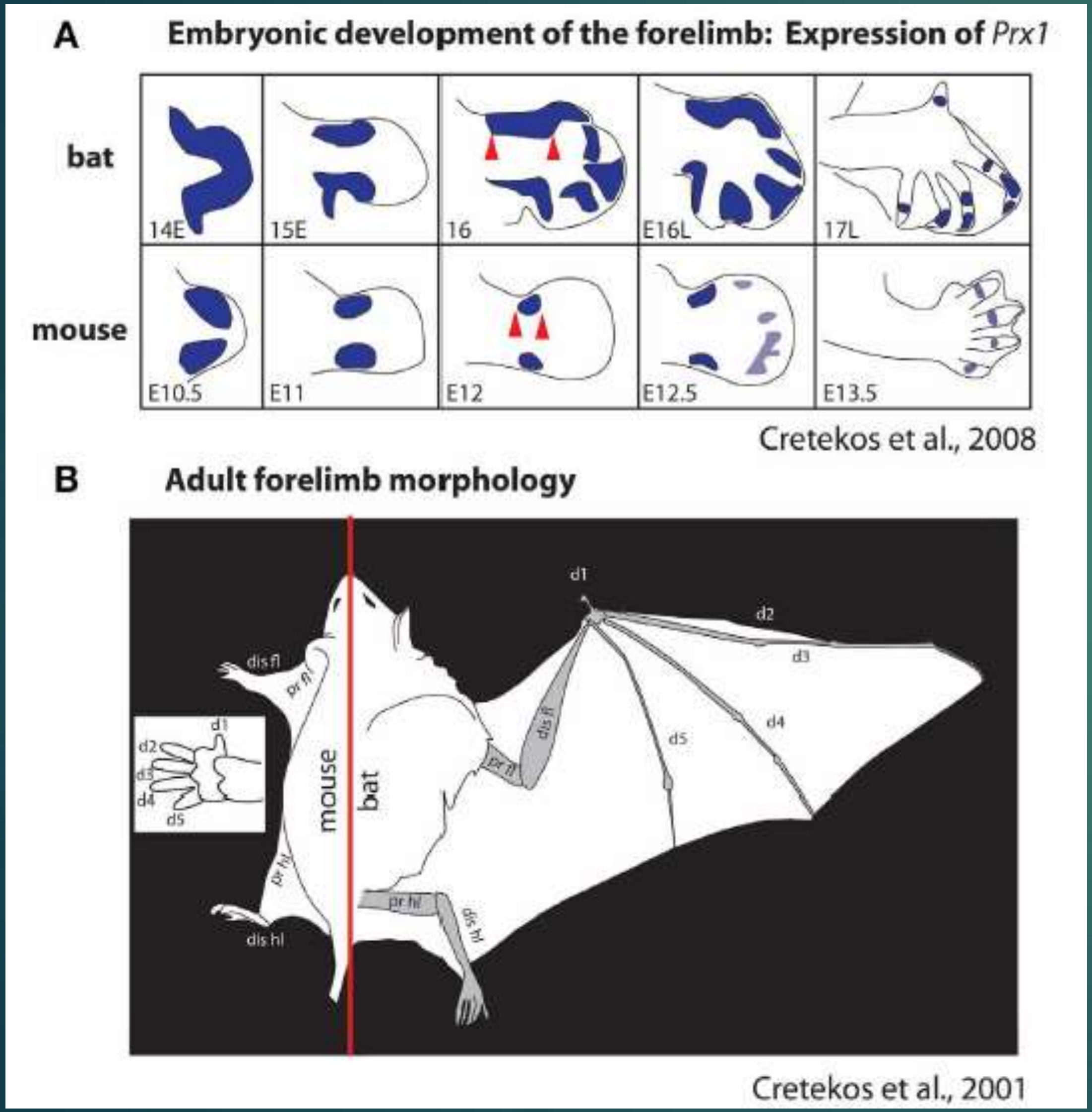
Z. Molinar

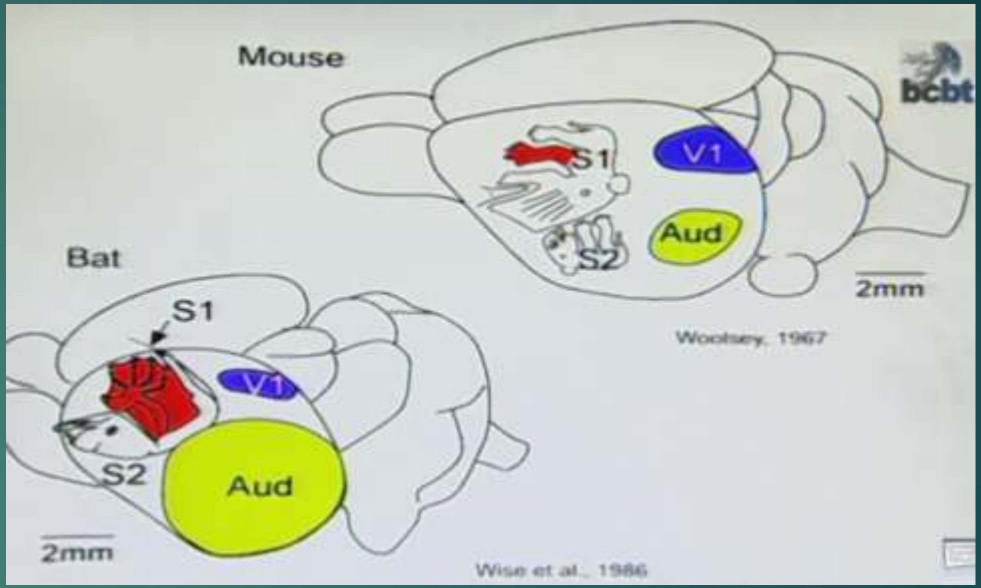
Neurogenesis in development: how glial cells become neurons



- In early development, neural stem cells rise from ventricular zone and migrate to final cortical area as neurons. Genetically mediated, but can be affected by maternal diet.
- During the late stages of cortical development, radial glial cells divide asymmetrically in the ventricular zone to generate radial glial cells and intermediate progenitor (IP) cells and that IP cells subsequently divide symmetrically in the subventricular zone to produce multiple neurons
- Process is more complex in humans, but is basically similar to evolutionarily earlier forms. In humans, exponential increase in brain size due to this process.

A change in gene PRX1: alters morphology & in turn alters regional area size & location





Bat & Mouse cortical region differences; note limb representation in S1 & size of A1

Regulatory divergence modifies limb length between mammals. _The bat Prx1 limb enhancer increases forelimb length in mice during development_.
Differences in DNA sequences regulating gene expression may be a primary source of variation

How do cortical modules change

- Cortical field/module is a unique pattern of connectivity that shifts and redistributes within a lifetime of an individual and in a species over time.
- Is there a redistribution of afferents on the cortical sheet
  - Alteration in cortical sheet size
  - Alteration of intrinsic or extrinsic genes to neocortex – yes; can shift region areas
  - Changes in peripheral morphology and use (environmental effect)
- Natural differences in physical environment in which individuals develop induce alterations in cortical field size, organization & neuronal number.

Rat brain is prototypical: All rodent brains are not the same; environmental diversity produce different neocortices

- Neocortex is a highly dynamic structure that is capable of assuming a unique organization and pattern of connectivity to match the physical demands and fluctuations that occur naturally in the environments in which an animal develops

- Rodents:
  - highly diverse in distribution and lifestyle (2,277 species);
  - variety of niches
  - vary along several lifestyle dimensions such as diel pattern (diurnal vs. nocturnal), terrain niche, diet, wild vs lab.

Leah A Krubitzer

Rodents: variable neocortex

- Terrain niches of rodents includes arboreal, aerial, terrestrial, semi-aquatic, burrowing, and rock dwelling.

- Their environmentally dependent behaviors are also highly variable and thus the neocortex, which generates these behaviors, has undergone corresponding alterations across species

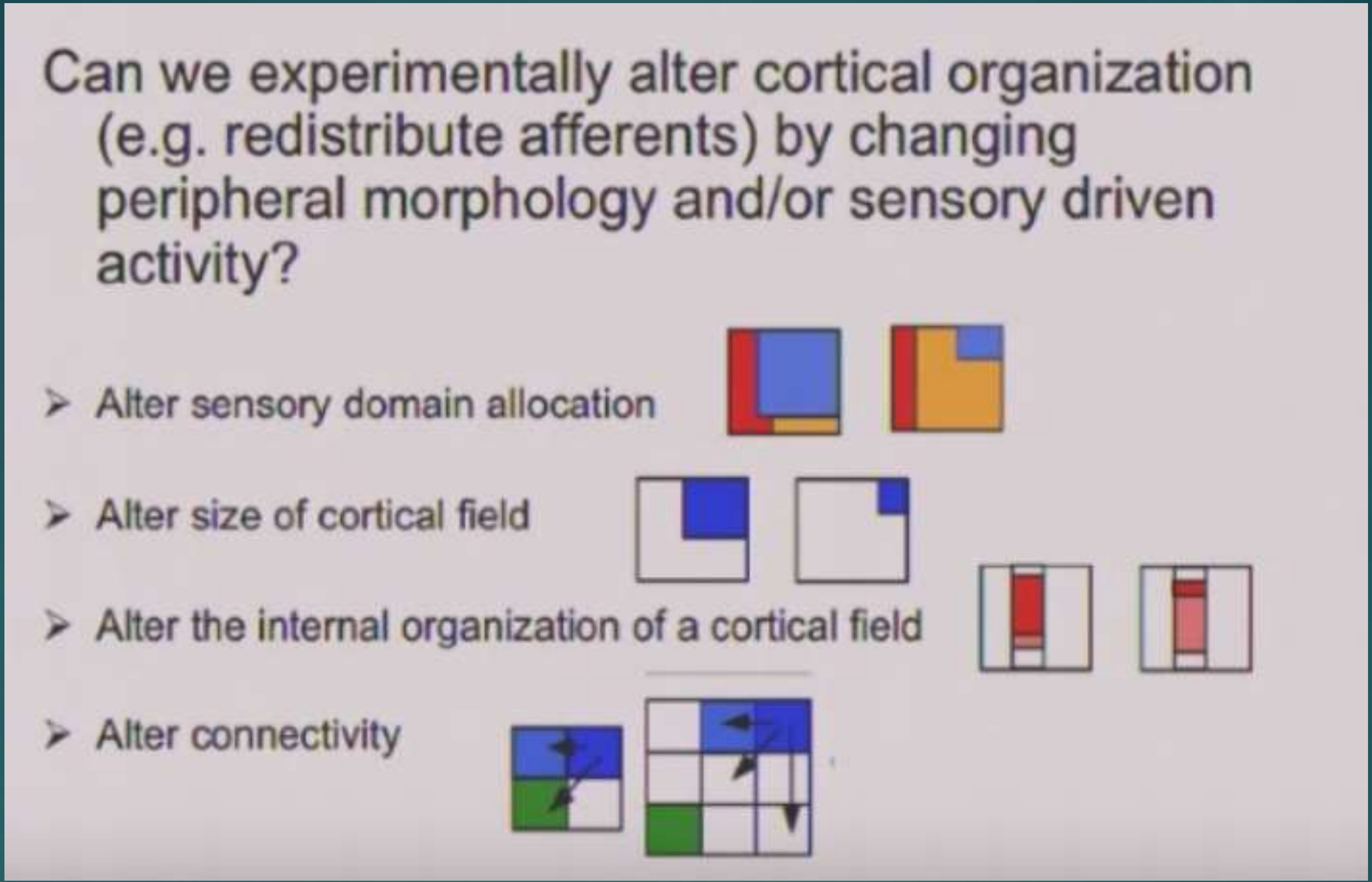
Rodents: totally variable cortex

- Size and number of cortical fields can be highly variable (differences in VI, S1, etc.).
- Internal organization of a cortical area reflects lifestyle differences between species and exaggerates brain representation of behaviorally relevant effectors such as tactile hair, teeth, or lips.

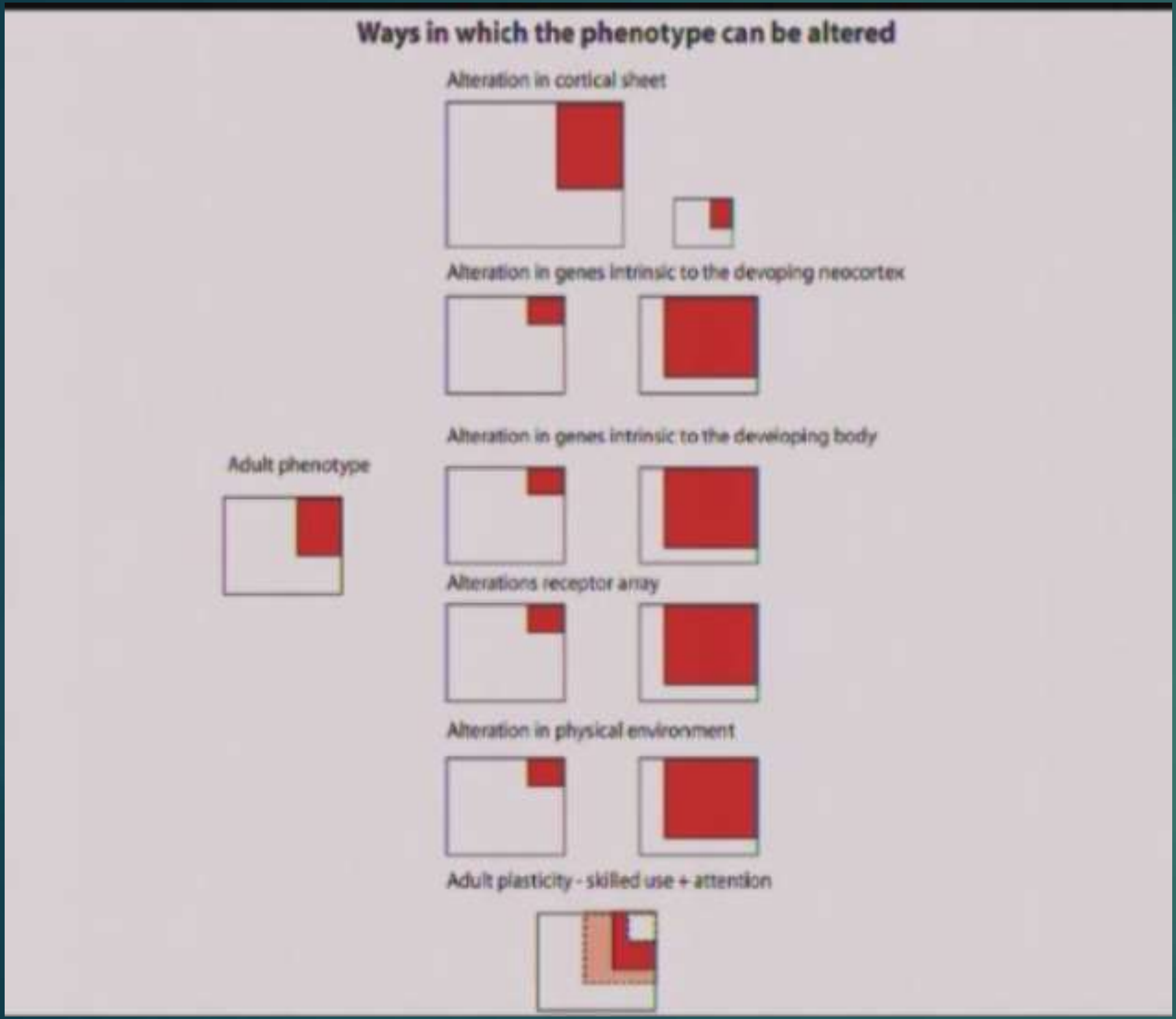
- Neuronal number and density varies for the same cortical field in different species and is even different for the same species reared in different conditions (laboratory vs. wild-caught; latter has higher EQ).

Rodents: brain variability

- No generic rodent model.
- There are rodent models suited for specific questions regarding the development, function, and evolution of the neocortex.
- Points to a complex, multilayered relationship between genes, brains, bodies, environment, and targets of selection.
- Any talk about the “gene” for autism, schizophrenia, etc. are misguided.

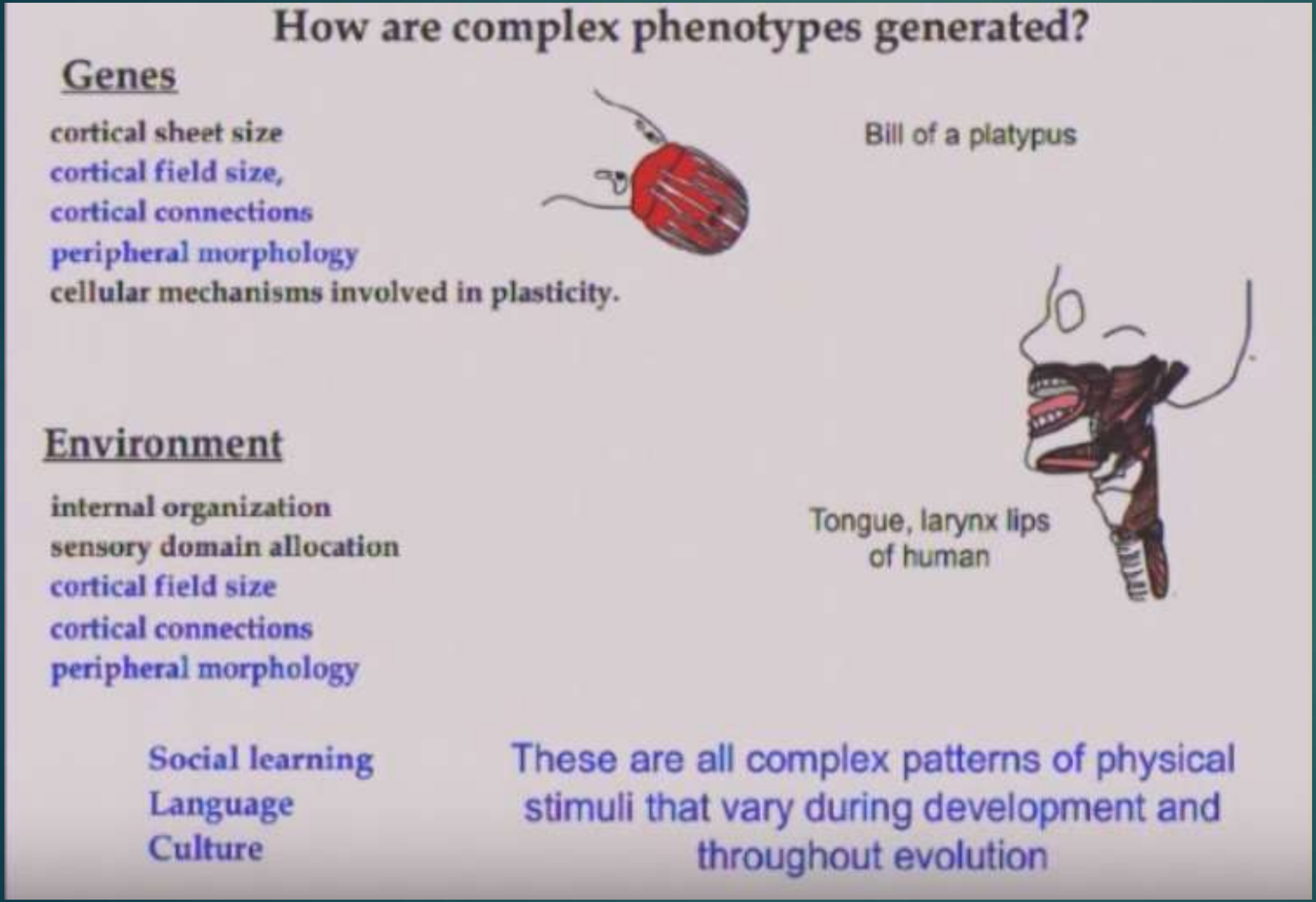


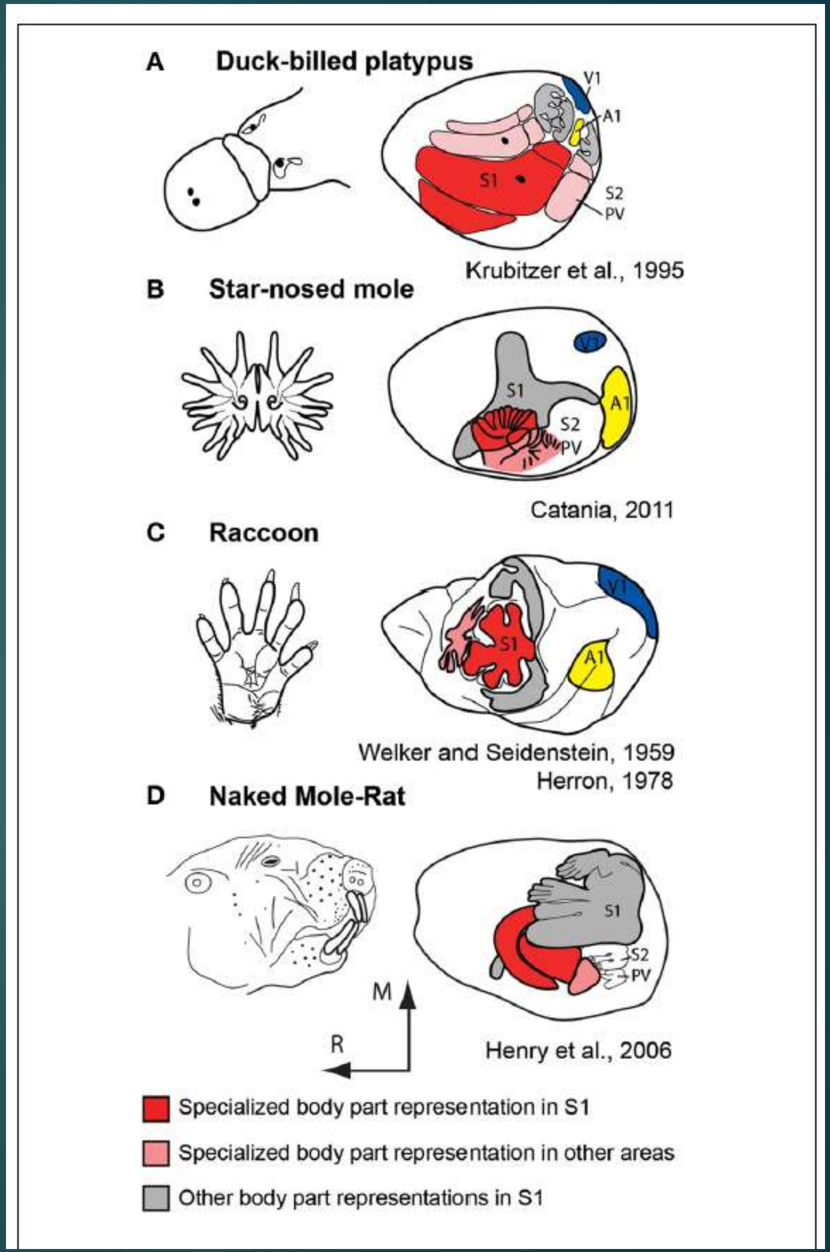
Yes!: cortical field size, functional organization, connectivity; recent work on poverty & stress in children (reduce regions by 20%) & Romanian orphan children



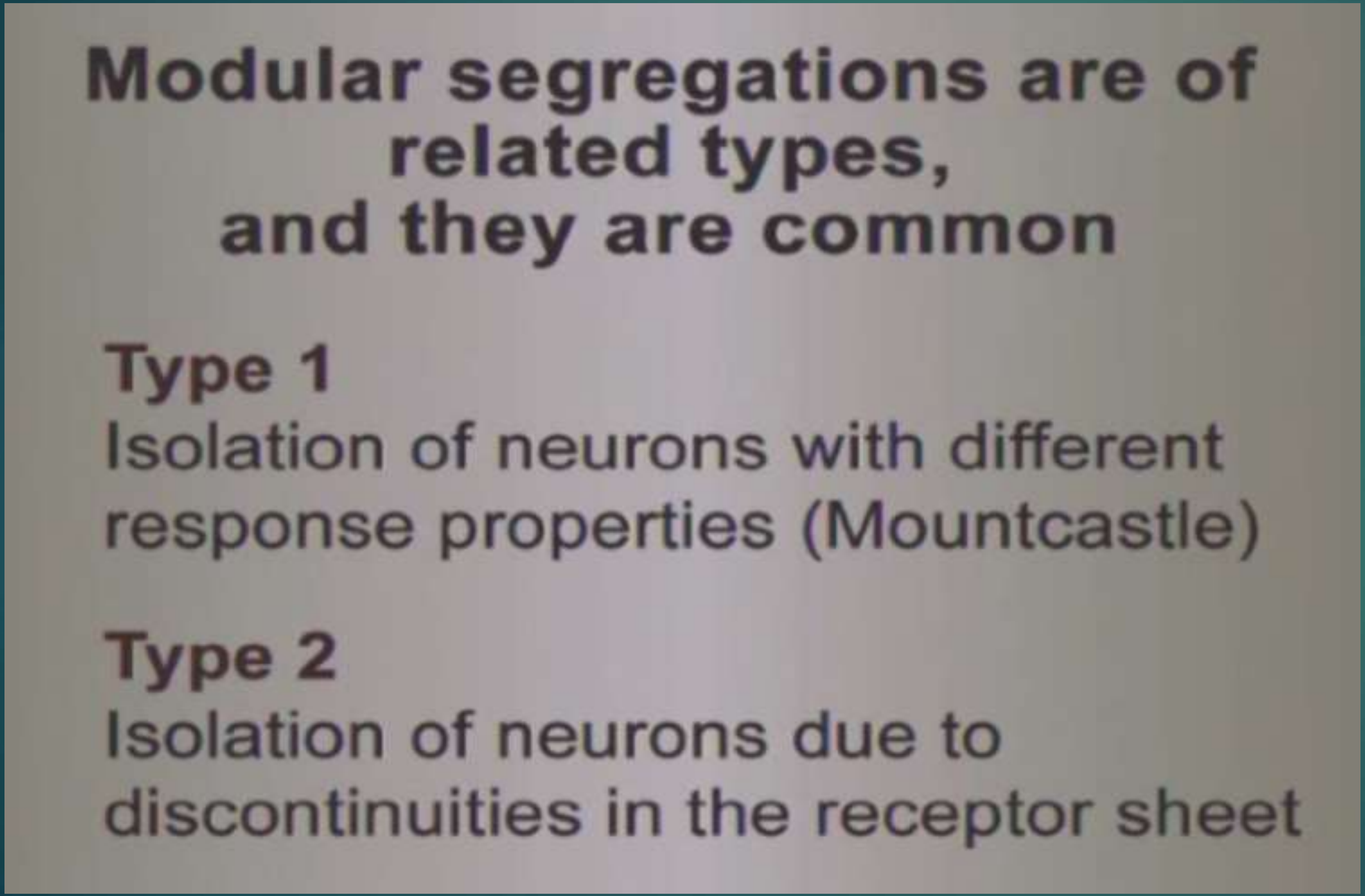
Can change cortex:
Cortical field size
Genes in development of neocortex & body
Receptor arrays
Physical environment
Adult plasticity

Ways to change brain





Brain module: brain area of common cognitive processing specialization



Mountcastle = vertical array of columns, densely interconnected with properties in common because of dense connections; form a module

There are multiple intrinsic & extrinsic mechanisms that can change the same aspect of the cortical phenotype

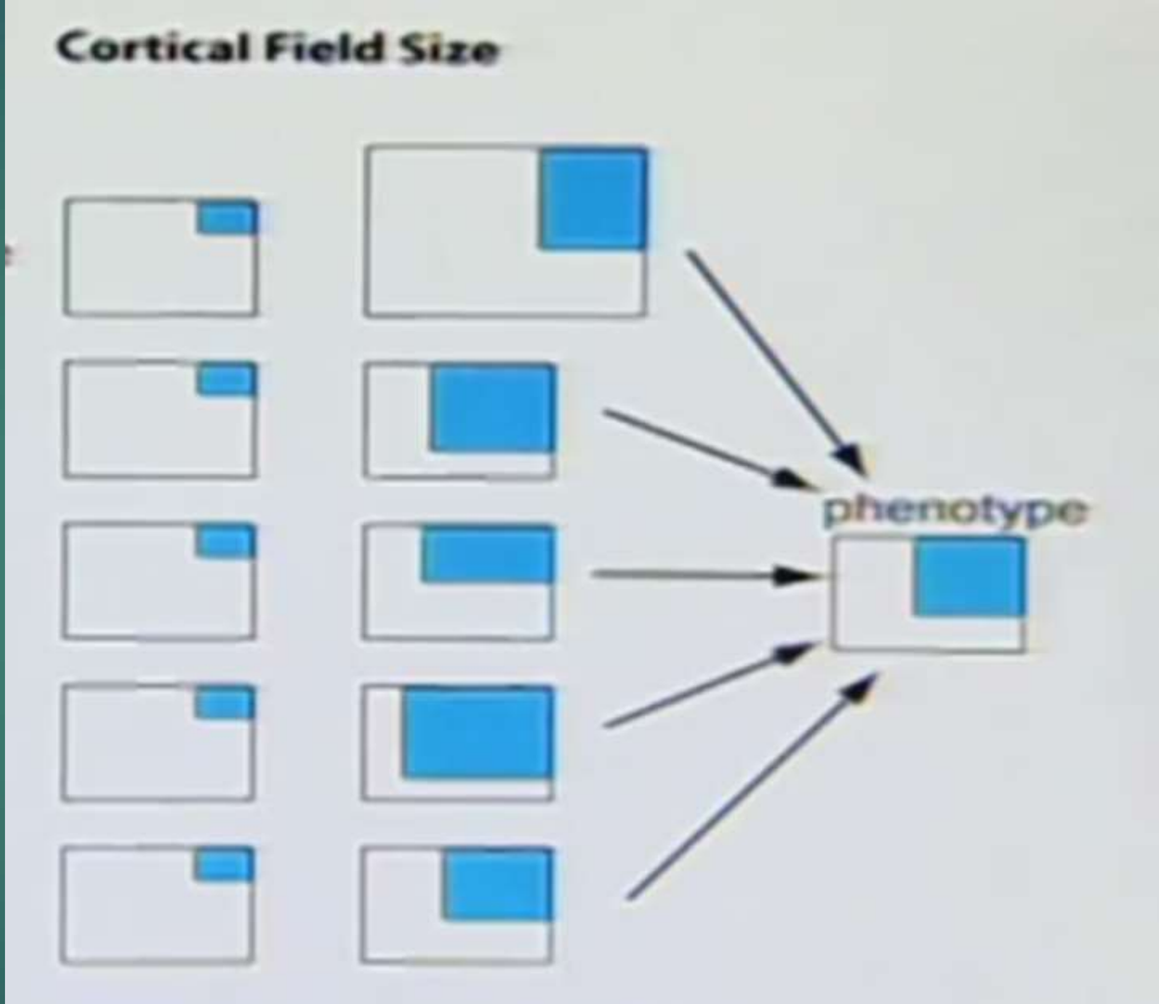
1 Alteration in cortical sheet size

2 Alteration in genes intrinsic to the developing neocortex

3 Alteration in genes intrinsic to the developing body

4 Alteration to the receptor array

5 Alteration to the physical environment



Krubitzer & Seeike, 2012

Brain Modules

- Modules (vertical columns of neurons) are adjacent groups of neurons separated by activity differences and activity dependent mechanisms (i.e. digit 1 vs digit 2, or seeing red vs blue in V1)
- Brain uses activity differences to create patterns of organization (module)
- Activities isolate neurons in the brain into modules with narrower range of inputs

Brain modules

- Module shapes and sizes reflect the relative magnitude of two competing inputs with different activity patterns and the developmental timing of the competition.

- It is relatively easy for modules to evolve or be lost within the branching lines of evolution

Ways external world drives cortical change

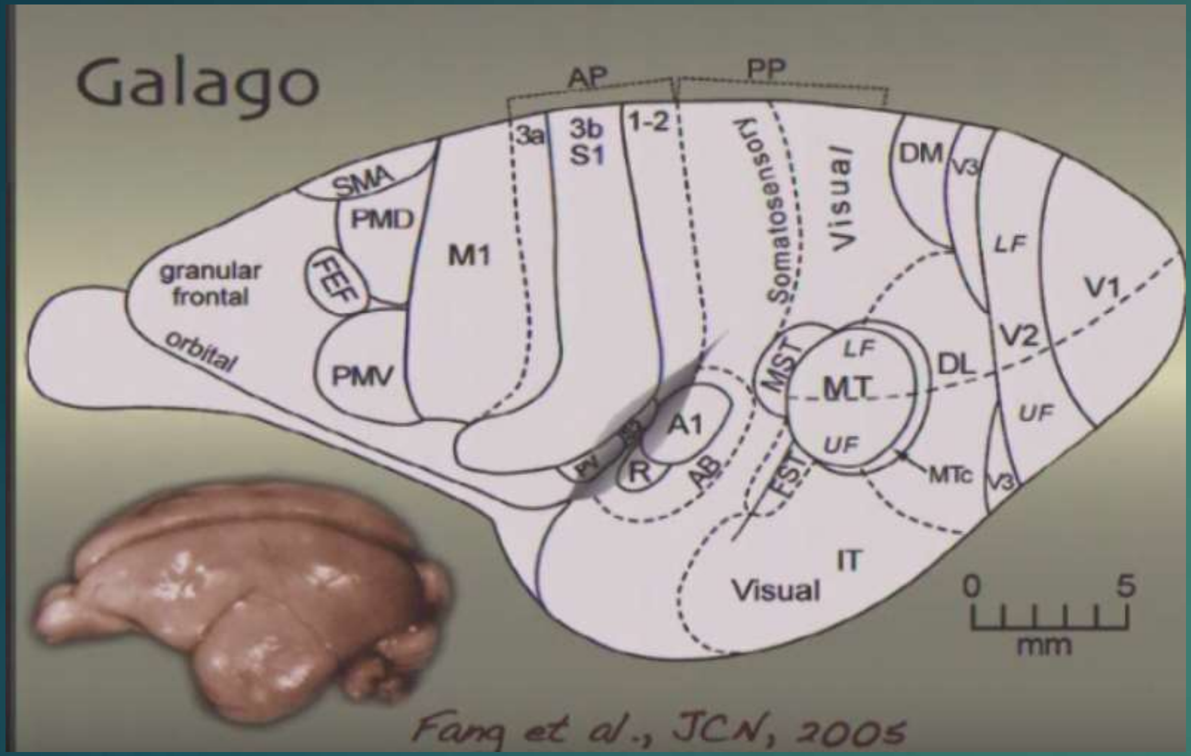
- Natural differences in the physical environment in which individuals develop induce alterations in cortical field size, organization, and neuron number.

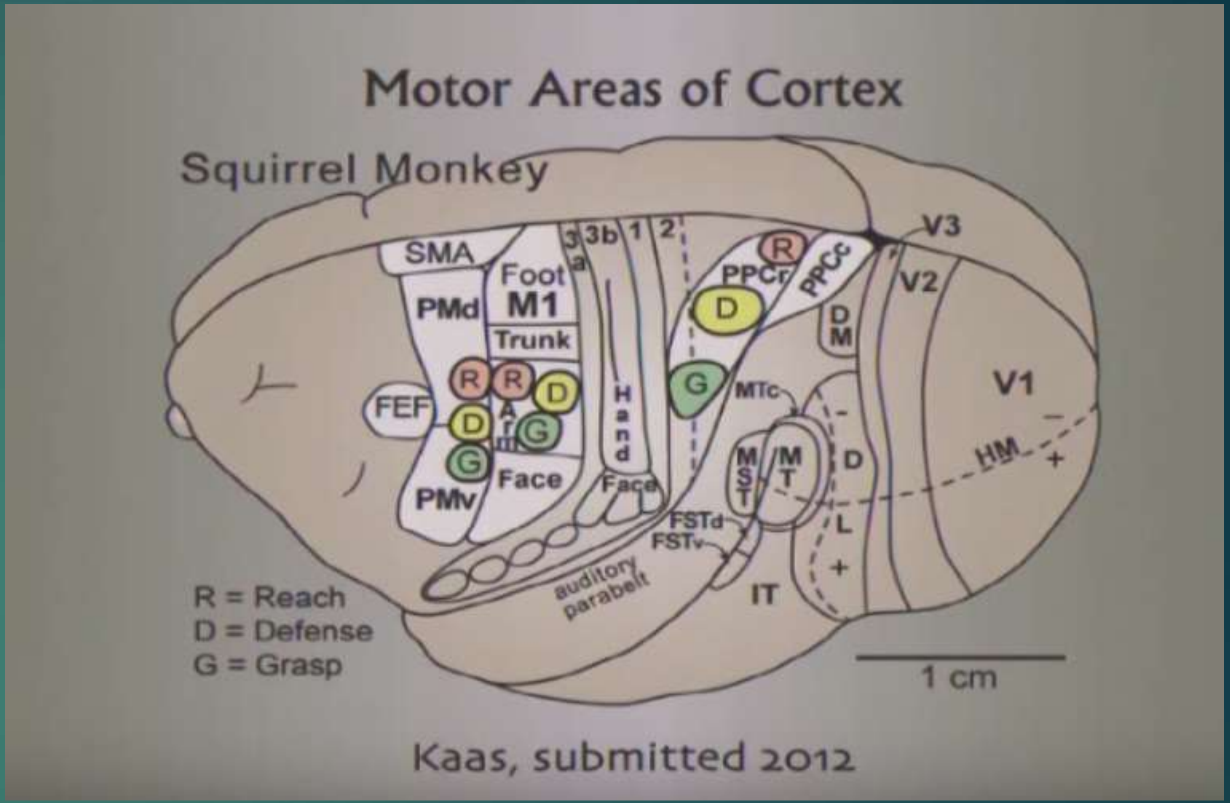
- Changes in sensory inputs or rearing behaviors change regional cortical representation.

Ways external world drives cortical change

- Example:
  - Visual ability in lab vs wild caught rats: significant differences in number of and density of neurons & glial cells in V1 (wild caught significant higher).
  - Behavior: being recipient of high parental rearing (tactile contact) behavior in monogamous prairie voles increases size of S1 (oral facial area) & connectivity

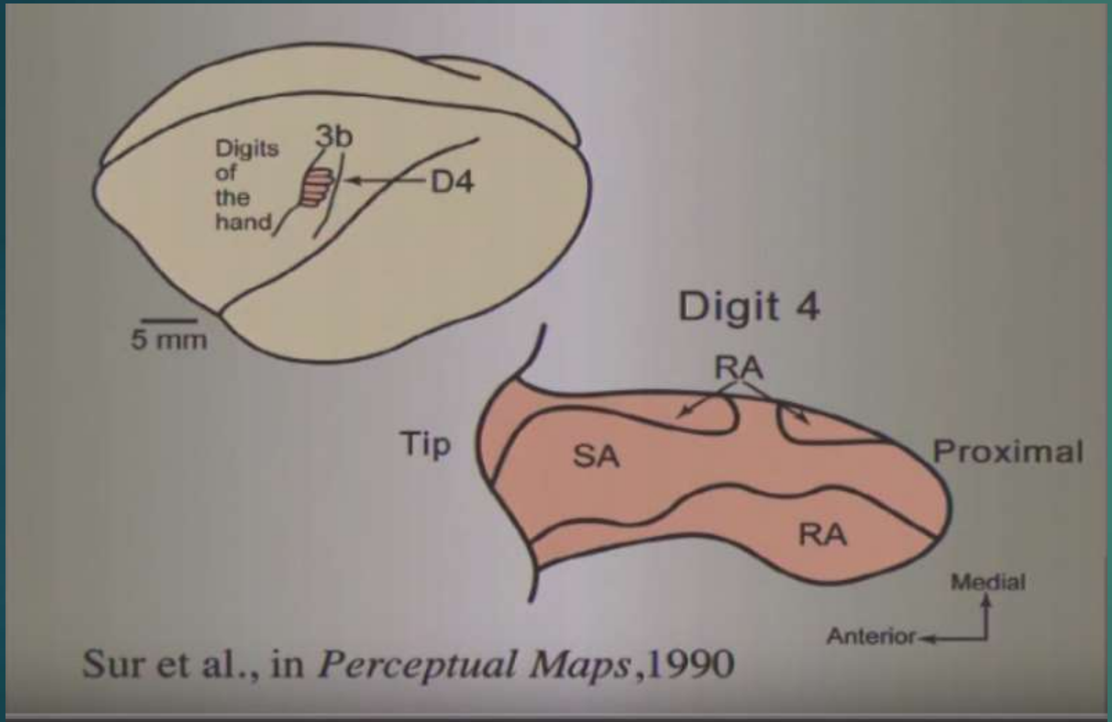
Typical primate brain modules

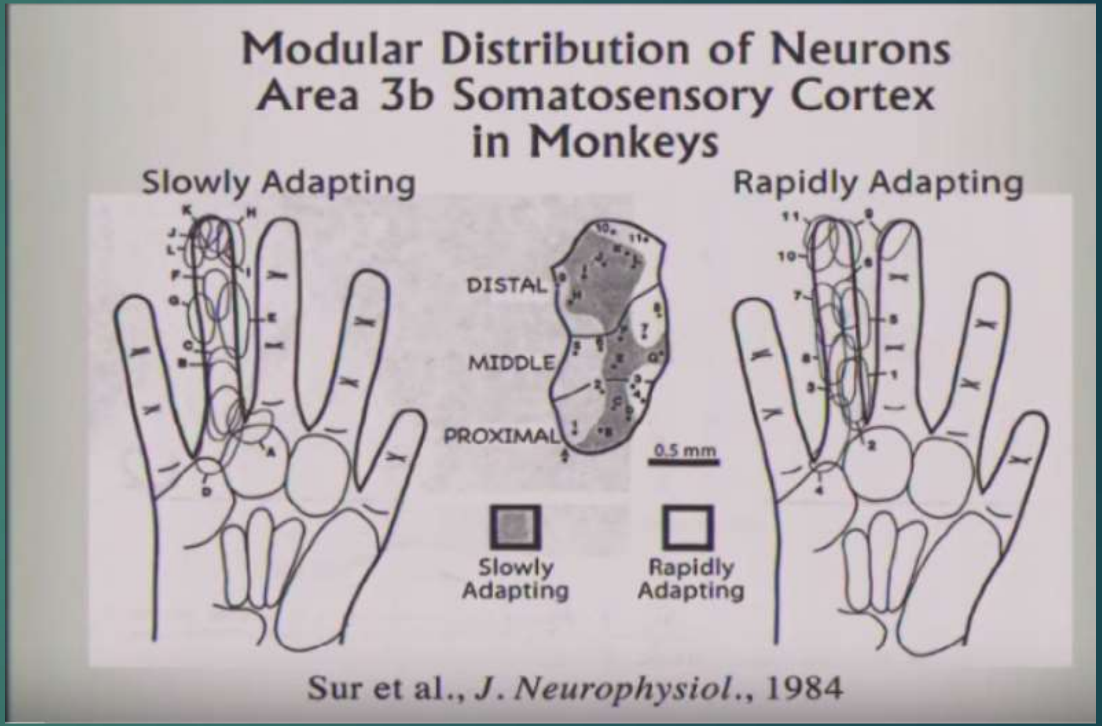




Often <u>regions/modules begin as innate, ecologically relevant behaviors</u>; <u>highly conserved; very important behaviors</u>, i.e. sucking, grasping, reaching; Organized in same way and in same areas; <u>can then be impacted by experience, learning, training</u>

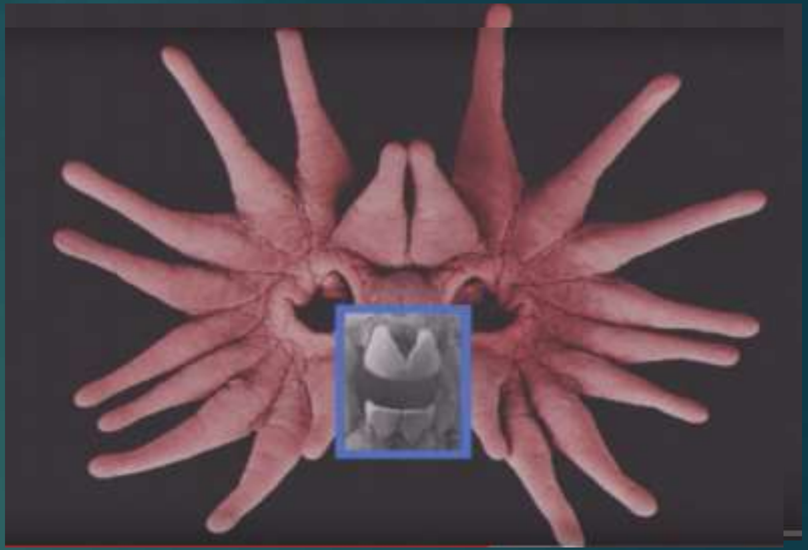
Classic brain modules:
Somatosensory cortex – digit representation of monkey & human hand





Size of digit representation dependent on peripheral reception & environmental experience; Based on differences in their response to inputs

Invertebrate eating semiaquatic Alien

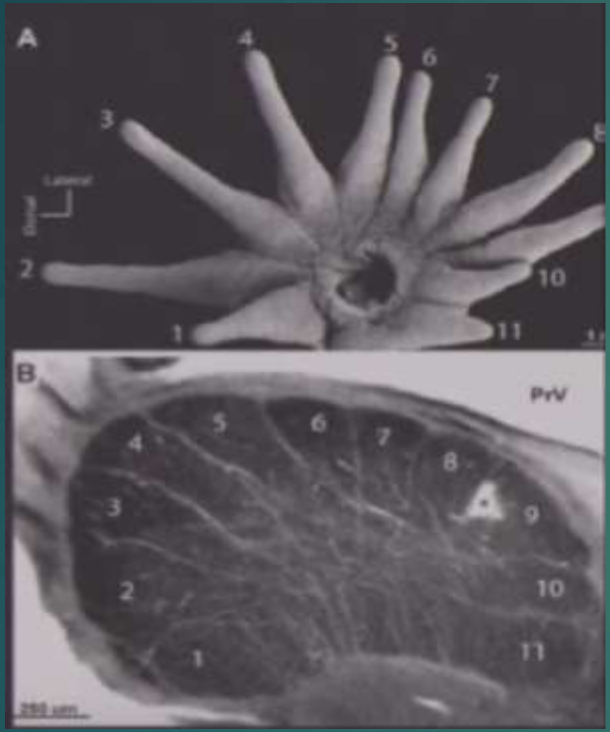


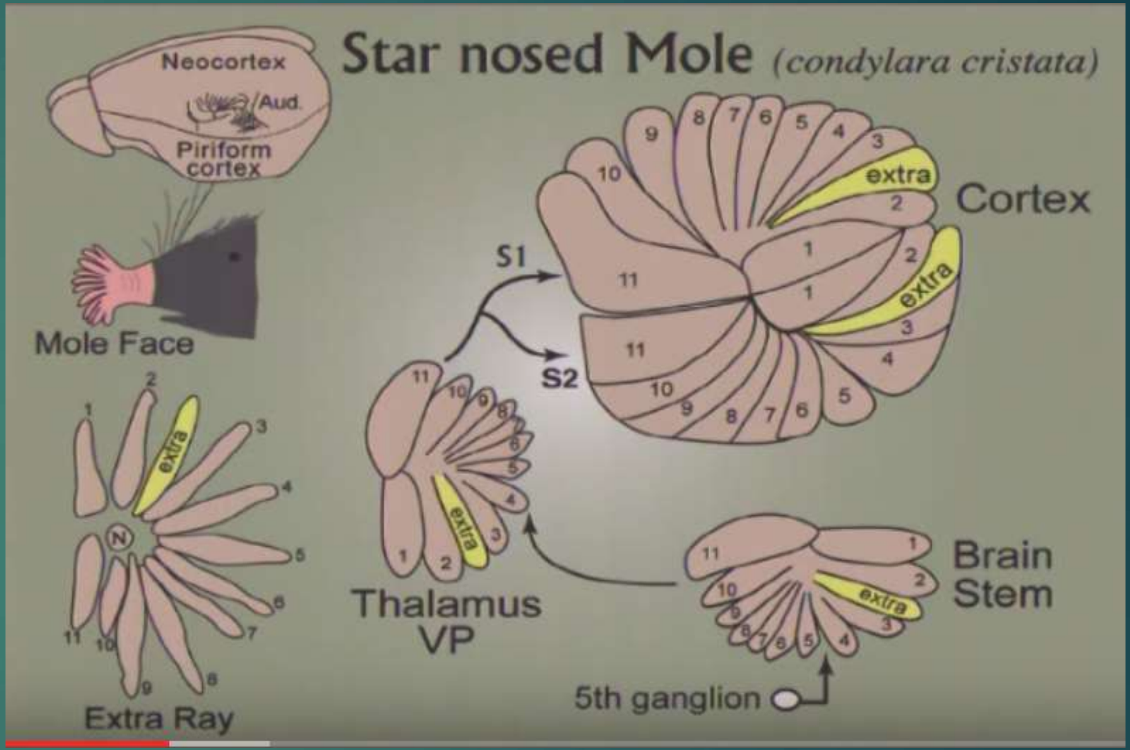
1 cm Somatosensory/Touch organ:
100,000 mylenated afferents
Human hand : only 17,000

Creation Magazine states that, just like human eye, it could not have evolved by natural selection

Guinness World Records, 2006: fastest food forager = 230 ms (8ms to tell if sg is edible)

Somatosensory representation for star nosed mole:
periphery or skin instructs the brain





Or in rats: each whisker has its own small module with representation;
always matched perfectly for peripheral number (rays in mole or whiskers in rat)
Environmental activity instructs cortex on what to build

Digit representation in macaque monkey; areas are highly segregated

If lose fingers (sensory loss), physical subdivisions stay same for life, but face can replace innervations

Blind use visual areas of brain for tactile processing

- Congenitally blind reading Braille: activation of primary visual area from tactile sensation = radical reorganization of brain

- Tactile processing pathways usually linked in the secondary somatosensory area are rerouted in blind subjects to the ventral occipital cortical regions originally reserved for visual shape discrimination.

- Used TMS to prove causal link.

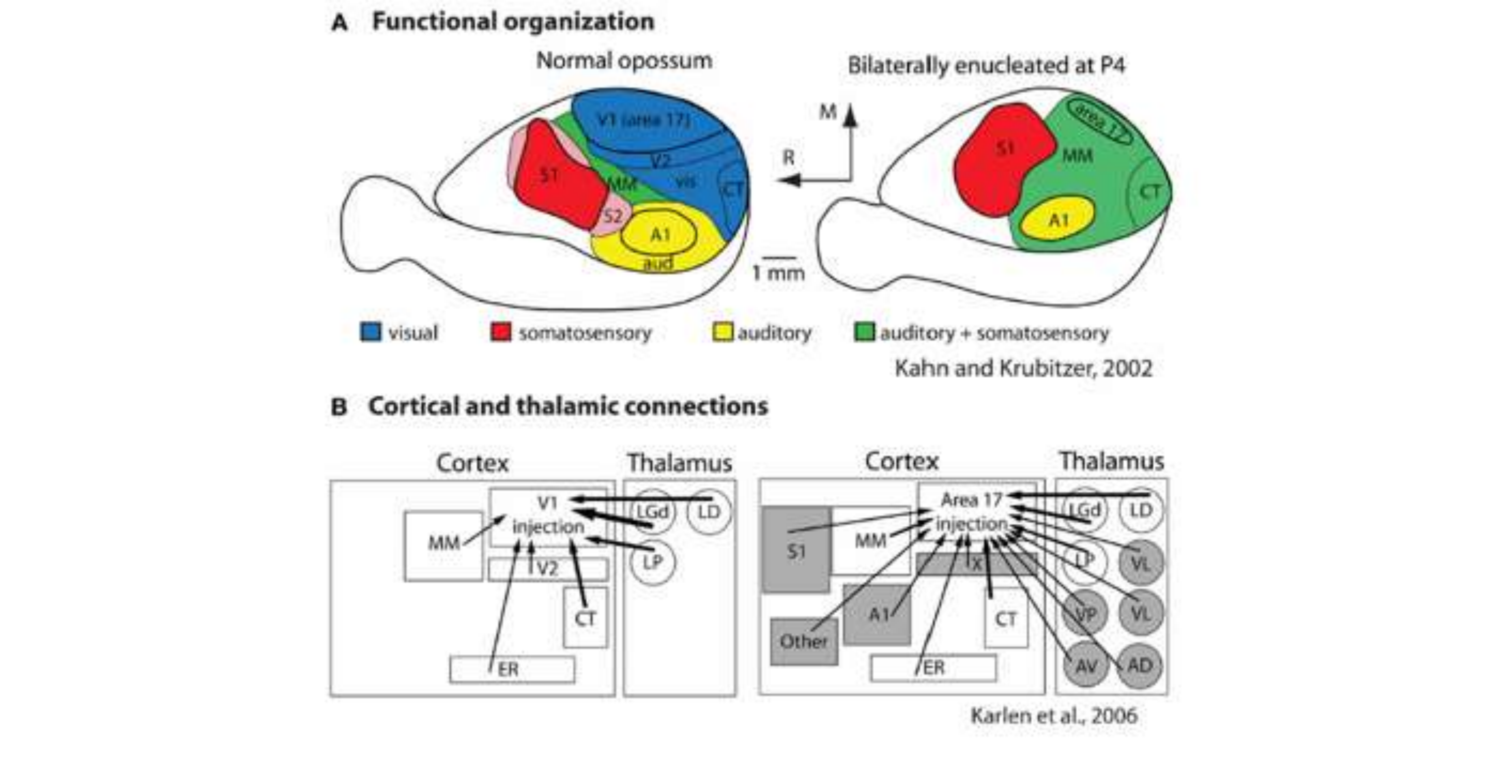
•N Sadato, A Pascual-Leone, et al., 1998

Brain fills in holes: Finger removal & arm deafferentation

- Michael Merzenich, UCSF, 1984:
- Microelectrodes to map sensory cortex:
  - mapped hand in monkey, removed a finger;
  - months later, brain map for missing finger was gone & replaced by maps for 2 adjacent fingers
- First evidence of brain reorganization: neuroplasticity

- Tim Pons, 1991: first proof that neurons in face map invaded area of missing arm map; 14 mm of arm map reorganized to process sensory input from face
- Lead to Ramachandran's 1992 work on phantom limbs: brain hallucinates a missing limb

If you remove inputs in V1 (blind opossum), major brain changes



<u>**Alterations in the functional organization (A) and connectivity (B) in bilaterally enucleated opossums**</u>**.**
In normal animals (left) much of cortex is devoted to visual processing. <u>With early & complete loss of vision (right) all of what would normally develop into visual cortex is taken over by the spared sensory systems</u>. This functional reorganization is accompanied by alterations in thalamocortical and corticocortical connections **(B)**.

Modified from Kahn and Krubitzer(2002) **(A)**; Karlen etal.(2006) **(B)**.

Sensory representation:
Mouse - whiskers & Duck billed platypus - bill

Your environmental world is reflected in your cortical sensory representation.

60-70% of cortex devoted to processing the bill

Somatosensory maps: Whiskers in a rat

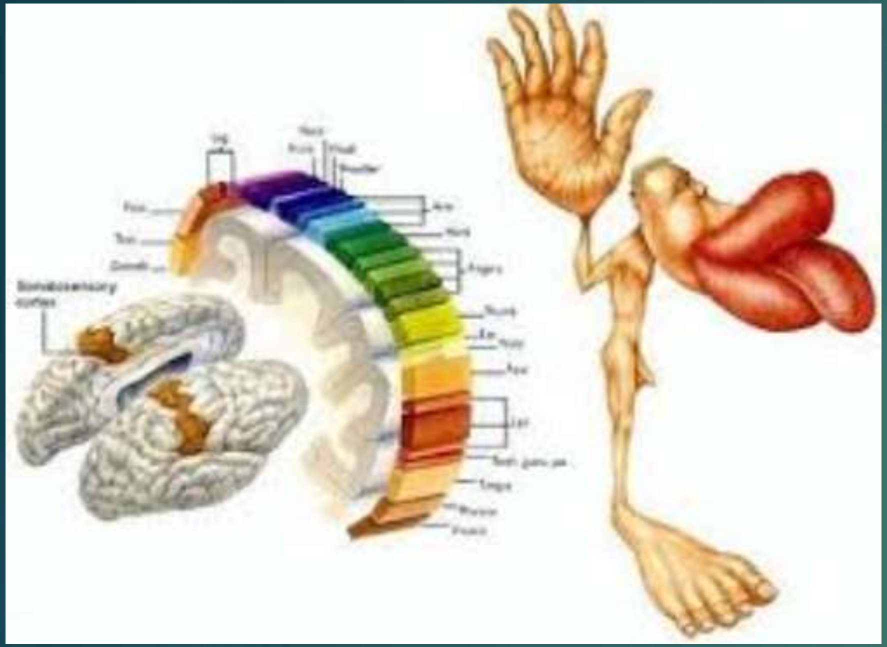
Head

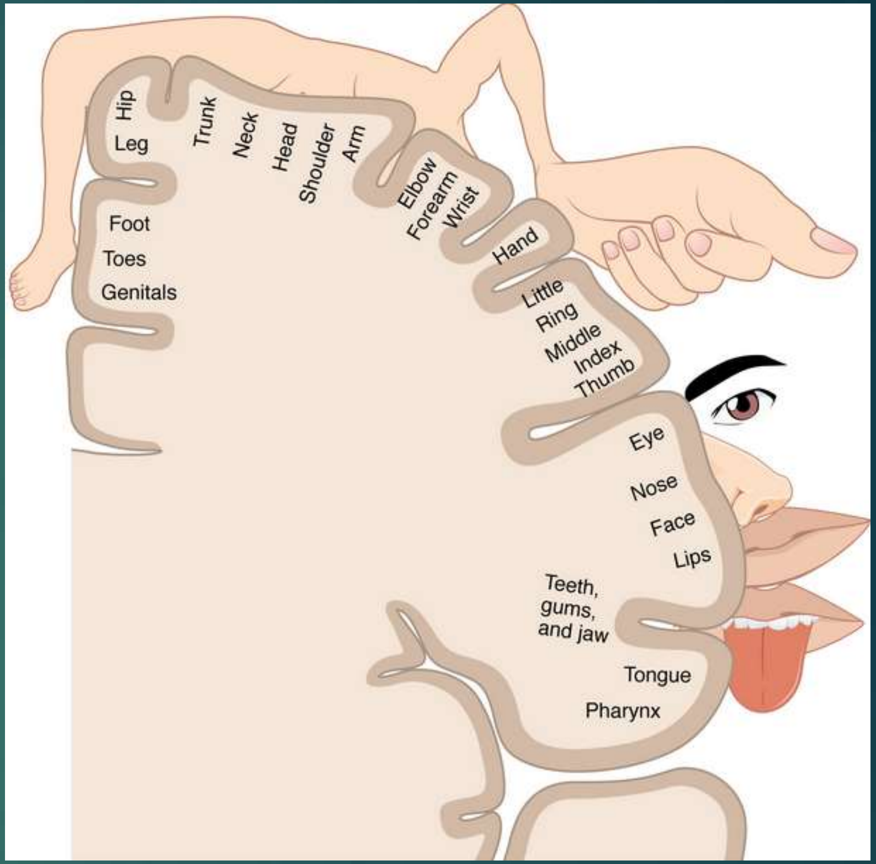
Hand

Rat whiskers representation

1 spot per whisker

Sensorimotor representation in human brain (& star nosed mole)



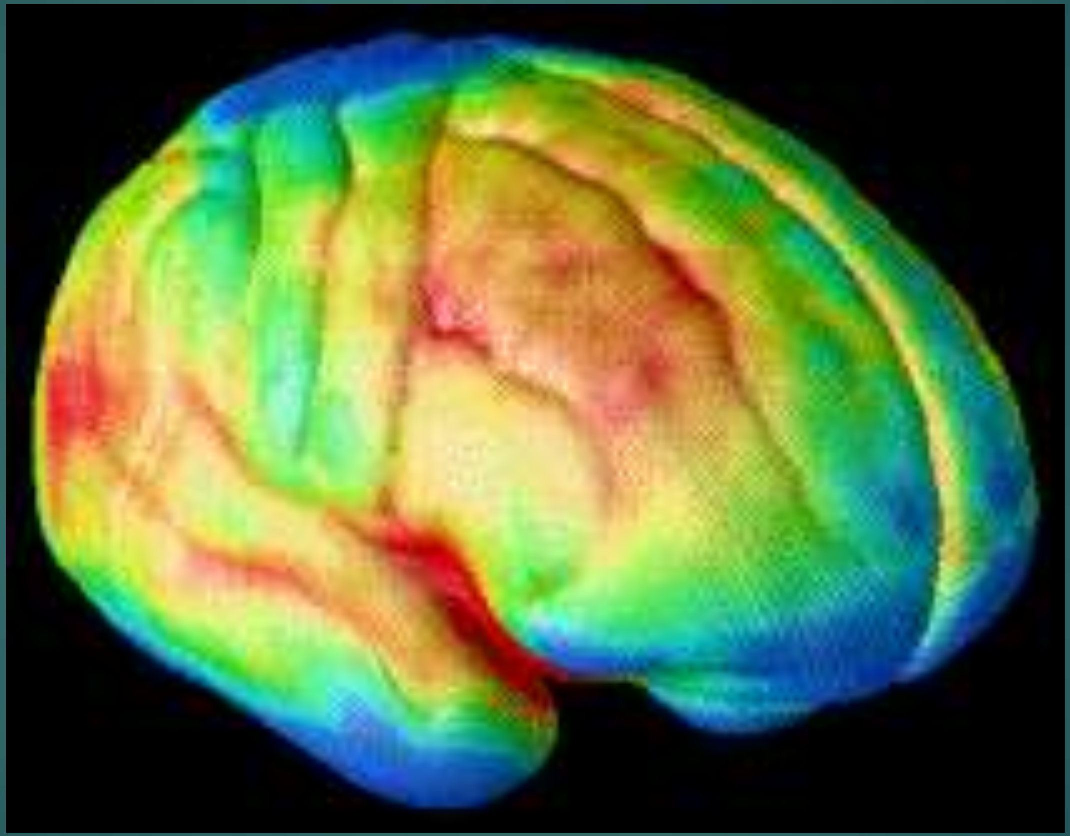


All primates have discrete sensorimotor representation areas in frontal cortex. Humans have 8 separate maps (cortex, cerebellum, inferior olive; parietal has multimodal maps)

Mapped by using microelectrodes for 1/50th of a second to trigger specific area movement

Great Adolescent Pruning: Age 5-21:

Effect of environment and experience on brain



Infant primates may have up to twice the adult number of neurons. Circuits are sculpted from the brain by pruning away cells and synapses.

Mechanisms: Programmed cell death (apoptosis), passive loss due to lack of stimulation, learning

Posterior parietal cortex: Another major shift of function

- In primates, PPC involved in visuo-spatial perception and spatial attention and behaviors like grasping and reaching.

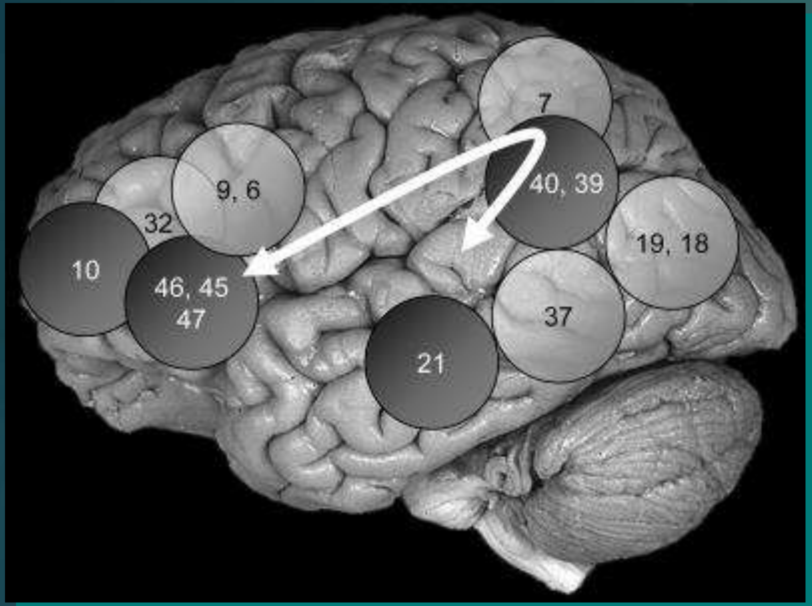
- In humans, PP involved in much broader cognitive abilities: attentional control, spatial working memory, long-term memory, ranking of topographic signals, motor plans for limb movements, relational learning, episodic memory, abstract spatial representation, numerosity, categorization, decision-making, planning, cognitive control, reward expectation, rules, categories, associations, DMN.

Christos Constantinidis, et al., 2013

Posterior Parietal

- Dorsal areas of the parietal cortex, including the superior parietal lobule (SPL) are involved in top-down attentional orienting (focus on book), while
- Ventral regions including the temporo-parietal junction (TPJ) are involved in bottom-up attentional orienting (truck horn outside).
- Fronto-parietal network: The dorsolateral prefrontal cortex (PFC) and posterior parietal cortex (PPC) are two parts of a broader brain network involved in the control of cognitive functions such as working-memory, spatial attention, and decision-making

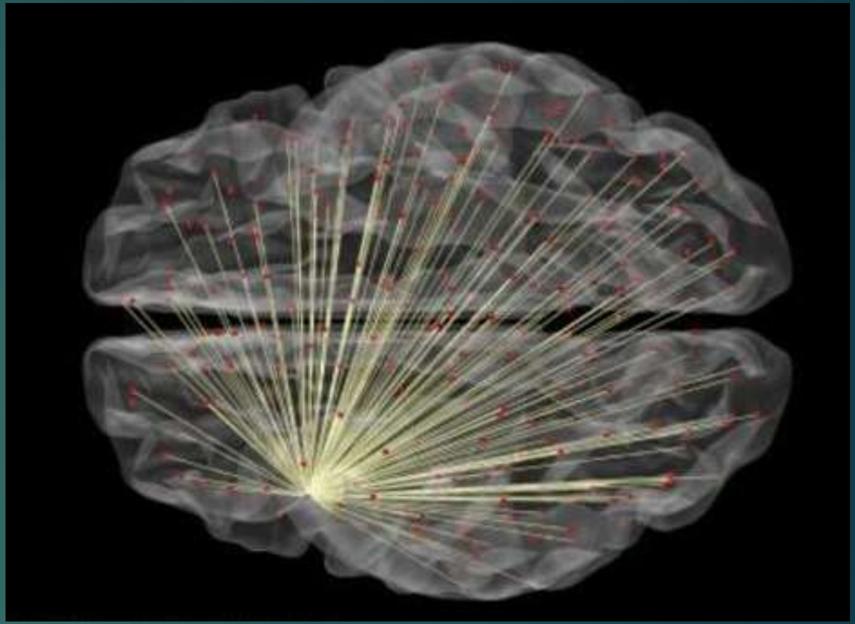
P-FIT: Parieto-Frontal Integration Theory: Biological basis of IQ



Dark Grey: Left Hem

Light Grey: Right Hem

Arcuate Fasiculus: connector



Their Parieto-Frontal Integration Theory (P-FIT) identifies a brain network related to intelligence, one that primarily involves areas in the frontal and the parietal lobes:

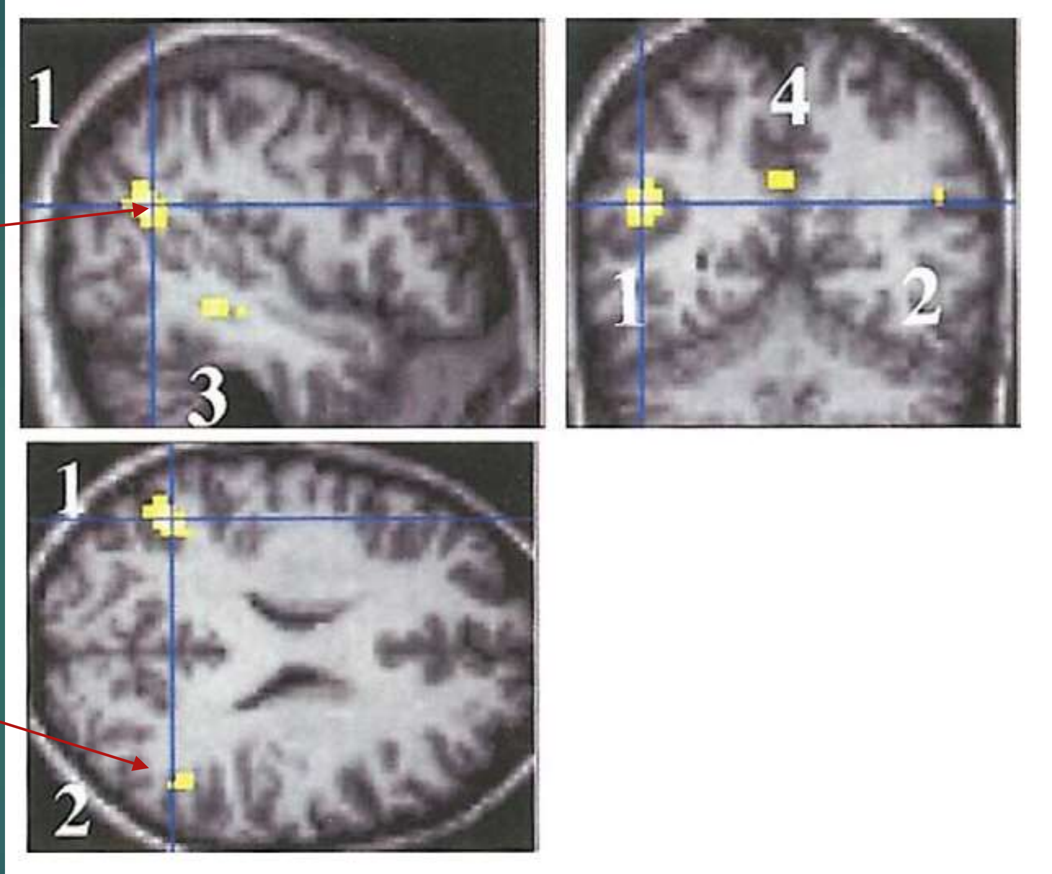
High intelligence probably requires *undisrupted information transfer among the involved brain regions along white matter fibers*

10% of Fluid IQ: Connectivity to Left DLPFC: goal monitoring

rTPJ: Reading Thoughts, Theory of Mind

left TPJ
verbal

rTPJ
pictures



Reading stories that describe or imply a <u>character's goals and beliefs</u>

Theory of mind vs. mechanical inference stories. Crosshair marks the most significant voxel in the left TPJ

Saxe & Kanwisher, 2003

Temporal Parietal Junction (bilateral VPC):
Theory of Mind (think about what others are thinking)

"I know you think you understand what you thought I said, but I don't think you realize that what you heard is not what I meant."

rTPJ is critical for representing mental state information, irrespective of whether it is about oneself or others.

Lower RTPJ activation: harsh, outcome-based judgments of accidents
(e.g., she *poisoned* her friend; deliberate murder)
Higher RTPJ activation: more lenient belief-based judgments
(e.g., she *thought* the poison was sugar; accident)

RTPJ allows a person to *identify* harmful actions as being either deliberate or inadvertent.

AutismSD: atypical, only outcome-based moral judgments, blame even for accidental outcome

Psychopaths: more likely to "forgive" accidental harms; blunted response to harmful outcome

Functions of the Precuneus

- Precuneus is major evolutionary advance of Homo sapiens
- Right - Control of spatial aspects of motor behavior; execution of spatially guided behavior
- Shifting spatial attention/tracking of different targets in space and between different object features, and in motor imagery tasks
- Visually goal-directed hand movements (optic ataxia)
- Mental imagery (visual rotation, deductive reasoning, music processing; visual reality)
- Episodic memory retrieval; R - regeneration of contextual autobiographic memory

Precuneus (& ACC) & Self Perception/Processing

- Precuneus: neural network supporting the mental representation of the self.
- Personal identity and past personal experiences
- Self versus non-self representation:
  - self-referential judgments,
  - first- versus third-person perspective taking,
  - perceived agency
  - mind reading/social cognition (TOM - judgments requiring empathy)
  - Description of your own personality traits and physical appearance
- Part of the DMN: All of these structures show high activity during rest, mind wandering, and conditions of stimulus-independent thought

Prefrontal Cortex

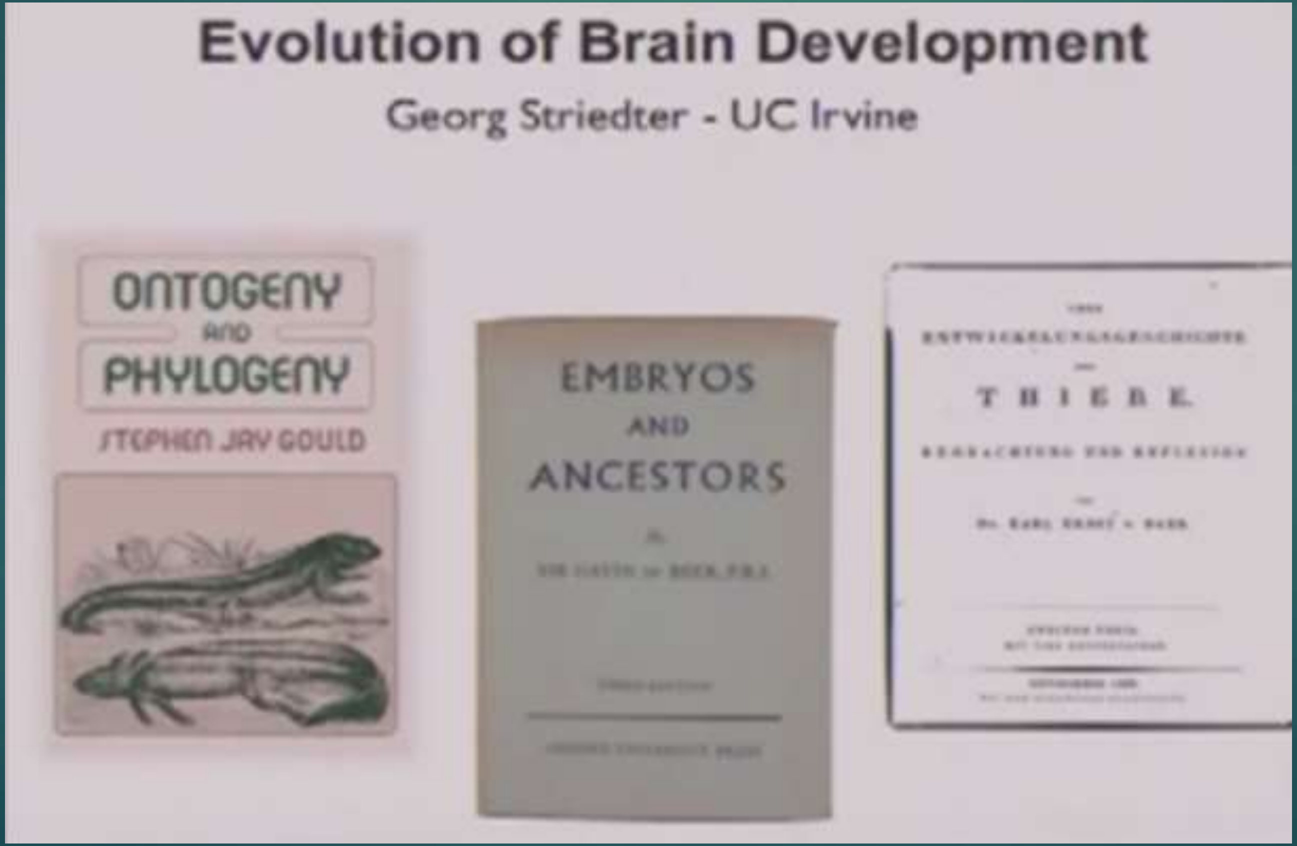
- The prefrontal cortex (PFC) has traditionally been viewed as the brain area associated with higher cognitive operations and executive function: working-memory, perceptual decisions, abstract rules, reward expectation, associative learning, categories, numerical quantities, planning of sequences of actions, memory retrieval strategies.

- PPC & PFC co-activated in a range of cognitive operations requiring attention and working-memory.

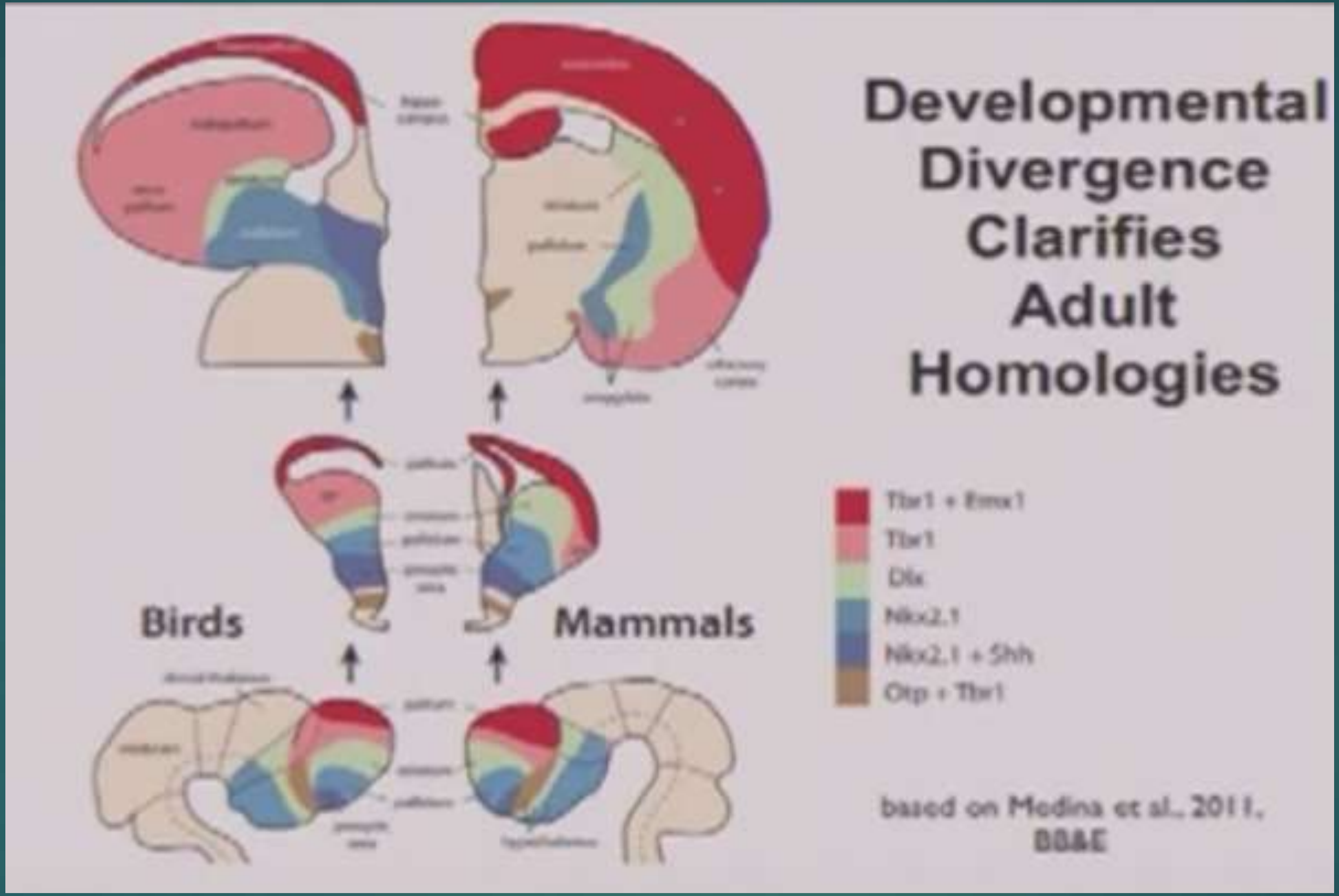
- Inactivation of the PFC causes more severe impairments in a wider range of attention, working-memory and motor functions. The PFC is able to resist interference by distracting stimuli during working-memory.

Evo-devo of Brain Development

- Not only has final product (adult human brain) evolved, but the process of brain development has evolved.



Evo-devo neurobiology:
Developmental differences produce adult homologies



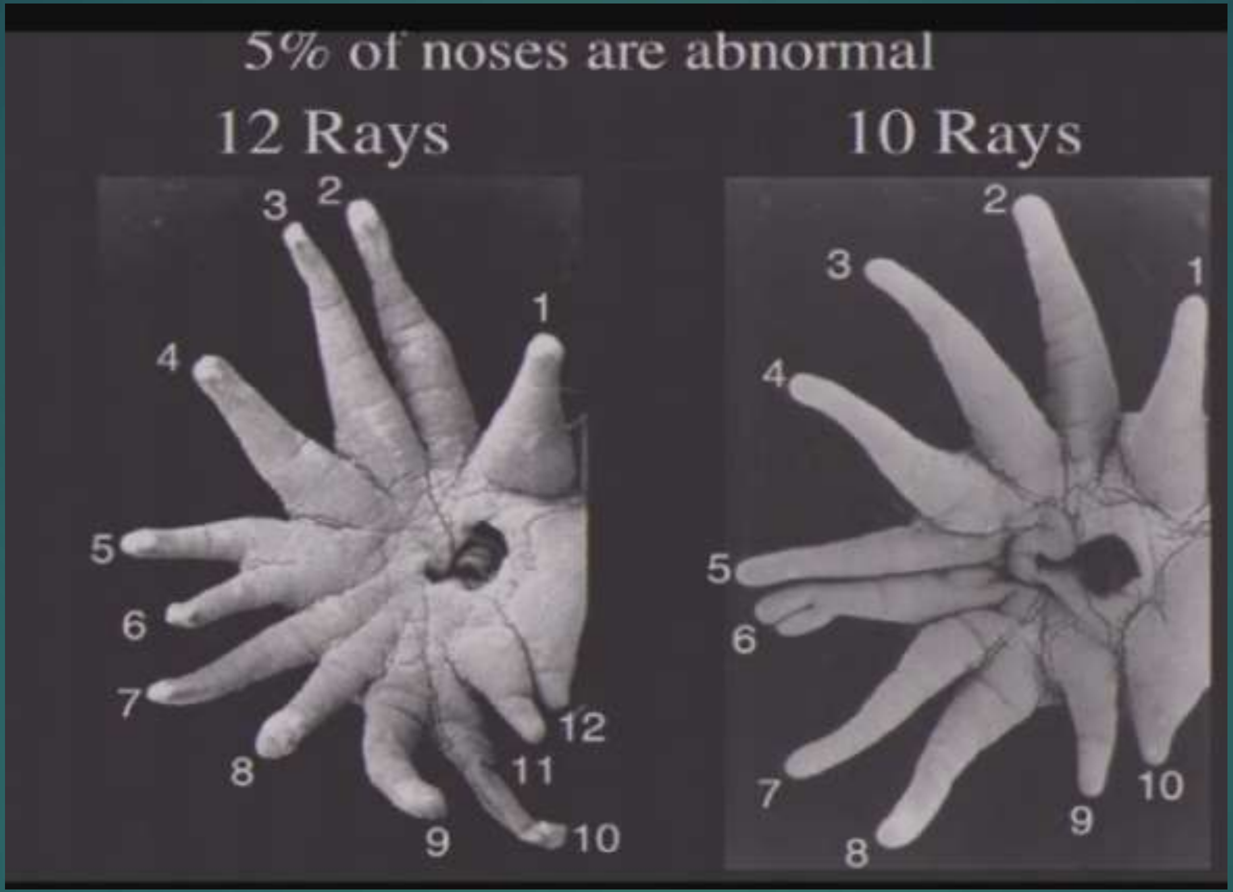
Young embryos look very similar; even subdivisions of forebrain, in size and position; but in development, pallium in birds and cortex in mammals (red) diverge, with enlargement in latter life; ventral pallium (pink)in birds increases;

Homology: existence of shared ancestry between a pair of structures, or genes, in different species.

Evolution is a tinkerer

- Linden: "In evolution, you never build something new if you can adapt something you've already got. It's the ultimate tinkerer and the ultimate cheapskate."
- Brain is not a well-designed machine, but a terrific set of compromises.
- Our brain has been put together with parts from jellyfish and lizards and mice.
- Messages on a telephone wire move a million times faster.
- Gene duplication is method of change; duplicate can change function while leaving original gene for original purpose

Tinkering: 5% of star nosed moles don't have 11 appendages



Cerebral Rubicon

- When hominid brains became more human than ape (650cc??)
- Relation of cranial capacity and brain size in endocasts
- Encephalization quotient (brain vs body size)
- Increased cranial capacity variation in Home erectus

Great Ape Cognitive Capacity: Understanding physical causality

- An important facet of physical cognition is the ability to quantify objects in one's environment.

- Monkeys, apes, and humans share a system for adding as well as subtracting quantities.

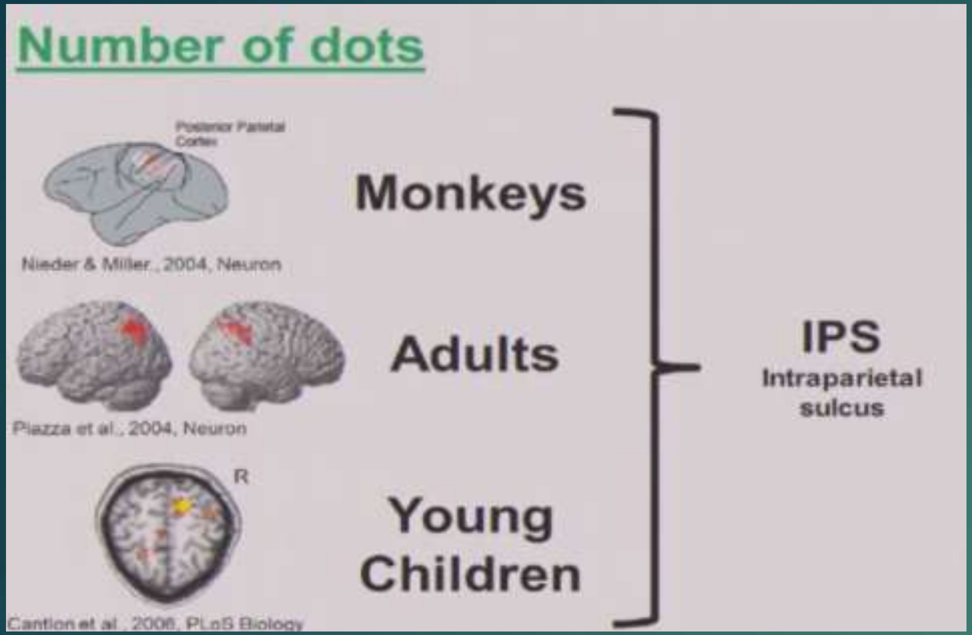
- No significant qualitative differences between chimpanzees' and monkeys' understanding of the non-verbal aspects of number or of unobservable physical causes.

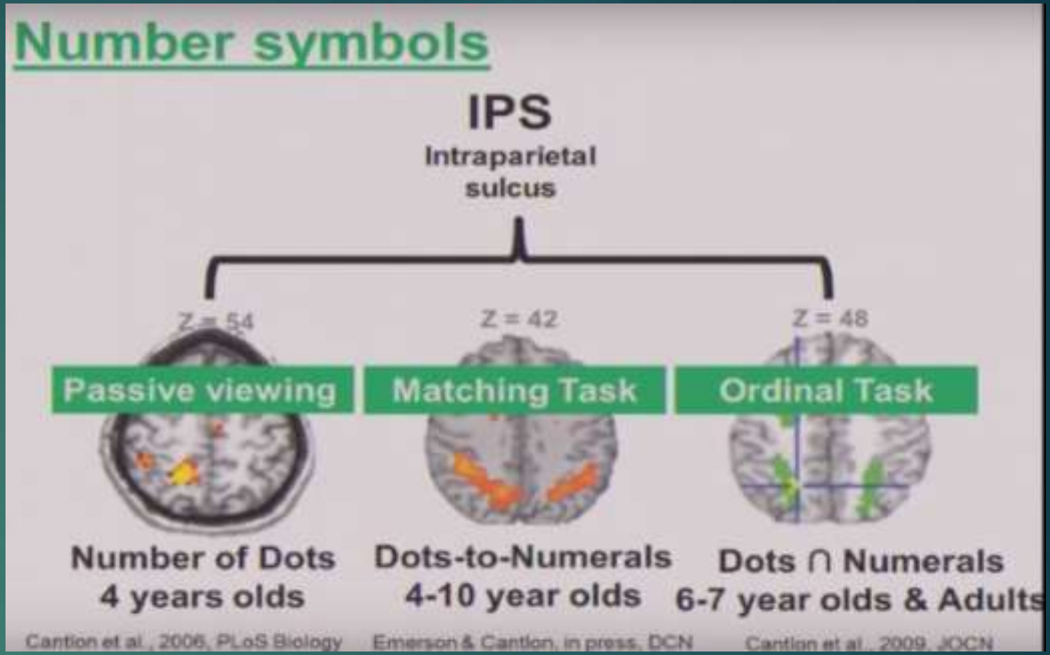
- Exemplified by tool use; great apes' understanding of simple mechanics may not differ substantially from that of monkeys

Old neural system for numbers

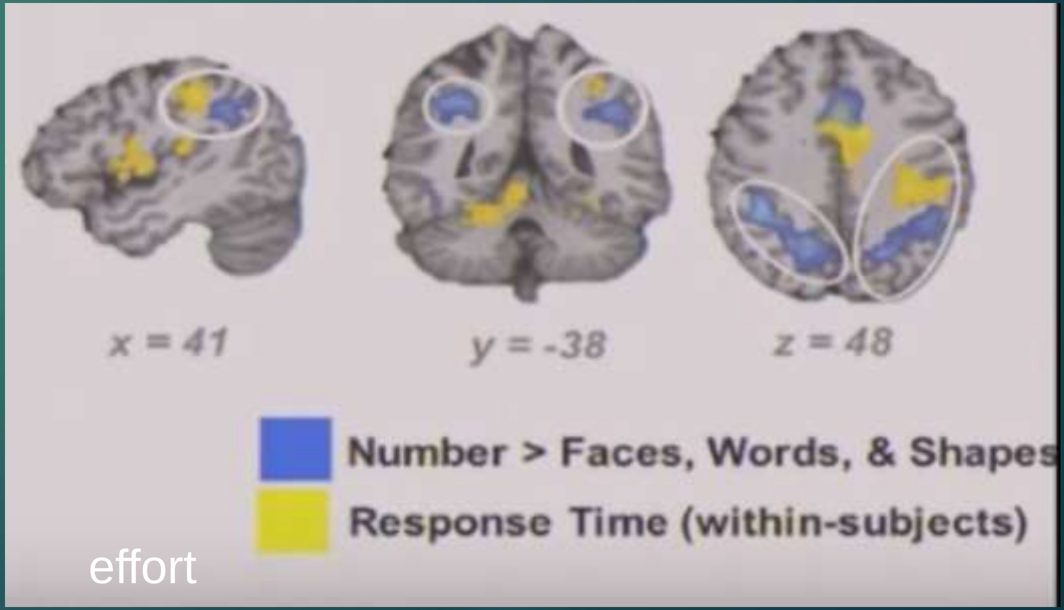
- Is arithmetic primitive? Adding/subtracting; used pointing to nonverbal objects in screen movies;
  - monkeys successfully added and subtracted
  - show same strategies as humans (easier to add same numbers (3+3); harder to add larger numbers (5+8); but not better if practice similar problem (may need symbols for this))
- Primitive homologous abilities in primates: number representation, number comparison, basic arithmetic (addition & subtraction)
- Children with better analog numerical abilities have higher math IQ
- Activated area: Intraparietal Sulcus

5+1	10-8
5+3	11-5
6+2	12-10
7+1	12-4
	12-8
	14-6





<u>Intraparietal sulcus involved in all number counting & all numerical symbolic processing</u>; Not a general effect of difficulty or effort; <u>Only IPS activation related to math test scores</u>



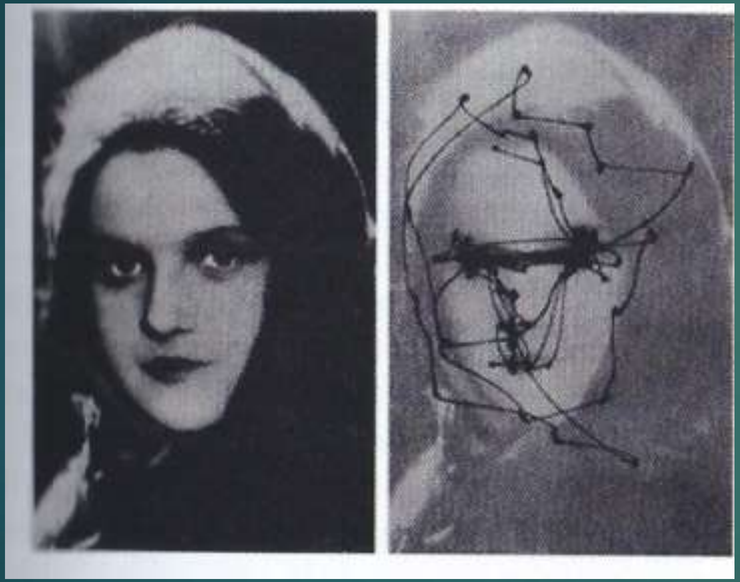
IPS is numerical processing center – conserved analog quantity processor

Cognitive skills that appear to be unique to great apes

- Self-awareness: mirror self-recognition in great apes; monkeys continue to display social behaviors toward their mirror image; most gorillas fail to recognize their mirror image

- Gaze following: Great apes are acutely sensitive to the direction of others' gaze.
  - Important for the location of objects such as food and predators.
  - In social settings, a great deal of information is communicated by means of following other individuals' gaze to specific individuals or to call attention to specific events.
  - Monkeys don't. Chimpanzees use the direction of gaze to reason about the intentions of conspecifics

Eye Gaze:
Significant key to social interactions



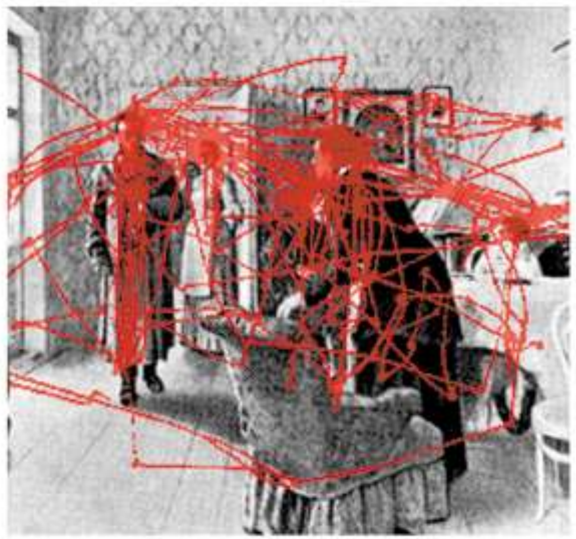


Fig. 1. Eye movement scanpath (in red) of a person viewing a painting by Rein; note the tendency to fixate on the faces. Adapted from Yarbus (*Eye Movements and Vision*, Plenum, New York, 1967).

Human & Dog Eye Gaze

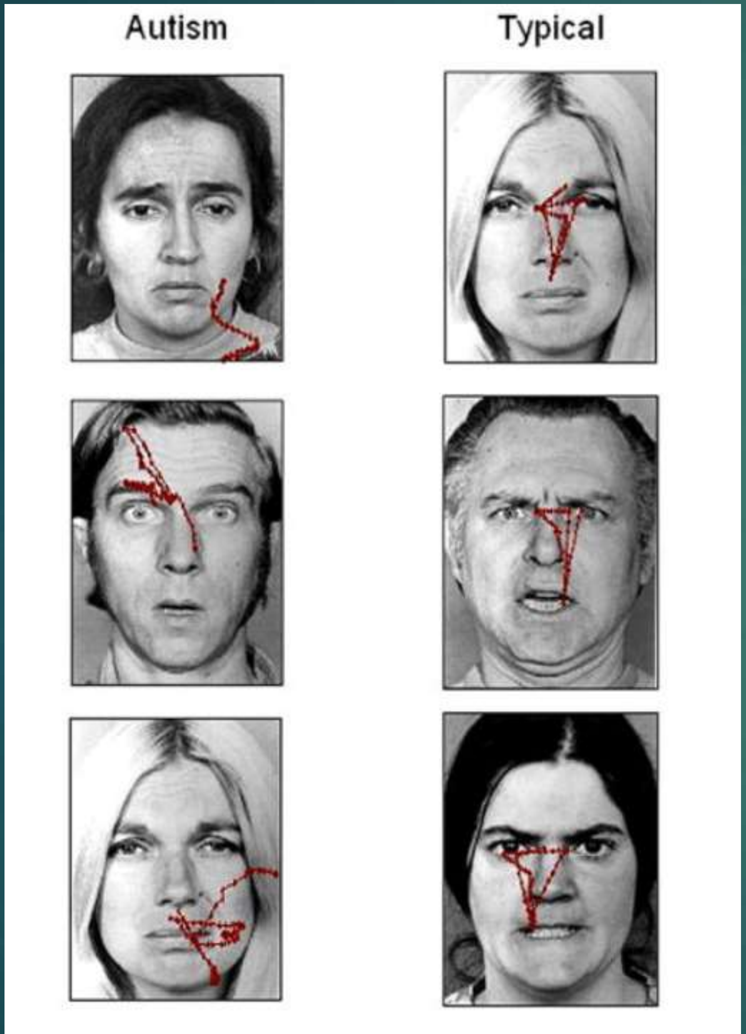
- Preverbal infants: Must first talk to them, then turn your head and they will follow your gaze

- Dogs too: Vocally address them “Hi dog”, then look them in eye; then they will follow your gaze

- Dog's gaze at its owner increases owner's urinary oxytocin during social interaction

E. Téglás, et al., 2012; Nagasawa, et al., 2008

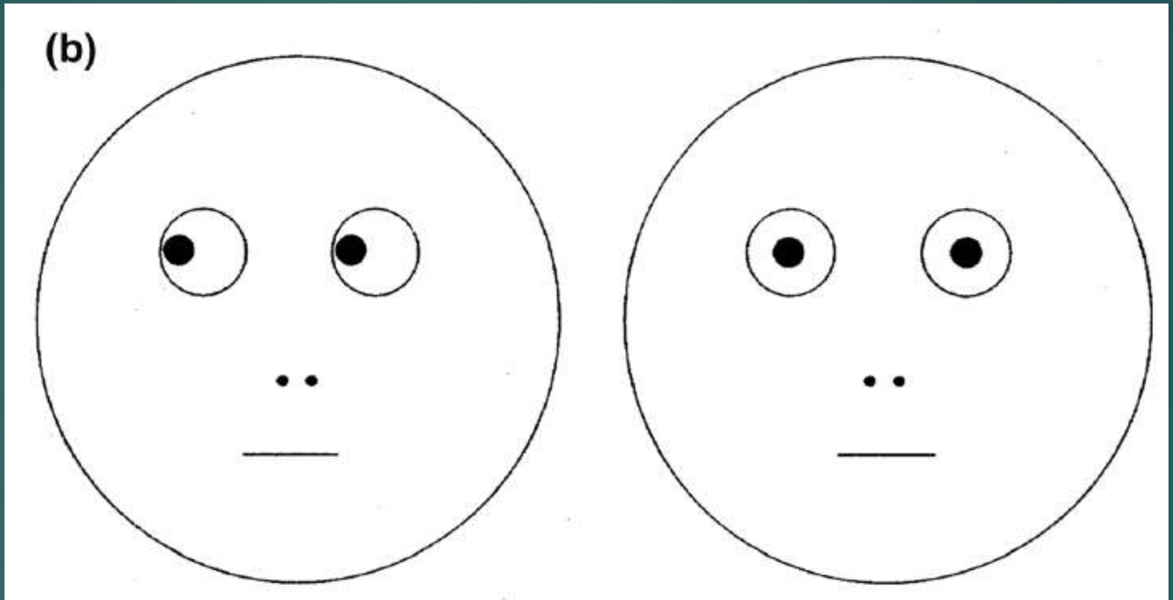
Autism: Deficit in social eye tracking



- Neurologically normal focus on the eyes, nose and mouth).
- Individuals with autism did not look at the eyes
- Using gaze information to infer mental states and intentions is consistently impaired even in high-functioning adults with autism

Pelphrey et al. (2002).

Autism: Able to perceive the direction of gaze



- When asked 'which one is looking at you?', autistic children score as well as normal children.

Autism: Can do gaze following, but not it's meaning

When asked which candy 'Charlie' prefers, most normal children point to the Polo Mints, but autistic children are less likely to do so.

Social tolerance & Executive functioning

- Great apes appear to be able to delay gratification longer than rhesus monkeys and may be more tolerant of conspecifics than monkeys.
- Tolerance appears to play a major role in the frequency and diversity of cooperative behaviors in chimpanzees and bonobos.
- Great apes' more sophisticated social and physical cognition skills rest in part on greater inhibitory control relative to monkeys – an executive function of the prefrontal cortex – which may allow them to better focus attention, in turn enhancing learning and memory

Evolution of human brain: Neocortex

- Since the last common ancestor, the lineage leading to *Homo sapiens* has undergone a substantial change in brain size and brain organization.

- Neocortex: defining feature of mammalian brain evolution, and its expansion becomes the pinnacle of human evolution

- Modern humans display striking differences from the living apes in the realm of cognition and linguistic expression.

Evolution of
the Prefrontal Cortex

Key to Function: Frontal Lobes are Well Connected!

- Frontal division recapitulates thalamic anatomy
  - One method for defining cortical regions relies on the thalamic projection system

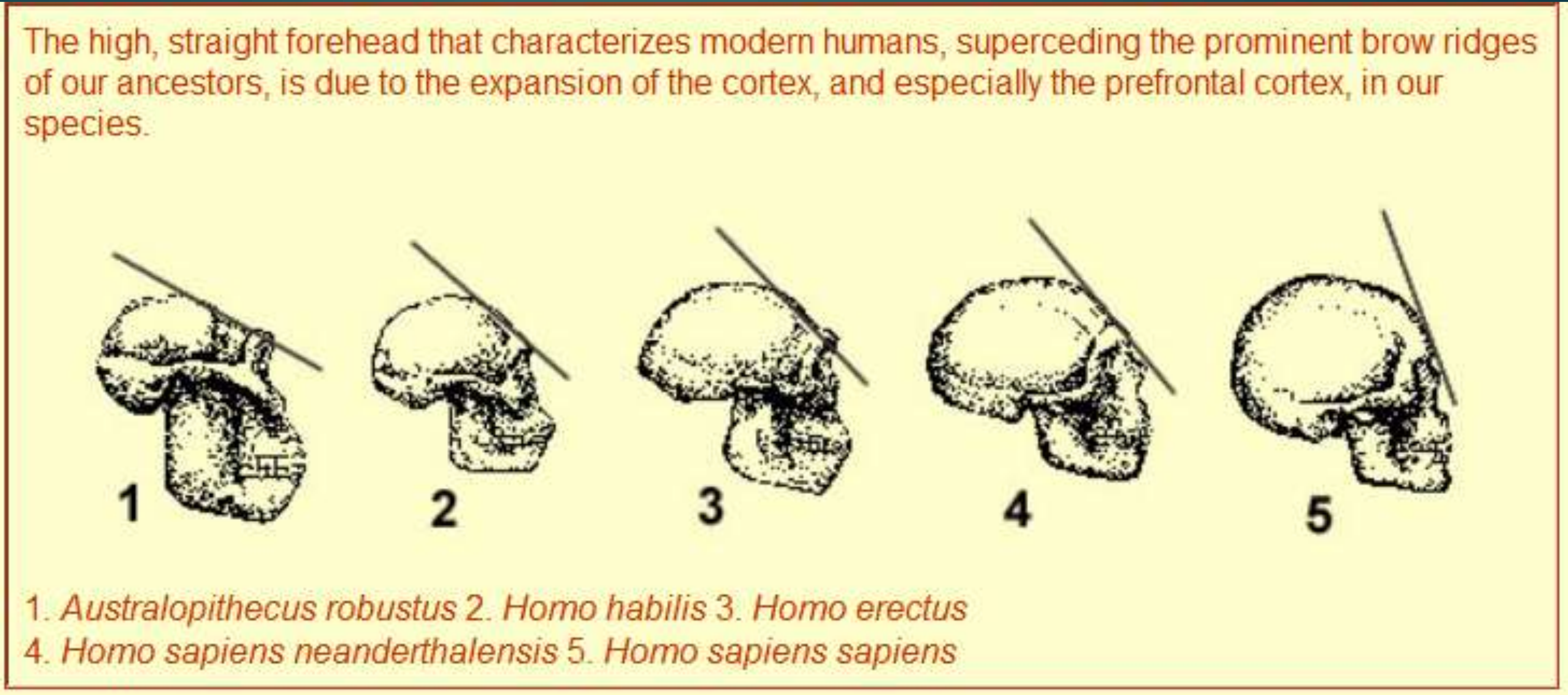
- Frontal “circuits” more important than frontal “regions”

- Frontal “systems” mediate activation states across the entire brain

Significant frontal-thalamic circuits

NUCLEUS	MAJOR INPUT	MAJOR OUTPUT	FUNCTIONS	FUNCTIONAL CLASS
Anterior	from mammillary body of the hypothalamus	cingulate gyrus of limbic lobe	mediates visceral, emotional information	specific, limbic
Ventral Anterior	globus pallidus, substantia nigra and intralaminar and midline thalamic nuclei	premotor and primary motor cortices	motor	specific motor
Ventro-lateral	Contralateral cerebellar hemisphere through superior cerebellar penduncle, globus pallidus	primary motor cortex	motor: coordinates basal ganglia with cerebellum	specific motor
Ventral Posterior (lateral and medial)	spinothalamic tracts and medial leminscus (medial=trigeminal nerve)	postcentral gyrus	somatosensory	specific, sensory
Lateral Geniculate	retinal ganglion cells	Lingual and cuneate gyri of the occipital lobes	vision	specific, sensory
Medial Geniculate	Inferior colliculus	auditory cortex	auditory	specific, sensory
Dorso-medial	Prefrontal cortex, substantia nigra, amygdala, hypothalamus	prefrontal cortex, amygdala	limbic	specific, limbic
Pulvinar	primary associational visual cortex	inferior parietal cortex (association cortex)	language formulation, language processing	specific, associational
Centromedian	globus pallidus, vestibular nucleus, superior colliculus, reticular formation, spinal cord, motor / premotor cortices	basal ganglia and thalamus	modulates excitability of cortex (cognitive) and overall functions of basal gaglia (sensorimotor)	non-specific
Reticular	thalamocortical projections	thalamic nuclei and reticular formation	integrates and regulates thalamic neuronal activity	non-specific

Forehead is the thing!



"Larger facial angles and more fully developed foreheads" were attributed to whites rather than blacks, and an increase in the facial angle was found when apes and humans were compared in the "natural chain of being" (Finger, 1994).

Frontal theory history

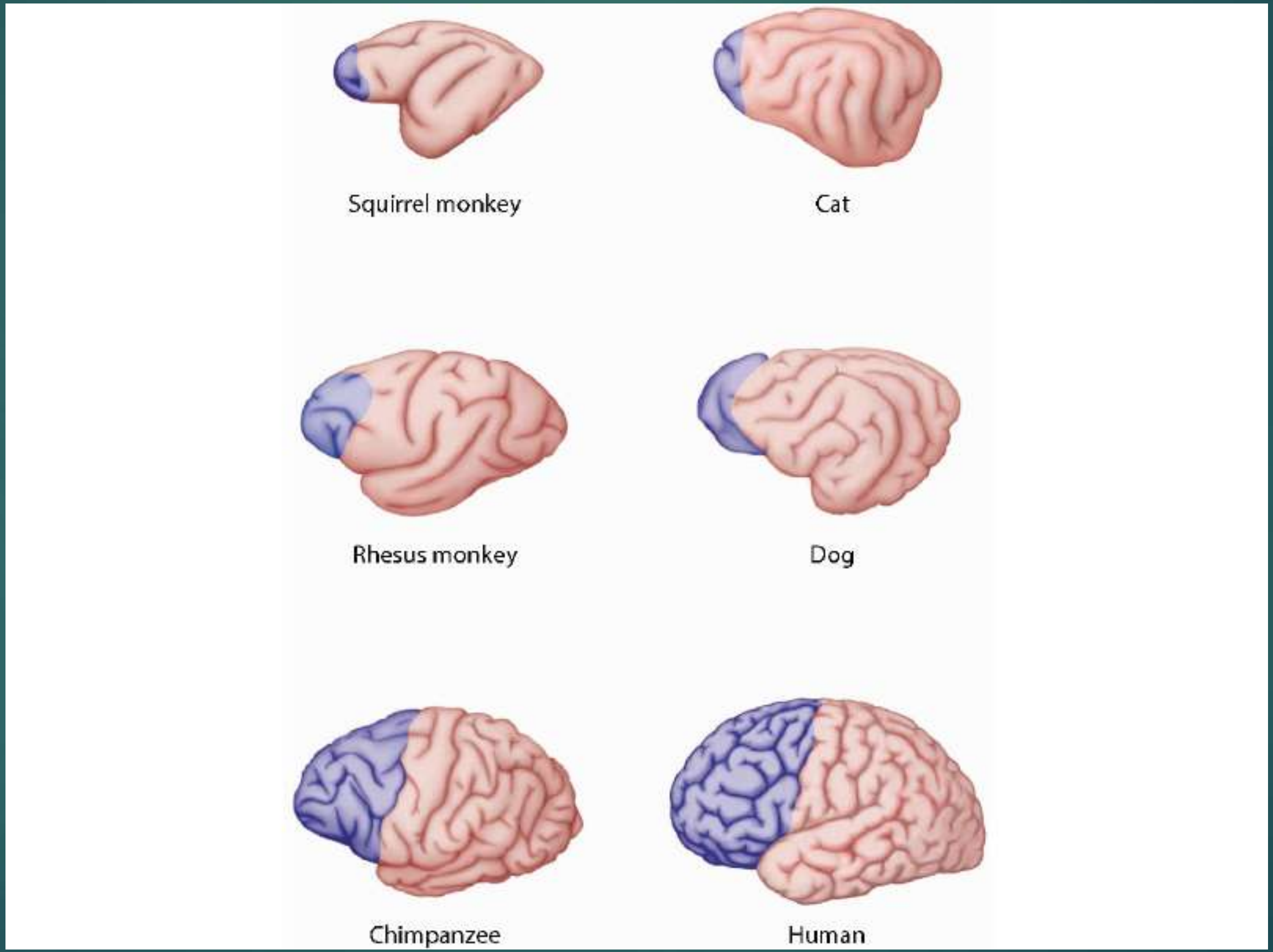
- Humans have tall, cliff like foreheads. Apes do not. Prefrontal cortex expansion
- Histological architecture of prefrontal region is conservative. Humans & macaques don't differ; but significant functional reorganization (language areas, EF, abstraction);
- Original support for PFC expansion in humans:
  - Deacon (1997) claimed that frontal lobe is 2 x bigger than expected for primate
  - No significant variation within humans in gyrification related to sex, body, brain size or cortical volume; but significant difference with other primates;

Frontal reorganization

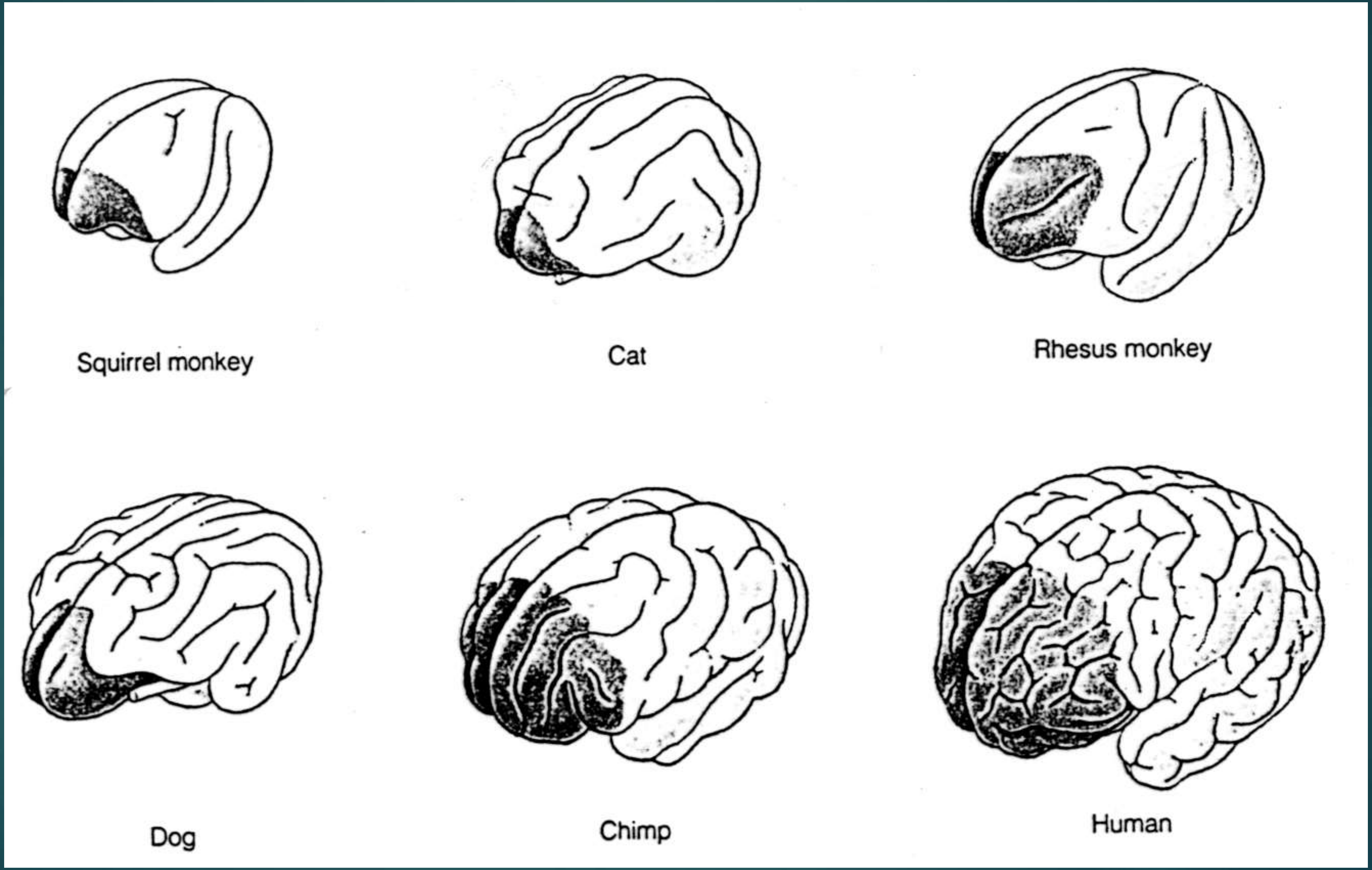
- Frontal lobe has been identified as a region that is noticeably enlarged and widened in Neandertals and modern humans compared to other hominins
- Primate frontal cortex hyperscales relative to the rest of the neocortex and brain. The total frontal lobe in humans is as large as expected for an ape of human size.
- Frontal pole region (area 10) is both absolutely & relatively larger than in other primates (6% larger than expected for an ape of human size)
- The whole prefrontal cortex is larger than expected by allometry for both grey and white matter

Semendeferi et al., 2002; Schoenemann et all. 2005

Older Comparative Anatomy of Frontal Lobes



Do you think Humans have lager frontal lobes than other primates?



Prefrontal Cortex in Humans and Primates

Primate frontal cortex hyperscales relative to neocortex and brain; human frontal cortex does not differ

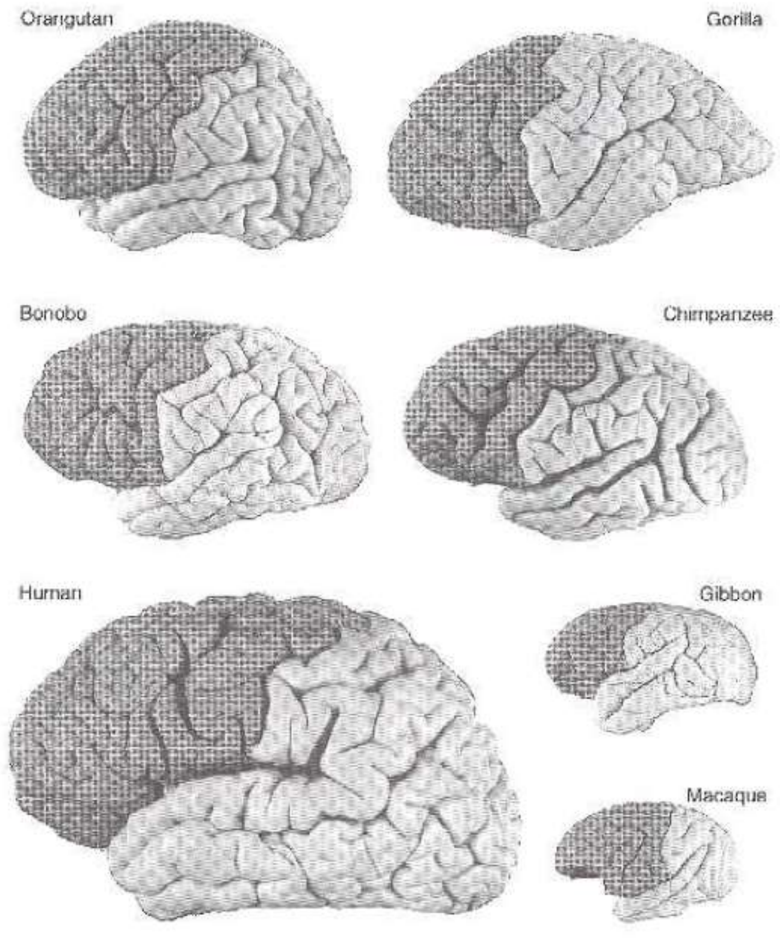


Figure 3.2 Photographs of the lateral view of the brain of all hominoids and the macaque. The frontal lobes are highlighted. The relative scale is only an approximation.

(Figure courtesy of K. Semendeferi, 1997)

Katerina Semendeferi: Total human prefrontal lobe is as large as expected for ape of human size

Humans and great apes share a large frontal cortex

K. Semendeferi[1], A. Lu[1], N. Schenker[1] and H. Damasio[2]

[1]*Department of Anthropology, University of California at San Diego, La Jolla, California 92093*

[2]*Department of Neurology, University of Iowa, Iowa City, Iowa 52242*

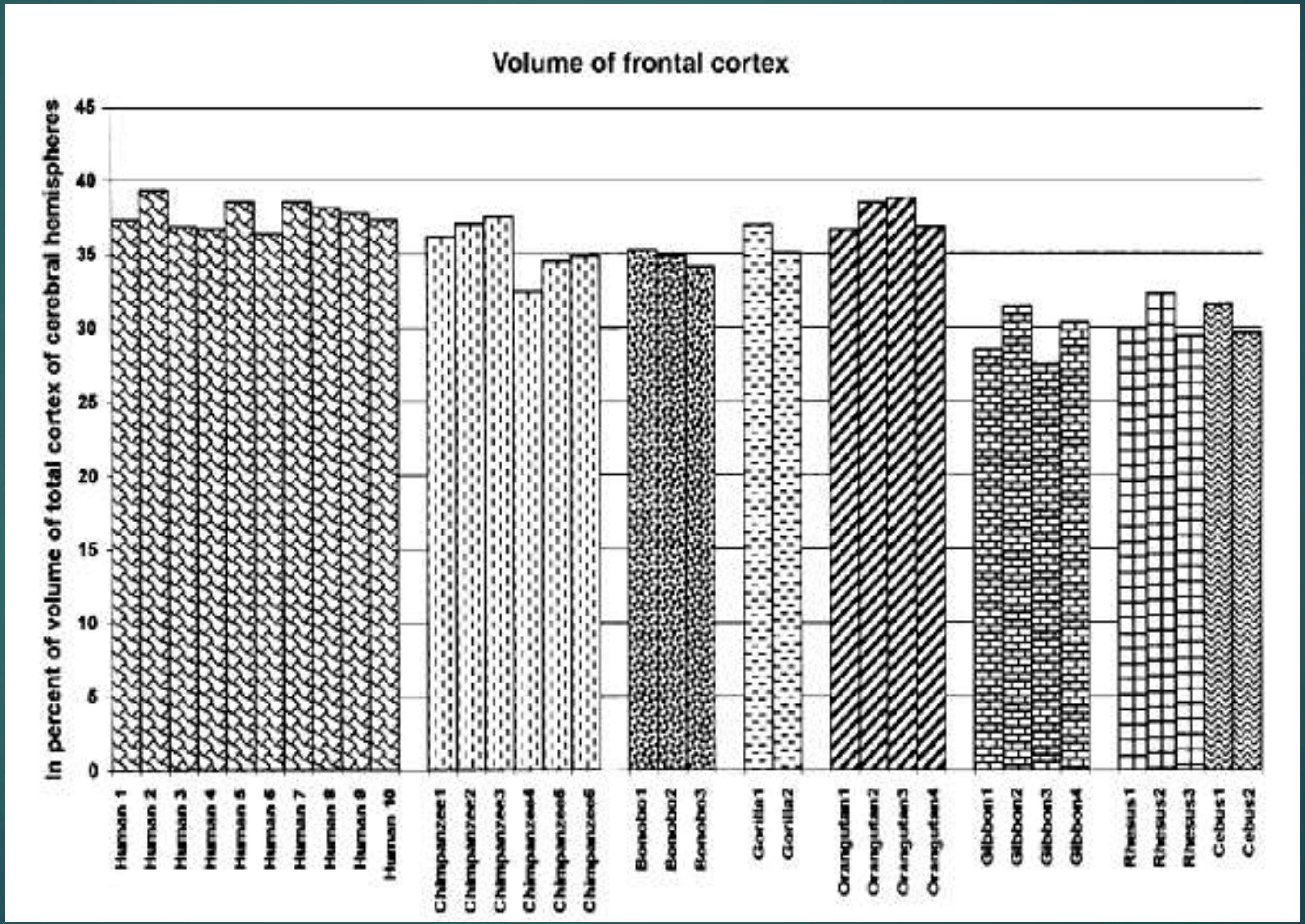
Correspondence should be addressed to K.S. (ksemende@ucsd.edu)

Published online: 19 February 2002, DOI: 10.1038/nn814

Some of the outstanding cognitive capabilities of humans are commonly attributed to a disproportionate enlargement of the human frontal lobe during evolution. This claim is based primarily on comparisons between the brains of humans and of other primates, to the exclusion of most great apes. We compared the relative size of the frontal cortices in living specimens of several primate species, including all extant hominoids, using magnetic resonance imaging. Human frontal cortices were not disproportionately large in comparison to those of the great apes. We suggest that the special cognitive abilities attributed to a frontal advantage may be due to differences in individual cortical areas and to a richer interconnectivity, none of which required an increase in the overall relative size of the frontal lobe during hominid evolution.

The Answer: All Primates have~ 34%

Human frontal cortex, though absolutely larger in humans, occupies same proportion of cortex as in nonhuman primates.



Semendeferi et al., Nature Neuroscience, 5, 272-6, 2002

Relative size of the frontal cortex in hominids: ~34%

Table 1. The relative size of the frontal cortex.

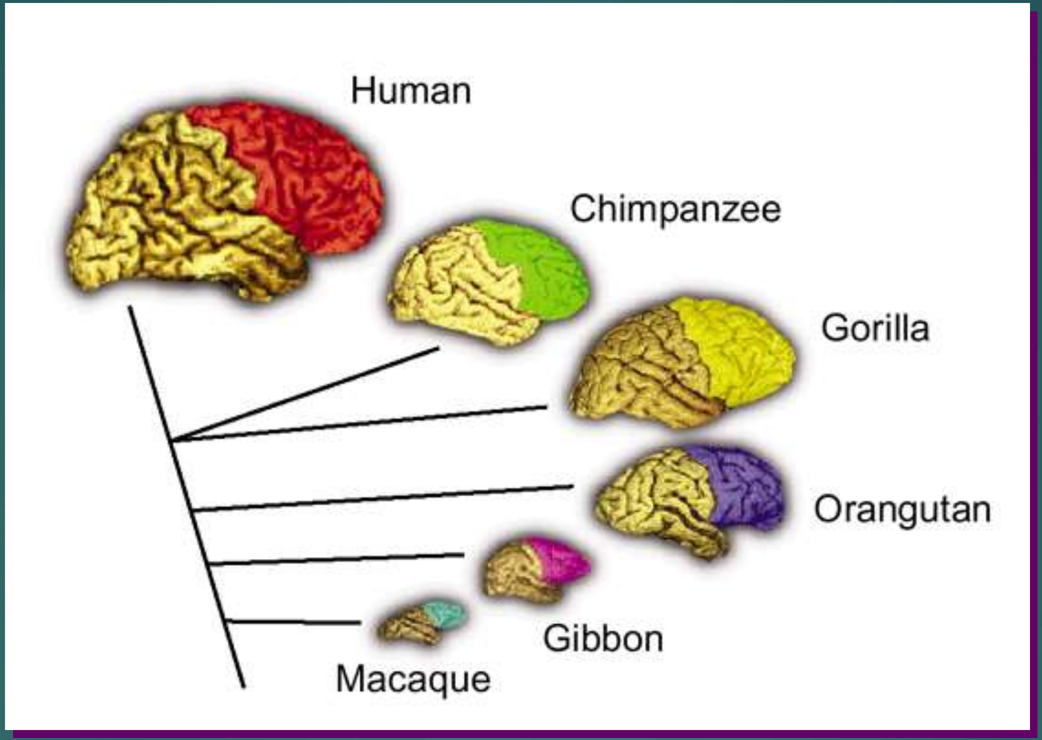
	Brodmann (1909)[7]*	Blinkov & Glezer (1965)[8]*	Present study**
Human	36.3	32.8	37.7 (± 0.9)
Chimpanzee	30.5	22.1	35.4 (± 1.9)
Bonobo	NA	NA	34.7 (± 0.6)
Gorilla	NA	NA	35.0 and 36.9
Orangutan	NA	21.3	37.6 (± 1.1)
Gibbon	21.4	21.2	29.4 (± 1.8)
Macaque	NA	NA	30.6 (± 1.5)
Cebus	22.5	NA	29.6 and 31.5

*Surface of frontal cortex in % of surface of cortex of cerebral hemispheres. **Volume of frontal cortex in % of volume of cortex of cerebral hemispheres. NA, not available.

The main reason that the prefrontal cortex is slightly larger is that humans have a larger volume of white matter in their prefrontal cortex.

Semendeferi et al., Nature Neuroscience, 5, 272-6, 2002

Frontal Lobes in Primates: 34%



Semendeferi and colleagues found that human frontal lobes are not disproportionately larger than predicted for a primate brain of its size.

Humans have greater white matter: greater white matter connectivity.

(Semendeferi, et al, 2002
Figure courtesy of K. Semendeferi and H. Damasio)

Prefrontal Cortex

- Katerina Semendeferi (1997, 2002)(much larger samples):
  - PFC is not larger or smaller than expected for great ape (34%); only area 10 (frontal pole) is larger in humans & has increased connectivity;
  - area 13 (part of limbic OFC) is smaller;
  - white matter in human PFC has greater amount in gyral portion than in the core (more intensive local connectivity between areas of PFC)
- Allen: Volumes of frontal and parietal lobes are strongly negatively correlated (larger F have smaller P & vice versa)
- Gray and white matter are larger than expected by allometry in humans
- In primates, larger the primate brain gets, the larger the frontal gets

Disproportionately large Prefrontal Cortex are not a hallmark of hominid evolution

- The idea of relatively "larger human frontal lobes" is incorrect.
- A relatively large frontal lobe is not a uniquely human feature, but is shared among all hominoids.

- Relative sizes of the dorsal, mesial or orbital sectors of the frontal lobe also do not stand out in the human brain.

- Humans have largest frontal lobes only in absolute size;
  Humans and great apes have overlapping relative values (33-39% of the volumes of the hemispheres, 1996; 35-37%, 2000)

- Orangutans had smallest socially mediating OFC (solitary style?)

K. Semendeferi et al., 1996; Semendeferi & Damasio, 2000

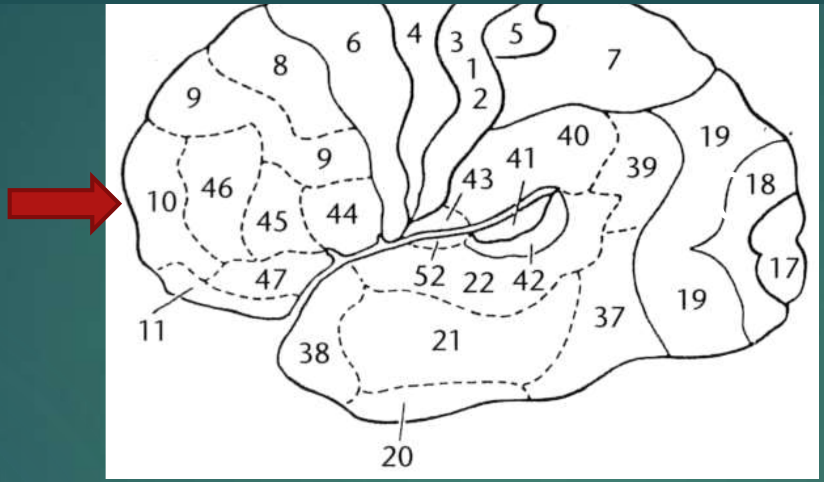
PFC: greater white matter connectivity

- Aspects other than relative volume of the frontal lobe have to be responsible for the cognitive specializations of the hominids.

- This region may have undergone a reorganization that includes enlargement of selected, but not all, cortical areas to the detriment of others

- The relative volume of white matter underlying prefrontal association cortices is larger in humans than in great apes; compatible with the idea that neural connectivity has increased in the human brain

Area 10 (frontal pole) = only connects to association areas

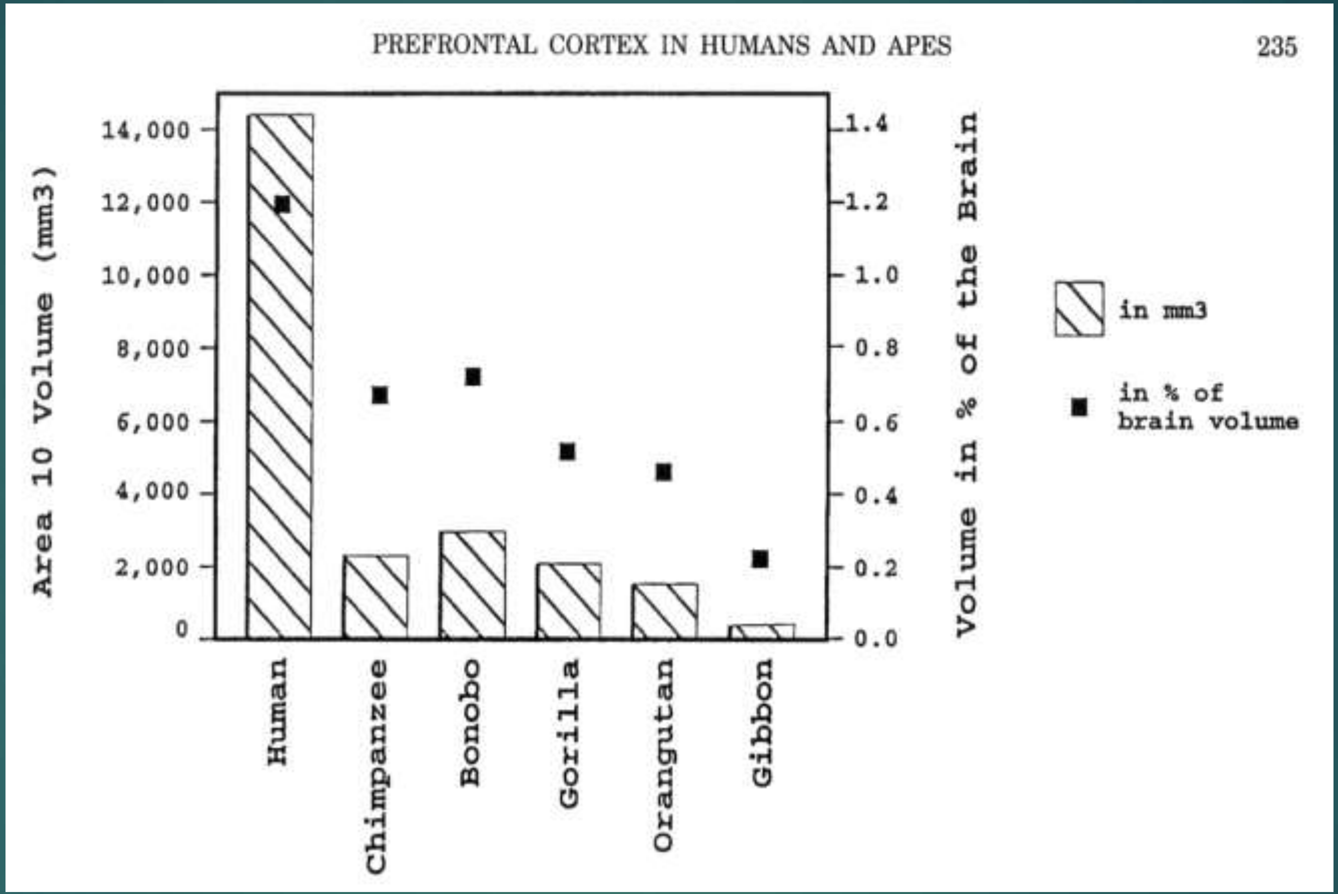


Area 10 (frontal pole) is both absolutely and relatively larger in humans (though only 6% larger than expected).

There is a specific increase in connectivity, especially with other higher-order association areas.

Endocasts of Australopithecus indicate increase in size of frontal pole.

Larger area 10 in humans than in apes



Area 10 in the right human hemisphere has an estimated 254 million neurons, while the great apes have less than one third of that amount.

Semendeferi et al., Am. J. Phys. Anthropol., 114, 224-241, 2001

Smaller human motor cortex and more gyrification in PFC

- Proportionally larger frontal cortex is to be expected in primates with big brains such as hominids
- Dorsal frontal cortex of hominids has a more complex pattern of gyral folding than in other primates, with distinct precentral and superior frontal sulci evident.
- The enlargement of frontal cortex in hominids has involved mostly the dorsolateral prefrontal cortex; Lateral prefrontal cortex is disproportionately large (as it tends to enlarge with increasing absolute brain size); increased ability of humans to suppress reflexive responses to stimuli and to develop language

- Primary motor and premotor cortex in humans occupy a smaller proportion of the frontal lobe compared with other primates, suggesting that the remainder is comprised of a relatively large prefrontal cortex (Preuss, 2004).

Frontal White Matter Volume Is Associated with Brain Enlargement and Higher Structural Connectivity in Anthropoid Primates

- Hyperscaling of neocortex to the rest of the brain is mainly due to the effect of white matter
- The hyperscaling of the frontal lobe with the rest of the brain is mainly due to the effect of white matter and frontal white matter (but not non-frontal white matter) is found to correlate significantly with the rest of the brain.
- Frontal white matter can be considered a principal component in explaining variation in brain size.
- Frontal white matter is at the heart of increased structural connectivity associated to brain enlargement and higher cognitive capacities.

J.B. Smaers et al., 2010

Auditory sequence processing reveals evolutionarily conserved regions of frontal cortex in macaques and humans

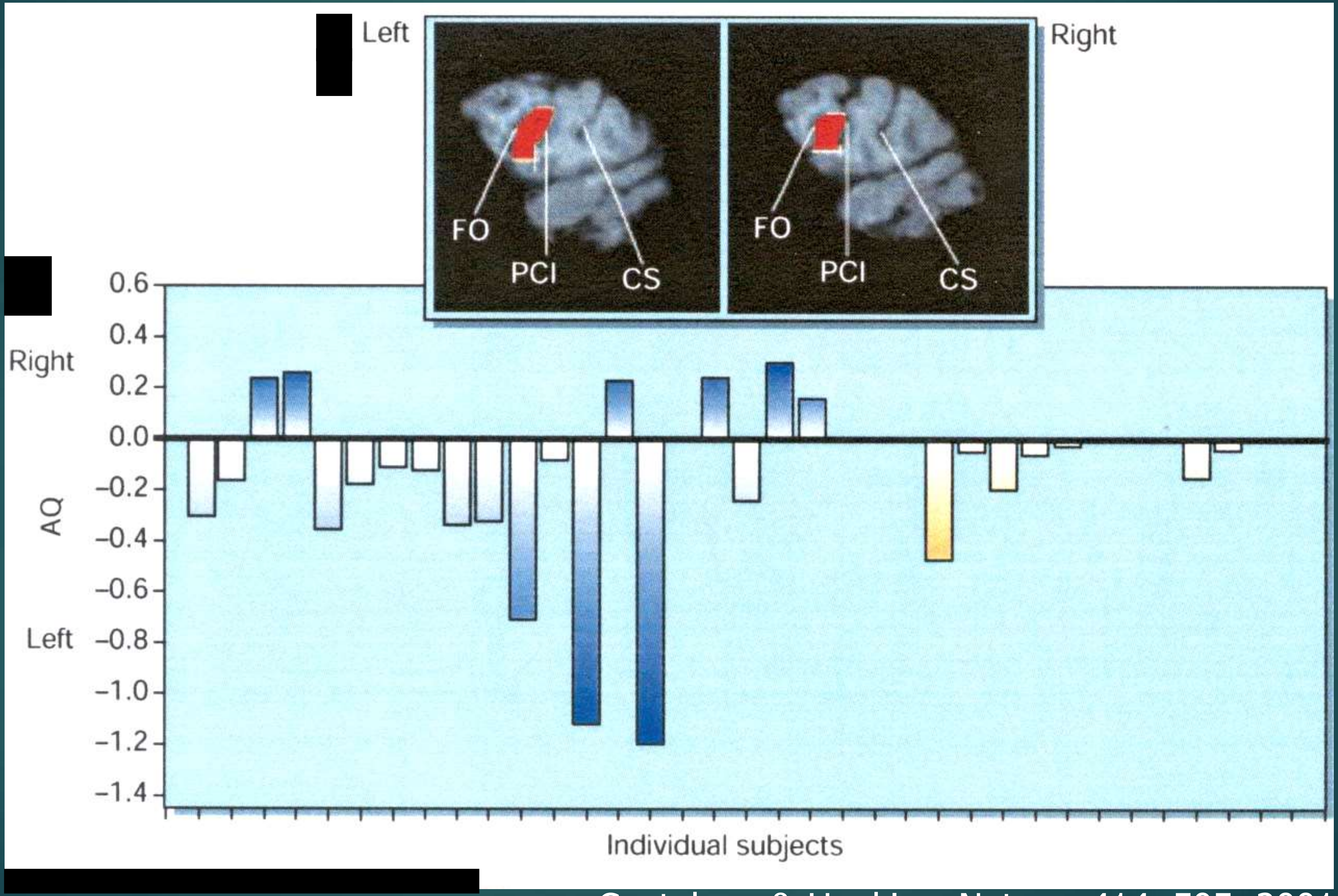
- use functional magnetic resonance imaging in *Rhesus macaques* and humans to examine the brain regions involved in processing the ordering relationships between auditory nonsense words in rule-based sequences. We find that key regions in the human ventral frontal and opercular cortex have functional counterparts in the monkey brain. These regions are also known to be associated with initial stages of human syntactic processing. This study raises the possibility that certain ventral frontal neural systems, which play a significant role in language function in modern humans, originally evolved to support domain-general abilities involved in sequence processing.
- regions of vFOC are comparably functionally engaged in monkeys and humans by sequences that violate the ordering relationships of an auditory artificial grammar

Benjamin Wilson, et al., 2015

Asymmetric area 44 (Broca's) in great apes: Left larger than right

Right

Left



Cantalupo & Hopkins, Nature, 414, 505, 2001

Other Regional Reorganizations

Brain growth: development & neocortex

- At the time of birth, human brains are already about two times larger than great ape brains.

- Subsequently, postnatal brain growth in humans continues at its fetal rate through the first year, whereas in other primates, brain growth rates decrease shortly after birth.

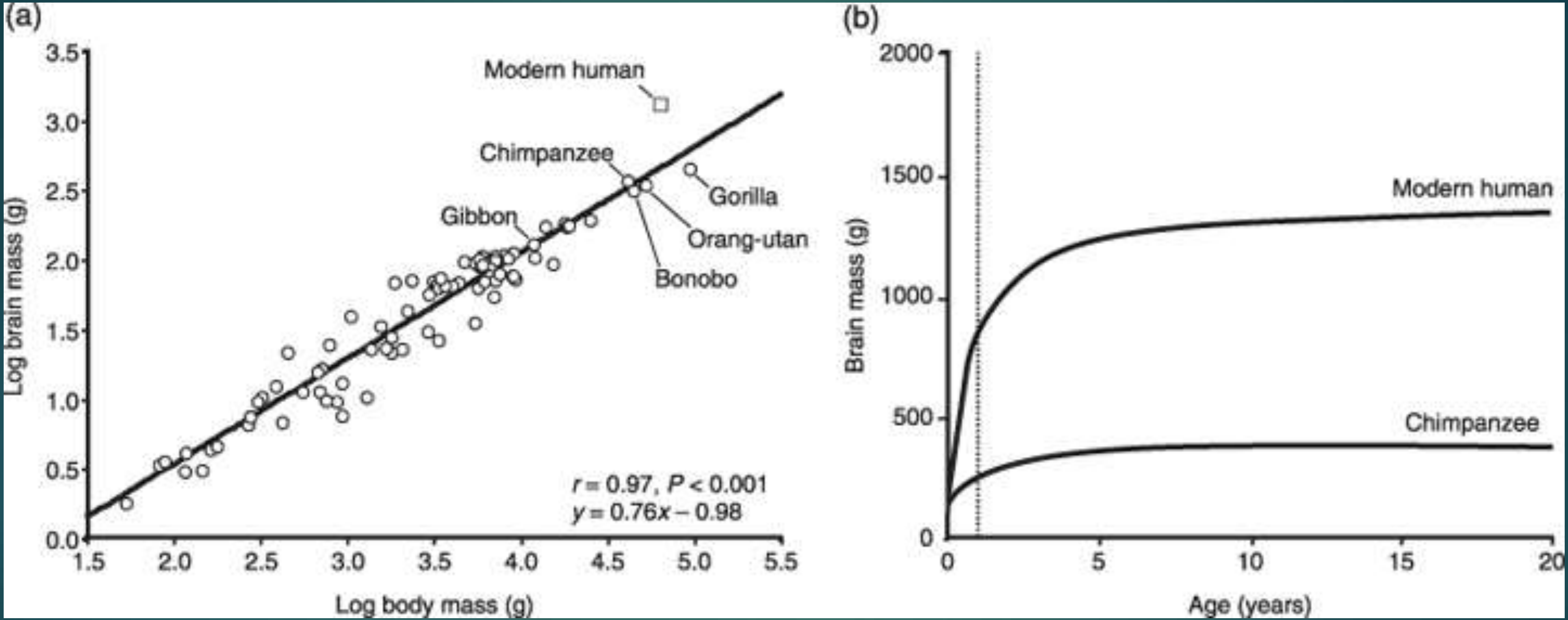
- This unique human brain growth schedule is critical to achieving a high level of encephalization in the face of the obstetric constraints associated with pelvic adaptations for bipedality

Brain growth: development & neocortex 2

- The human neocortex (including both gray and white matter) exceeds predictions for a hominoid of the same total brain size.
- Because of the particularly steep allometric scaling slope of the neocortex relative to other brain parts, larger brains become composed of progressively more neocortex.
- Across mammals, as overall brain size enlarges, various parts of neocortex do not increase at the same rate.

- Thus, brain size enlargement led to a greater degree of regional functional 'neocorticalization'.

A natural history of the human mind: tracing evolutionary changes in brain and cognition



Modern humans have brains that are approximately three times larger than would be predicted for a primate of the same body mass.

Journal of Anatomy Volume 212, Issue 4, pages 426-454, 1 APR 2008 ;http://onlinelibrary.wiley.com/doi/10.1111/j.1469-7580.2008.00868.x/full#f2

Great Ape brain differences

- Asymmetry: In right handed humans, the anterior part of the right hemisphere is longer and wider than the left, & posterior left is wider & longer. Present in gorillas, but not chimps.

- Hominid skull endocasts also exhibit wider anterior right frontal & longer posterior left

- Larger mediodorsal nucleus of thalamus (heavy connections to prefrontal)

- Larger cerebellar dentate nucleus in humans

- Area 13 (posterior OFC; social emotional) and area 10 present in humans and all great apes.

- Gorillas have larger cerebellum, smaller temporal lobe, and larger parietal-occipital area.

- Left-right asymmetry of planum temporale is present in all the great apes.

K. Semendeferi, 2001

Functional Region Changes: Bigger is different

- Absence of change in volume is not evidence of absence of change in functional structure;

- Increases in brain size are likely evidence of regional functional changes in structure

Regional brain changes

- Lieberman: Increased cranial globularity and facial retraction in modern humans

- These morphological changes, some of which may have occurred because of relative size increases in the temporal and possibly the frontal lobes,

- Regional reorganizations very likely tied to type of synaptogenic response to environment (neocortical adaptations to different ecological niches) that occur early in development

- Shift in primates toward diurnal niche with increased reliance on vision (with vision area size negatively correlated with size of olfaction areas); but visual areas reduced relative to other brain areas in humans

Lieberman, 2002; Bruner, 2008

Functional changes

- Bipedality did not significantly increase brain size, but produced likely functional brain changes in motor and visual cortex
- Increased laterality of function; humans are unique in extent of "handedness" ~90% right handed. Language and memory enhancements
- Structure, but not location, & relative size of hippocampus has been highly conserved in mammals; significant size variability (sex, how much storage activity, seasonal, London Taxi cab driver success); laterality changes: spatial memory is lateralized to right, episodic memory to left
- Amygdala, & its fear response, is highly conserved, but with some reorganization. Orangs have smaller amygdala & OFC; more solitary

Temporal Lobe

- The temporal lobe also shows extraordinary enlargement in humans.
- Temporal lobe in humans is larger than expected, as well as temporal lobe surface area and white matter (maybe due to adaptations for language)
- The relative increase in the volume of the human temporal lobe, furthermore, is related to coordinated reorganization of nuclei in the amygdala.
- Compared with great apes, an anteriorly expanded and laterally pointing temporal lobe characterizes endocasts of *Australopithecus africanus*, suggesting reorganization of the cortical areas involved in some aspects of the these multimodal functions might have preceded brain size enlargement in human evolution

Parietal regional differences

- Semendeferi & H. Damasio: occipito-parietal region is as large as expected, but more fine-grained reorganization is evident

- Bruner: Parietal lobe has become more rounded in humans (due to intraparietal junction and cuneus); results in globularization of skull

Parietal Expansion: reason for Homo sapiens globular skull

- Bruner: expansion of parietal and temporoparietal regions

- Change in the brain's spatial organization, with changes in the relative brain proportions and in the underlying patterns of connections, esp. in intraparietal sulcus, and the precuneus

- Crucial areas for visualspatial integration processes, namely the coordination of the inner and outer environment; capacity for internal virtual reality.

- Cost may be Alzheimer's

Bruner, et al., 2003, 2014; Bruner, 2008

Increased size of higher-order unimodal and multimodal areas of the neocortex and their connections to other brain structures

- Currently, the most compelling evidence for 'new' neocortical areas in humans that are not homologous with macaques include regions within posterior parietal cortex which provide additional central visual field representations and greater sensitivity to extract three-dimensional form related to motion.

- Same regions in the dorsal interparietal sulcus are activated in PET imaging of humans learning how to fashion Oldowan-style stone tools.

Importance of Parietal expansion

- 35 year fight between Holloway (yes) & Falk (no) over lunate sulcus.
- Several endocasts of *Australopithecus afarensis* and *Australopithecus africanus* (4–2.5 Ma) show evidence that the lunate sulcus, which marks the border between primary visual cortex and parietal cortex, had already shifted to a more humanlike configuration prior to dramatic brain size expansion.
- Because posterior parietal cortex is active in object manipulation tasks and motor planning, it is possible that this cortical reorganization opened the door to stone tool production in later hominins.
- Further geometric expansion of the parietal lobes appears to distinguish modern *Homo sapiens* endocasts from other hominins (Bruner, 2004).

Parietal : Social cognition & Theory of Mind

- Tomasello & Rakoczy (2003) have argued that there are two (initial) stages of uniquely human social cognition.

- The first stage is observable in one year olds, who have an understanding of other persons as intentional agents,
- This enables them to take part in pretend play, and is important as a prerequisite for shared attention and early social and linguistic learning.
-
- The second stage is the "Theory of Mind" belief-desire psychology which normally starts around 4 years of age, but which is **dependent on several years of linguistic communication**.

Mirror Neurons

- Mirror neurons found in primates.
- Recently shown in humans; object use or seeing use appears to trigger
- (fMRI) studies of humans have found that the inferior parietal lobe and frontal operculum are activated during the observation and execution of actions and, thus, form a putative human mirror neuron system (hMNS)
- Predisposition to take the perspective of others is associated with selective tuning of the hMNS to simulate socially informative facial movements.

K. Montgomery, 2009

Smaller visual areas

- Human primary visual cortex is also substantially smaller than predicted by allometry for total human brain size. V1 is only about 1 1/2 times larger in humans than in great apes; neocortex is 3 times larger.

- The relatively small size of primary visual cortex in humans suggests that adjacent areas of the posterior parietal cortex have disproportionately increased in volume.

- Pushing back of primary visual cortex in humans was in part a result of an expansion of the parieto-occipital association areas, which may have expanded in response to evolution of language or tool use.

Other areas

- Enlarged thalamus
- The cerebellum is large relative to body size. Cerebellar enlargement in humans is not surprising given that it is linked by extensive connections with the neocortex and these two structures have evolved as a coordinated system across primates (Whiting & Barton, 2003).
- Ventral portion of the cerebellum's dentate nucleus is relatively larger in humans than in the great apes (Matano, 2001). This part of the dentate nucleus projects to non-motor regions of the frontal lobe by way of the ventrolateral thalamus. Greater development of the connections with frontal association areas that play a role in cognition and language

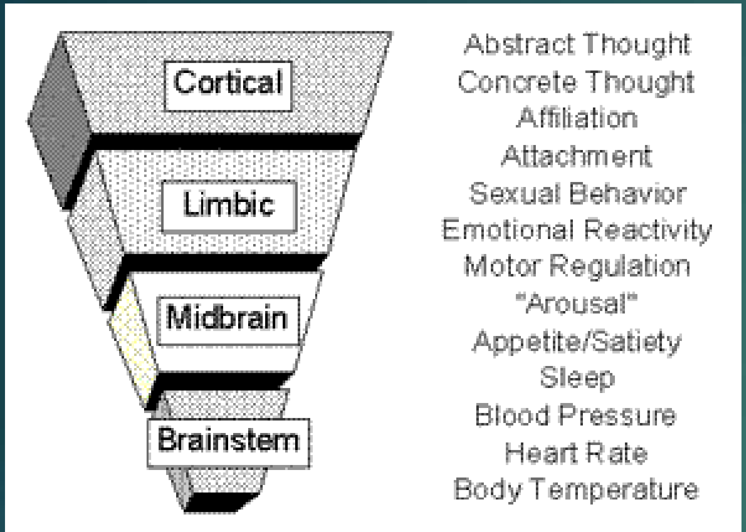
More elaborate asymmetries

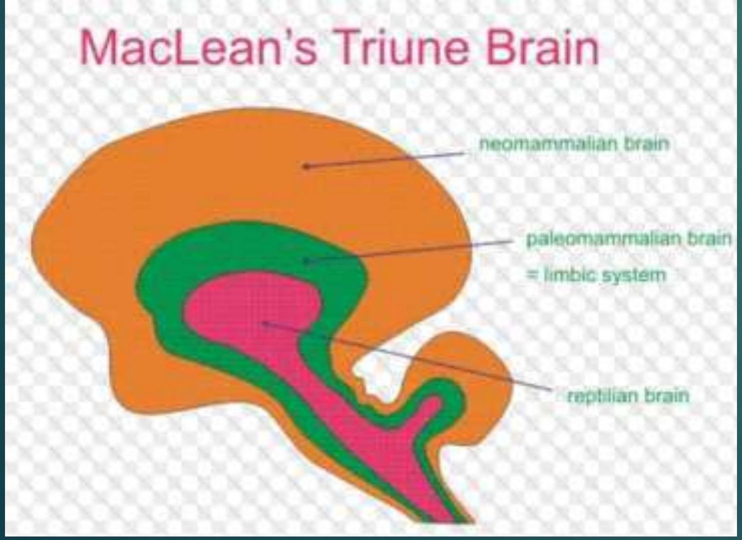
- Humans have elaborated on these asymmetries and evolved a much greater degree of hemispheric lateralization. Across *Homo sapiens* the incidence of right-handedness is approximately 90%, particularly for fine motor tasks involving precision grip and manipulation of tools.
- In contrast, most other primates do not display such pronounced bias for hand use at the population level. No evidence that any great ape species displays the same high degree of population-level handedness that is present in humans.
- There is a pattern of combined left-occipital and right-frontal petalias. These asymmetric lateral protrusions at the frontal and occipital poles of the cerebral hemispheres are a common feature of human brains.
- Present consistently present since *Homo erectus*

Asymmetries

- The human brain displays strong population-level left hemisphere dominance for language functions, especially among right-handed individuals.
- Some of the cortical areas associated with language function in humans also display asymmetries in extant great apes, suggesting that they were present in the LCA. Specifically, population-level left hemisphere dominant asymmetry of the planum temporale, in Wernicke's area, is shared by humans, chimpanzees, bonobos, gorillas, and orangutans
- This might be due to the computational demand to process sequential information, such as species specific vocal calls and dexterous manual actions, with temporal fidelity by reducing conduction delay across hemispheres
- The neural machinery for processing complex acoustic signals contained in species-specific communication was present and lateralized in the LCA, providing a scaffold upon which language functions later evolved.

MacLean's Triune Brain hypothesis: outdated idea in search of facts





- Triune brain theory has not survived well; basal ganglia (reptilian complex) are much smaller portion of the of reptiles and birds. Since the basal ganglia are found in the forebrains of all modern vertebrates, they most likely date to the common of the vertebrates, more than 500 million years ago, rather than to the origin of reptiles. Also bird cognition is impressive.
- The limbic system, which MacLean proposed arose in early mammals, have now been shown to exist across a range of modern vertebrates.
- The "paleomammalian" trait of parental care of offspring is widespread in birds and occurs in some fishes as well. Neocortex was already present in the earliest emerging mammals. Non-mammals also have pallial areas which mediate similar functions as the cortex. Old theory casts emotion as more primitive than reason, an idea that is no longer held.

White Matter Connectivity

White Matter: bigger brain needs more wiring

- Barton and Harvey: hyperscaling of the neocortex in primates is entirely due to white matter, with grey matter scaling only isometrically (in direct proportion with the rest of the brain).

- Due to the larger distance between neurons and the length of the axons connecting them, longer axons need to be thicker and more heavily myelinated in order to maintain optimal conduction times, causing white matter volume to hyperscale with cortical volume

Connectivity: Distance is time in the brain

- More neurons lead to more and longer connections; more of brain devoted to connections; ultimately have to be organized differently than small brains
- Neural computations more readily done if distance between neurons is smaller;
- Hemispheric specialization reduces distance between functionally related areas
- Regional functional asymmetry is a solution to connection problem.

Greater connectivity

- Whole brain neocortical white matter increases disproportionately with gray matter in mammals
- Frontal lobe white matter connectivity is reason for frontal lobe increase in bigger brain. White matter to gray matter ratio in PFC is greatest in humans.
- Primates demonstrate hyperscaling of left PFC, with white matter volume showing larger volume than gray in apes and especially in humans;
- Prefrontal–cerebellar connectivity is highest in humans
- Language evolution: Broca's and Wernicke's connectivity is especially high in humans; left arcuate fasciculus in humans enlarged
- Mirror neuron connectivity: humans have highest dorsal pathway connectivity (extracting detailed info from observed action); chimps higher ventral; parietal-frontal connections highest in humans; better tool use and making ability and imitation of highly detailed actions

Von Economo Neurons: Distinctly Human

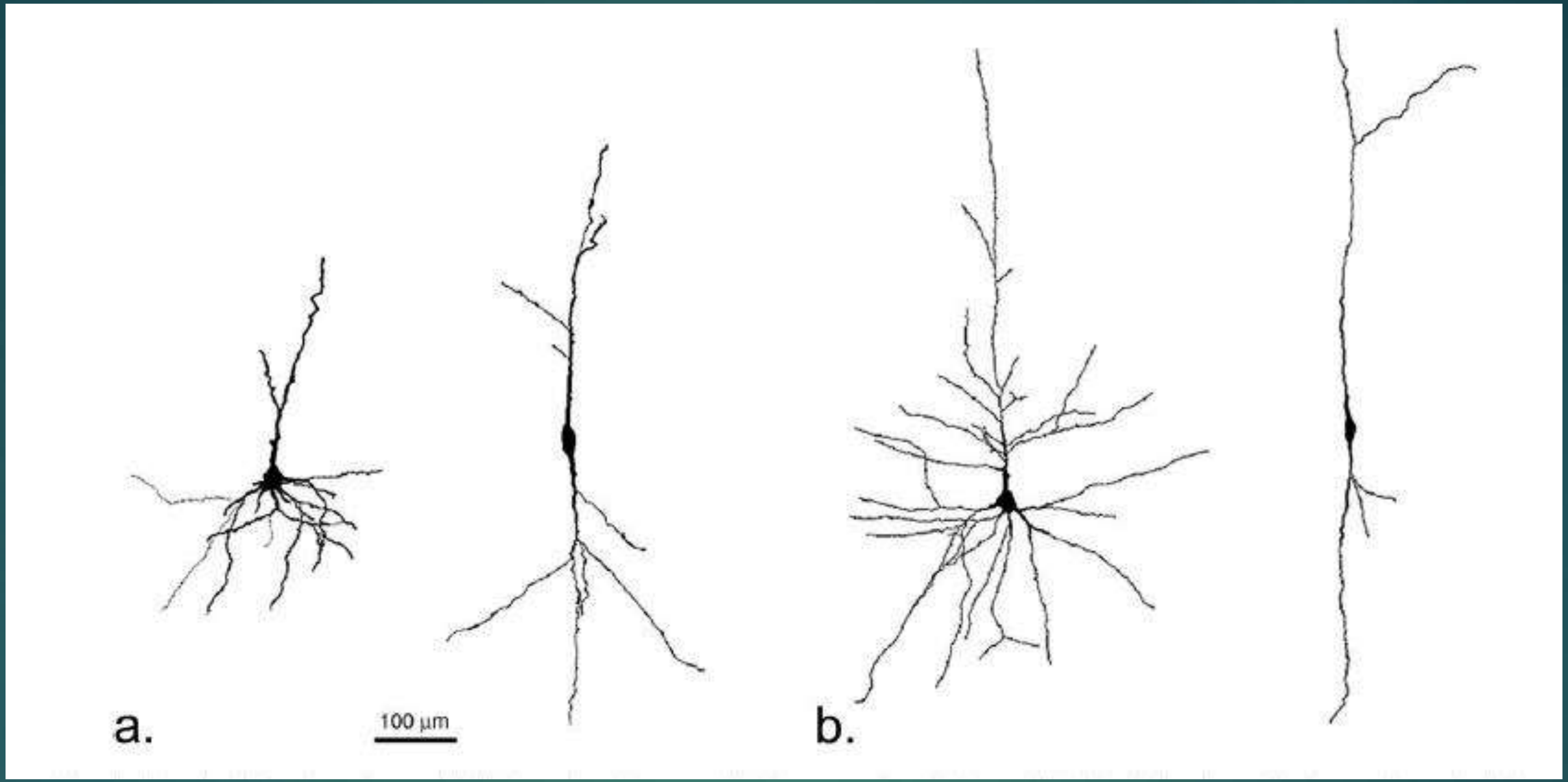


Fig. 4. Neurolucida tracings of pyramidal (left) and von Economo (right) neurons from Fronto-Insular (a) and Anterior Cingulate Cortex (b). Notice the vertical symmetry and relative sparseness of the VEN dendritic tree. [Allman et al., 2005]

VENS: While present in many mammals, humans are loaded with them

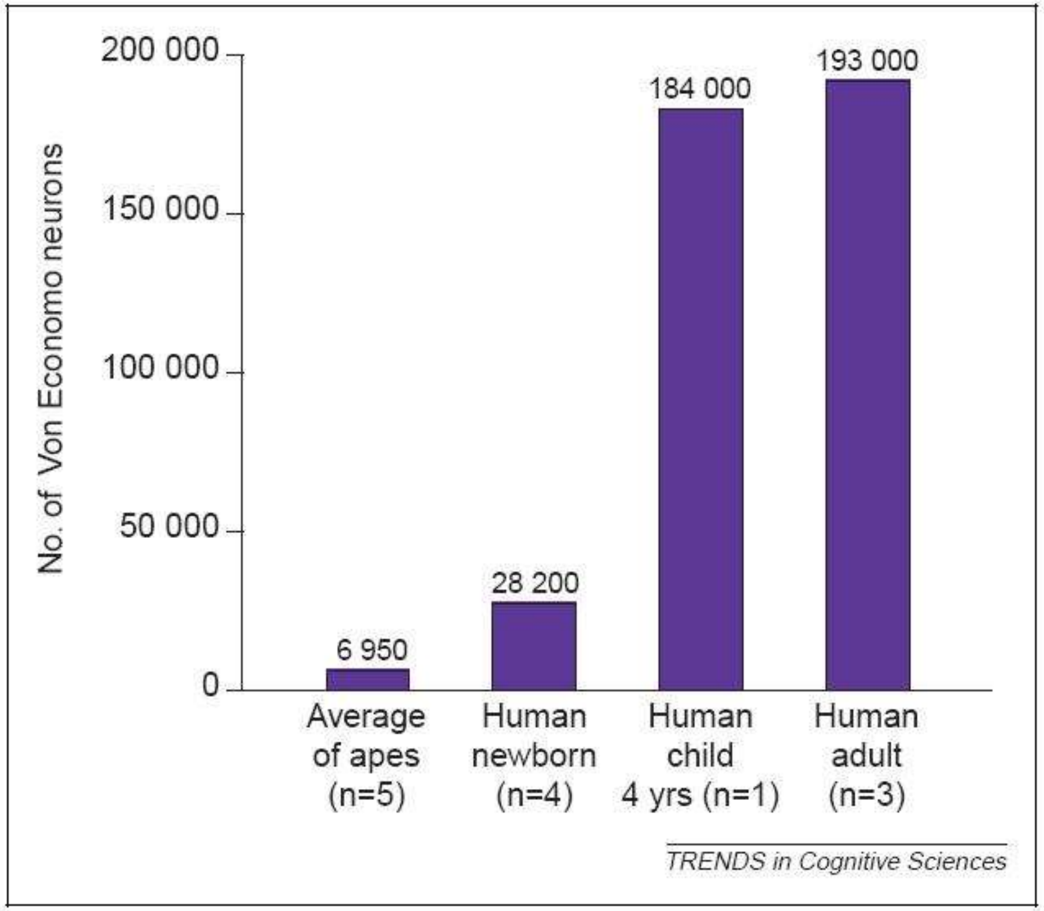


Figure 2. Comparison of Von Economo neuron numbers. Total number of VENs in FI (total of right and left hemispheres) is shown for apes, human neonates, a four-year-old child, and an adult human. The number of subjects is given in parentheses. The data are stereological counts by the authors on brains in the Yakovlev Collection at the National Museum of Health and Science and the Semendeferi Collection at the University of California, San Diego.

[Allman et al., 2005]

Von Economo Neurons

- Von Economo neurons are large bipolar cells that are found in cortical layer Vb of the anterior cingulate, fronto-insular and dorsolateral prefrontal cortex regions
- Strongly express the dopamine D3 and D5 receptors, as well as serotonin-1b and serotonin-2b receptors.
- John Allman: 'air traffic controllers' for emotions. Signals from the ACC are received in Brodmann's area 10.
- Initial analysis of the ACC layer V in hominids revealed an average of ~9 spindle neurons per section for orangutans (rare), ~22 for gorillas, ~37 for chimpanzees, ~68 for bonobos, ~89 for humans.
- Selective degeneration in FTD and agenesis of corpus callosum and overly abundant in autism (heightened introspection?)

Watson, Karli Kiiko (2006)

Von Economo Neurons: large-brained, social species

- All of the primates examined had more spindle cells in the fronto-insula of the right hemisphere than in the left.
- An adult human had 82,855 such cells, a gorilla had 16,710, a bonobo had 2,159, and a chimpanzee had a mere 1,808 - despite the fact that chimpanzees and bonobos are great apes most closely related to humans; In DLPFC, areas 9 and 24
- The brain networks recruited during a humorous experience & and embarrassment did indeed include FI and ACC
- Interoceptive feedback and cognitive monitoring of conflict to mediate rapid non-rational behavioral selection in ambiguous social interactions,
- FTD reduction produces deficits in empathy, social awareness, self-control.

Specializations of projection cell types

- In layer V of anterior cingulate and frontoinsular cortex, neurons with a spindle-shaped cell body (VENs) are only found in great apes and humans among primates.
- Designed for quick signaling of an appropriate response in the context of social ambiguity
- von Economo neurons have now also been identified in large-brained cetaceans, indicating that they have independently evolved in multiple lineages.
- VENs perform important social cognitive functions in species that have both large brain size and complex social organization.

Theories of Causation of Brain Enlargement

Theories of Brain Enlargement

- Radiator Theory – need for cooling system
- Smaller Facial Muscles & Bones
- Sociality
- Environment
- Weather
- Endurance running
- Diet
- Genetic mutation

Why the Hominid Brain Enlarged

Changes in Hominid Physiology

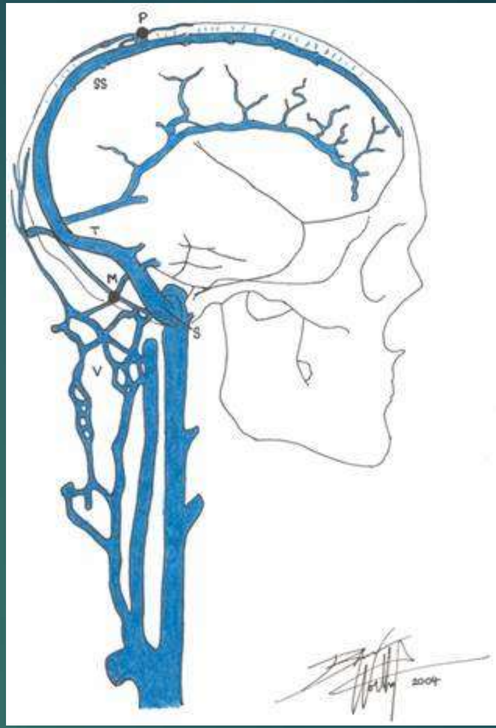
Radiator Hypothesis (Falk, 1990)

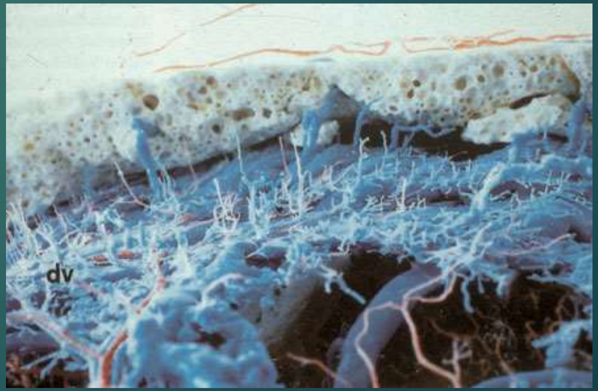
– The more active the brain is, the more heat it generates

- Increased Blood Circulation
- Improved Brain Cooling
- Enabled Size of Hominid Brains to Increase

The Radiator Hypothesis

- In hot environment, brain temperature may be the one biggest limit on survival (and human brains generate energy).
- *A. afarensis* began to develop openings in the skull (valveless emissary veins & foramina; connect the veins outside the cranium to the venous sinuses inside the cranium) through which blood could flow out to cool the brain.
- Brain temperature was constraint; 'radiator' released this constraint.

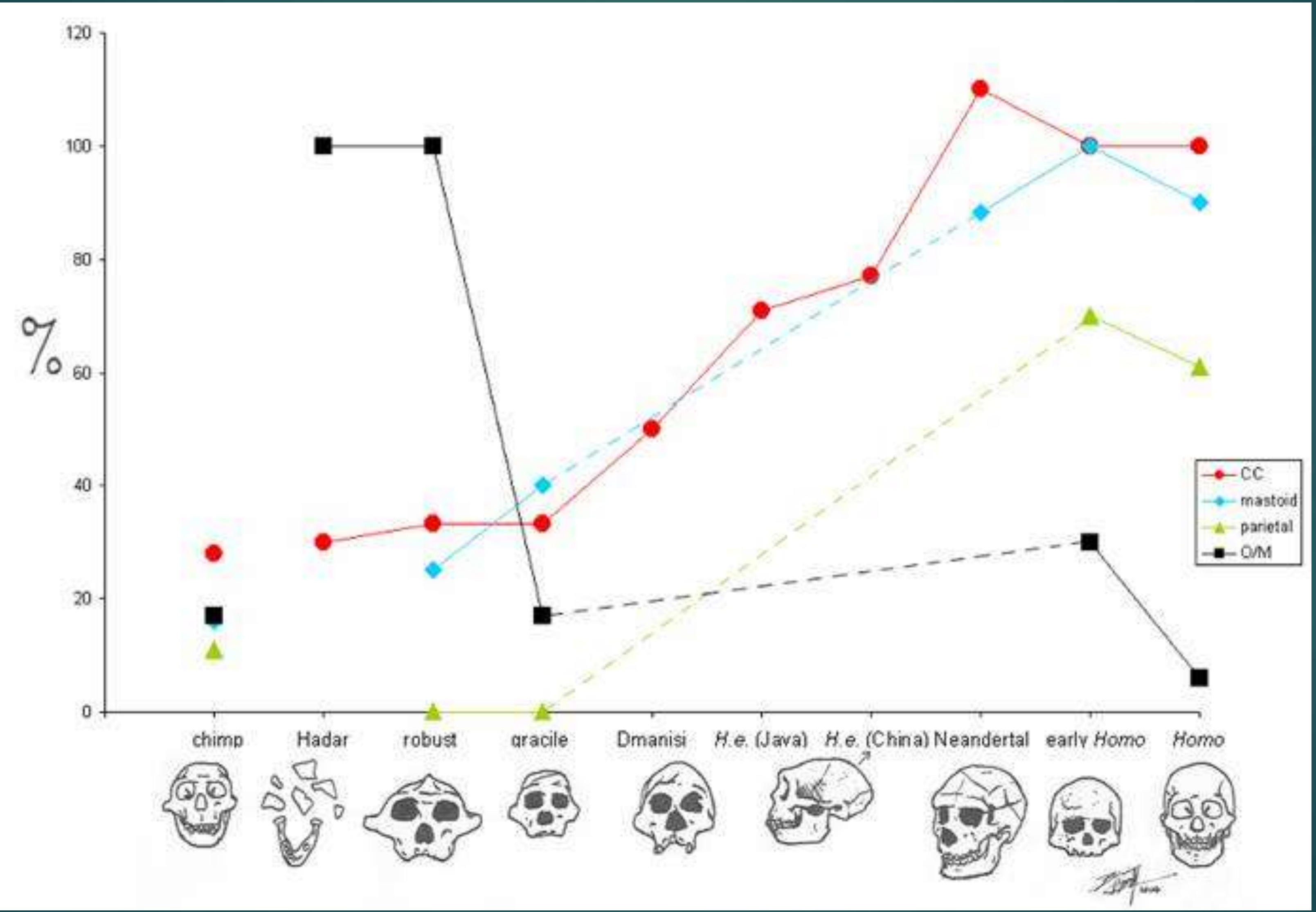




Lower photo from Wolfgang Zenker and Stefan Kubik (1996:4); illustrations from http://www.anthro.fsu.edu/research/falk/concepts.html

Images and discussion from Dean Falk, http://www.albany.edu/braindance/Theories.htm.

The Radiator Hypothesis



Cranial capacity

Mastoid foramina

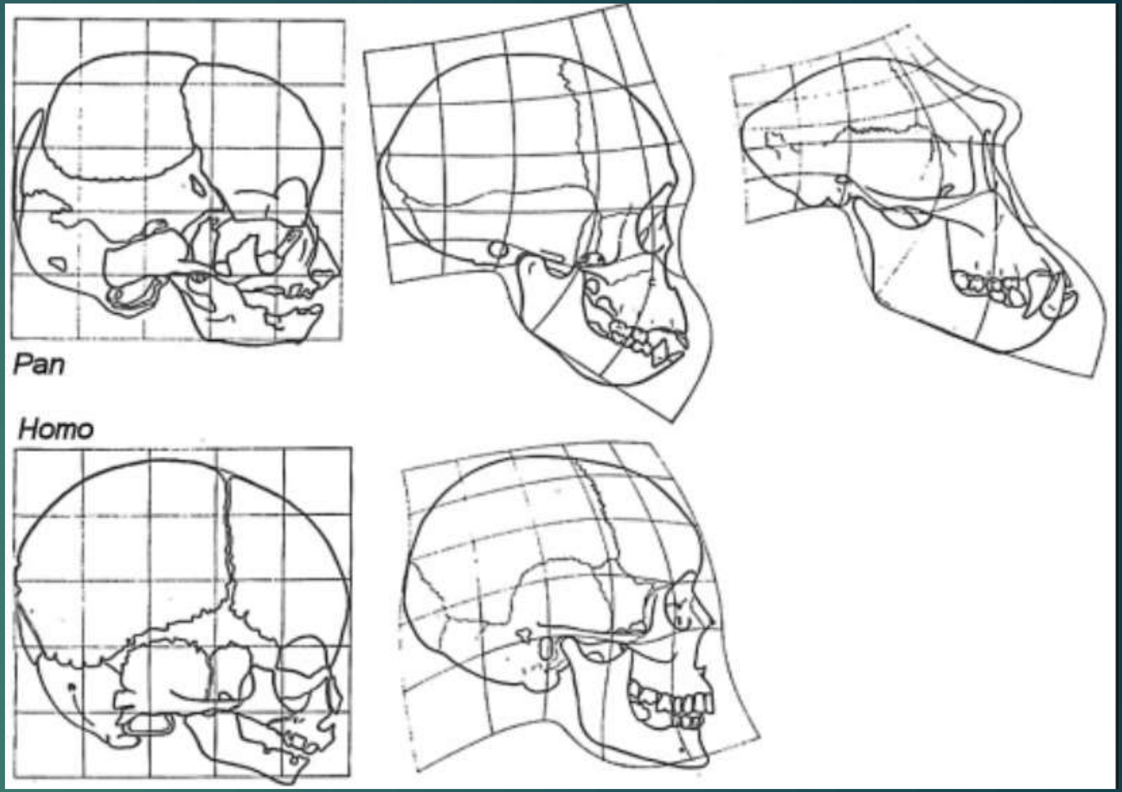
Parietal foramina

Cerebral Vasculature Malformations

Facial bones got smaller: more room for brain in skull

Why the Hominid Brain Enlarged? Neoteny

Neoteny (juvenilization)
Mutations that affect development are a major mechanism of evolution
•
Rate of brain development is slowed
– Allows more brain cells to be produced
• Adults retain some infant characteristics
•
Newly evolved species resemble the young of their common ancestors
– Human heads look more like the heads of juvenile chimpanzees than adult chimpanzees
-



Proportion of brain size to body size is greater in infants than in adults, developmental changes result in increases in brain size

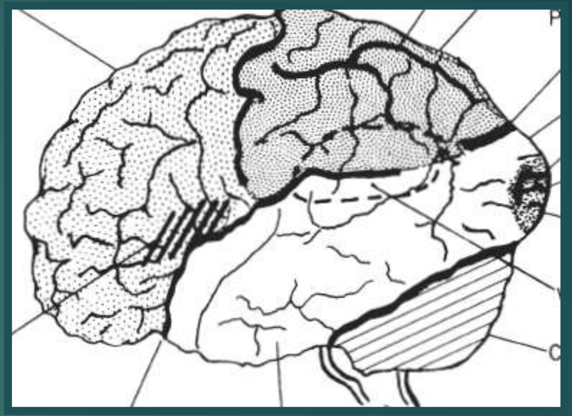
Social Brain Hypothesis:

Posits that primates evolved big brains to keep track of complex social rivalries when living in big groups.

Social Brain Hypothesis (Robin Dunbar)

Relationship between:

- size of neocortex
- size of social groups

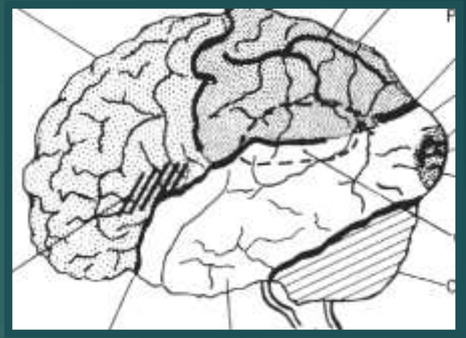


- Prosimians have smallest neocortex ratios for their social group sizes
- Monkeys are intermediate
- Apes have the largest

Strier (2003) Primate Behavioral Ecology

Social Brain Hypothesis (Robin Dunbar)

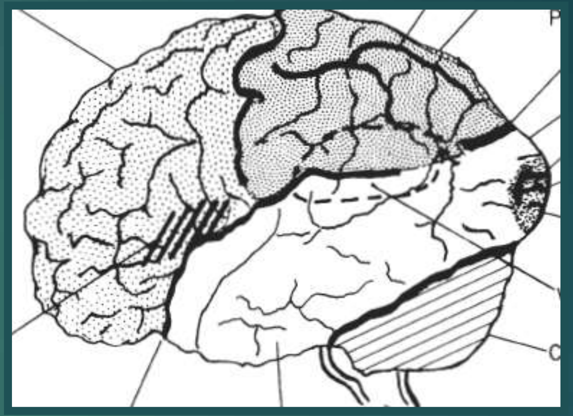
Within each of these grades:



- Primates with the largest grooming networks are those with the largest neocortex ratios ! !
- The ability to maintain the social alliances was the PRIMARY selective factor in the evolution of large primate brains.
- Primates have social brains

Strier (2003) Primate Behavioral Ecology

Social Brain Hypothesis



Relationship between:

- **size of neocortex**
- **size of social groups**

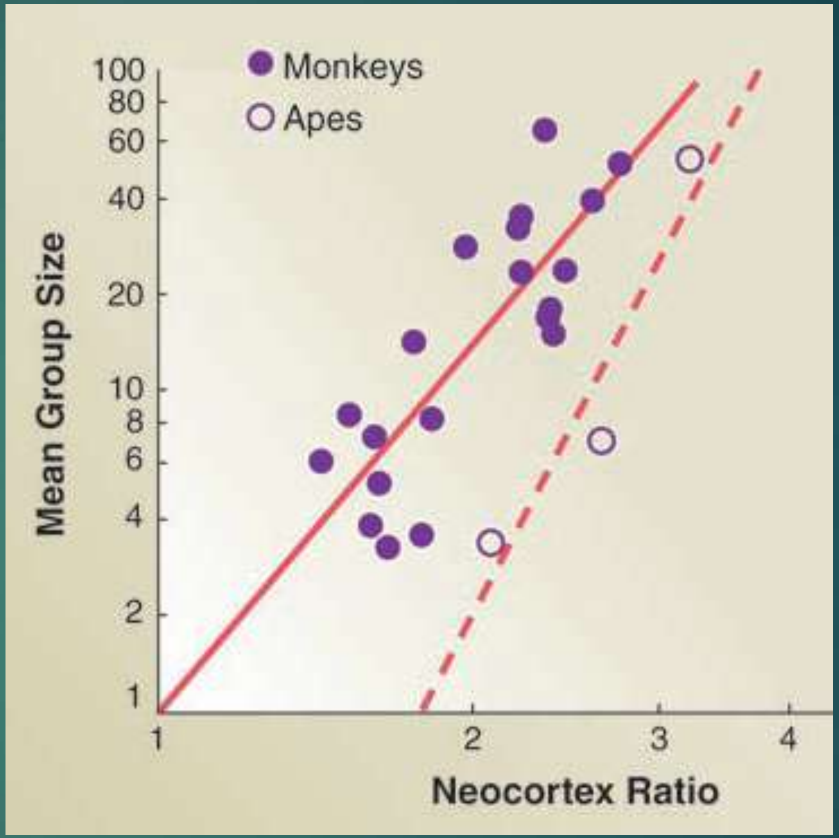
Also in :

- **Bats**
- **Carnivores**
- **Whales**

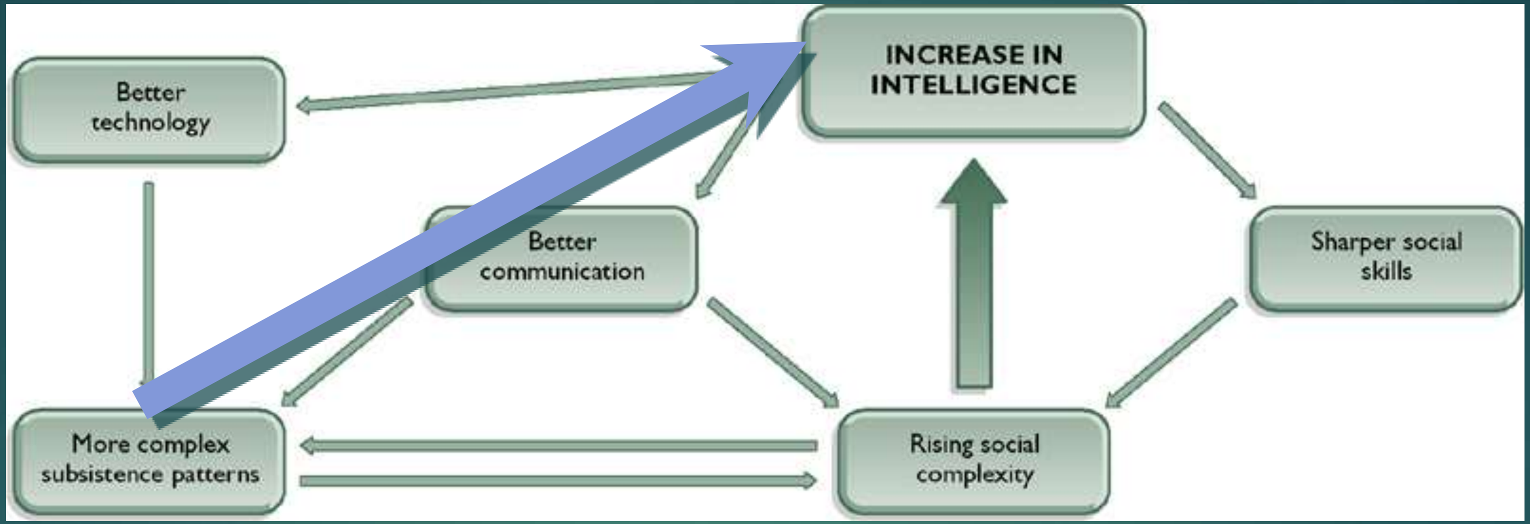
Reader and Laland (2002)

Social brain hypothesis

- Robin Dunbar (1992): brain size in primates, expressed in terms of neocortex ratio, shows an outstanding correlation with the size of the social group.
- Dunbar: Average social group size correlates with the ratio of neocortex to the rest of the brain.



R. I. M. Dunbar, *et al.* 2007. Evolution in the Social Brain. *Science* 317, 1344-1347.



Possibility: dietary change?

Social brain hypothesis

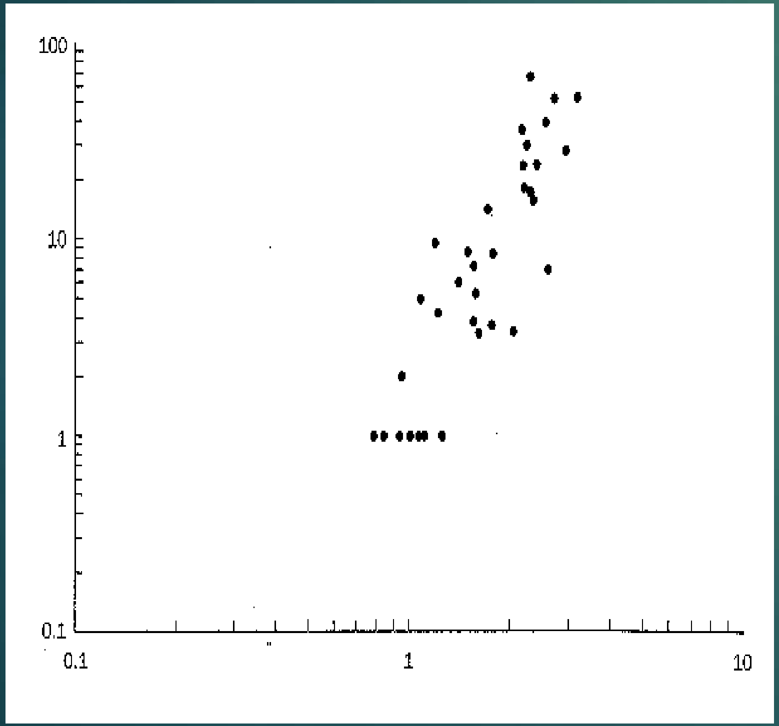
Problem: What kicks off the process?

Larger brain only adaptive once social life is complex.

Dietary change?

Neocortex Size and Group Factors.

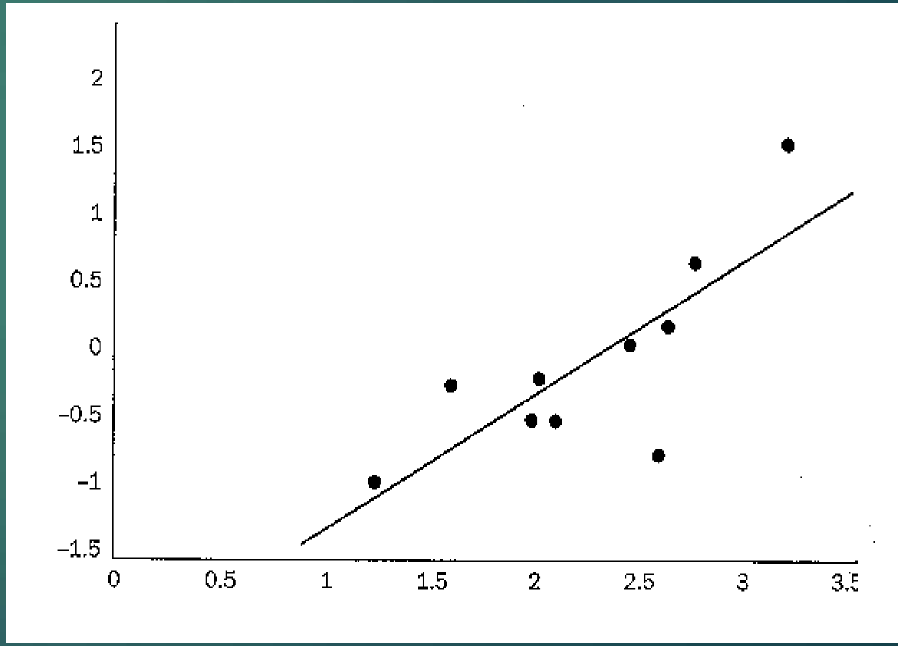
- Dunbar (1992) argues there is a direct correlation between group size and neocortex size across the primate order.



Neocortex ratio

- Byrne & Whitten (1988) argued that social living requires 'Machiavellian intelligence'.

Tactical deception



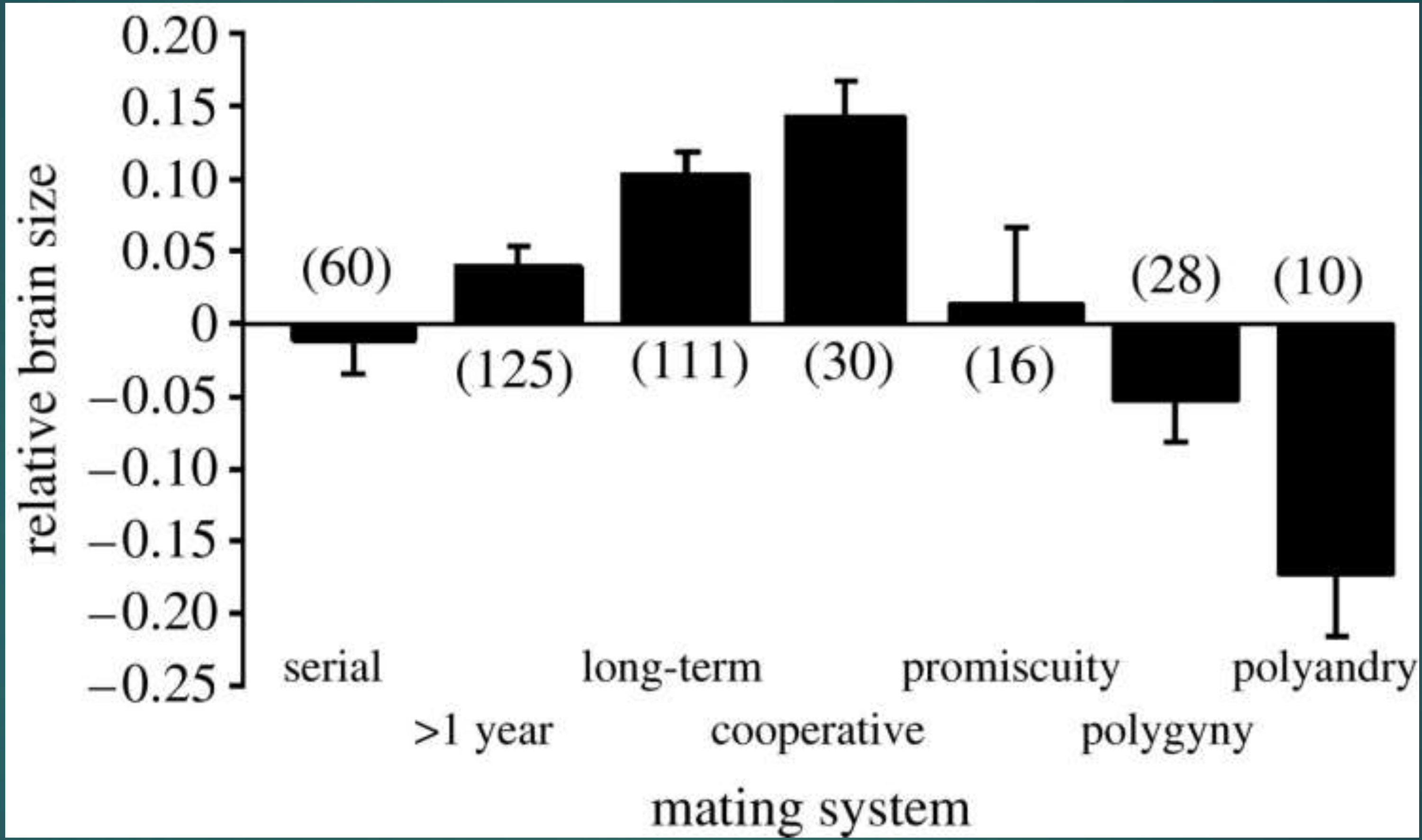
Neocortex ratio

Sociality, ecology, and relative brain size in lemurs

- The social brain hypothesis proposes that primates have evolved relatively large brains for their body size primarily as an adaptation for living in complex social groups. Studies that support this hypothesis have shown a strong relationship between relative brain size and group size in these taxa. Recent reports suggest that this pattern is unique to primates; many nonprimate taxa do not show a relationship between group size and relative brain size.
- Rather, pairbonded social monogamy appears to be a better predictor of a large relative brain size in many nonprimate taxa. It has been suggested that primates may have expanded the pairbonded relationship beyond simple dyads towards the evolution of complex social groups.

Evan L. MacLean, et al., 2009

Long-term pair-bonded species appear to have the largest brains within birds.



Mating system and relative brain size across 480 species of birds **(raw brain volume data from Iwaniuk & Nelson (2003); mating system data from various sources).**

Emery N J et al. Phil. Trans. R. Soc. B 2007;362:489-505

Hunting/Gathering is highly social.

- Acting cooperatively in a group.
- Shared information and communication.
- Sharing.
- Bartering.
- Food preparation and ritual.
- Making tools.
- Tracking, navigation.
- Meat is highly valued both in hunter-gatherer societies and chimpanzees. It is a valuable resource conferring power and status.
- In human foraging societies women prefer successful hunters as mating partners.

Stanford, 1999

Social Complexity and Brain size

- Dunbar found a close correlation between the ratio of neocortex to the rest of the brain on the one hand and social group size and complexity of social relationships on the other.

- For example, baboons show a remarkably high degree of sociability and have the largest neocortex of Old World monkeys.

- Byrne and Whiten found a highly significant correlation between neocortical size and the prevalence of tactical deception.

- VENs: Damage to uniquely human VENS result in significant social impairment

Socialization as antecedent to big brain

- Socialization: food cooperation, social standing detection
- Social complexity may drive social intelligence
- Dunbar: 66% of human talking is dedicated to gossip
- Theory of Mind: inferencing other people’s thoughts, detection of deception, feel for other’s

Environment & Neuroplasticity

Humans: more neuroplasticity

- Aida Gómez-Robles: compared the effect of genes on brain size and organization in 218 human and 206 chimpanzee brains. They found that although brain size was highly heritable in both species, the organization of the cerebral cortex—especially in areas involved in higher-order cognition functions—was much less genetically controlled in humans than in chimps.
- One potential explanation for this difference is that because our brains are less developed than those of our primate cousins at birth, it creates a longer period during which we can be molded by our surroundings.

Environment

- Longer exposure to environment while developing because of
  - 1) premature birth
  - 2) longer juvenile period.
- This allows for greater impact of environment – culture and specific learning – on the actual "building" of the brain itself.

Examples of neuroplasticity: training & synaptic increase

- Positive relationship between training in anything and increase in size of various brain structures
- Music:
  - Right inferior frontal & pitch
  - Musical training before age 7, larger anterior CC
  - String players, increased cortical representation in left motor hand region
  - Musicians have increased GM in Broca's
- Reading: left VWFA
- Juggling: motor regions
- London Taxi drivers: right hippocampus

Neuroplasticity and evolution: bigger is better

- Is there relationship between brain changes due to training and brain changes due to evolution?
- Increased brain size is associated with increased cognitive performance; more GM & WM associated with more training
- Hominid cultural environment has a direct influence on brain anatomy
- As early Homo spread into diverse ecological environments, behavioral neuroplasticity of our genus was a significant factor in our evolutionary survival
- Intensity of training is sufficient to alter normative morphology of the brain
- Selection in any cognitive domain could contribute to evolution of overall brain size. Increase in brain volume in hominid evolution could have been a function of the cultural environment that conferred fitness advantages to tasks or skills that required years of intensive training.

Visual Word Area: Reading changes brain

FFA

VWFA
Ventral
occipitotemporal
cortex

PPA

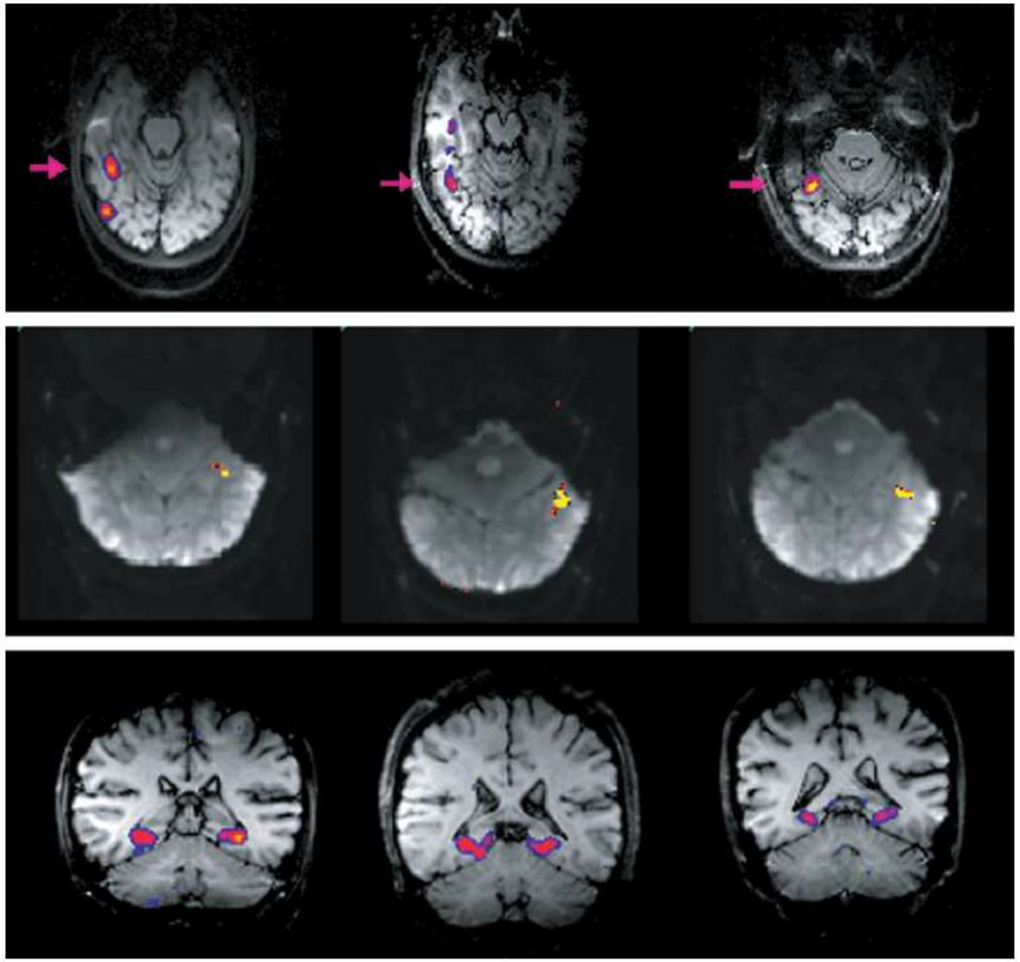


Fig. 6. Three of the functionally specific regions that have been discovered using the individual-subjects functional ROI approach. Top panel: the fusiform face area (FFA), which is defined by a higher response to faces than objects shown in three individual subjects (data from Kanwisher et al. 1997). Middle panel: a word and letter-string selective region, which is defined by its higher response to visually presented words than line drawings of objects shown in three individual subjects (data from Baker et al. 2007). Lower panel: the parahippocampal place area (PPA) which is defined by a higher response to scenes than objects shown in three individual subjects (data from Epstein et al. 1999).

Faces

Right VWFA: Faces

Left VWFA:
Visual Words
based on
experience

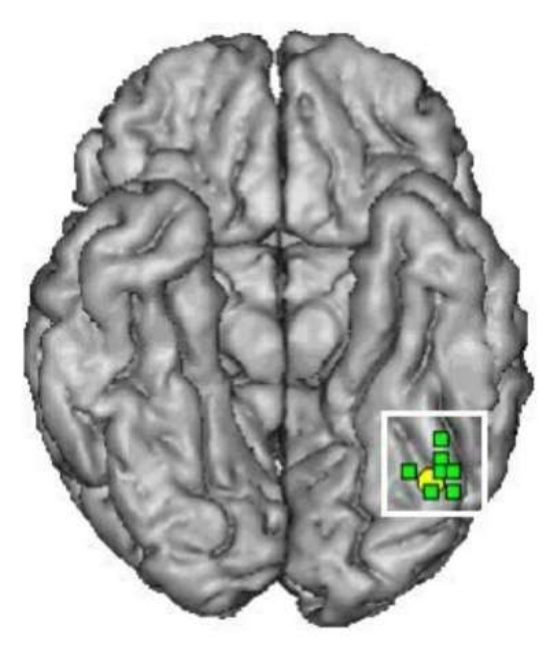
Scenes

Reading letters area: Culture & literacy changes brain

- Visual Word Form Area localized to the left occipito-temporal region that is responsible for recognizing visual letters and words (reading written words).

- The VWFA's right hemisphere analogue is the fusiform face area, which allows us to recognize faces.

- In young children and people who are illiterate, the VWFA region and the fusiform face area both respond to faces.
- As people learn to read, the VWFA region is co-opted for word recognition. Brain circuits originally evolved for object recognition converted to become tuned to recognize frequent letters.



Result of experience

Both Hebrew & English Words

Kanwisher; Dehaene

Not evolutionary brain change: Current Literacy

- Literacy, whether acquired in childhood or through adult classes, enhances brain responses in three distinct ways:
- 1 – increases activation of left VWFA
- 2 - allows practically the entire left-hemispheric spoken language network to be activated by written sentences.
- 3 - enhanced phonological activation to speech in the planum temporale
-
- These largely positive changes should not hide that literacy also leads to cortical competition effects
  - At the left VWFA site, a significantly reduced activation found for checkerboards and faces.

S. Dehaene et al., 2010

Weather: Brain Development & Environmental Change

- Weather: The landscape early humans were inhabiting transitioned rapidly back and forth between a closed woodland and an open grassland about five to six times during a period of 200,000 years; such variability of experience can trigger cognitive development.
-
- Early humans went from having trees available to having only grasses available in just 10 to 100 generations, and their diets would have had to change in response
- The result can be increased brain size and cognition, changes in locomotion and even social changes -- how you interact with others in a group.
- The environment changed dramatically over a short time, and this variability coincides with an important period in our human evolution when the genus Homo was first established and when there was first evidence of tool use.

Weather & larger brains

- Normal human heads are longer than wide
- Cranial index (width/length x 100) positively correlated with cranial capacity (.37)
- Distribution of CI and cranial capacity correlated with climate, with larger heads more common in colder regions (Beals, 1984); using fossil hominid (*Homo*) skulls, larger brain size correlated with climactic variation
- Weather as driving force for evolution of larger brain: cold winters and variable climates put a premium on cognitive flexibility to cope with seasonal fluctuations in temperature and food availability

Endurance Running

- Aerobic exercise increases levels of brain derived neurotrophic factor (BDNF), insulin-like growth factor 1 (IGF-1), and vascular endothelial growth factor (VEGF), which appear to lead to exercise-induced neurogenesis in the rodent and human hippocampus
- Study: variation in brain mass across a wide range of nonhuman mammals is significantly positively correlated with variation in maximal metabolic rates
- There is an association between total brain size and the capacity for aerobically supported, endurance-type exercise across a wide range of mammals.
- Novel hypothesis that details a possible evolutionary mechanism. The evolution of exercise capacity may lead to the upregulation of neurotrophins and growth factors that increase brain growth and development.

D. A. Raichlen & A. D. Gordon, PLoS One, 2011

Linking brain and brawn: exercise and the evolution of human neurobiology

- Hypothesis that human neurobiology was influenced by our evolutionary history as endurance athletes. As early as 1.8 Ma, our ancestors began walking and running longer distances than previous hominin taxa and morphological adaptations for increased aerobic activity levels during human evolution are correlated with increases in brain size Evolution of increased aerobic capacity had a significant effect on brain evolution in athletic mammals, including humans.
- In particular, aerobic physical activity (APA) generates, and protects new neurons, increases the volume of brain structures and improves cognition in humans and other mammals.
- There is an evolutionary relationship between APA and the brain, including a positive correlation between aerobic capacity and brain size across a wide range of mammal. However, at the same time as brain size began to increase in the human lineage, aerobic activity levels appear to have changed dramatically. Our ancestors, beginning with *H. erectus*, shifted to a hunting and gathering lifestyle that required higher levels of aerobic activity, with morphological evidence showing adaptations for increased long-distance trekking and the adoption of endurance running (ER; aerobic running for distances of more than 5 km) as a new hunting method.

David A. Raichlen, John D. Polk, 2012

Aerobic physical activity 2

- Aerobic physical activity (APA) appears to lead to neurogenesis, neuroprotection and cognitive improvements in adults primarily through the upregulation of neurotrophins and growth factors.
- Brain-derived neurotrophic factor (BDNF) is among the more important neurotrophins involved in APA-induced neurogenesis. Voluntary and forced running in rodents and humans results in a significant upregulation of BDNF, which improves neuronal survival
- In addition to BDNF, concentrations of two growth factors—insulin-like growth factor I (IGF-1) and vascular endothelial growth factor (VEGF)—increase with physical activity, and both are known to play a role in neurogenesis
- Long-term endurance training increases circulating levels of IGF-1 and VEGF in humans at rest

Diet: Evolution of Feeding Behavior

Feeding Behavior: keep a high bit rate for signaling neurons

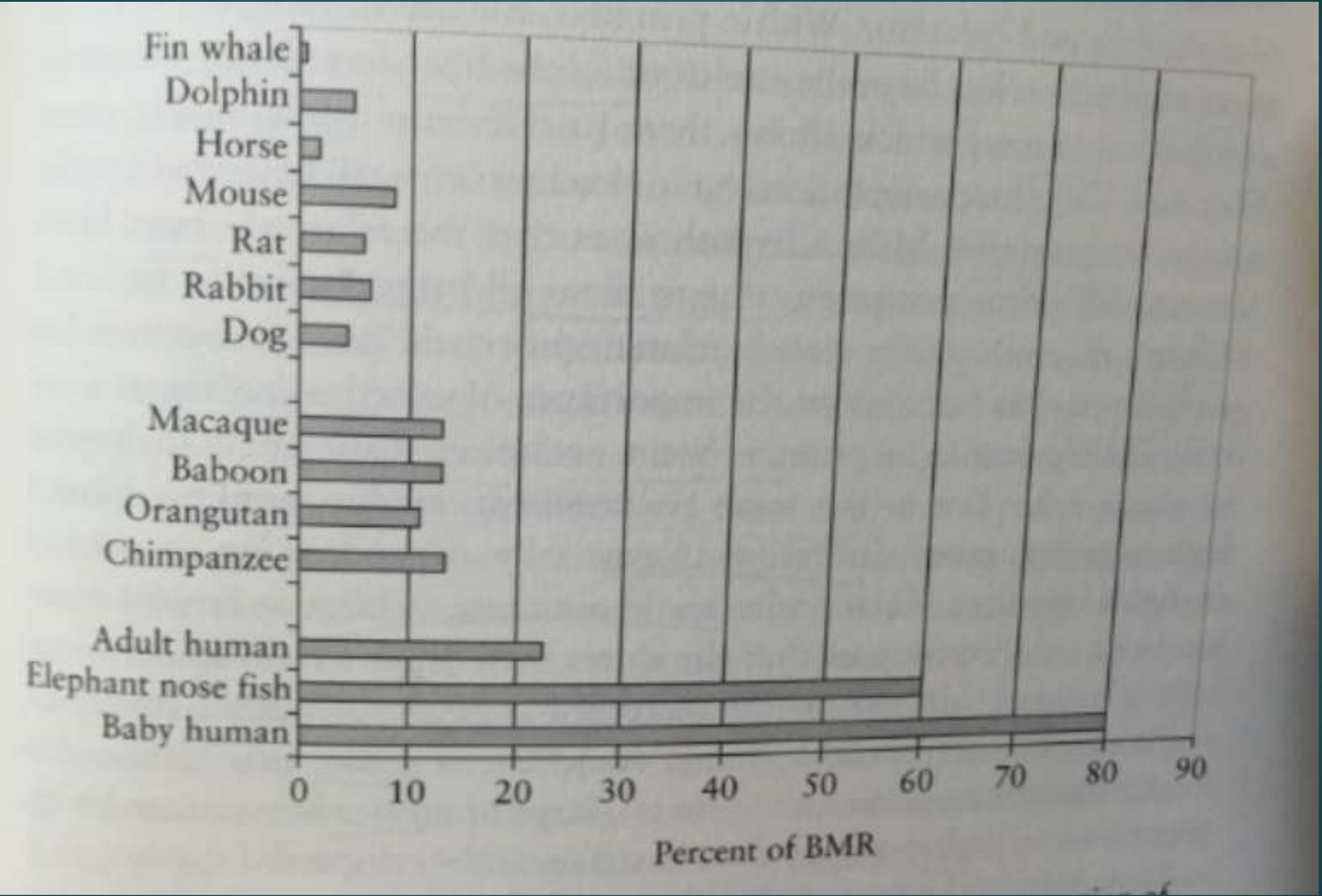
- Feeding behavior is at the core of a species adaptive ability; from the beginning human brain has been shaped by eating and nutrition
- Larger brains are energetically expensive; 16 x more energy than muscles; mitochondria in axons and synapses are primary users; neuronal signaling uses 50% of energy
- Brain is 2% of body mass, but accounts for 20-25% of BMR; 80% in infants (in other primates its 8-13%; in non-primate mammals, its 3-5%); only elephant nose fish uses more (60%)
- Humans did not increase BMR, which is as expected for mammal of its size.

‘Expensive tissue’ hypothesis (Aiello & Wheeler, 1995)

- Large brain is **energy hungry** — human brain consumes 25% of our energy when resting.
- In infants, 80**%** of body’s energy!
- GI tract is 60% smaller than expected.

Graphic from Getty Images

Human Babies use 80% & adults use 24% of BMR in brain



Expensive Tissue Hypothesis

- The human brain occupies only 2% of body mass, but consumes about 20% of total metabolism. Other organs (heart, liver, kidney, GI tract) are equally 'expensive'. All organs consume about 70% of BM.
- According to the 'expensive tissue hypothesis' by Aiello and colleagues, every increase in brain size must be balanced by a reduction of the demands of the other 'expensive' organs.
- The solution for the 'energy crisis' of the human brain consisted in a reduction of gut size, which had to be compensated by an increase in the quality of food, that is, higher nutritional value and digestibility.
- In most primates, diet quality and brain size are significantly positively correlated and evolutionary changes in diet quality are related to changes in relative brain size.

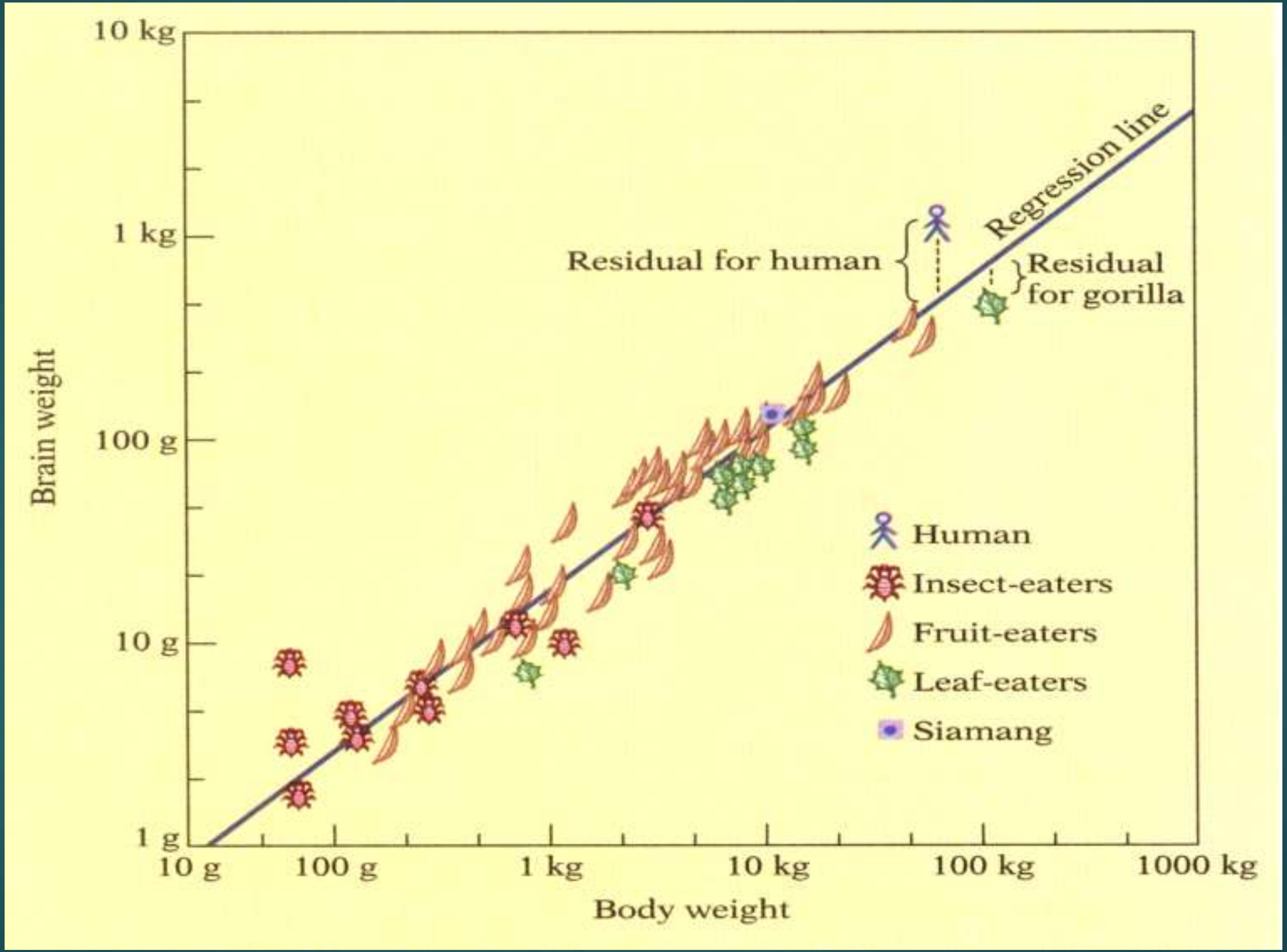
Why is the Hominid Brain Enlarged ? Eating fruit

The Primate Lifestyle

- Eating behavior of primates is more complex than other animals
  - Finding fruit is more difficult than eating grass
  - Color vision & enlarged visual area required for finding ripe fruit

- Fruit eaters need good sensory, spatial, and memory skills
  - Fruit eaters have larger brains

Fruit eaters have larger brains

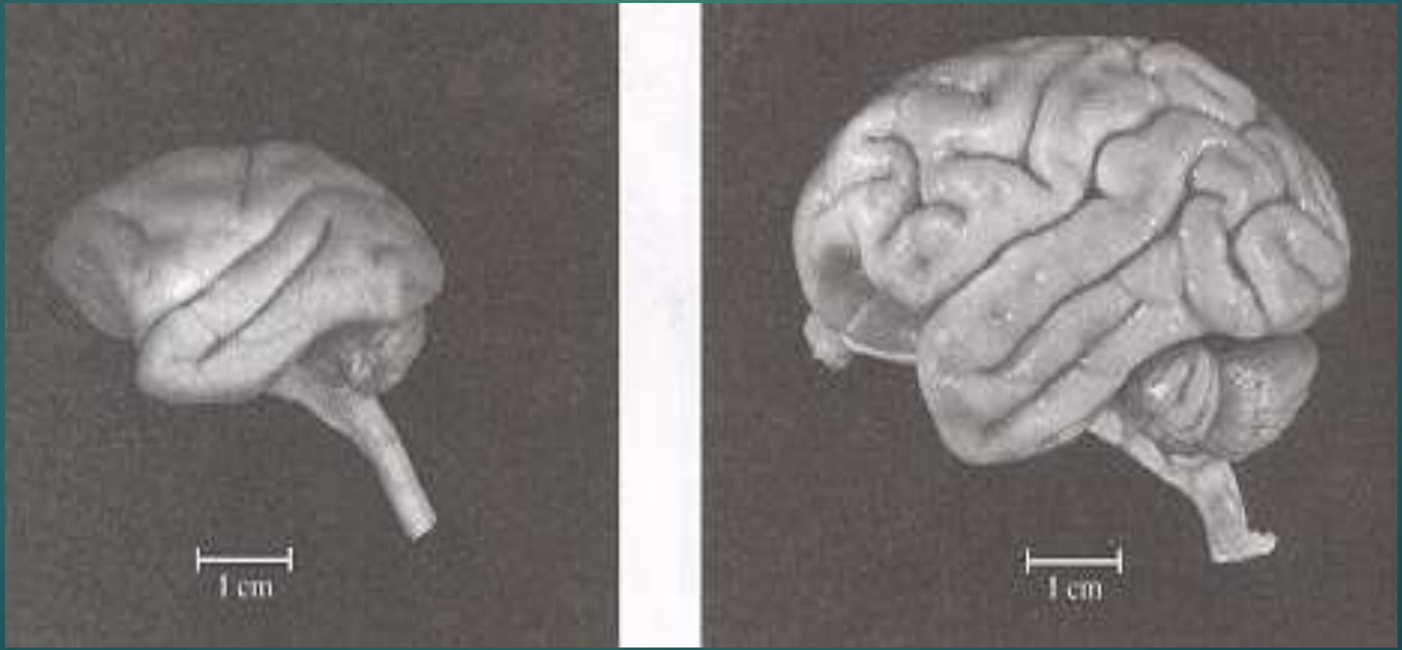


Allman J., 1999

Brains of Fruit-Eaters

- Howler monkeys and spider monkeys are approximately the same size but the fruit-eating spider monkey has a much larger brain and well-developed brain than the leaf-eating howler monkey.

Photos from Allman, 2000, p 166



howler monkey **spider monkey**

Diet

- Finding fruit and meat require memory for food locations, and increased social co-operation.

- The Australopithecines were herbivores and small brained.

- As the early hominids moved from vegetarian to more protein-based diets (meat and fish) their teeth and jaws became smaller and brain size increased.

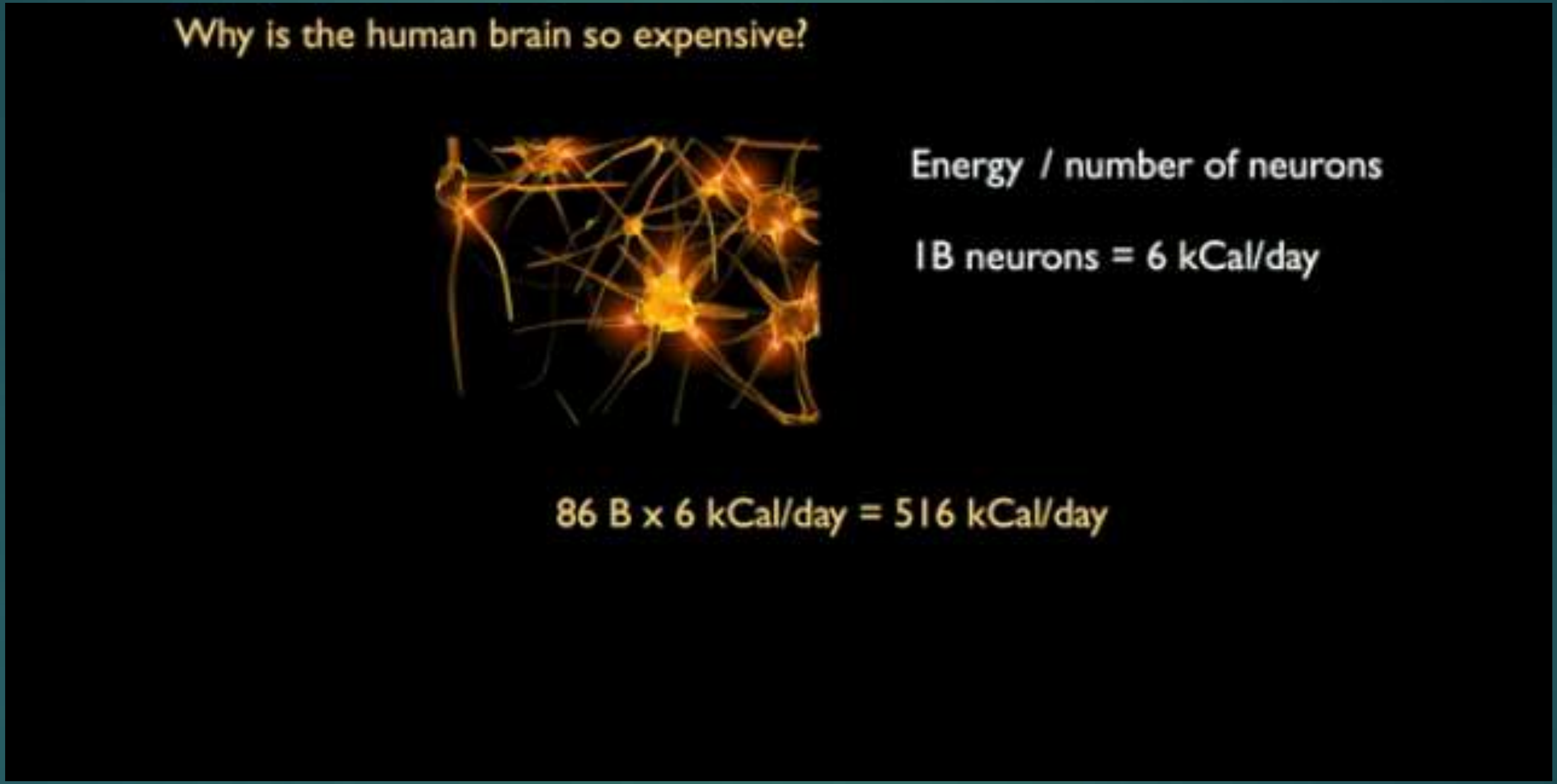
- Leaf-eaters (folivores) have smaller brains with proportionally less neocortex in relation to body size than frugivores (fruit eaters) and carnivores.

Brain is metabolically expensive

- Large brain is metabolically expensive tissue, requiring increase in quality of hominid diet
- Among primates, large brain size correlates with more diverse, higher quality diets; diet quality also associated with gut size
- Size of digestive organs is negatively correlated with brain size
- Did we need fish, meat or nuts?
- Smaller brain, shorter gut

Chimp, A. Afarensis, H. sapiens

Energy is just right



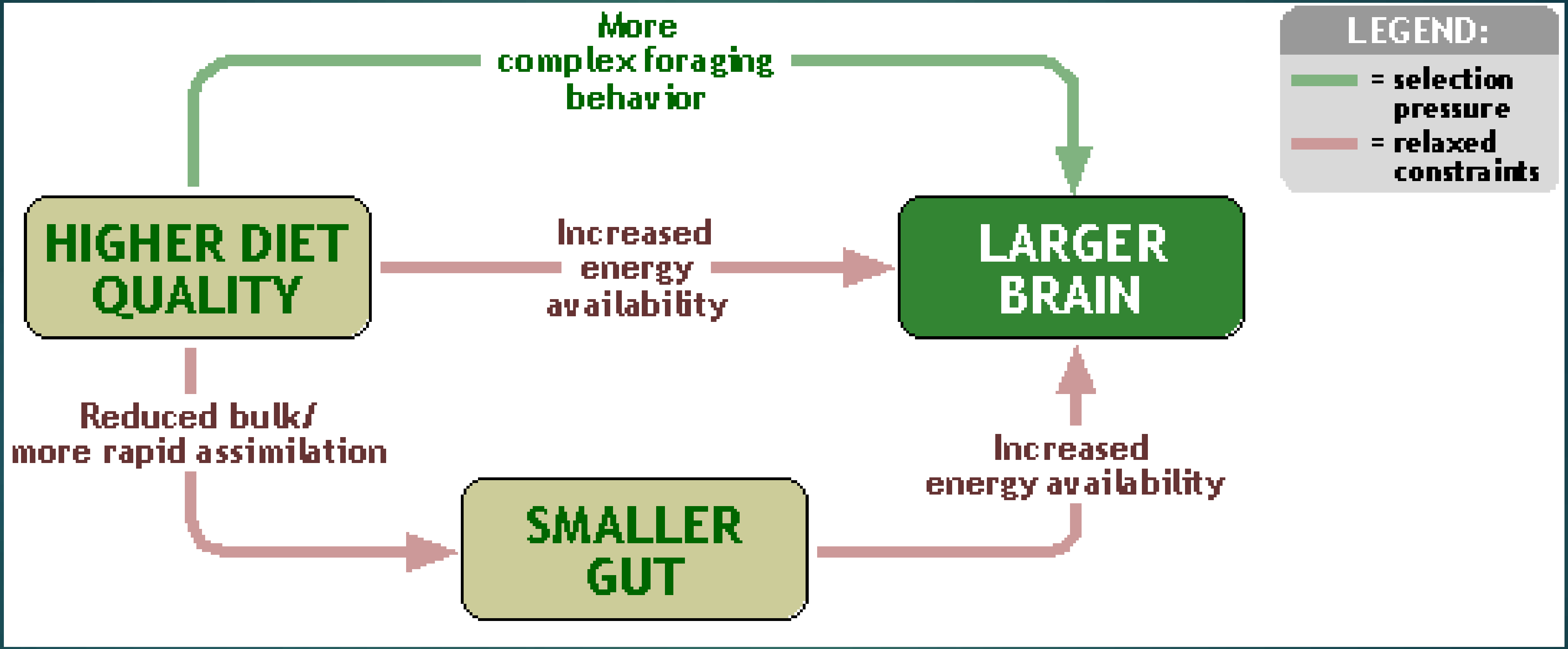
Amount of human brain energy is linear function of the number of neurons

Suzana Herculano-Houzel, , TED, 2013

Brains and Guts!

- Gibbons (1998) pointed out that while the human brain has expanded greatly, our basal metabolic rate is similar to our ape relatives.
- Brain expansion was accompanied by a reduction in the gastrointestinal tract due to a shift from relatively indigestible vegetarian matter to a diet rich in protein and fat which requires less digestion and provides more energy.
- The human gut is around 60% smaller than would be expected for an animal of our size
- The guts of chimpanzees and gorillas are optimised for fruit eating and leaf eating respectively, the human gut is optimised for high energy diets (principally derived from eating meat).

Diet, selection and reduced pressure

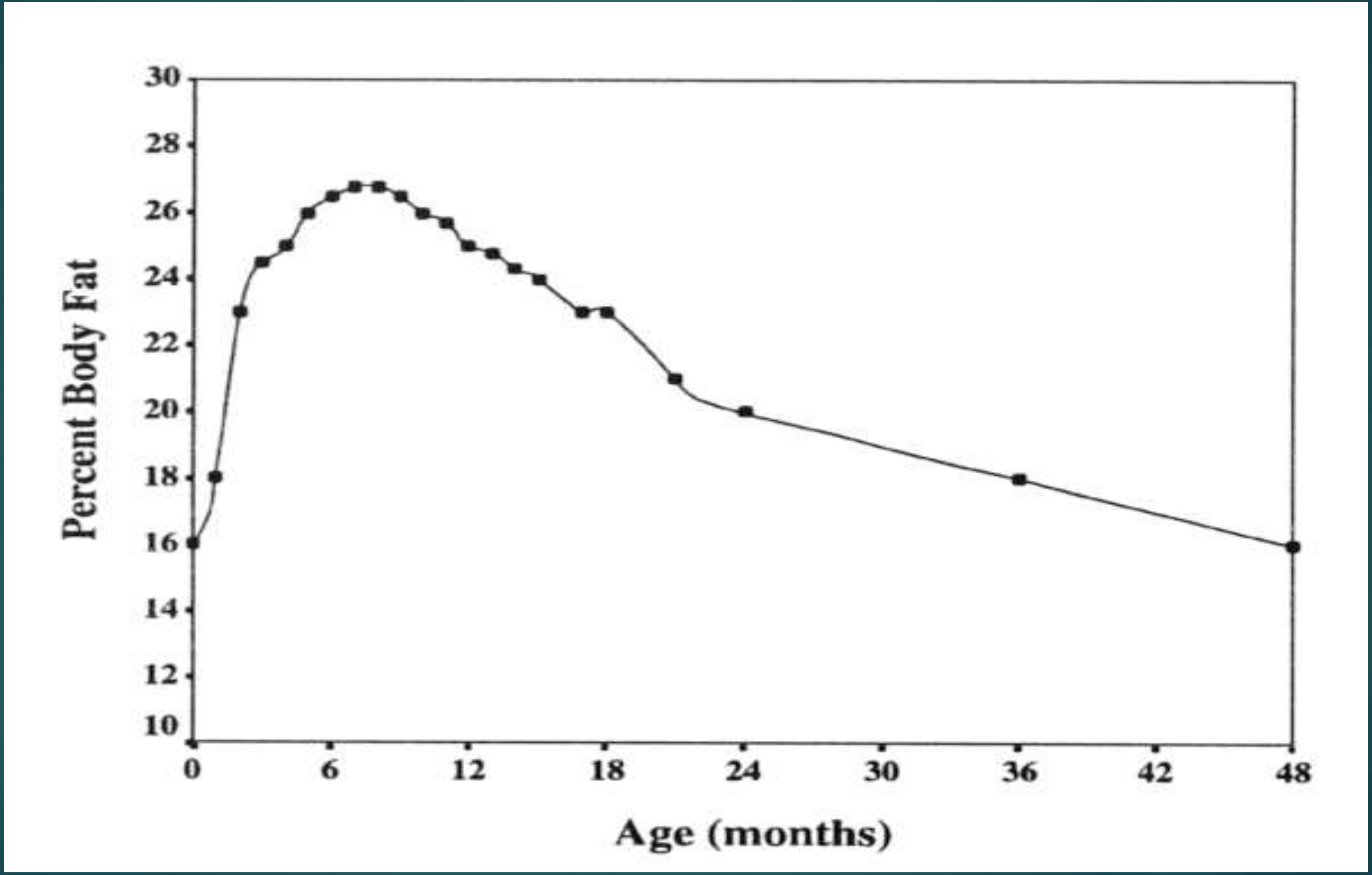


Brains need fat

- Neural connectivity is determined by the availability of phospholipids, which make up 60% of the brain.

- Axons and dendrites rely on a supply of the essential fatty acids (arachidonic acid, and docosahexaenoic acid) and the essential amino acids, and can only be obtained from a diet rich in animal protein (meat, fish, eggs).

Changes in percent body fat in human infants



Leonard et al., Comp. Biochem. Physiol., 136, 5-15, 2003

Survival of the fattest

- Human babies are fat; 15% body fat (substantially fatter than other mammals); infant brains use over 80% of BMR
- Fat babies were the key to evolution of the large human brain.
- The fattest infants became mentally the fittest adults. Importance of fat and cholesterol for myelin & white matter (brain has 20% of all cholesterol in body)
- Body fat in infants provided fuel store for the brain.
- Breast fed babies have bigger brains & higher IQs
- Need for reliable source of fatty acids (DHA): fish and shellfish

Cunnane & Crawford, Comp. Biochem. Physiol., 136, 17-26, 2003

Baby body fat enables brain growth by
(1) having a ready supply of stored energy in periods when food is lacking
(2) Reducing total energy costs (e.g., by not having to explore the environment for food)

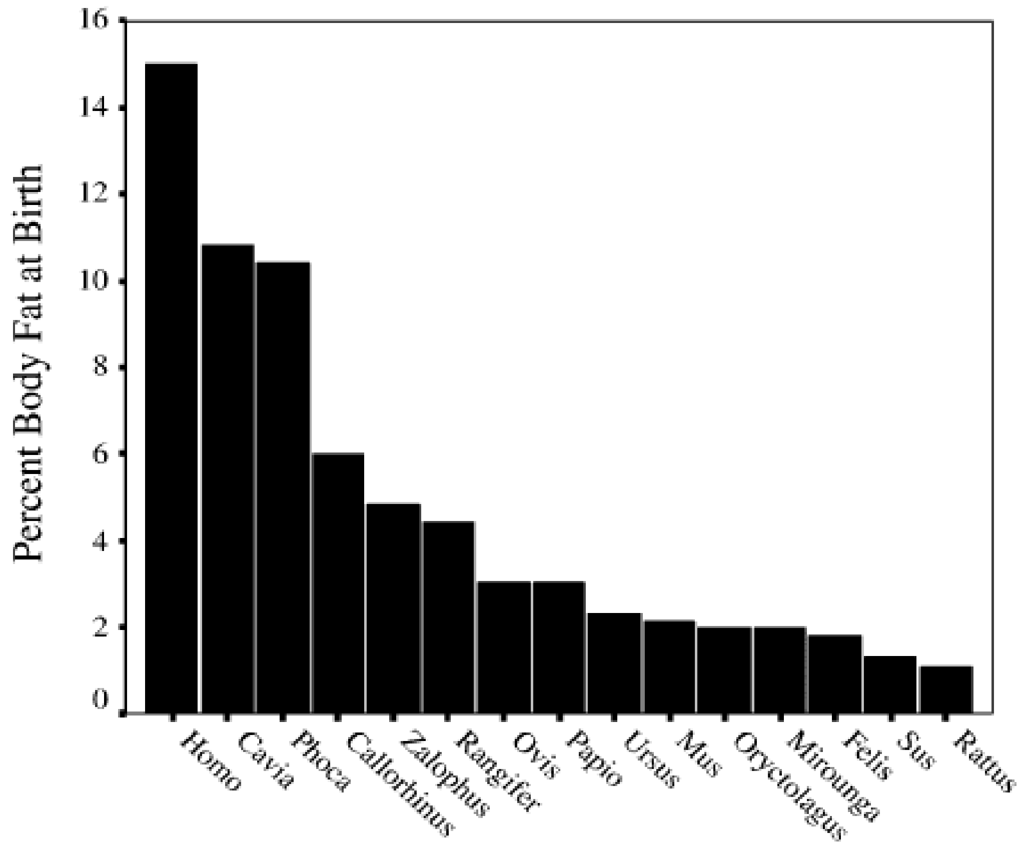


Fig. 6. Percent body fat at birth of 15 mammalian species (adapted from Kuzawa, 1998). At 15–16% human infants have the highest level of adiposity.

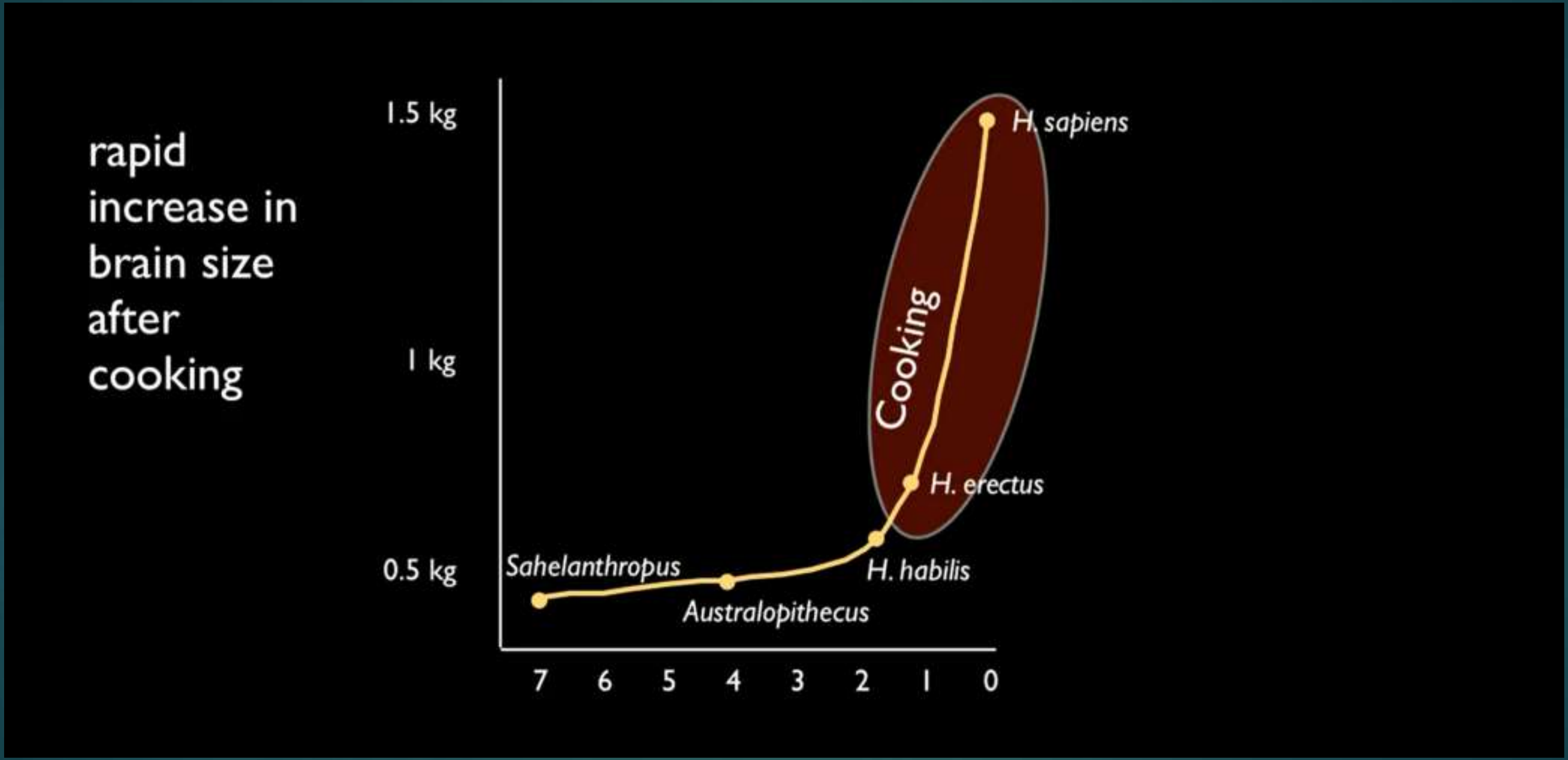
Something fishy about the brain?

- **Shoreline foraging** provided high protein frogs, clams, fish, & bird eggs (fish bones with *H. habilis*).
- **Shore rather than savannah** as the crucial niche.
- Eating fish as a diet adaptation that is strongly implicated in human brain development?
- Omega 3 in humans

‘Man the hunter’ hypothesis

- Did **hunting** drive human evolution by fueling hungry brain?
- Evidence of **butchering** in stone marks on bones & refuse piles.
- Modern foragers get **50% of calories** from meat (chimps <3%).
- Might seek especially **rich foods** (like brains or marrow).
- Would also help explain **expanding range** of *H. erectus* (out of Africa).
- But data and jaw suggests **small animal hunting** (not romantic image of big game hunting).

Rapid increase in brain size after cooking



Meat and cooking

- Meat is a high-quality food, esp. from wild game animals, lean & low in saturated fats; good source of omega-3

- Richard Wrangham: role of cooking in hominid evolution

- His cooking hypothesis: enhanced food, social dynamics, male-female sexual bonding, decrease in sexual dimorphism

Dietary hypotheses: We were omnivores

- Hunting revolution was first dietary revolution idea linked to increased brain size
- Scavenging hypothesis
- Aquatic food hypothesis
- Cooking revolution
- Absence of compelling evidence

- Reality: flexibility and variability were keys in dietary behavior; we were omnivores

Diet of early Homo?

- Evidence suggests no single pattern (‘unspecialized frugivore’)
- Perhaps the best evidence of dietary versatility and ability to inhabit variety of ecological niches
- The most interesting thing is the ability to meet energy demands from varied niches with underdeveloped guts, jaws and teeth.
- Humans were likely omnivores for a very long time; clearly occupied a different niche from other living Great Apes
- Paleo diet: Modern health problems are not because we are eating the wrong food; the problem is the lack of activity and surplus of calories.

Coevolution of increased brain size & longevity: Brains and Time

- Big brains live longer:
  - Brain size & longevity are highly correlated in mammals and primates

- The primate sex who is the child caregiver lives longer:
  - social mediation? – male competition; higher BMR for bigger males
  - female chimps live 42% longer;
  - human women live 10 years longer than men
  - Males in species, where fathers are caretakers, live longer

Grandmother hypothesis

- Grandmother hypothesis: menopause is adaptive & basis for longevity selection in humans
  - fitness gains obtained through a relative's reproductive success (assist daughters by feeding children; reduce weaning age, allow daughters to become fertile and reduce birth spacing)
  - Intergenerational caregiving
  - Intergenerational information transfer, esp. about food resources, esp. about rare crises events
  - Extended family: nurturing of growing dependent brain & sharing memories of a life time of information
  - White matter & hippocampal volume peak with menopause

Genes

Large portion of brain reorganization took place at genetic and molecular level during human evolution independent of brain size changes

Genes and Behaviour
The Nature Nurture Fallacy

Genes do not determine, control or cause behaviour.

Rather, they influence the probability that behavioural differences will be expressed in a given environment.

And they do this by interacting with the environment.

Behaviour Genetics: Themes from model organisms with applicability to humans

1) There is significant genetic variation for most behavioral traits (familial, artificial selection).
2) Multiple genes affect each behavioral trait. Most have small effects.
3) Pleiotropy rules.
4) Gene x Environment interactions are pervasive.
5) Environment affects gene expression.
6) Genes affect social behavior- animals self select environments (risk prone)
7) Sex differences are pervasive (>50%) of genes are differentially expressed between the sexes.
8) Genetic background (gene-gene interactions)
9) Single gene effects-downstream genes.

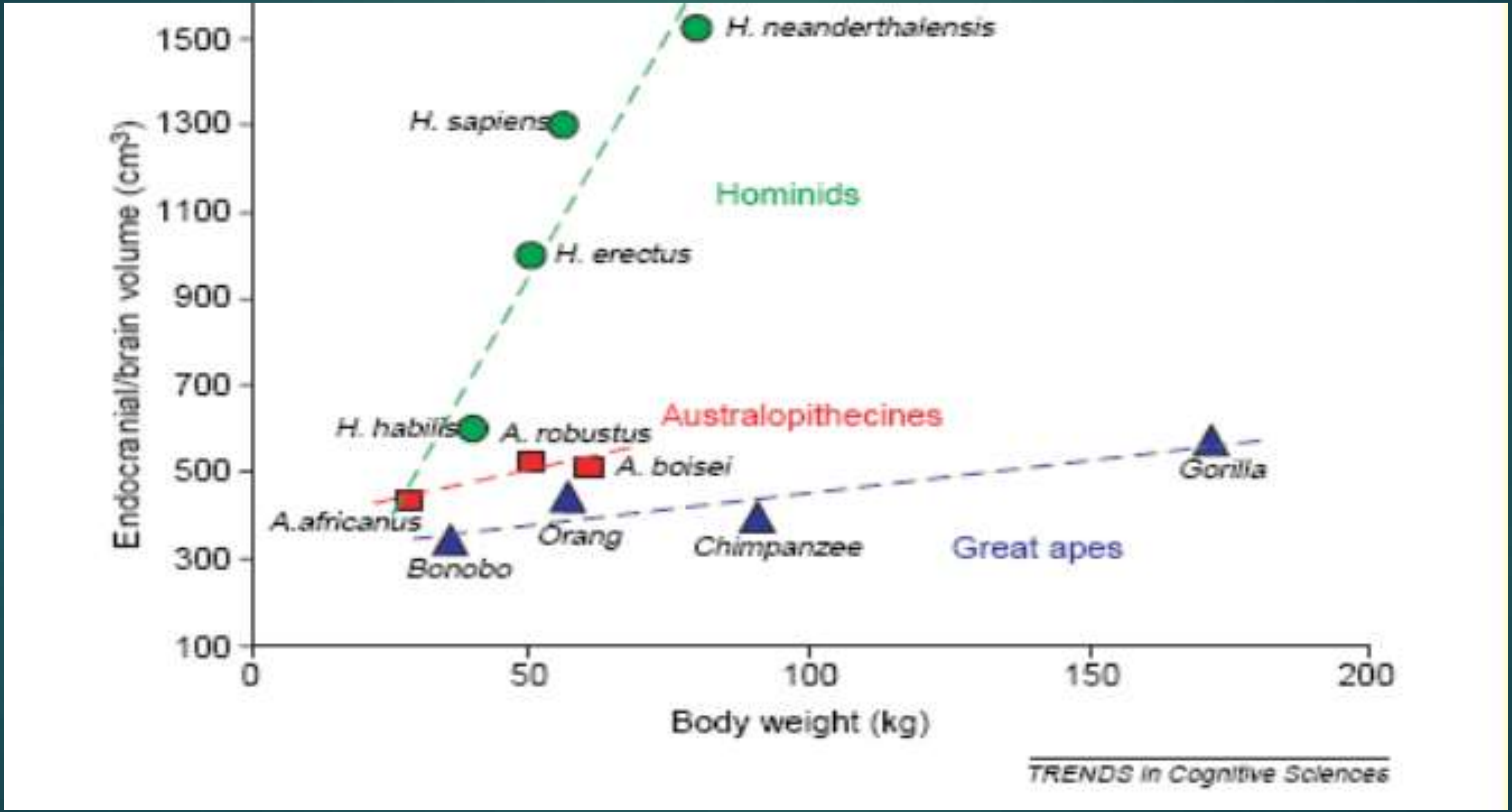
Sokolowski 2001. Nature Reviews Genetics;
Kendler and Greenspan 2006. Am. J. Psychiatry

Some major effects

Different alleles of gene have consequences

Pleiotropy rules: A gene that affects behavior will have multiple phenotypes; 1 gene affecting many things (behavior, development, etc..

The steep increase in brain size in hominides is possibly due to genetic mechanisms affecting cell devision during embryonal cortical grow.

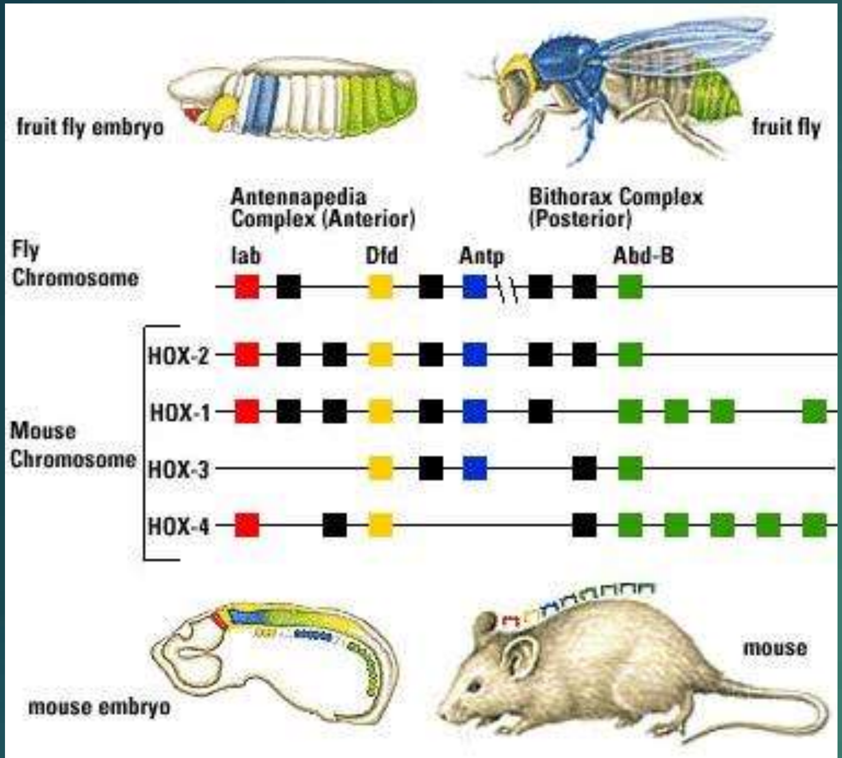


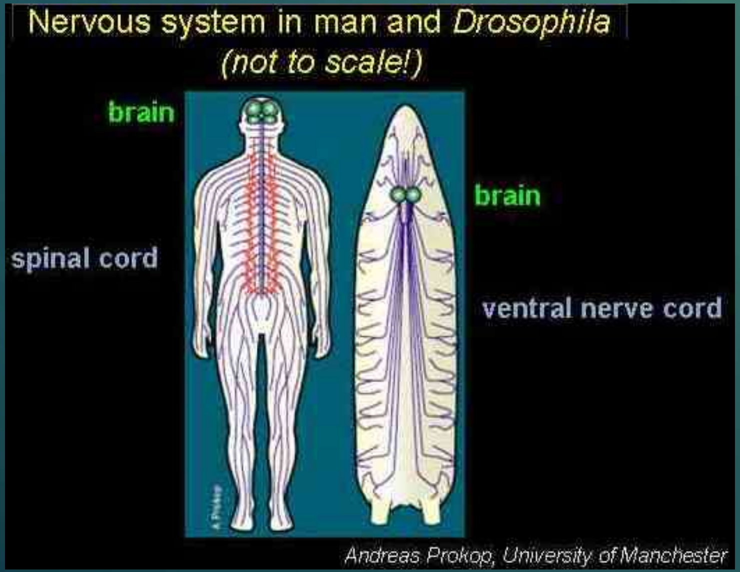
Gene expression

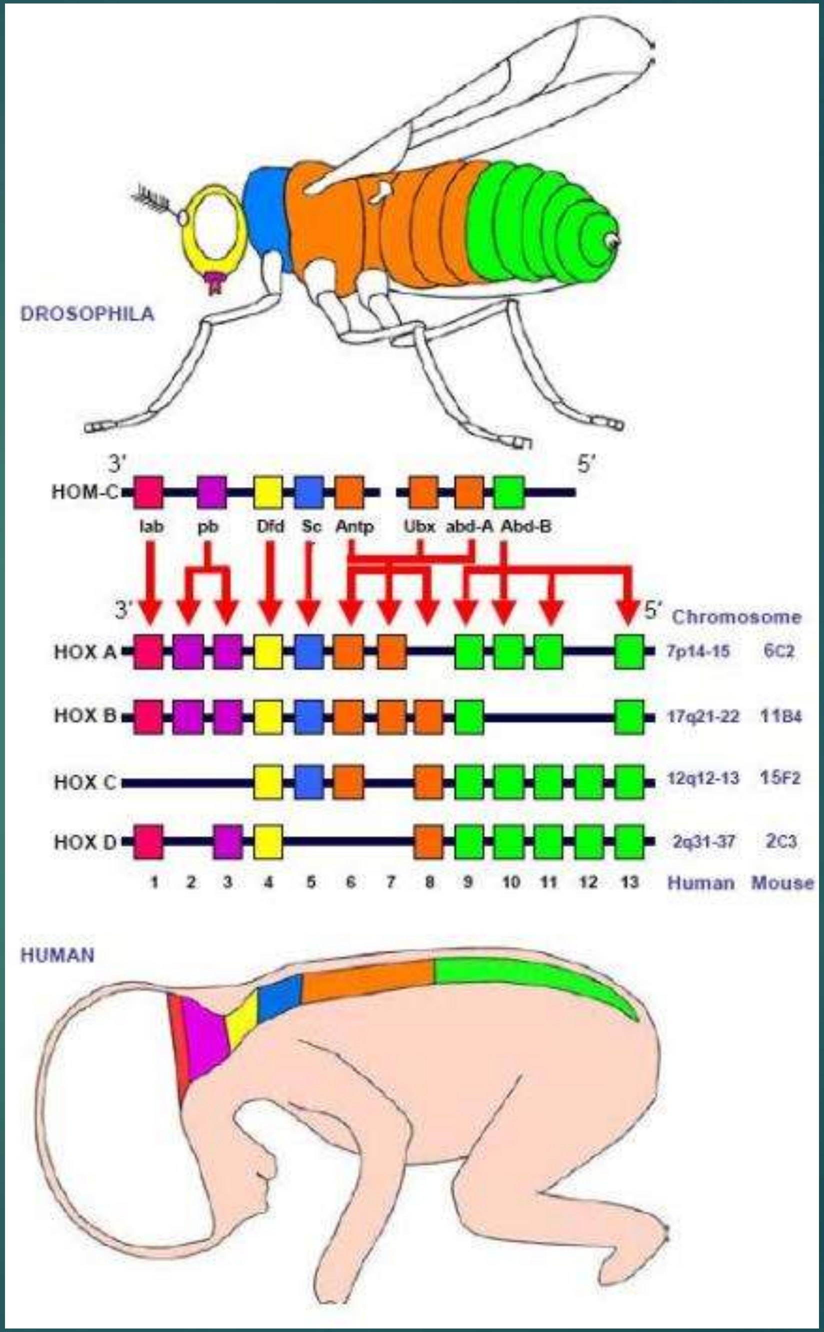
- Gene expression is highly conserved between human and chimp brain; more variability in it among regions of human brain
- Gene expression associated with neural development is delayed in humans
- Timing of expression associated with synaptic function in prefrontal cortex is extended.
- Most differences in human gene expression involves up-regulation or increased expression level (energy metabolism, synaptic plasticity, cell growth, cellular maintenance, protein targeting)

Elevated neuronal activity?

- Caceres et al. (2003) applied a variety of genetic techniques to the cortical tissue (removed post-mortem) of humans, chimpanzees and rhesus macaques.
- These suggested that humans and chimpanzees are more similar to each other than to the macaques, which is as expected,
- But here were dozens of genes that were expressed very differently in human and chimpanzee cortex, with 90% of these being expressed more actively in humans.
- The human is brain is characterized by "**elevated levels of neuronal activity**".
- As a contrast, comparing gene expressing in the human and chimpanzee heart and liver revealed very little difference of this kind.



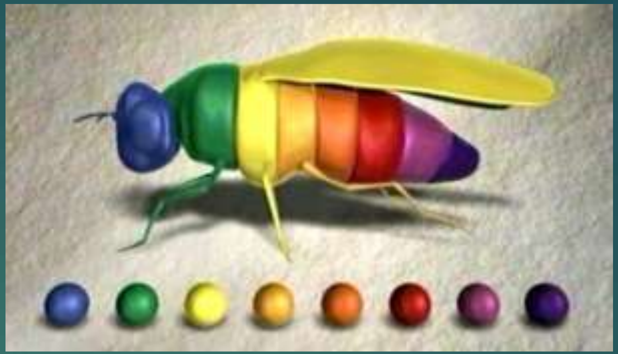


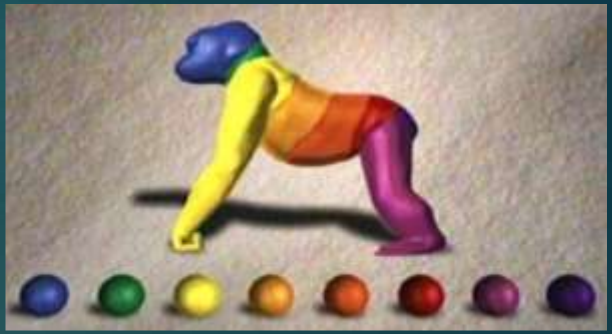


500 MY old Homeobox genes (180 base-pair DNA sequence; encode 60 amino acids) and their effect on structural development are active in humans

Lappin et al., 2006

Genes





- Transcription factors regulate patterns of cell adhesion molecules and their downstream target genes (regulate where and when genes activate) covary with aspects of cortical organization, such as cortical field size, location, and connectivity

- Homeobox genes from the *Hox* family are highly conserved across animals; a product of gene duplication; homeobox genes play an important role in vertebrate forebrain development (becomes neocortex), promote migration of GABAergic interneurons to the neocortex

More genetic suggestions for human uniqueness

- Prabhakar et al, (2006) found many human-specific changes in regulatory sequences of DNA with almost no overlap with chimpanzee equivalents and suggest that these may have contributed to uniquely human features of brain development.
- Homeobox gene *Emx-1 & Emx-2* in mammals: regulate formation of cortex; disruption leads to corpus callosal agenesis (so 500 MYA gene disrupts a placental mammal brain structure – clearly a new function); mutation of Emx-2 causes formation of deep clefts in cortex (Schizencephaly)
- *BF-1 & BF-2:* expressed exclusively in developing forebrain (cell division before migration)
- *Tailless:* ancient formation of gut gene also controls forebrain growth; mutation reduces size of cortex and amygdala in mammals

Genes: Humans have 83 genes that are unique

- Gene expression in humans is similar and different from nonhuman primates
- There is a regionality of gene expression, consistent with idea of specific brain regions. In cerebral and cerebellar cortex in humans, 1,600 genes are differentially expressed in 2 tissues; 89 genes are specifically expressed in 1 or other. These genes are functionally related to signal transduction, neurogenesis, synaptic transmission, and transcription (all related to neuronal function).
- Substantial overlap in genes expressed in prefrontal cortex in humans & great apes.
- 62% of human genes present in apes (vs. 46% in monkeys)
- 98% identical DNA between chimpanzees and humans; differences between them due to changes in gene expression; only 83 genes have higher expression in humans

Gene Duplication

- Gene duplications are an essential source of genetic novelty that can lead to evolutionary innovation.
- Duplication creates genetic redundancy, where the second copy of the gene is often free from selective pressure — that is, mutations of it have no deleterious effects to its host organism. If one copy of a gene experiences a mutation that affects its original function, the second copy can serve as a 'spare part' and continue to function correctly.
- Thus duplicate genes accumulate mutations faster than a functional single-copy gene, over generations of organisms, and it is possible for one of the two copies to develop a new and different function
- Protein domain amplification (Intragenic copy number increase of a protein domain), the process by which a protein domain undergoes a copy number increase, has recently emerged as important.

DUF1220 Domain Copy Number

- DUF1220 domains show the largest human-lineage-specific increase in copy number of any protein-coding region in the human genome and map primarily to 1q21, where deletions and reciprocal duplications have been associated with microcephaly and macrocephaly, respectively.

- Humans have more than 270 copies of [the protein] DUF1220 encoded in the genome, far more than other species. The closer a species is to humans, the more copies of DUF1220 show up. Chimpanzees have the next highest number, 125. Gorillas have 99, marmosets 30 and mice just one.

- The more copies of DUF1220 in the genome, the bigger the brain. And this held true whether we looked at different species or within the human population.
- DUF1220 copy number exhibits the strongest correlation with brain gray-matter volume

Laura J. Dumas, et al., 2012

Genome	PDE4DIP	Total DUF1220	NBPF Genes
Human	2	272	23
Chimp	3	125	19
Gorilla	3	99	15
Orangutan	4	92	11
Gibbon	3	53	10
Macaque	1	35	10
Marmoset	1	31	11
Mouse Lemur	1	2	1
Bushbaby	1	3	2
Tarsier	1	1	0
Rabbit	1	8	3
Pika	1	1	0
Mouse	1	1	0
Rat	1	1	0
Guinea Pig	1	1	1
Squirrel	1	1	1
Tree Shrew	1	4	3
Cow	1	7	3
Dolphin	1	4	1
Pig	1	3	1
Horse	1	8	3
Dog	1	3	1
Panda	1	2	1
Cat	1	3	2
Megabat	1	1	0
Microbat	1	1	0
Hedgehog	1	1	0
Shrew	1	1	0

- DUF1220 shows greatest human specific copy number expansion of any protein coding sequence in the human genome
- Show signs of positive selection
- Human increase primarily due to domain amplification (rather than gene duplication)

O'Bleness *et al*. Evolutionary History and Genome Organization of DUF1220 Protein Domains. G3 (Bethesda). Sept (2012).

Noteworthy DUF1220 Copy Number Totals

	DUF1220 Copies
Total in Human Genome	272
Total in Chimp Genome (CLS)	125 (23)
Total in Last Common Ancestor of *Homo/Pan*	102
Total of Newly Added Copies in Human Lineage	167
Total Human-Specific Copies Added via Domain Amplification	146
Total Human-Specific Copies Added via Gene Duplication	21
Avg. Number Added to Human Lineage Every Million Years	28

O'Bleness, *et al*, G3: Genes, Genomes, Genetics, 2012

Volume correlation in Twins vs Environmental impact

Genetics (high correlation in twins)	Environment
Overall brain volume (highly corr. In twins, .7-.9)	Surface contours (not identical in twins)
Total White and Grey areas	Sulcal-gyral morphology
Cerebrum	Visible appearance of brain
Cranial capacity	Cerebellar volume
Volume of major lobes	
Corpus callosum (.8-.9)	Hippocampus (.4)
MFC, SFC, STC,	Content of left visual word recognition area
Left occipital cortex	
Amygdala	
Brain size & IQ (.5), Grey matter & IQ	

Brain plasticity: genetic basis of brain size

- Genetic studies indicate brain size and sizes of some brain regions are highly heritable, others are not.

- Interaction of genetics and intensive training: Several genes that are known to participate in regulating the dynamics of proliferation and programmed death of cerebral precursor cells show evidence of positive selection in the hominin clade since the LCA.

Gene Expression

- Many genes related to brain development and function show signs of accelerated evolution exclusively in humans
- Human cerebral cortex displays up-regulation of genes related to neuronal signaling, plasticity, and metabolic activity
- There are increasing numbers of glial cells relative to neurons in the primate neocortex as a function of brain size, and humans have the highest glia-neuron ratio

Reports of “human-specific” genes ?

- FOXP2
  - Highly conserved, but mutated in family with language disability
- ASPM/MCPH
  - Mutated in individuals with microcephaly
- HAR1F
  - Gene sequence highly changed in humans
- SRGAP2 (neuronal migration?)
  - Partial human-specific gene duplication
- DUF1220 protein domains
  - Highly increased in copy number in humans; expressed in important brain regions

FoxP2

- The transcription factor *FOXP2:* Based on the association of certain point mutations of this gene with grammatical impairment and orofacial dyspraxia, accompanied by functional under-activation and structural abnormalities of language-related brain regions,
- *FOXP2* has been suggested to play a role in the development of language and speech in humans; The human variant of *FOXP2* has been reported to also be present in Neandertals

Genetic Brain Evolution

- Of 23 most conserved positions affected by amino acid changes, 8 affect genes that are associated with brain function or nervous system development (NOVA1, SLITRK1, KATNA1, LUZP1, ARHGAP32, ADSL, HTR2B, CBTNAP2)
- 4 are involved in axonal and dendritic growth (SLITRK1, KATNA1) and synaptic transmission (ARHGAP32, HTR2B); 2 have been implicated in autism (ADSL, CNTNAP2).
- CNTNAP2 is also associated with susceptibility to language disorders and it is one of the few genes known to be regulated by FOXP2, a transcription factor involved in language and speech development as well as synaptic plasticity.
- It is thus tempting to speculate that crucial aspects of synaptic transmission may have changed in modern humans.

Meyer M, et al.,. A High-Coverage Genome Sequence from an Archaic Denisovan Individual Science. 2012.

ASPM

- Wondered whether the genes that cause microcephaly, an inherited human disorder in which brain size is greatly reduced, might include genes involved in human brain evolution.
- In 2002, mutations in the genes *ASPM (abnormal spindle-like microcephaly associated) and microcephalin* were identified as two causes of microcephaly.
- Both these genes have been under selective pressure during primate evolution.
- *ASPM* encodes a protein involved in spindle formation, so it is tempting to think that changes in its sequence might result in an increased rate of cell division and hence brain size.

- Most recent research does not show large difference between humans and apes

Neurotransmitters are ancient

- Dopamine before the vertebrates: process of food intake in jawless vertebrates, like lampreys
- Dopamine related to novelty seeking, “response ready” adaptation

Sun, T., & Walsh, C. A. (2006). Molecular approaches to brain asymmetry and handedness. *Nature Reviews Neuroscience, 7*(8), 655-662

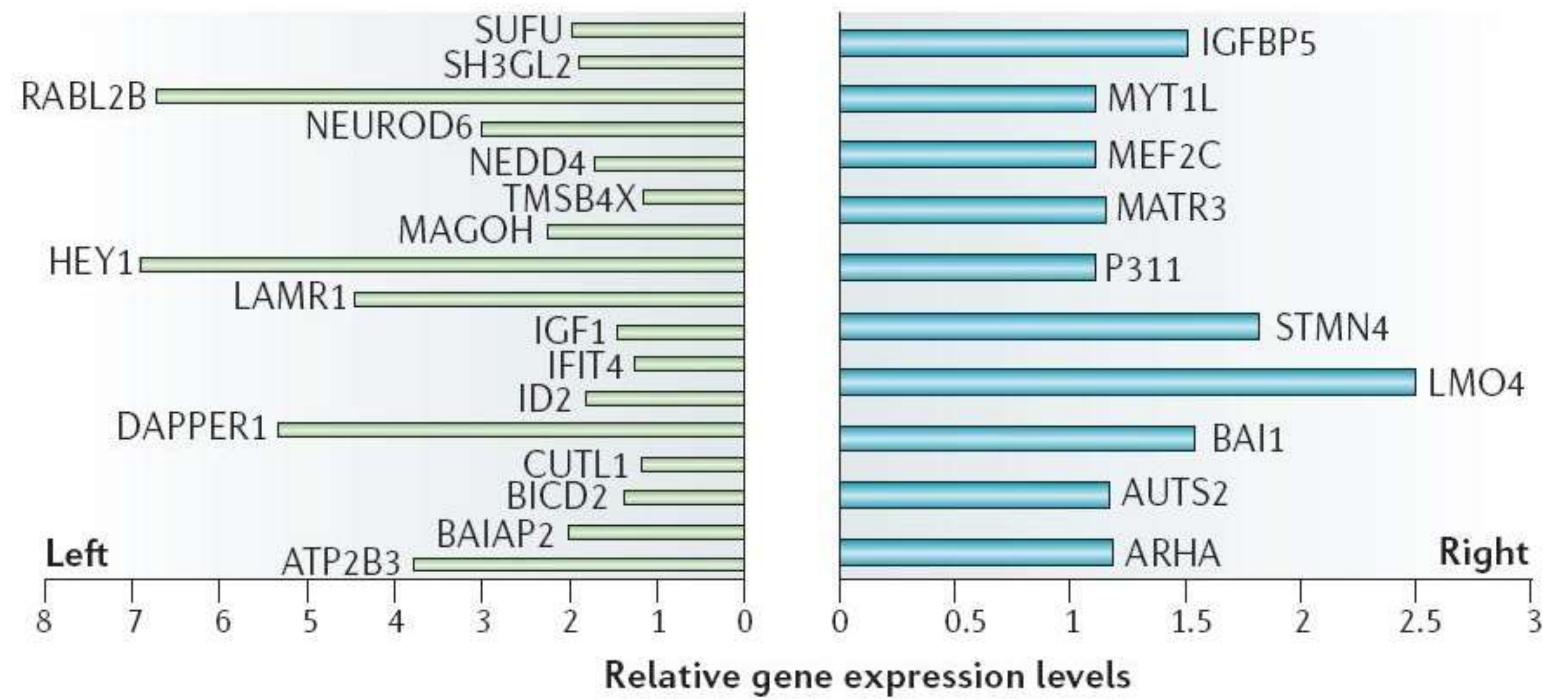


Figure 2 | **Asymmetrically expressed genes in 12-week-old human fetal brains,**

Gene expression differences in left and right hemispheres of two brains. 27 genes showing consistent differential expression are listed. Among them, 17 genes were highly expressed in the left perisylvian regions, whereas 10 genes were highly expressed in the right.

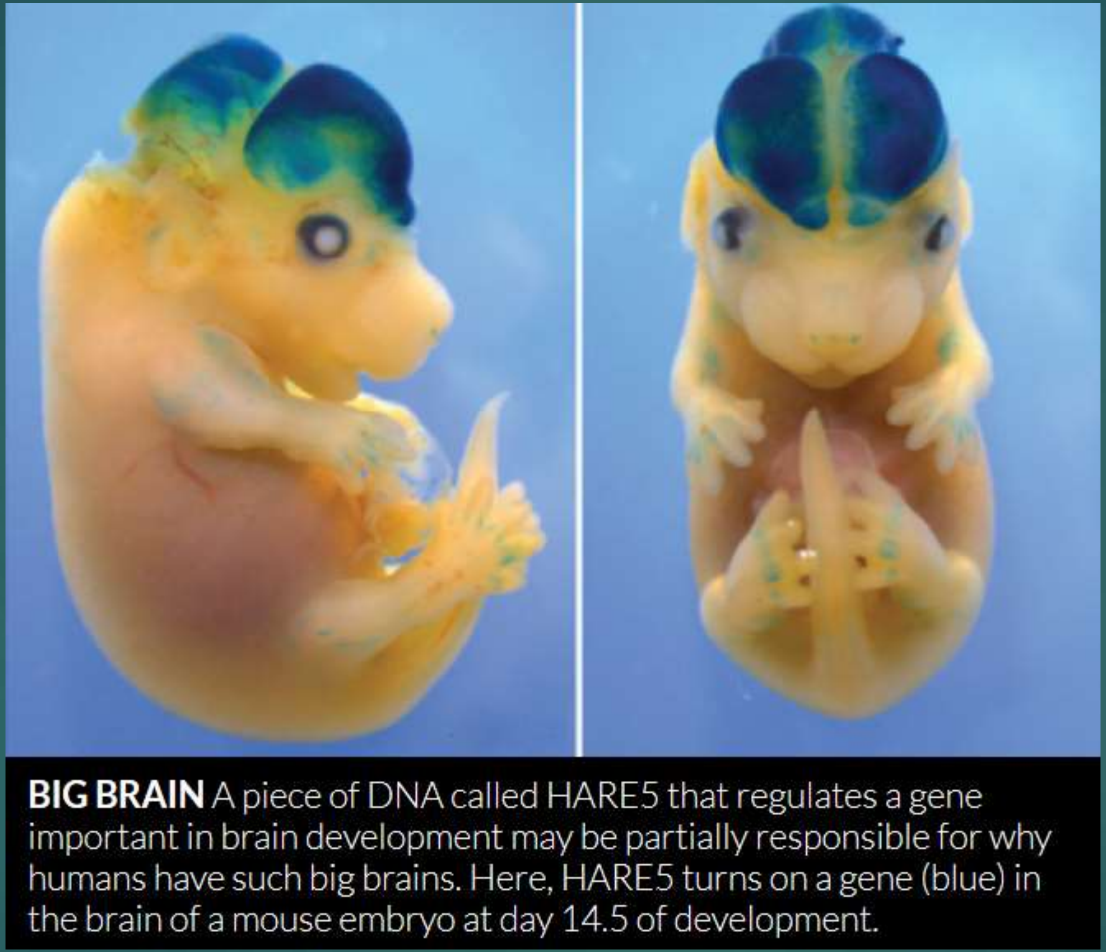
miR-941

- Gene – miR-941 – is unique to humans. The researchers say that it emerged between six and one million years ago, after humans had evolved from apes.
-
- The gene is highly active in two areas of the brain that control our decision making and language abilities. The study suggests it could have a role in the advanced brain functions that make us human.

Gene Expression: AHI1 & HAR1

- *AHI1* is another gene that shows evidence of positive selection in human evolution. This gene is required for normal axonal pathfinding in development that leads to decussation of the corticospinal tract and superior cerebellar peduncles. Lack of it leads to severe motor disease
- *HAR1*, is a 118-bp region in the last band of chromosome 20q that encodes a stable secondary RNA structure expressed in Cajal-Retzius cells during weeks 7–9 of gestation in humans. These cells types, which also express reelin, are critical in the early specification and migration of cerebral cortical neurons into their correct layers

Gene Enhancer: Bigger brain in mice via Human HARE5

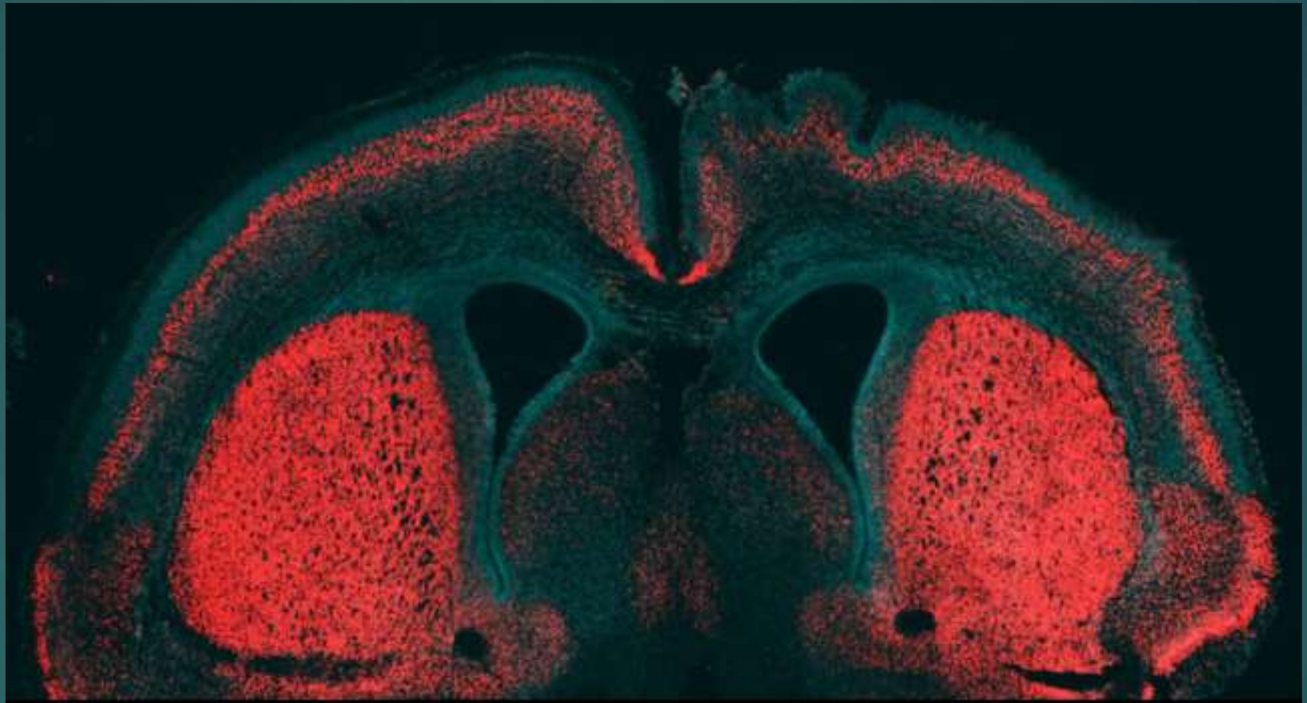


In mice engineered to possess a copy of the Frizzled 8 gene, adding the human version of HARE5 made nerve cells grow faster than in mice given the chimp version of HARE5. Mice with the human HARE5 developed a 12 percent bigger cortex than mice with the chimp enhancer

Genetics of Brain Size

- Gene enhancer HARE5, turns on a gene called Frizzled 8 in the brain during development.
- Human HARE5 has 16 differences from the chimpanzee version of the enhancer that alter brain development
- Genetic switch that boosts brain size. The human version of that switch produces a 12 percent larger cortex than a chimpanzee version does.

Genetic tweaks built humans' bigger brains



FOLD IT A gene that only humans have can make the normally smooth outer layer of mouse brains develop folds similar to those in human brains (upper right center). The gene may have been important for the evolution of big human brains.

When scientists inject a gene (*ARHGAP11B*) found only in humans into the brains of mouse embryos, the normally smooth mouse brain develops the crinkles and folds reminiscent of wrinkly human brains

Bigger brain gene

- A gene called *ARHGAP11B* can also build bigger brains
- The gene was duplicated about 5 million years ago — after the common ancestor of modern humans, Neandertals and Denisovans split from chimpanzees. but brain size didn't really start to change until about 2 million years ago
- *ARHGAP11B* causes one type of primordial brain cell to switch to another type. One part of the brain that makes new nerve cells in adults grew 50 percent thicker in mice that got a dose of the gene than in mice that didn't. Injecting the gene into mouse brains also caused the cortex folding.

J. L. Boyd et al., 2015

Other Possibilities

Brain Size in Primates as a Function of Behavioral Innovation

- Behavioral innovation, the capacity to invent new behavior patterns, may have played a pivotal role in primate brain evolution.
- Comparative analyses have revealed correlations between innovation rate and species' relative neocortex volumes, after correcting for phylogeny and differences in research effort.
- Thus, primate brain size and one measure of cognitive capacity, innovation rate, are correlated. Moreover, innovation rate correlates with a number of other cognitive measures (social learning, tool use, individual learning), suggesting that these capacities have evolved together.

S.M. Reader, 2007

Innovation rate & executive brain ratio

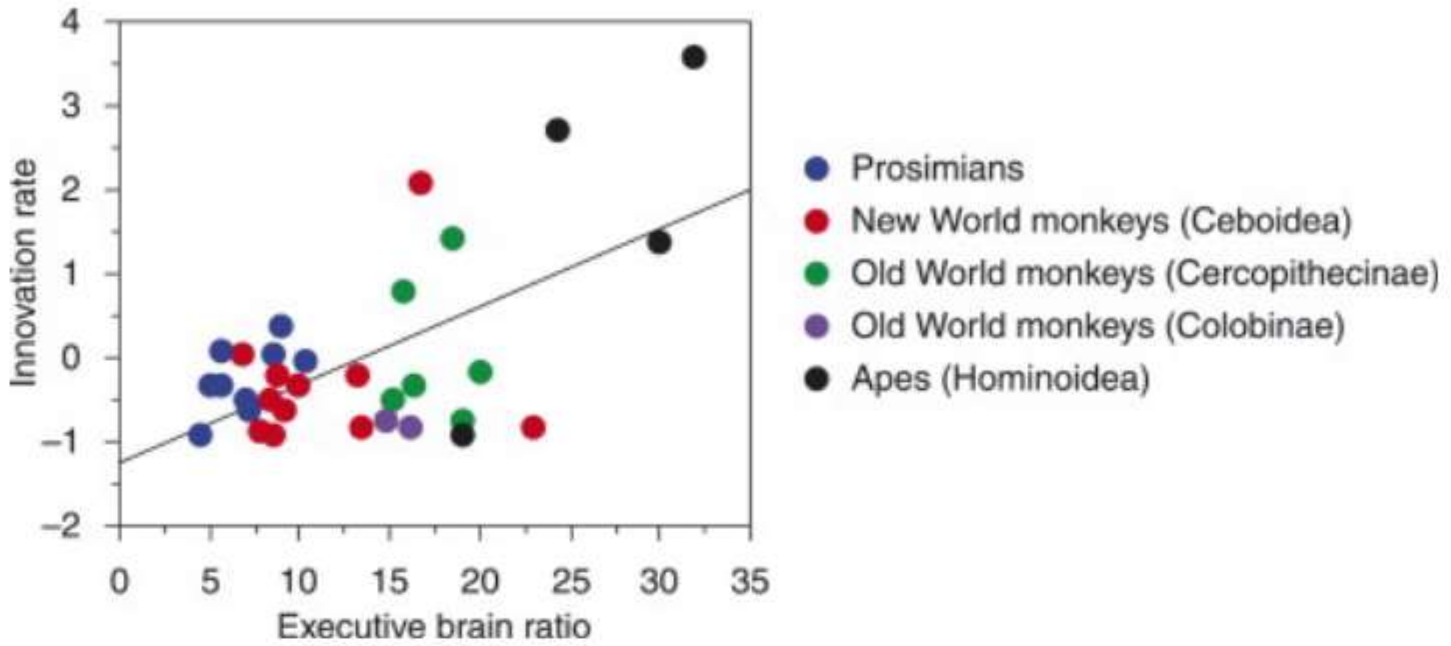


Figure 1. Innovation rate and relative executive brain ratio (executive brain volume/brainstem volume) are correlated. Innovation rate was corrected for differences in research effort by taking the residuals from a natural log-log plot of innovation rate against research effort, thus corrected innovation rate can take positive and negative values. For exposition the figure shows across-species data, with colored symbols indicating taxa. Independent contrast analysis gave similar results (Reader and Laland, 2002). Adapted from Reader, S. M. and Laland, K. N. 2002. Social intelligence, innovation and enhanced brain size in primates. *Proc. Natl. Acad. Sci. USA* 99, 4436–4441.

Evolution of Language

Early language

- Most birds and primates have vocalizations, alarm calls, that reference external world: aerial object, snake in the grass, whale songs
- Bird song is sexually selected: not for meaning, but for sex
- Chimps are terrible at vocalization; cannot train to vocalize a particular sound
- Martin Sereno theory: pre-existing (1) vocal control by sexual selection and (2) visual serial assembly of interpersonal glances; no 1 language area; ability to create fictive scenes from past; finally development of faster auditory/visual mapping

Unique to humans?

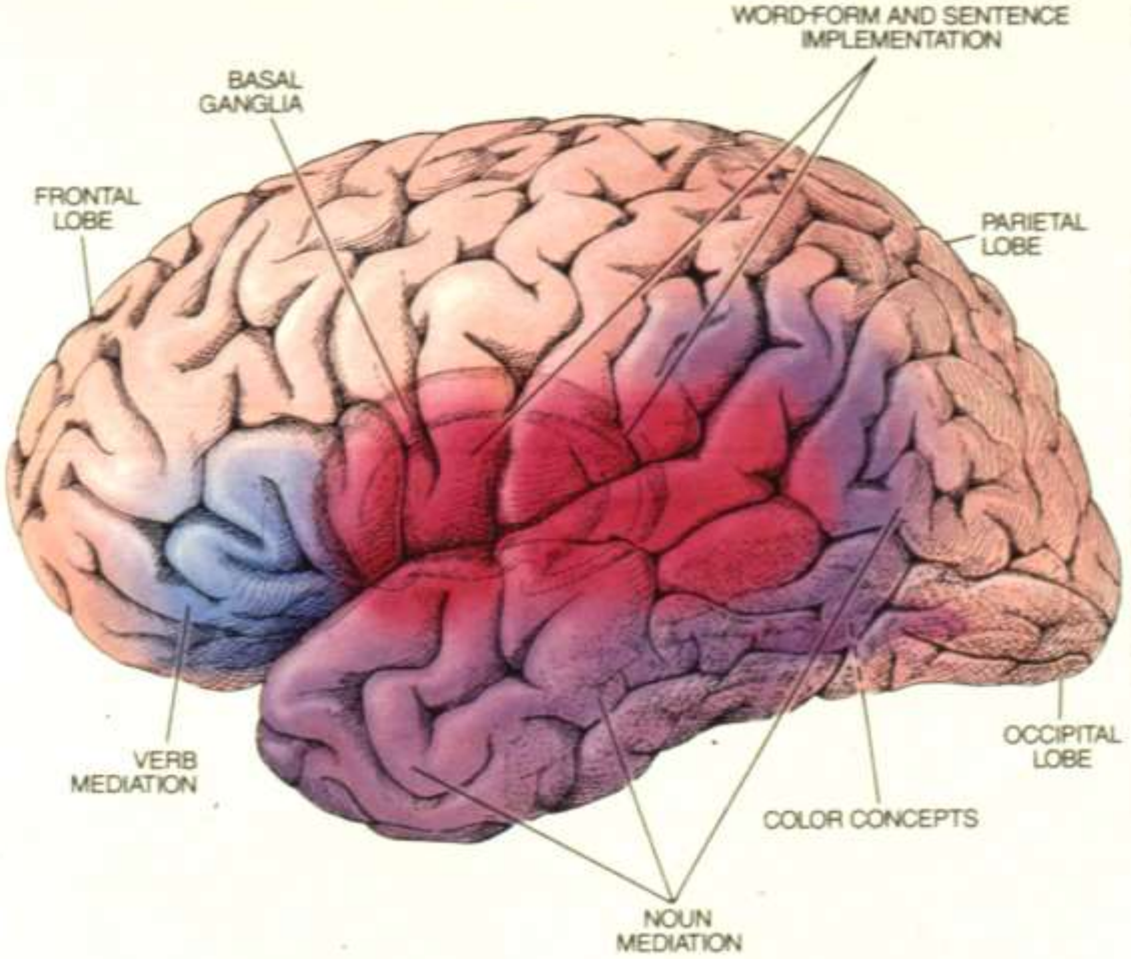
- There is a long tradition that ascribes properties to humans that are supposedly not found in other animals.
- The most cited are causal understanding of mechanisms of tool use, tool-making, syntactical–grammatical language, consciousness, self-awareness, imitation, deception and theory of mind.
- There is evidence, however that great apes possess at least some states of consciousness found in humans. Deception has been widely observed among monkeys; great apes and cetaceans show mirror self-recognition, and great apes and even corvids show an understanding of the mechanisms of tool use and tool-making.
- Existence of imitation, theory of mind and syntactical language in nonhuman animals is under debate.

Roots of language

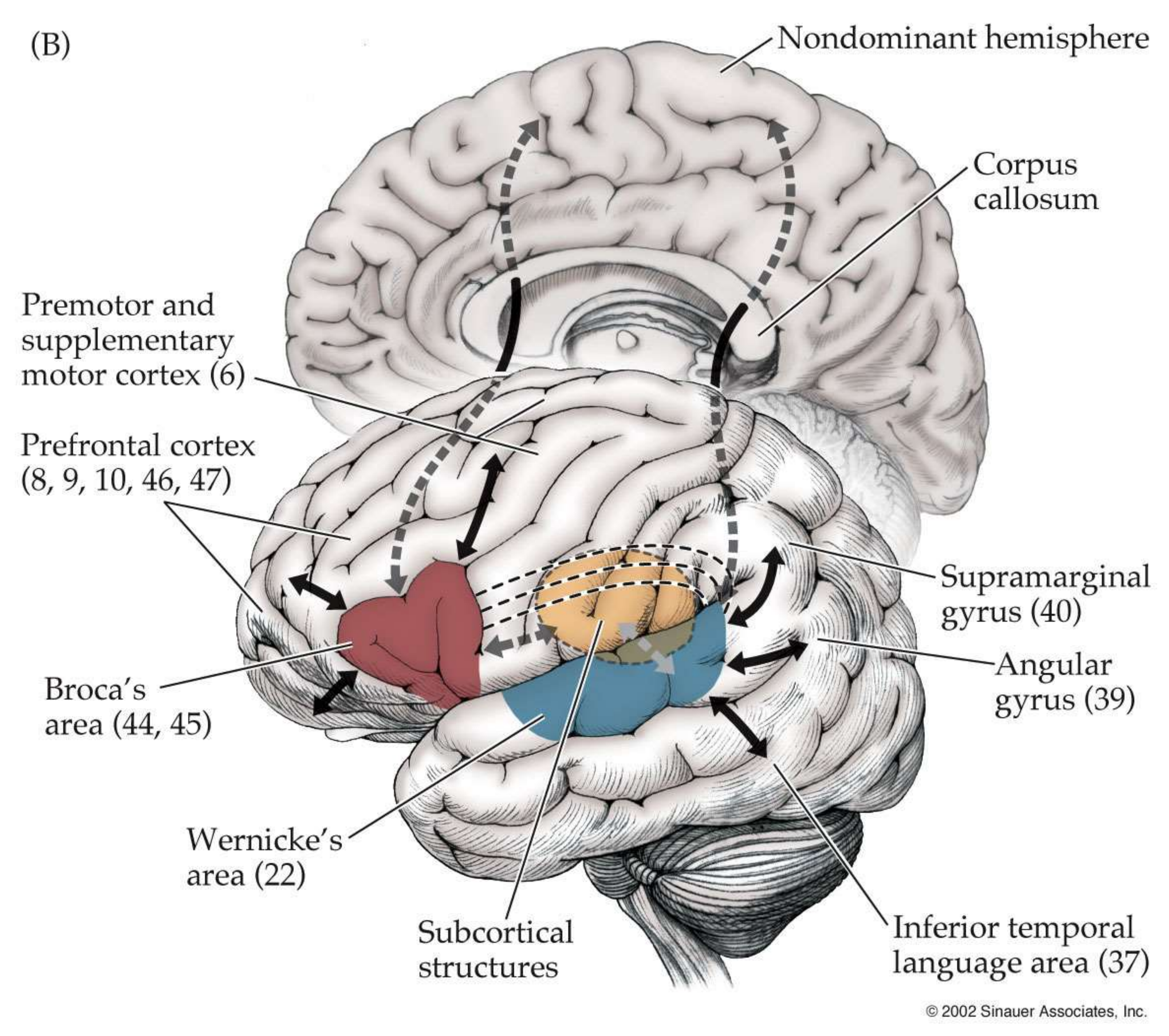
- There is a controversy about the roots from which human language evolved (vocal, mostly affective-emotional communication versus visual communication, gestures and mimicry, or a combination of both).
- Also been argued that speech and gesture develop in parallel, phylogenetically and ontogenetically.
- Accordingly, the ability of humans to use language without accompanying gestures would just be a further specialization, because under normal conditions humans use both components.

Is language unique to humans?

- The most-cited example for a unique human ability is syntactical–grammatical language.
- Most authors agree that sentences consisting of up to three words can be understood and used by chimpanzees, gorillas and dolphins.
- Savage-Rumbaugh and colleagues demonstrated that the 8-year-old bonobo chimp, Kanzi, who was raised in a language environment similar to that of children showed linguistic capabilities including signs of grammar and syntax typical of a 2-year-old girl, but Kanzi did not go beyond these abilities despite his long training period.



BRAIN SYSTEMS FOR LANGUAGE in the left hemisphere include word and sentence-implementation structures and mediation structures for various lexical items and grammar. The collections of neural structures that represent the concepts themselves are distributed across both right and left hemispheres in many sensory and motor regions.



Blumenfeld: Figure 19.2

Why in these places?

- Broca's area is next to the motor strip in the orofacial area: control of speech articulation there makes sense.
- Wernicke's area is next to auditory cortex, towards the visual and somatosensory areas: grounding of spoken word meanings there makes sense

Broca's in Great Apes

- Asymmetric Broca's area in great apes
- Brodmann's area 44 delineates part of Broca's area within the inferior frontal gyrus of the human brain and is a critical region for speech production, being larger in the left hemisphere than in the right — an asymmetry that has been correlated with language dominance.
- There is a similar asymmetry in this area, also with left-hemisphere dominance, in three great ape species (*Pan troglodytes, Pan paniscus*and *Gorilla gorilla*).
- The neuroanatomical substrates for left-hemisphere dominance in speech production were evident at least five million years ago and are not unique to hominid evolution.

Earliest Language: decreasing diversity with distance,

Quentin D. Atkinson looking not at words but at phonemes — the consonants, vowels and tones that are the simplest elements of language.

- A simple but striking pattern in some 500 languages spoken throughout the world: A language area uses fewer phonemes the farther that early humans had to travel from Africa to reach it:
  - Click-using languages of Africa have more than 100 phonemes
  - Hawaiian, toward the far end of the human migration route out of Africa, has only 13
  - English has about 45 phonemes.
- This pattern of decreasing diversity with distance, similar to the well-established decrease in genetic diversity with distance from Africa, implies that the origin of modern human language is in the region of southwestern Africa.

FOXP2

- Scientists discovered *FOXP2* in the 1990s by studying a British family known as 'KE' in which three generations suffered from severe speech and language problems. Those with language problems were found to share an inherited mutation that inactivates one copy of FOXP2.
- Most vertebrates have nearly identical versions of the gene, which is involved in the development of brain circuits important for the learning of movement. The human version of *FOXP2*, the protein encoded by the gene, differs from that of chimpanzees at two amino acids, hinting that changes to the human form may have had a hand in the evolution of language.
- A team led by Schreiweis' colleague Svante Pääbo discovered that the gene is identical in modern humans (*Homo sapiens*) and Neanderthals (*Homo neanderthalensis*), suggesting that the mutation appeared before these two human lineages diverged around 500,000 years ago.

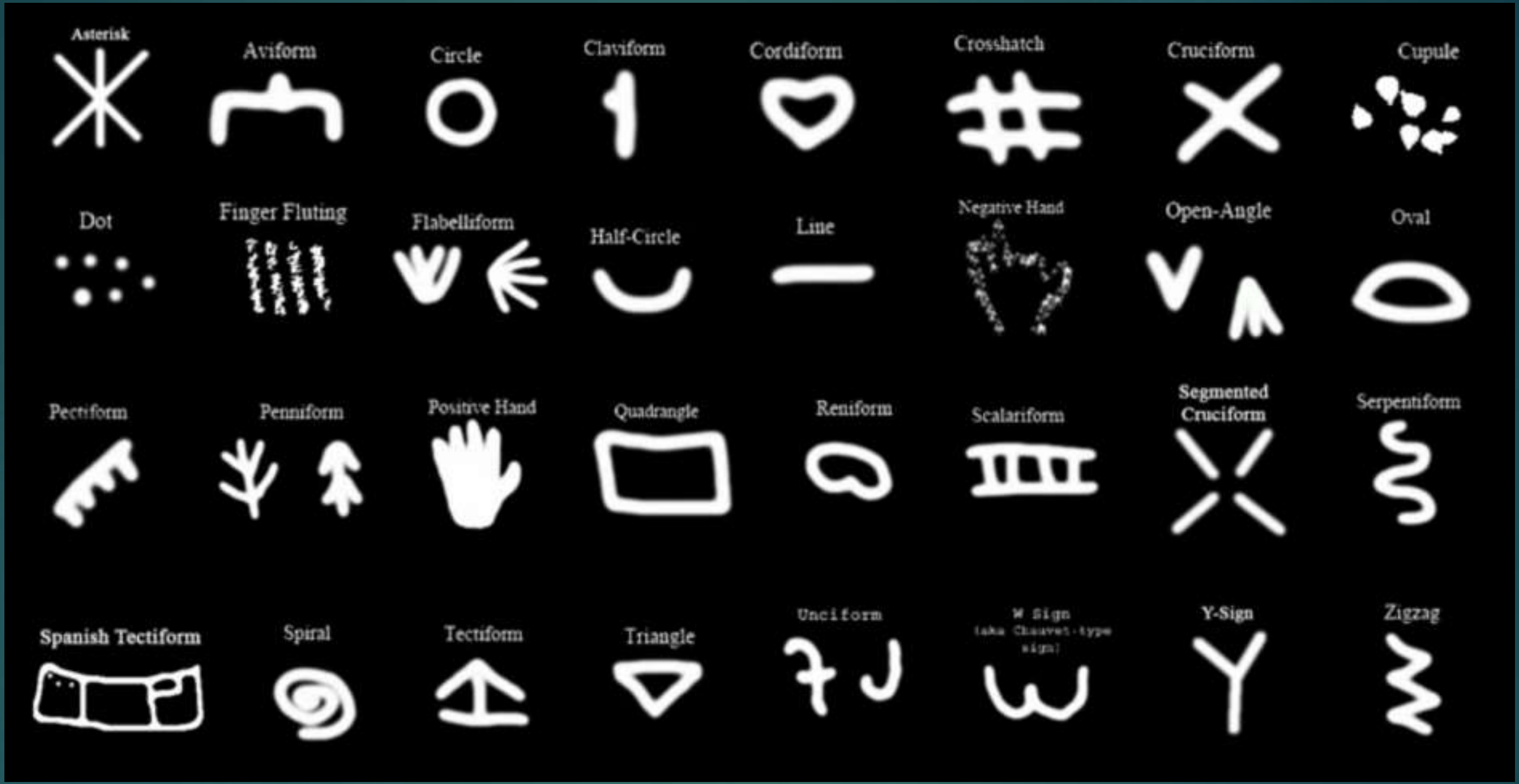
If language is so great, why doesn't every species get one?

Possible answers:

- It's too expensive, relative to the benefits
  - e.g. in terms of brain tissue requirements
- It's hard to get started
  - e.g. requires an unlikely evolutionary "invention"
    - not just an extension of animal communication systems
  - or, early "releases" are not very useful
    - "theory of mind" lacking
    - displaced reference can be confusing

Art and Culture

Graphic Communication



52 cave sites in Europe, over 30,000 year period: 75% had symbols; 32 symbols
65% of which stayed in use for entire time period; some clan signs?
Common origin in Africa?

2015, TED, **Genevieve von Petzinger**

Although we do not know when language first appeared in human history, there is substantial evidence for complex communication skills (*e.g.*, paintings, music) appearing in human populations at least 40,000 years ago.

Chauvet-Pont-d'Arc Cave contains the oldest known cave paintings: about 30,000 years BP

Figure 1 | A 35,000-year-old sex object. The newly described[1] Aurignacian figurine, 60 millimetres in height, viewed from different angles.

A female figurine from the basal Aurignacian of Hohle Fels Cave in southwestern Germany.

Conard, N. J. *Nature* **459**, 248–252 (2009).

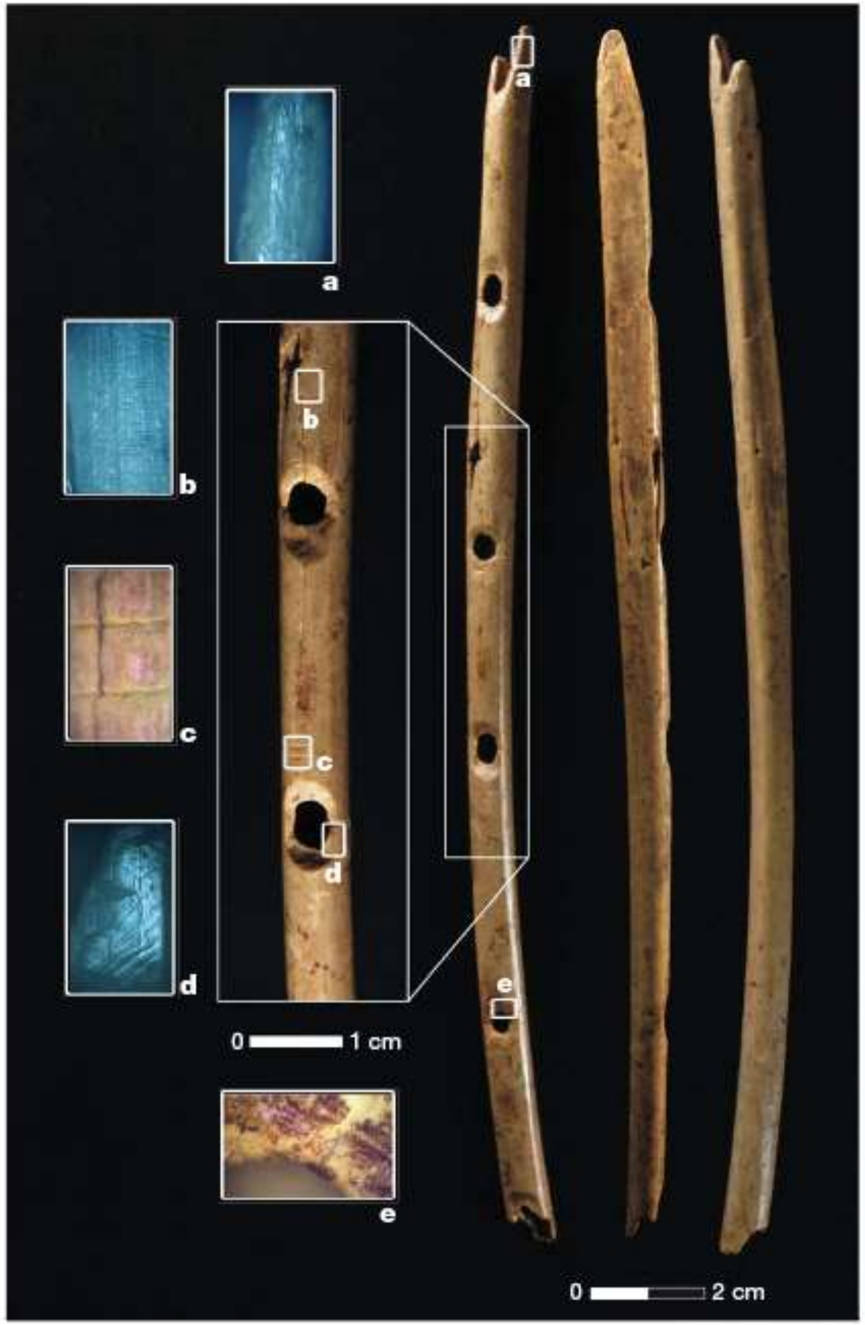


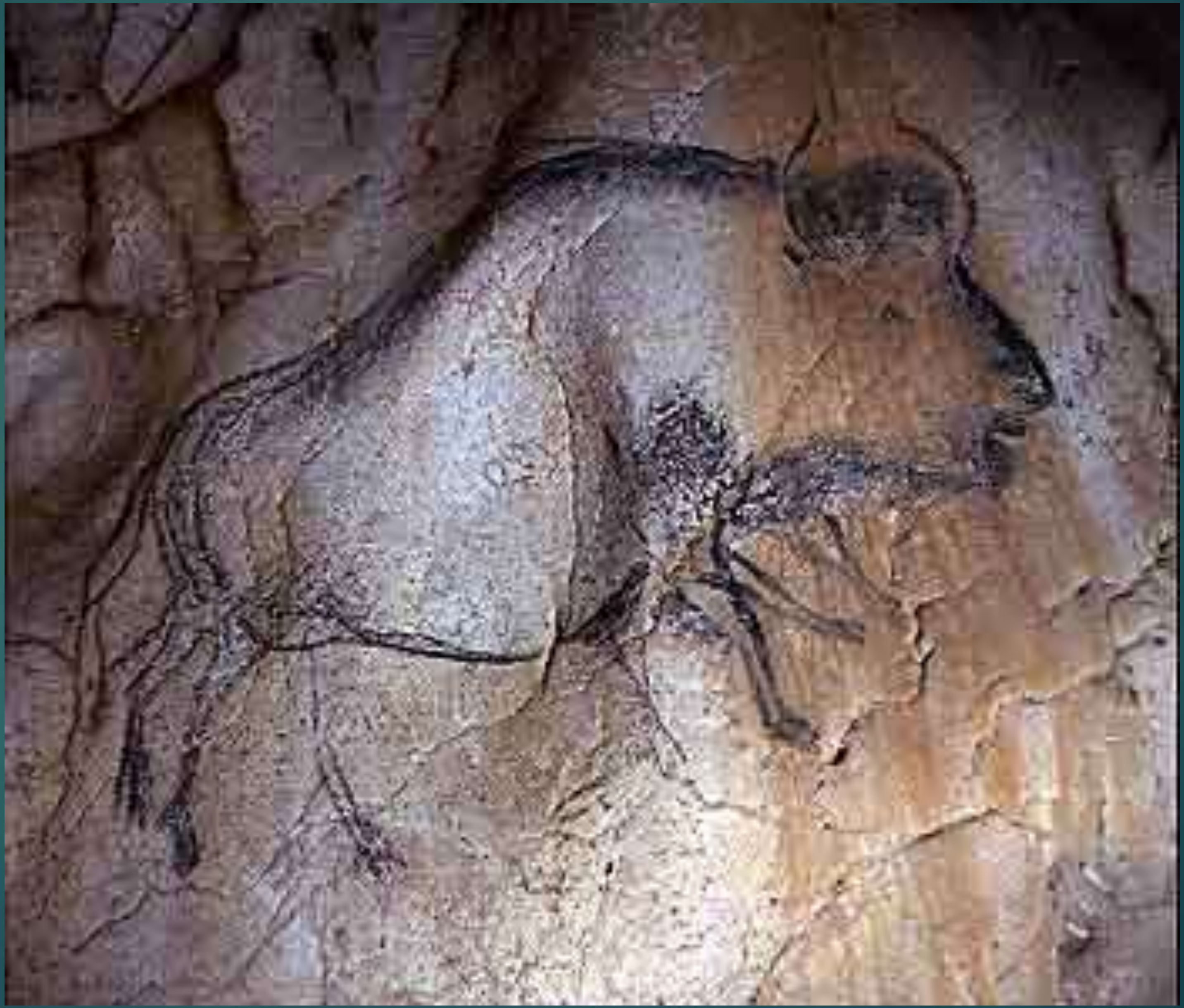
Figure 1 | Bone flute from Hohle Fels archaeological horizon Vb.

New flutes document the earliest musical tradition in southwestern Germany

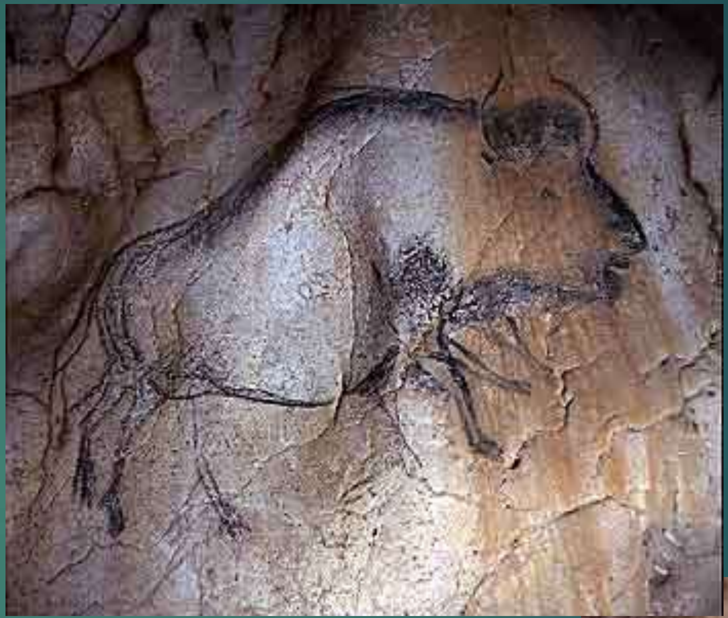
Nicholas J. Conard et al

Nature: **460:** 737-740, 2009

Chauvet (31k) bison with active legs



Detail of horses at Chauvet (31k)



Hand at Chauvet (31k)

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