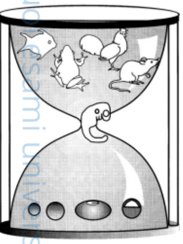
BRAIN PHYLOGENY AND ONTOGENY

Phylogeny focuses on the evolution of the species and studies brain evolution comparing species; ontogeny studies the developmental history and trajectory of an individual within its lifetime (from pregnancy, how the brain develops before and after birth)

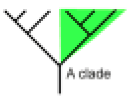
General phylogeny

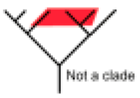
Basic concepts

- Evolution (Darwin)=many variations of each feature in each species, natural selection selects the most adaptive ones for the area in which the organism lives, the ones that are most fit to the environment
    - among all members of the species, survival of the fittest=has higher chances of survival and of transmitting this good variability to the progeny with reproduction→ explains the great diversity in species
    - common ancestors=many similar characteristics



- Hourglass model=represents the relationship between evolution and ontogeny, there is an intermediate stage of embryo in every species, where the embryo looks like other species
    - embryogenesis has a lot of similarities across species
    - phylum=taxonomic category, vs clade=group of organisms that have evolved from a common ancestor (ex apes and humans) → cladogram
        - the study the evolution of the brain in primates could provide insights in how the human brain works and how it is linked to the mind





- Ontogeny recapitulates phylogeny (Haeckel)=development from embryo to adult is a fast version of evolution
    - the initial state of embryos is very similar independent of species (as it reflects the common ancestor) but through development, they reach totally different end points and develop species-specific features
    - problem: theory questioned (Richardson): cherry-picking→ better the hourglass model

How can we study the brain's evolution?

- Measuring cranial capacity at various stages of evolution
    - Two main turning points in evolution=main driving forces for brain evolution in the human capacities (language and executive functions)

        - the emergence of the primate cerebral cortex=brain size expansion
            - ++ volume and convolutions=birth of associative areas
            - birth of new (and unique) areas
        - the overcoming of natural selection (replaced by an interaction of ecological constraints, neural constraints and cognitive factor)
            - our cognitive system can allow us to evolve even further but also to go extinct
            - acceleration of the expansion of the brain and of cranial capacity, which made the development of language possible (and then other executive functions)
            - culture could shape our brain evolution in this new transition of our brain evolution
        - prediction of a third phase: accelerating human brain capacity through AI
- Through radiometric dating=use of carbon-14, uranium-238 to identify the age of a cranium
    - when an individual is alive, it absorbs radioactive impurities and radioactivity decays in a very well known rate: possibility to measure the decadence in a skull to understand when that individual was alive
        - C-14 only for thousand of years, better P-14 or U-238
- Through endocasts to infer the structure of the brain=fossil cranial shapes to reconstruct the real shape of the brain
    - internal shape of hollow objects to indicate the cranial vault
    - the brain leaves an imprint: the vault is modelled by what is contained
- Through genome phylogeny=sequencing genomes to get a precise reconstruction about phylogeny and the evolutionary distance between species
    - similarities between two species=number of genes in common divided by total number of genes→ differences in functions and number of genes
    - the evolutionary distance between two species can be interpreted in terms of acquisition of genes or functions (through loss or gain of genes)

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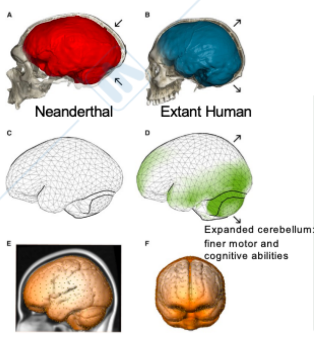
Comparisons with other species



Neanderthal man vs homo sapiens (us): endocranial differences in shape

- expanded cerebellum: finer motor and cognitive abilities
    - based ganglia
    - fine motor skills: success of the homo sapiens
- N is more elongated, modern human more globular
    - globularity shows what changed
    - the cerebellum has many connections (premotor and prefrontal cortices), relevant for cognitive abilities

- Gunz: 1-2% of total genome is identified in Neanderthal: 40% of the Neandertal genome is still represented today

    - association with reduced cranial globularity (round vs elongated) proportional to the quantity of N DNA→ brain globularity is coded in chromosomes 1 and 18, responsible for myelination and neurogenesis are affected
    - homo heidelbergensis=common ancestor between us and neanderthal

Species of mammals have different brains

- Common features: hemispheres (interhemispheric fissure), central sulcus/rolandic fissure
- Differences: shape, size, gyrification complexity, patterns
    - the most evident difference is size (considering brain/body weight ratio)
        - humans and primates are an outlier=usually animals with larger bodies have larger brains ("passive growth"), but here brains are too heavy compared to their body
            - how did such an energy-demanding organ survive selection?
                - 25% of body energy (it's the 2% of our weight)
                - active growth=brain size is increased
            - hypothesis: higher cognitive abilities? Huge numbers of neurons: relative high cost
            - we cook our food=+ energy=+digestion=+ assimilation of nutrients
                - we are able to sustain our brain without spending a lot of time eating=possibility to develop new skills
                - since mankind started cooking, there has been a rapid increase in brain size

Hypothesis about brain evolution:

- Concerted brain hypothesis=brains evolve mainly by global modifications during neurogenesis, increasing or decreasing all of its components together
    - major dimensions of covariation in brain structures are due to developmental events: any evolutionary change in the brain cannot occur without a change in the whole brain
- Allometry brain hypothesis=not all regions have the same rhythm of evolution, changes in the relative size of individual brain regions reflect selection-mediated adaptive divergence in brain function
    - differences in development and growth in different areas of the brain (both in phylogeny and ontogeny)
    - study: diverging allometric trajectories for humans (blue) vs papionini (red)
    - change in relative size of individual brain regions reflects selection-mediated adaptive divergence in brain function
- Mosaic brain hypothesis=network-specific selection→ selective forces act on specific brain areas/networks, whose adaptive responses do not concern other brain areas/networks
    - heavily interconnected brain structures are forced to change together, despite selective forces may act on only one of the two (independent regions evolve independently)
        - functional constraints drive allometric scaling in evolution (also in ontogeny) → patterns dependent from connectivity

- variation in the size of individual brain regions reflect adaptive divergences mediated by natural selections
- no correlation between brain volume and proportion of neocortical GM→ evolution concerns not only the number of neurons, many other factors put pressure on brain evolution (activity patterns=diurnal vs nocturnal, diet quality, social complexity)
  - the proportion of grey matter is uncorrelated to the whole brain volume

- factor influencing relative size of specific brain regions changes in primates
  - the relative sizes of specific brain regions increase across primate species, according to suborder and socioecology (activity pattern, diet quality, social complexity)
  - group-living species&high quality have developed olfactory systems if they are nocturnal, if they are diurnal, developed visual system
  - diet quality predicts (what?) more than social complexity
- mosaic or concerted evolution? BOTH: The most likely alternative for brain evolution is a combination of both the mosaic and the concerted evolution hypothesis -> e.g. songbird brains evolved as a coordinated whole but also experienced significant, independent modifications to dedicated systems from specific selection pressures
  - concerted or mosaic changes could be related to the degree of functional interdependence: changing together in a coordinated manner (concerted changes) despite the factor on only one of the area
  - two independent structures can evolve autonomically→ mosaic evolution

Did the prefrontal cortex have a differential evolution?

- Differential evolution of prefrontal cortex? Based on the allometric view, emphasis on the difference in the evolution of the frontal lobes in primates -> the frontal lobes carry out functions that make humans humans (emotional regulation, language production) -> can the size of the prefrontal cortex explain the complexity of human cognition?
  - Deacon: emergence of symbolic capacities due to larger prefrontal cortex in human brain evolution
  - hot colours: need to be stretched more to show equivalence in the two species (areas that developed the most)
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    - big resemblance between children brains and apes: comparison of evolutionary and postnatal cortical surface expansion→ comparison between ontogeny and phylogeny
  - differential evolution of prefrontal cortex size? probably not
    - issues with this theory
      - based on study of few primates and mammals (excluding apes)
      - terminological confusion between frontal and prefrontal
    - the relative size of frontal cortex with respect to the rest of the brain does not change much→ HP: special cognitive abilities attributed to a frontal advantage due instead to differences in individual cortical areas and to a richer interconnectivity

- NB! Data is often inconsistently named => difficult to truly understand what researchers are referring to (results may change!). From comparisons between rhesus monkeys and humans, many areas have expanded in evolution and those same areas are the ones which develop the most after birth => ontogeny follows phylogeny (with some differences)
  - Humans do not differ that much from great apes in FC size => higher cognitive abilities may be due to differences in individual areas and richer connectivity, which do not imply a change in size => evolutionary rewiring. When a WM/GM ratio is computed in the PFC, humans are shifted towards WM => more WM than other primates => stronger hierarchical interaction between areas, which could explain the higher cognitive abilities.
    - special cognitive abilities attributed to the frontal advantage in humans can be led to differences in individual cortical areas and to a richer interconnectivity
  - connectoms: macaque and human regions exhibiting homologue matching index similarity in terms of connectivity patterns
- Which tracts are different and similar in a whole brain perspective? For monkeys axonal tracing (antero- and retrograde, with radiotracers), for humans Diffusion Weighted Images to reconstruct WM tracts (from how constrained is water movement inside a specific brain area -> CSF = free = isotropic, myelinated axons = direction of the axons = anisotropic, e.g. fractional anisotropy). Similarities between man and monkey may explain phylogenetically conserved cognitive abilities. NB! Structures can be recycled -> new skill in evolution uses an area previously used for other functions.
  - intervariability; low variability in ancient regions (hippocampus, olfactory system) → archicortex
- white matter tracts between human and monkey:
  - Similarities
    - Superior longitudinal fasciculus: divided into 3 branches (first – second – third, from dorsal to ventral). Connects frontal and parietal structures, probably bidirectional. Involved in visuospatial attention orienting, working memory -> if cut, visual neglect, WM deficits and optic ataxia. NB! For a lesion, deficits are common to both species -> probably a common ancestor developed this system.
    - cingulum: connects default mode network="think about nothing" and cingulate cortex -> autobiographical memory, emotion control, error monitoring, mind wandering, self-representation.
    - uncinate fasciculus: ventro-medial connection between the frontal cortex and the anterior temporal lobe and amygdala . Involved in emotional memory, risk estimation and social behaviour.
  - Differences: must be interpreted with caution -> might derive from different methodology, but might as well explain emerging functions in humans.
    - arcuate fasciculus: in monkeys not arcuate at all, similar only to a subsection of the human one. The majority of fibres are only typical for humans (blue). NB! Humans have bigger brains => possibility to extend connections.
      - language in the human brain

            - comparison between post-mortem axonal tracing in monkey and human in vivo tractography
        - inferior frontal-occipital fasciculus: shorter in monkeys, doesn't reach the occipital pole => large development in humans following the gyrification of the occipital lobe
    - map of the within-species white matter variability→ evolution of WM across species
        - U shaped short range connections between nearby associative regions; white matter tracts (associative) are variable; occipital lobus too went through evolutionary pressure
        - the archicortex (hippocampus and olfactory parts) hasn't changed much within species

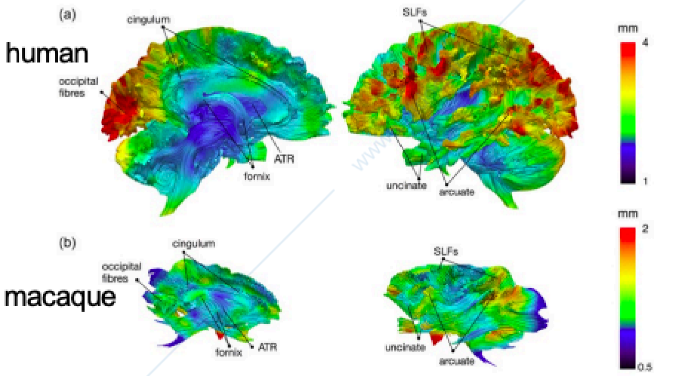
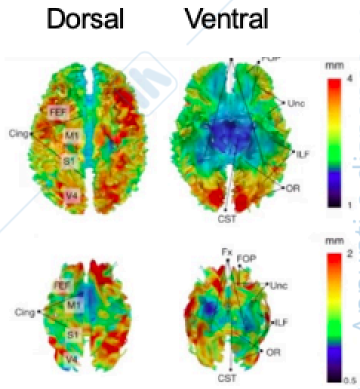


Figure 3. White matter variability. Three-dimensional projection of the average deformation measured for white matter in humans (a) and monkeys (b). SLFs, branches of the superior longitudinal fasciculus; ATR, anterior thalamic radiation.



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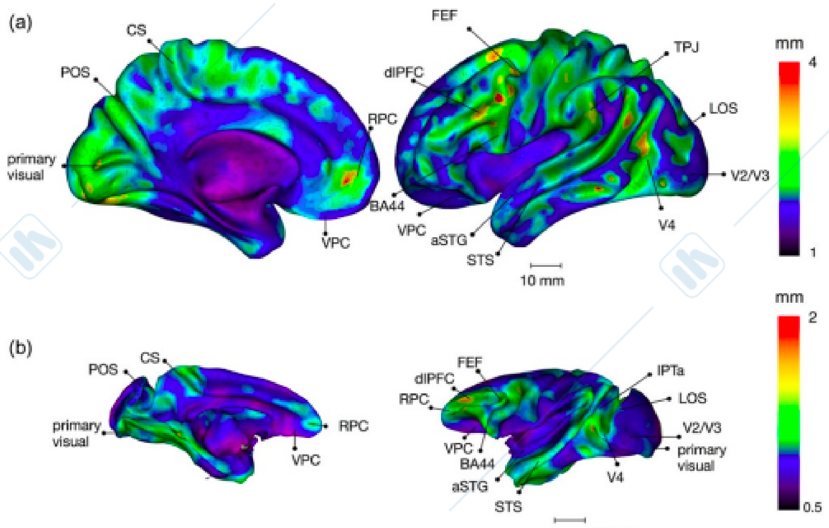
- Intraspecies (interindividual) variability
    - Due to genetic or epigenetic factors, might be exploited by natural selection to identify the fittest => good for the survival of the species. Highly variable regions are the same in humans and monkeys, both in GM and WM. According to the dual origin theory of the brain, more ancient regions have low variability (olfactory system, hippocampus) -> the whole brain evolved from this archicortex -> moving away from it variability grows: newer regions have more variability = new level of complexity and testing new configurations => evolutionary pressure still at play.



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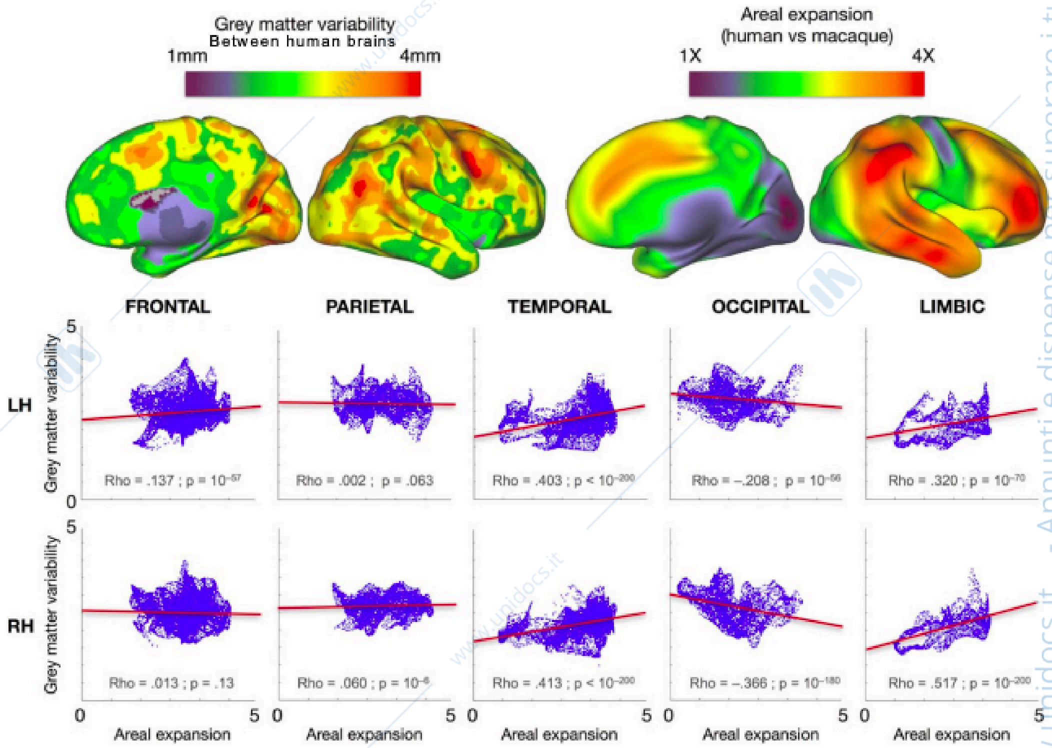
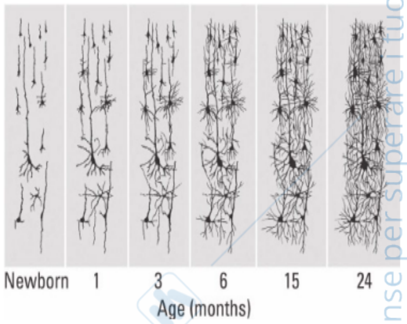


- When GM variability is measured and compared between humans and macaques (= amount of deformation needed for a macaque brain to fit a human one) and within humans, areas with the most differences are newer ones (= more variable) => define a human as human. The same can be observed for WM -> U-shaped association tracts are the most variable: changed a lot in evolution and support new functions, in older structures lower variability (e.g. fornix, corona radiata). Occipital tracts are less variable in monkey.
- Variability can also be compared in the two hemispheres => lateralization of certain functions is mirrored by a higher variability (e.g. Heschl's gyrus is more variable in the left hemisphere, where it is used for language, areas of the MTL for social and emotional processing more variable in the right hemisphere). In general, asymmetry in monkeys is lower/different (NB!

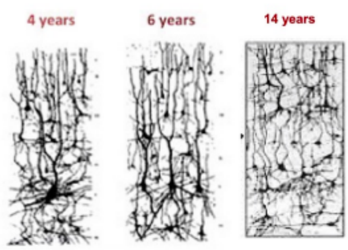
Monkey brains cannot be considered as “ancient human” ones, as we just share a common ancestor => some further differentiation).
  - Smaers: regression of left prefrontal white matter volume to grey matter volume
    - more white matter than grey matter in the prefrontal cortex: strong hierarchical interaction in associative areas or a higher level of integration

Brain ontogeny

- Learning implies changes in neural transmission: better neural communication=signals travelling quickly and efficiently
  - synaptogenesis=process of formation of new synapses→ + synapses=+efficiency
    - prenatal period, but also in adults
    - interaction of
      - nature=genetic substrate
      - nurture=experience stimulates changes
    - arborization of the dendritic tree



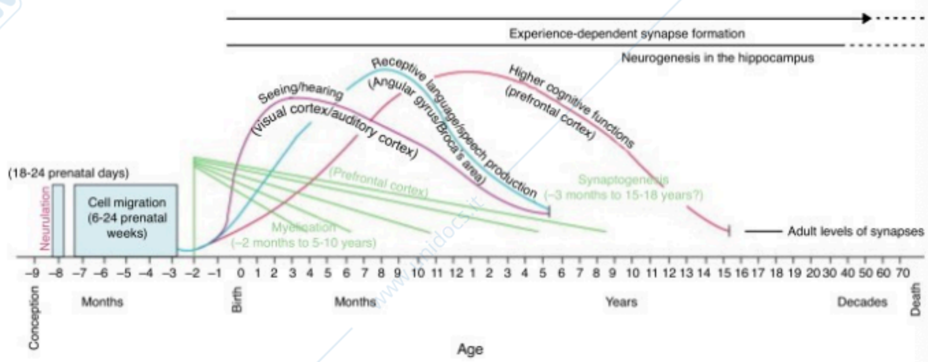
  - neurogenesis=formation and growth of new neurons
    - early development→ only exception: hippocampus (hippocampal-dependent functions, such as memory encoding/consolidation and mood regulation)
  - myelination=development of myelin sheaths around axons (oligodendrocytes and Schwann’s cells)
    - last step of neural development, allows plasticity
    - within the first 24 months, until adulthood in some regions
      - projection bundles (primary regions: motor and sensory circuits) → limbic system→ commissural bundles→ association bundles
        - ontogeny follows phylogeny: bundles that developed later in evolution are myelinated last
    - functions
      - the axon’s insulation prevents the loss of electricity in AP
      - more efficiency in transferring informations
    - myelin=lipidic substance that shields axons to encapsulate them and raise speed and frequency of action potentials
- During neurodevelopment, regressive mechanisms=eliminate what has been built:
  - synaptic pruning=synaptic elimination between early childhood and puberty
    - to eliminate irrelevant connection, as they waste energy and material (metabolic reasons)→ improvement in networking capacity
    - until optimal density of the brain
    - slow but constant: from 4 to 14 years



- the timing depends on the area: much later in frontal cortex, visual cortex in perinatal period
- the cut links depend on Hebb's rule: if neurons don't show co-activation for too long, the connections are destroyed

- apoptosis=programmed neuronal death for the absence of neurotrophic factors which guarantee survival
  - 20-80%: in children millions of cells die every day, allowing advancements in development
  - ≠ necrosis=cellular death caused by external factors (stroke, amyloid deposits)

- The human neurodevelopment is slower compared to other mammals
  - advantages
    - before pruning, a lot of neuroplasticity=productive phase
    - more opportunities because experience could shape the brain (volume, connectivity)
    - more cerebral volume and connectivity (white matter, associative regions)
    - complex behaviour in cognitive processes starting with minimal genetic prespecification by our genetic structure
  - changes in synaptic density during development
    - sensory areas→ motor→ language→ higher cognition
    - curve: generative processes than regressive phase
      - hippocampus keeps its neurogenesis capacity



Rise = synaptogenesis
Fall = pruning

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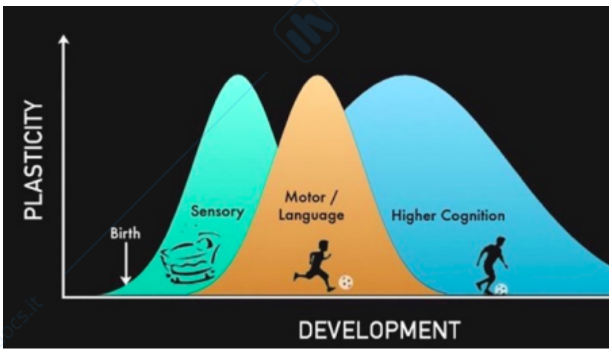
- sensitive periods="windows of plasticity" where the effects of environmental stimuli on neural and functional development are stronger→ important to detect, to ensure optimal exposure to stimuli and experiences to maximally exploit these
  - nuanced timing (depends on the faculty)



- example in language:
    - first month: more efficient and quicker learning of 2nd language
        - after that, our exposure to mother tongue has altered our capacity in perception and then production of phonemes
    - early exposure to language accounts for better syntax
    - cases of social isolation: “feral children” don’t fully develop language
        - miss the symbolic association=capacity of referring to something which is not present
- the visual system shows critical periods:
    - Hubel, Wiesel: when kittens are visually deprived in one eye during the critical period, the circuitry in the visual cortex is permanently altered and they remain blind on that eye
        - -neurons code for the deprived eye, +for the other
        - the ocular dominance columns change=in a normal visual cortex there’s an alternation of visual columns for the two eyes, but here dominance columns for the open eyes will expand so much that the other (for the closed eye) will be almost invisible
        - later experiments showed that ocular deprivation had an irreversible effect only in the first 3 months of development
    - if kittens are exposed only to an environment of only vertical stripes for the first month of their lives, they won’t recognize other shapes during the rest of their lives→ permanently blind to horizontal lines
        - not exposed to the richness of experience during the sensitive period