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Dipartimento di Scienze della Vita

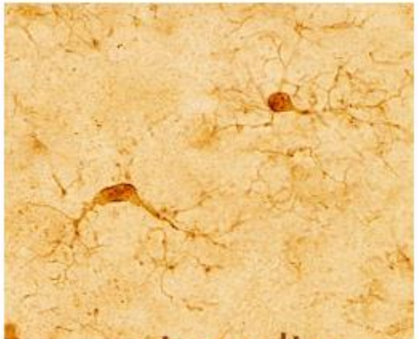
COMPARATIVE BRAIN EVOLUTION

Lecture 3:

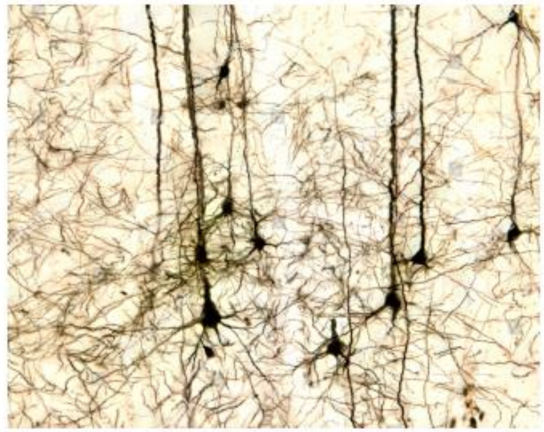
Principles of Comparative Neuroanatomy (II):

Neurons and Sensory Receptors

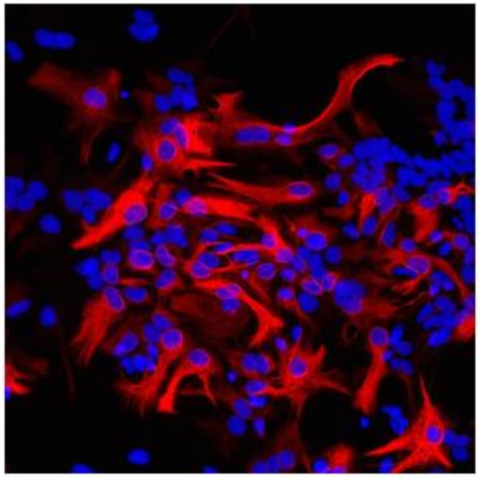
Nervous system: different types of cells



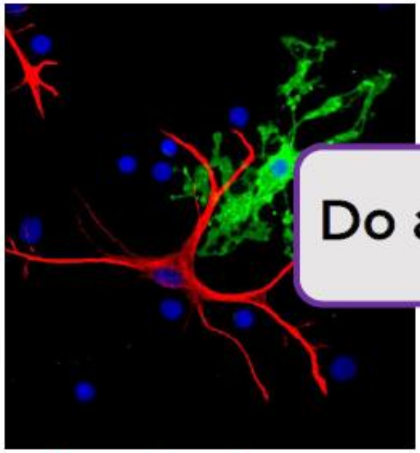
microglia



neurons



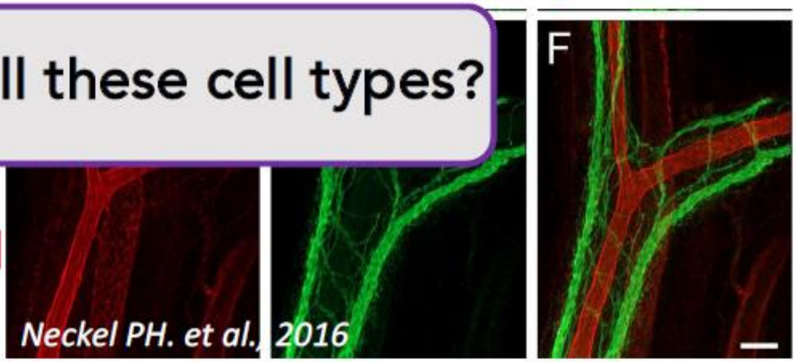
astrocytes



oligodendrocytes

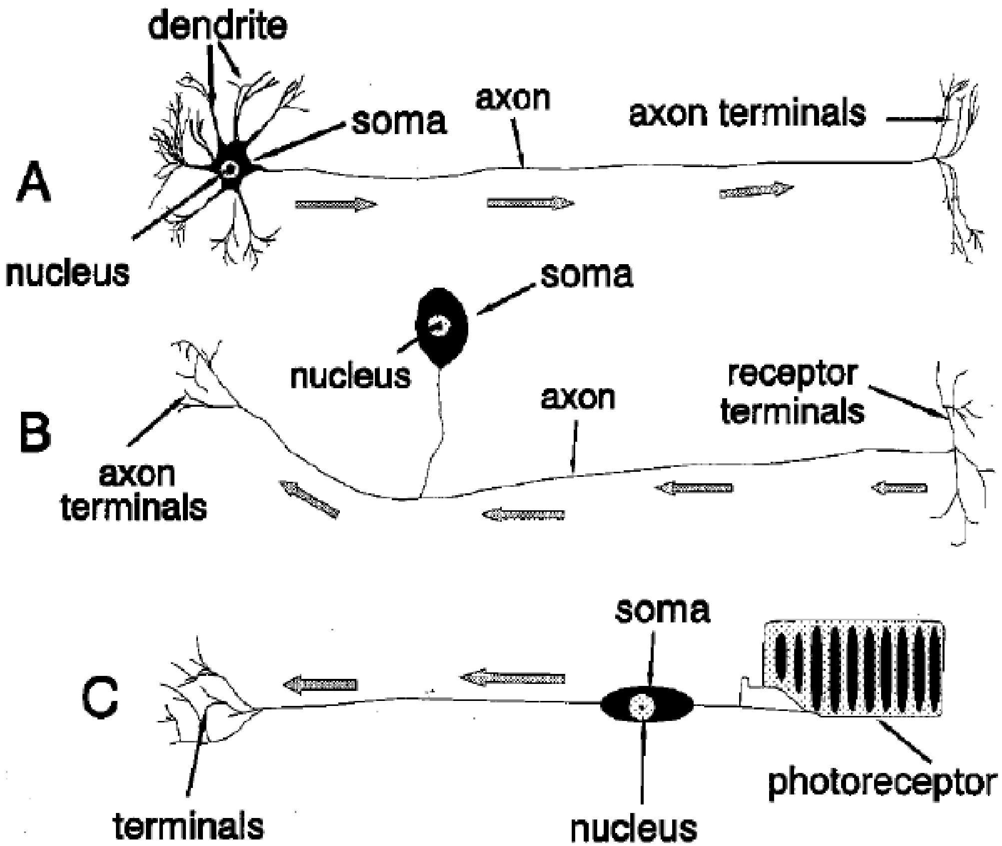
Do all vertebrates have all these cell types?

endothelial cells



Neurons & Sensory Receptors

motor neuron
Pyramidal neuron
axon & dendrites



sensory neuro
Piriform cell
no dendrites

receptor
Photoreceptor
no axon, no dendrites

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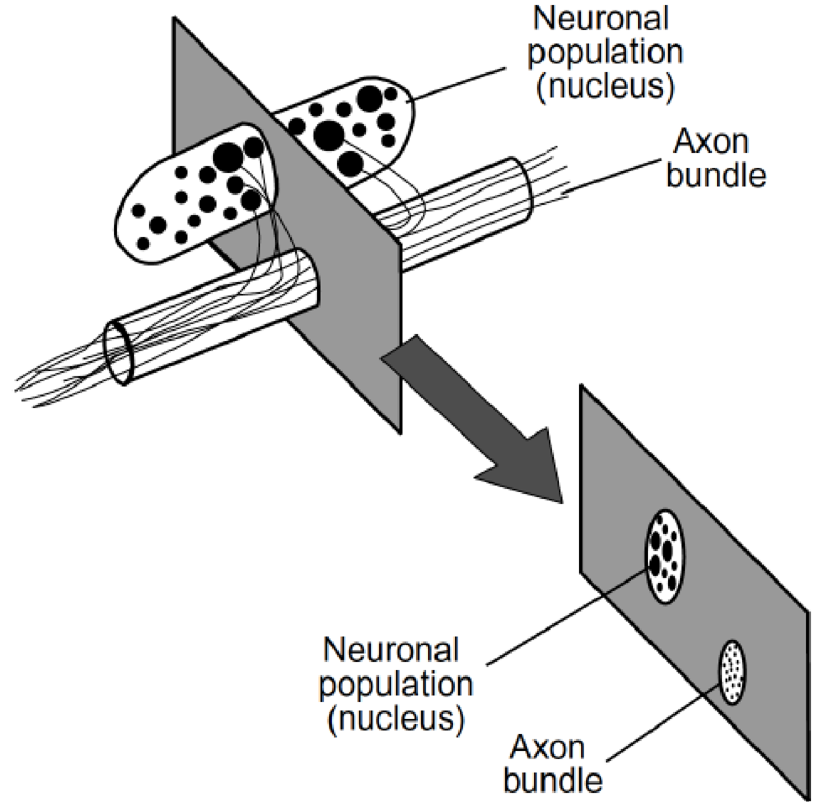
Nucleus

In neuroanatomy, a nucleus is a discrete population of neurons situated in a well-circumscribed boundary.

Synonims: locus, substantia, area, ganglia

Axon bundle, fibers



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Receptor and senses

Exteroceptors: receptors to the external world

Interoceptors: receptors to the inner world

Why are they important from an evolutionary perspective?

How many senses?

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How many senses?

- Vision
- Taste
- Touch
- Smell
- Hearing
- Pain

- Vestibular sense
- Temperature
- Various types of touch (deep, light, vibration)
- Proprioception
- Muscle stretch

and special senses..

Special senses

- Electrical field

lampreys

sharks

Ray-finned fishes

amphibians

monotremes

dolphins

- Infrared radiation

snakes

- Magnetic field

fishes

reptiles

birds

mammals

- Lateral line sensations

Non-tetrapods

amphibian larvae

Sensory adaptation

Receptor adaptation: receptors decrease their responsiveness to persistent stimuli.

Some receptors become adapted to a particular level of stimulation, will only respond to different level.

It is reversible, by a period of absence of the stimulus/ changing the stimulus.

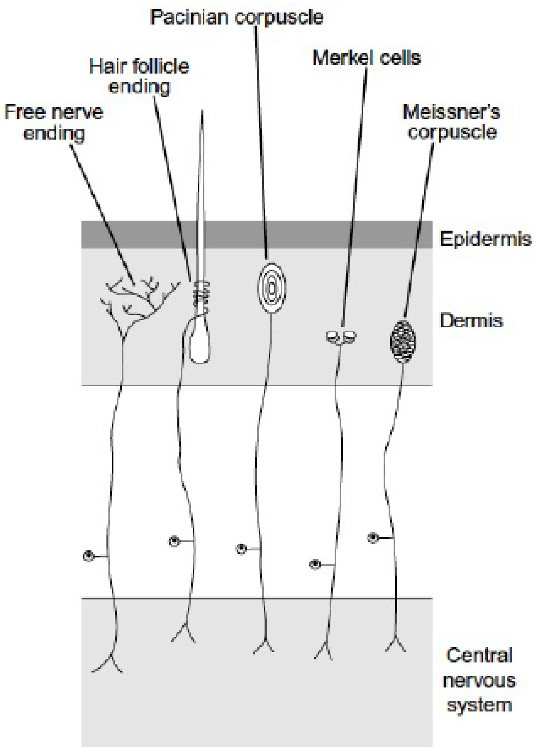
Receptor types

TABLE 2-3. A Classification of Receptors and Their Senses

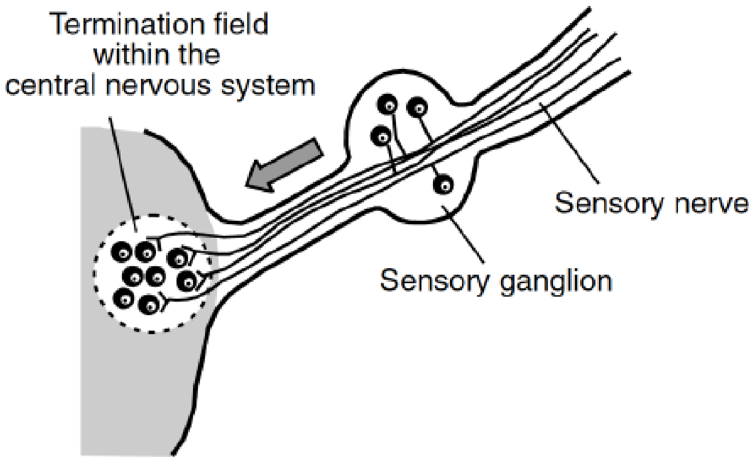
Receptor Class	Sensory Modality		Receptor Type
Mechanoreceptor	Touch	Fast adapting	Meissner's corpuscles
		Slow adapting	Merkel's disks
	Tendon stretch		Tendon organs
	Skin stretch		Ruffini endings
	Joint position		Joint receptors
	Muscle length and stretch		Muscle spindles
	Muscle contraction		Golgi tendon organ
	Vibration		Pacinian corpuscles
	Hearing		Hair cells
	Vestibular (gravity, acceleration, head position)		Hair cells
	Lateral line		Hair cells
Radiant-energy receptor	Light (including UV)		Photoreceptors
	Infrared radiation (pit organ)		Pit-organ receptors
	Infrared radiation (skin warmth)		Free nerve endings
	Infrared radiation (skin cold)		Free nerve endings
Chemoreceptor	Taste		Taste buds
	Smell		Olfactory receptors
Electroreceptor	Electric fields		Ampullae
			Tuberous receptors
Nociceptor	Pain		Free nerve endings
	General chemical sensitivity		Free nerve endings
Magnetoreceptor	Magnetic fields		Photoreceptors (?) Ampullae (?) Trigeminal receptors

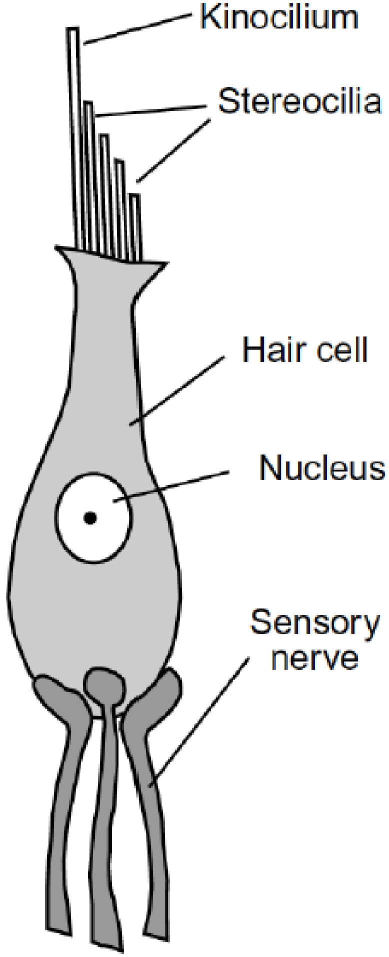
Receptor types

Examples of somatosensory receptors in the skin



Some are true **sensory neurons**, some are **specialized receptor cells** (innervated by sensory neurons).





1. Mechanoceptors

Touch/pressure, mechanical deformation

Most common/ubiquitous form

Best studied in Mammals

Amphibians & Reptiles

Sensitive to vibrations of the substrate;
On the ventral skin.

Birds

Mechanoceptros on/ near the base of the feathers. Why?

1. Mechanoceptors

Specialized mechanoceptors

- Hair cells
- Eimer's organs
- Lateral line organs

1. Mechanoceptors

Specialized mechanoceptors

- Hair cells
- Eimer's organs
- Lateral line organs

Do we have them?

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1. Mechanoceptors

Hair cells

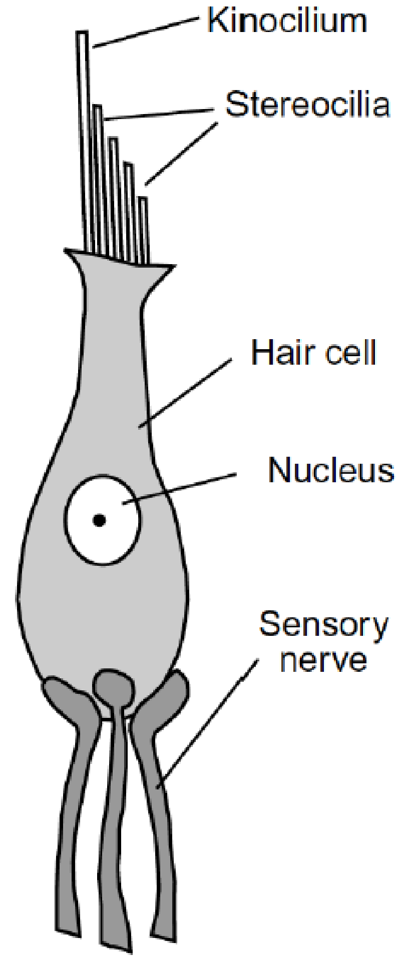
One/more hair: stereocilia

Longer hair: kinocilium ← Present in all vertebrates, In mammals they degenerate during development

e.g. auditory hair cells

In tetrapods, they are located in the basilar papilla

In mammals: Organ of Corti



1. Mechanoceptors

Specialized mechanoceptors

- Hair cells
- Eimer's organs
- Lateral line organs

Do we have them?

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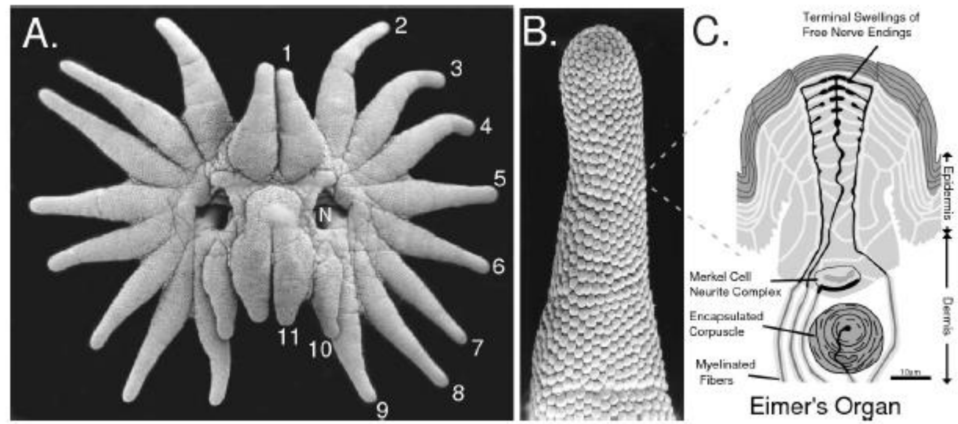
1. Mechanoceptors

Eimer's organs



Catania et al., 1999

Star-nosed mole

Unique sensory adaptation on the snout

Protuberances called rays
→ each ray has thousands of Eimer's organs
→free nerve endings in the organ: Merkel mechanoceptors

Environment exploration

1. Mechanoceptors

Specialized mechanoceptors

- Hair cells
- Eimer's organs
- Lateral line organs

Do we have them?

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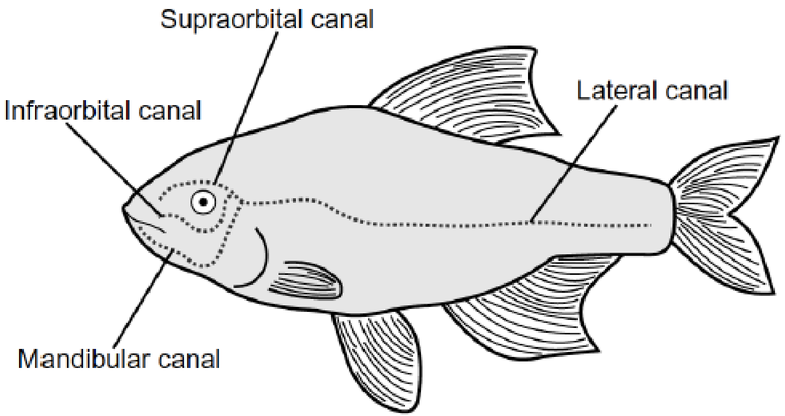
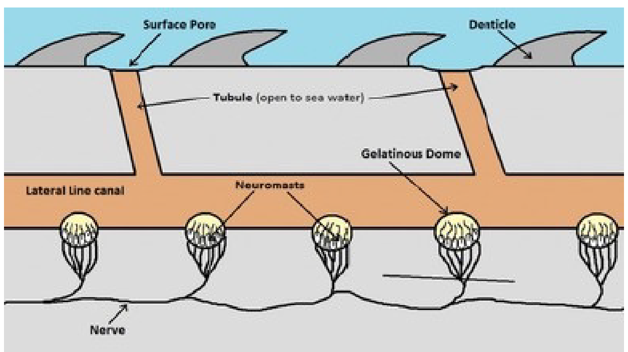
1. Mechanoceptors

Lateral line organs



Important for aquatic anamniotes

Located in the lateral line canals.



mechanoceptors called: neuromasts

- Hair like cells,
- Line the fluid-filled canals
- Some canals are closed (internally secreted fluid)
- Others are open (surrounding water enter)

2. Radiant-energy receptors

Radiant energy visible (to human) vs non visible

- Photoreceptors
- The median eye
- Pit organs

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2. Radiant-energy receptors

- Photoreceptors
- The median eye
- Pit organs

Do we have them?

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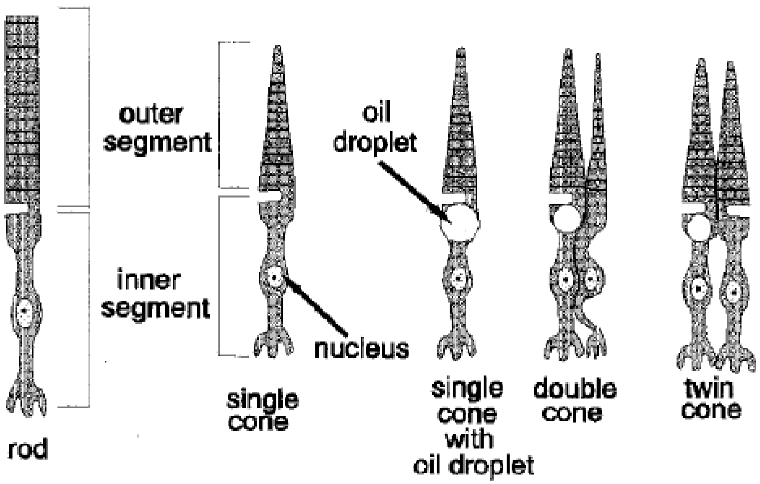
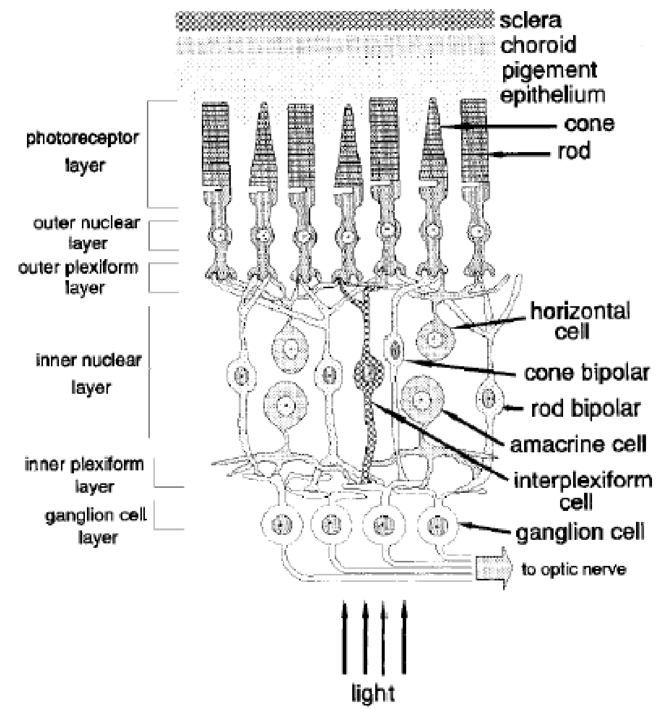
1. Radiant-energy receptors

Photoreceptors in the retina



Photoreceptors of the retina



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2. Radiant-energy receptors

- Photoreceptors in the retina
- The median eye
- Pit organs

Do we have them?

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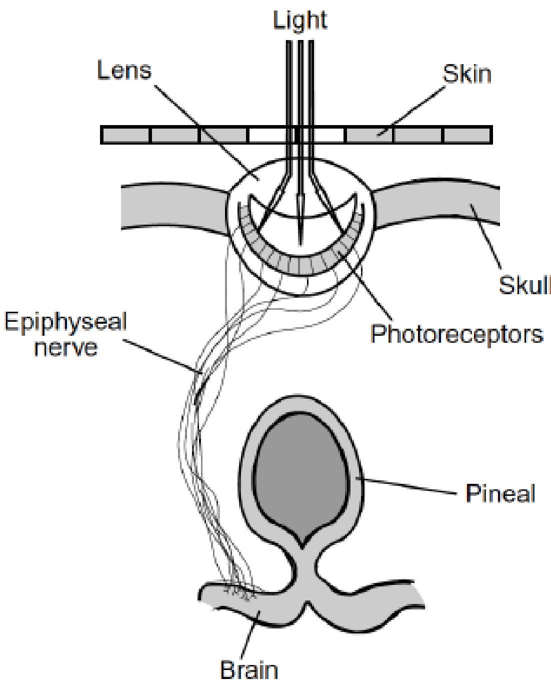
1. Radiant-energy receptors

The median eye



In some non-mammalian vertebrates.

- Single, unpared eye (at the top of the skin)
- Known as pineal eye or epiphysis

Structure: a layer of photoreceptors

Function: they gather light, do not form images

Synthesize melatonin → light/dark cycles

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1. Radiant-energy receptors

The median eye

In mammals and birds:

- The epiphysis is glabdular and it's the pineal gland

Produce melatonin → CNS pathways → light/dark cycles

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2. Radiant-energy receptors

- Photoreceptors
- The median eye
- Pit organs

Do we have them?

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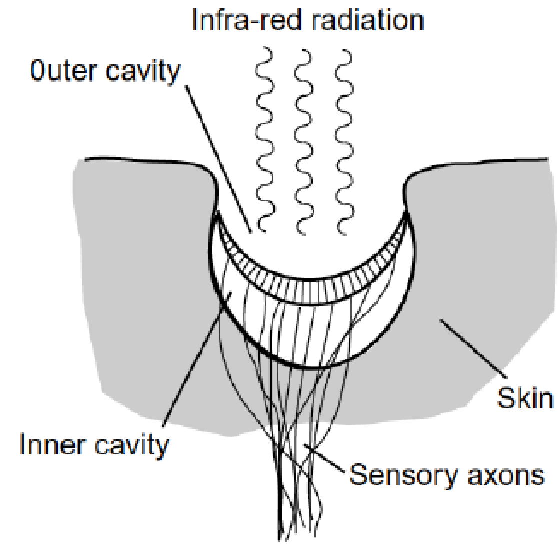
1. Radiant-energy receptors



Pit organs

Energy detector:
photoreceptor sensitive to **infrared** range.

In pit vipers (venomous snakes)

In the snout (btw. Lateral eyes and the nostrils)
Or in the non-venomous, on their upper/lower lips

Pit membrane innervated by sensory axons of trigeminal nerve.

Extremely sensitive.

Why are they useful?

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3. Chemoceptors

They sense the chemical properties of the environment.

Do we have them?

In water, both Gustation (Taste) and Olfaction (soluble chemical stimuli):

- act as distance receptors
- act as contact receptors

In air, only olfactory sense maintain dual role as distance and contact sense.

Taste in land animals is only a contact sense.

3. Chemoceptors

- Taste
- Olfaction
- Vomeronasal organ

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3. Chemoceptors

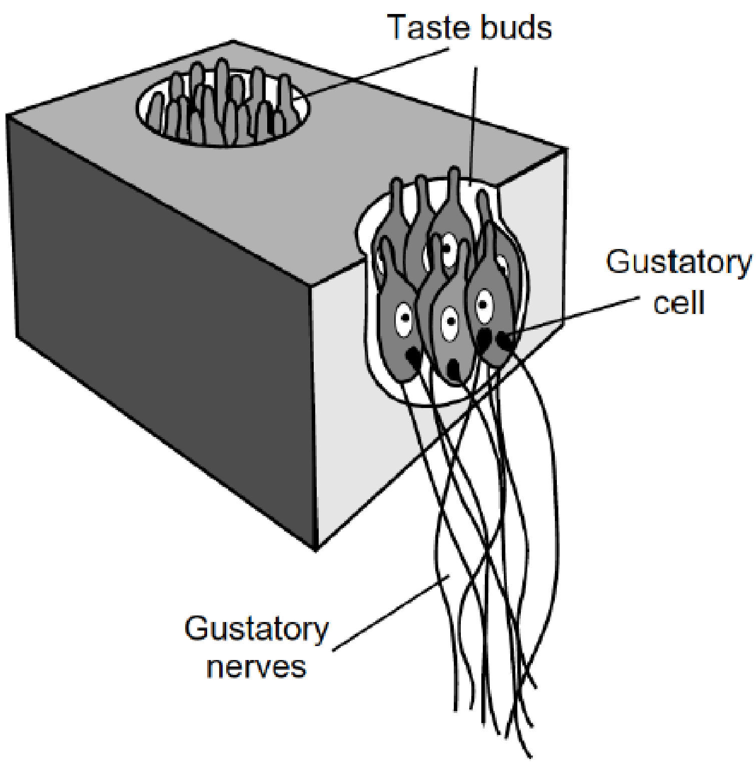
- Taste
- Olfaction
- Vomeronasal organ

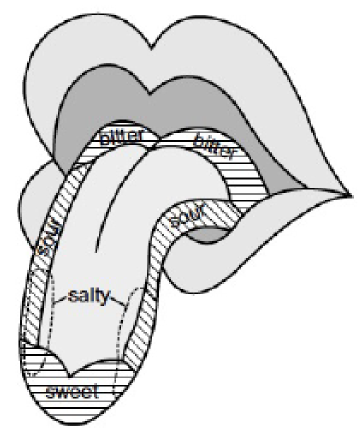
3. Chemoceptors

Gustatory receptors

Located within taste buds (located in gustatory papilla).

- In tetrapods: on the tongue (land animals).





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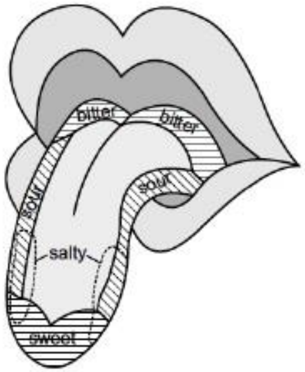
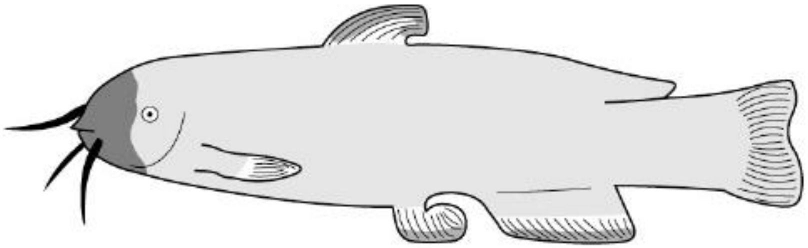
3. Chemoceptors

Gustatory receptors



- In **tetrapods**: on the tongue (land animals).
- In **non-tetrapods**: in the mouth, throat, on the head, all over the body surface.



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3. Chemoceptors

Gustatory receptors: what they respond to?

- In nonhuman land vertebrates: they respond to similar chemical compounds as gustatory receptors (sweet, acids, salts, alkaloids, bitter)

- In aquatic vertebrates: they respond to the same compounds + wide range of aminoacids.

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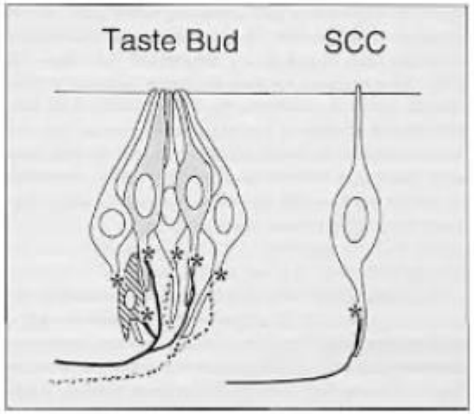
3. Chemoceptors

Solitary chemoreceptor cells: another taste system



On the skin surfaces, in the mouth and on the gills (in anamniotes, including hagfishes, teleosts, amphibians)

Amphibians: on the ventral skin.

Teleosts

Located on the fins

Ciliata

Detection of predators/ competitors.

Prionotus

Explore the bottom, involved in feeding.

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3. Chemoceptors

- Taste
- Olfaction
- Vomeronasal organ

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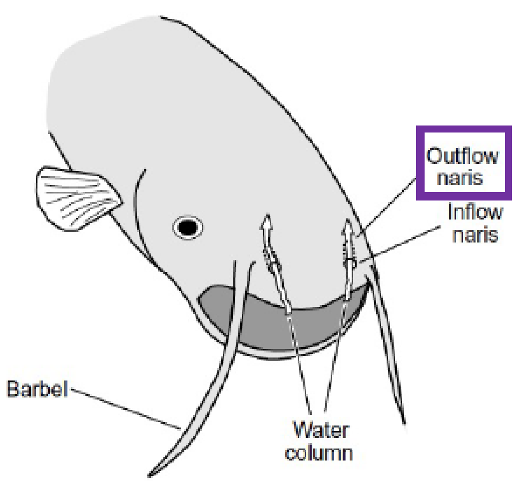
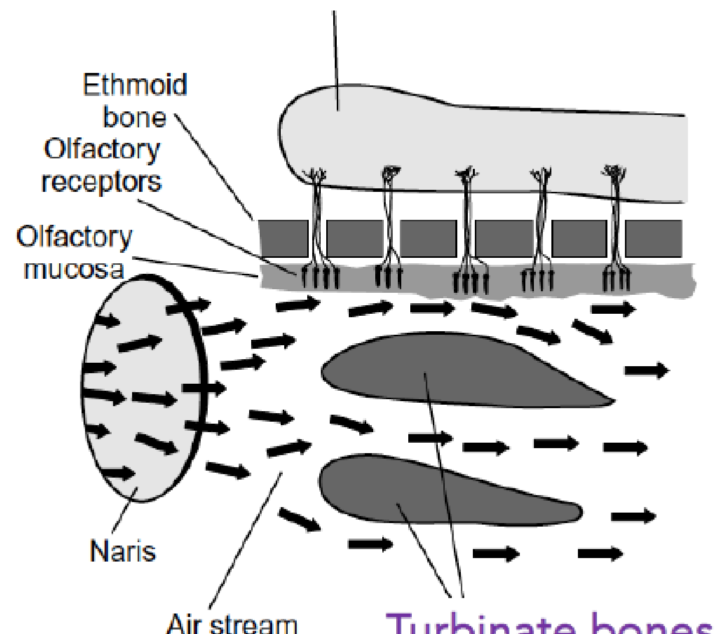
3. Chemoceptors

Olfactory receptors

Located in cavities with anterior and posterior openings
(e.g. nose,
in fish nasal sacs or outflow naris)





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3. Chemoceptors

Olfactory receptors

We are microsmatic!

Other animals (e.g. Canidae) are macrosmatic!

Larger olfactory bulbs

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3. Chemoceptors

- Taste
- Olfaction
- Vomeronasal organ

Do we have them?

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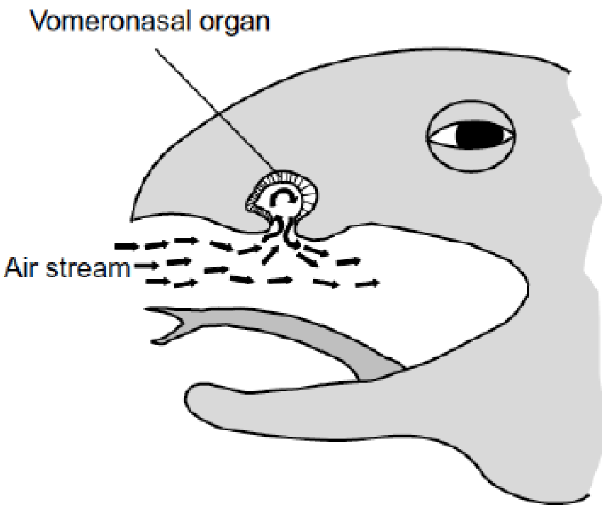
3. Chemoceptors

Vomeronasal organ



It senses the pheromones:

- Chemical communication substances secreted by one animal that produce a specific behavior reaction in another

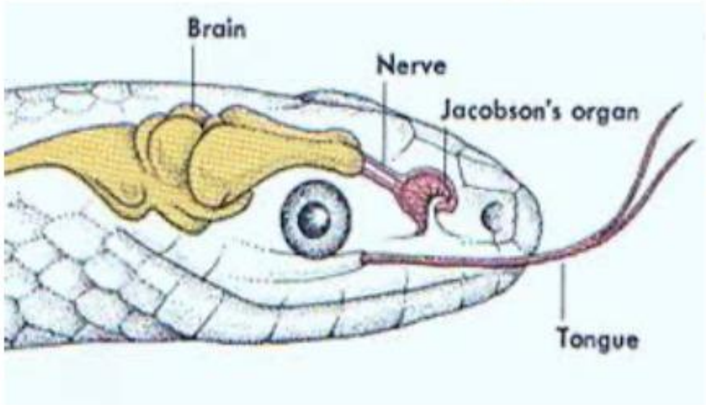
Humans do not detect "sex-attractant" pheromones.

In amphibians, reptiles and many mammals: located in the nasal cavity.

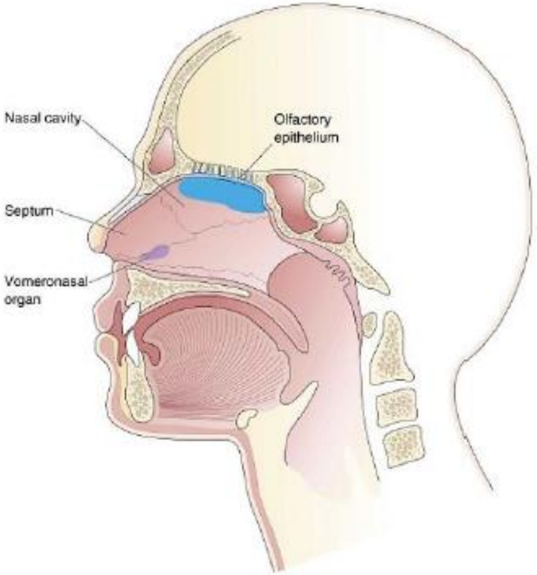
Different termination in the brain, they terminate in the accessory olfactory bulb.

3. Chemoceptors

Vomeronasal organ



Other vertebrates (snakes, lizards) have the Organ of Jacobson



Vomeronasal organ in primates

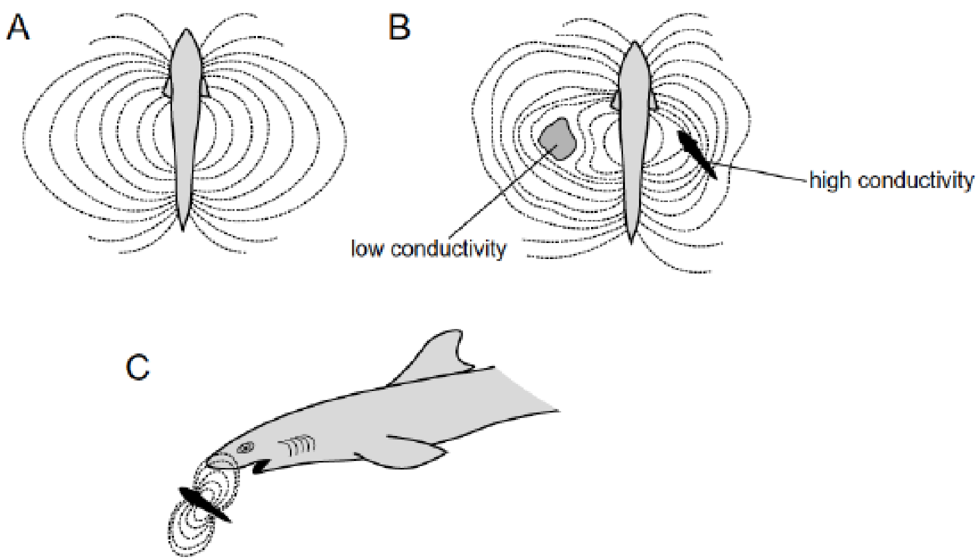
Well developed in strepsirrhini, middle in New World monkeys, underdeveloped in Old world monkeys and great apes.

4. Electroreceptors

Detection of electric fields. Do we have them?

Cartilaginous fishes ray-finned fishes

Detect self-generated and others' fields.



Electric organs

Generate electrical field.

4. Electroreceptors

- Ampullary receptors
- Tuberous receptors

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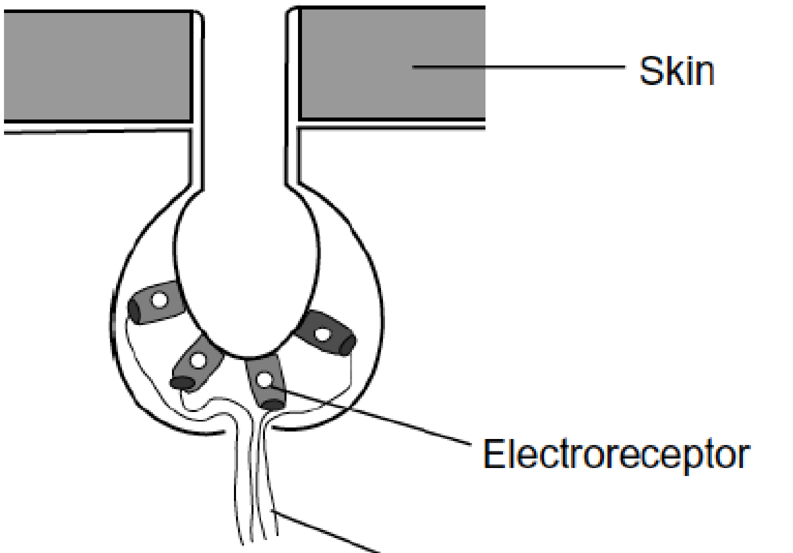
4. Electroreceptors

- Ampullary receptors
- Tuberous receptors

Ampullary

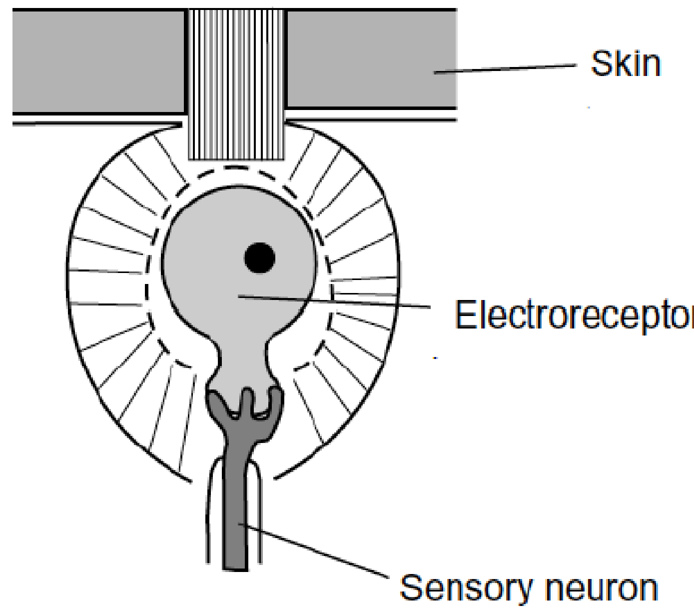


Low frequency electric rhytms

4. Electroreceptors

- Ampullary receptors
- Tuberous receptors

Tuberous



High frequency range of electric rhytms

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5. Nociceptors

Detection of unpleasant stimuli, pain.

Activated when tissues is cut, crushed, damaged or irritated by chemicals.

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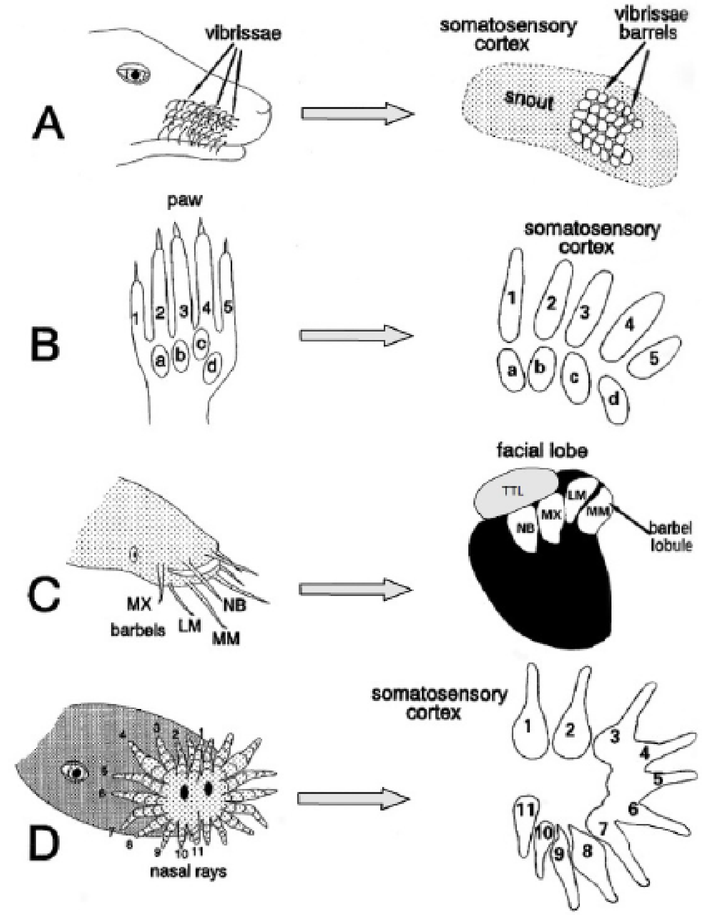
Topographic organization

Sensory systems have a spatial organization of the receptor surface that is preserved within the sensory parts of the CNS.



Sequential arrangements are maintained.

Summary

- different types of CNS cells in vertebrates
(different types of neurons or glial cells)

- Neuronal populations (nuclei)

- Receptors, senses and adaptation
(special senses)

- Mechanoceptors (hair cells, Eimer's organ, Lateral line organs)

- Radiant-energy receptors (photoreceptors, median eye, pit organs)

- Chemoceptors (taste, olfaction, vomeronasal organ)

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COMPARATIVE BRAIN EVOLUTION

Lecture 4

Comparative Neuroembryology (I):

Early Brain Morphogenesis

Lecture 4:
Comparative Neuroembryology (I): Early Brain Morphogenesis

1. Ontogenesis and Phylogeny

2. Neural tube formation

3. Different morphogenic events

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2 fundamental biological processes

Ontogeny
the development of an individual organism

Phylogeny
the evolutionary history of a species

Understanding how the nervous system forms during embryogenesis and how it has evolved across species provides critical insights into both normal brain function and neurological disorders

Comparative Neuroembriology

Importance of genetic neuromorphology: study of genes involved in the CNS development.

Ontogenesis does not recapitulate phylogeny, but creates it.
(Haeckel 1866)

All phylogenetic changes are correlated with genomic changes.

Relationship ontogenesis – phylogenesis are complex.

EVO-DEVO

The relationship between **ontogeny** (individual development) and **phylogeny** (evolutionary history) has long fascinated biologists.

While the 19th-century notion that “ontogeny recapitulates phylogeny” (Ernst Haeckel) has been largely revised, modern biology recognizes a **dynamic interplay** between these two processes.

This integration is especially evident in the development and evolution of the nervous system.

Ontogeny and Recapitulation (?)

"Ontogenesis recapitulate phylogeny."
Evolutionary changes results from the addition of new ontogenic stages to the terminal phase of the ancestor's development.

← Is this true?

Terminal additions occur in phylogeny, BUT the sequence of development in vertebrates does NOT recreate adult ancestral stages of the species' evolutionary history.

Developmental sequences do NOT recreate stages from "lower" to "higher" species

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Ontogeny and Recapitulation (?)

Developmental sequences do NOT recreate stages from “lower” to “higher” species

There is something true…

Resemblance among embryos within a group and this resemblance decreases as development proceeds.

- Von Baerian recapitulation Over evolution, there is conservation of many developmental stages

1. Developmental Biology Reflects Evolutionary History

Embryonic development often mirrors evolutionary stages. For example:

- The **neural tube**, a hallmark of vertebrate development, reflects the ancestral central nervous system structure.
- The **tripartite brain** (forebrain, midbrain, hindbrain) seen in vertebrate embryos is conserved across species, suggesting a common evolutionary origin.

These developmental stages are not literal recapitulations but **modular reuses** of ancient genetic programs.

2. Deep Homology and Conserved Genetic Pathways

Modern genomics has revealed that many genes involved in nervous system development are **deeply conserved** across species:

- **Hox genes**: Define segmental identity in both invertebrates and vertebrates.
- **Pax6**: Essential for eye and brain development in flies, fish, and humans.
- **Otx and Emx**: Involved in forebrain patterning across vertebrates.

This conservation supports the concept of **deep homology**, where similar structures arise from shared genetic mechanisms, even in distantly related organisms.

3. Evolutionary Innovations via Developmental Modifications

New nervous system features often arise from changes in developmental processes:

- **Heterochrony**: Changes in the timing of developmental events (e.g., prolonged neurogenesis in humans leads to larger brains).
- **Heterotopy**: Changes in the spatial expression of genes (e.g., expansion of cortical regions).
- **Gene duplication and divergence**: Allow new functions to evolve while preserving ancestral roles.

These mechanisms enable **evolutionary plasticity** while maintaining core developmental frameworks.

4. Comparative Embryology as a Tool for Evolutionary Insight
Studying embryonic development across species reveals both conserved and divergent features:

- **Amphioxus** (a basal chordate) shows a simple neural tube and brain vesicles, offering clues to vertebrate origins.

- **Lampreys and hagfish** (jawless vertebrates) exhibit primitive brain structures that inform early vertebrate evolution.

- **Mammalian embryos** show advanced cortical development, reflecting evolutionary expansion.

Comparative embryology helps reconstruct **evolutionary trajectories** and identify **ancestral states**.

5. Evo-Devo: Evolutionary Developmental Biology

The field of **evo-devo** (evolutionary developmental biology) bridges ontogeny and phylogeny by exploring how changes in development drive evolutionary change.

Key principles include:

- **Modularity**: Developmental units (e.g., brain regions) can evolve independently.

- **Plasticity**: Developmental systems can adapt to environmental and genetic changes.

- **Constraint**: Evolution is limited by developmental possibilities and historical contingencies.

Evo-devo has revolutionized our understanding of how complex nervous systems evolve.

6. Brain Evolution Through Developmental Expansion

In mammals, especially primates:

- **Neurogenesis is extended**, allowing more neurons and larger brains.
- **Cortical folding (gyrification)** increases surface area without expanding skull size.
- **Radial glia** and **intermediate progenitors** contribute to layered cortical architecture.

- Von Baerian recapitulation Over evolution, there is conservation of many developmental stages

Ontogenic sequences → adult phenotype

↑

Changes in the genome

Swifts in the timing
during development
(heterochrony)

Developmental studies help reconstructing phylogeny

Features common to most groups in developmental sequences and in the adult phenotype can be used to reconstruct the condition of the brain in the common ancestral vertebrate.

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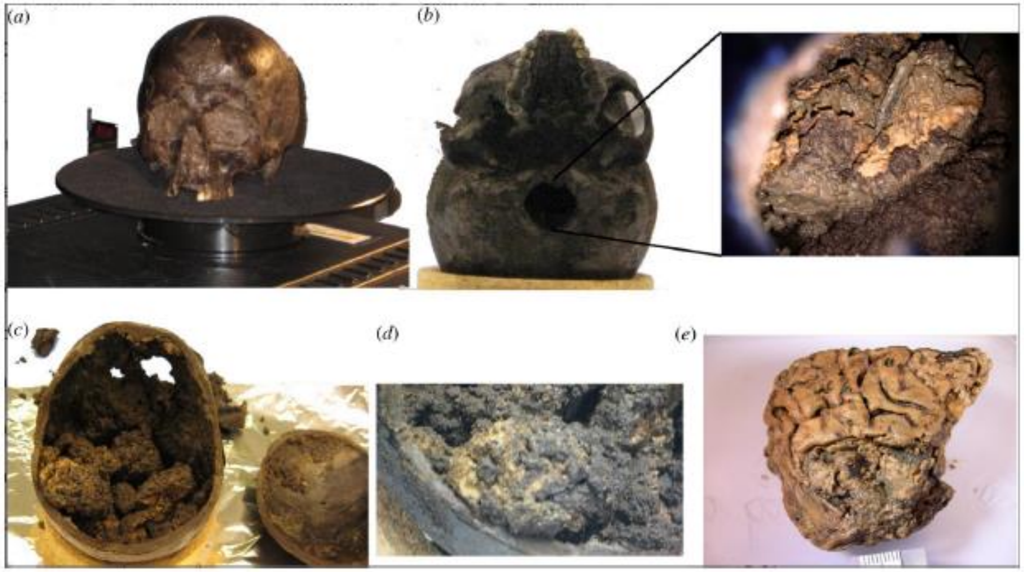
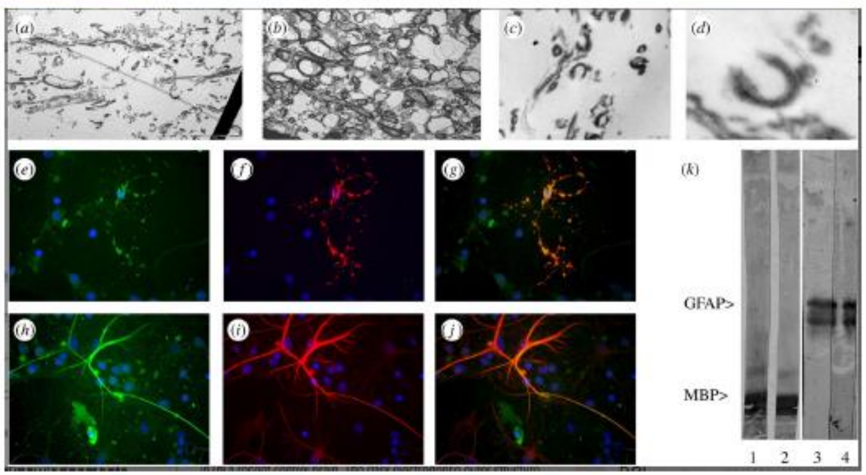




Research articles

Protein aggregate formation permits millennium-old brain preservation

Axel Petzold, Ching-Hua Lu, Mike Groves, Johan Gobom, Henrik Zetterberg, Gerry Shaw and Sonia O'Connor

Published: 08 January 2020
https://doi.org/10.1098/rsif.2019.0775

Ontogeny refers to the sequence of events that occur from the fertilization of the egg to the formation of a fully functional nervous system in the adult organism.

This process is highly orchestrated and involves several key stages:

1. Neural Induction

Neural induction is the first step in the formation of the nervous system. It begins during **gastrulation**, when the three germ layers—ectoderm, mesoderm, and endoderm—are established. The **ectoderm**, which will give rise to the skin and nervous system, receives signals from the underlying **mesodermal notochord** to become **neuroectoderm**.

2. Neural Plate and Neural Tube Formation

The neuroectoderm thickens to form the **neural plate**, which then undergoes **neurulation**—the process of folding into the **neural tube**, the precursor to the central nervous system (CNS).

- **Primary neurulation**: The neural plate folds to form the neural tube.
- **Secondary neurulation**: Occurs in the caudal regions, forming the lower spinal cord.

3. Regionalization and Patterning

Once the neural tube is formed, it undergoes **regionalization** into distinct domains:

- **Forebrain (prosencephalon)**
- **Midbrain (mesencephalon)**
- **Hindbrain (rhombencephalon)**
- **Spinal cord**

4. Neurogenesis and Gliogenesis

Neural progenitor cells within the ventricular zone of the neural tube begin to divide and differentiate:

- **Neurogenesis**: Formation of neurons
- **Gliogenesis**: Formation of glial cells (astrocytes, oligodendrocytes)

Radial glial cells serve as scaffolds for migrating neurons, guiding them to their final destinations.

5. Migration and Layer Formation

Neurons migrate along radial glia to form the layered structure of the brain, particularly the **cerebral cortex**. This process is tightly regulated and involves:

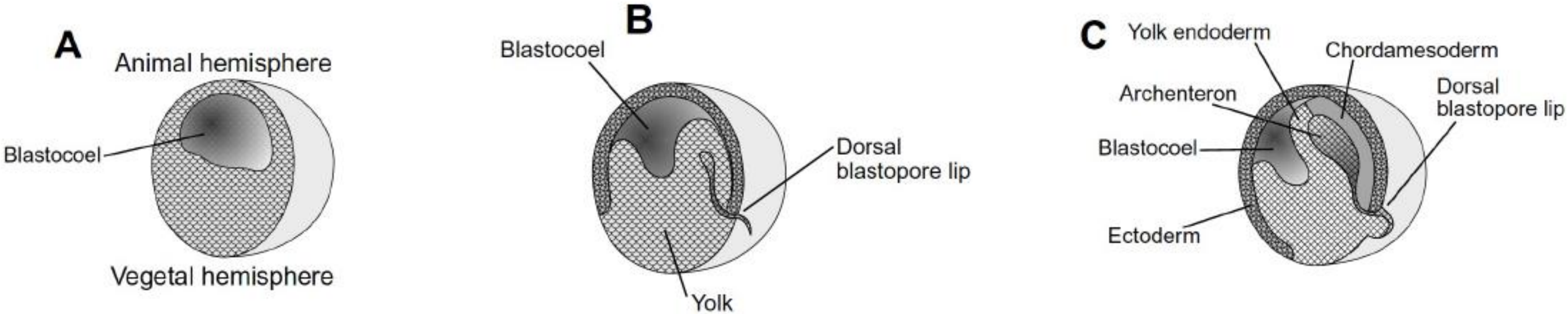
- **Reelin signaling**
- **Cell adhesion molecules**
- **Cytoskeletal dynamics**

6. Synaptogenesis and Circuit Formation

Neurons extend axons and dendrites to form synapses. This involves:

- **Growth cones**
- **Guidance cues** (e.g., netrins, semaphorins, ephrins)
- **Activity-dependent refinement**

Early brain morphogenesis



Blastula

Gastrula

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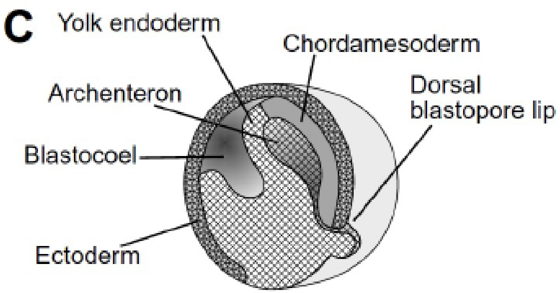
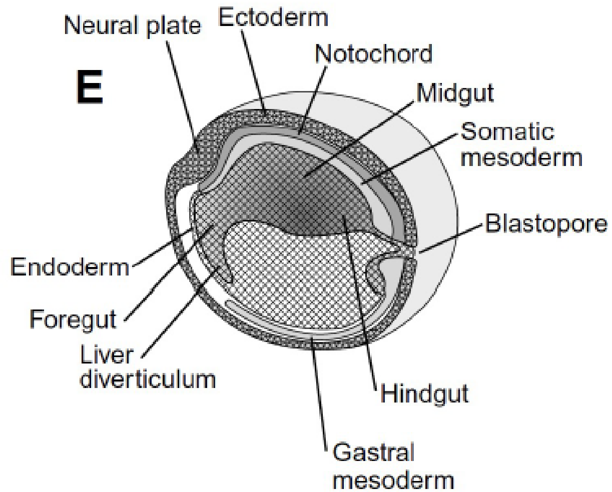


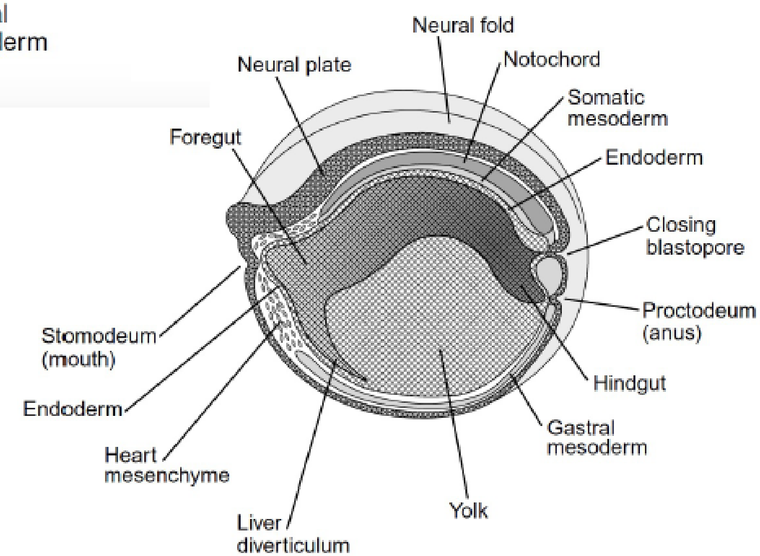
Gastrula



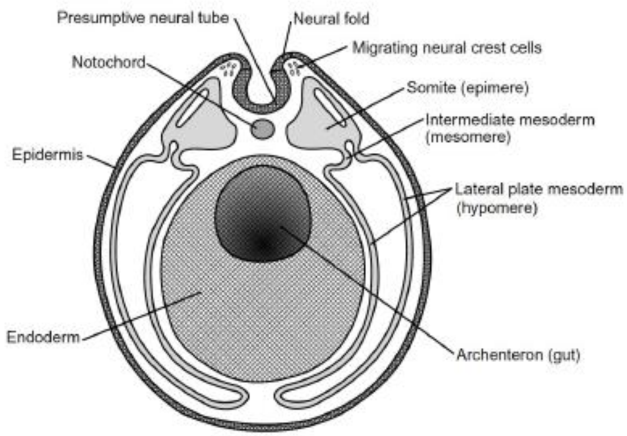
ectoderm → Neural tube

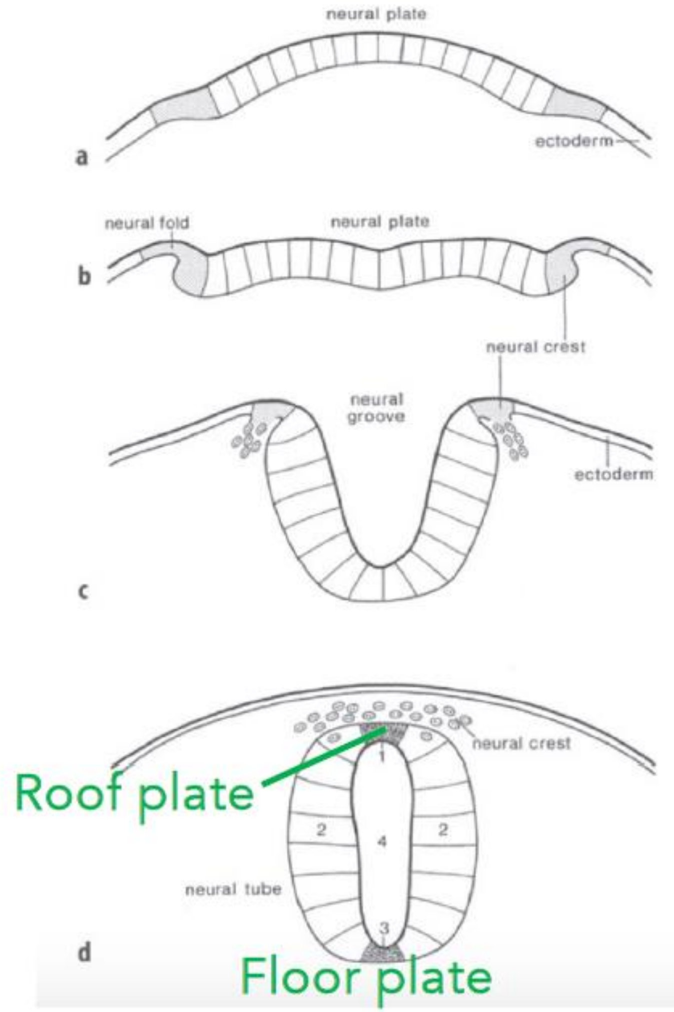
↑

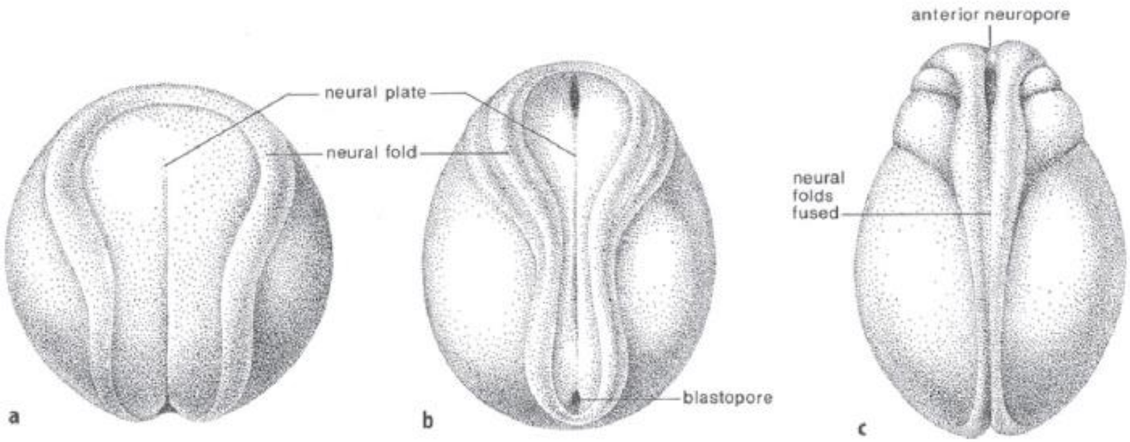
notochord



Neural tube formation





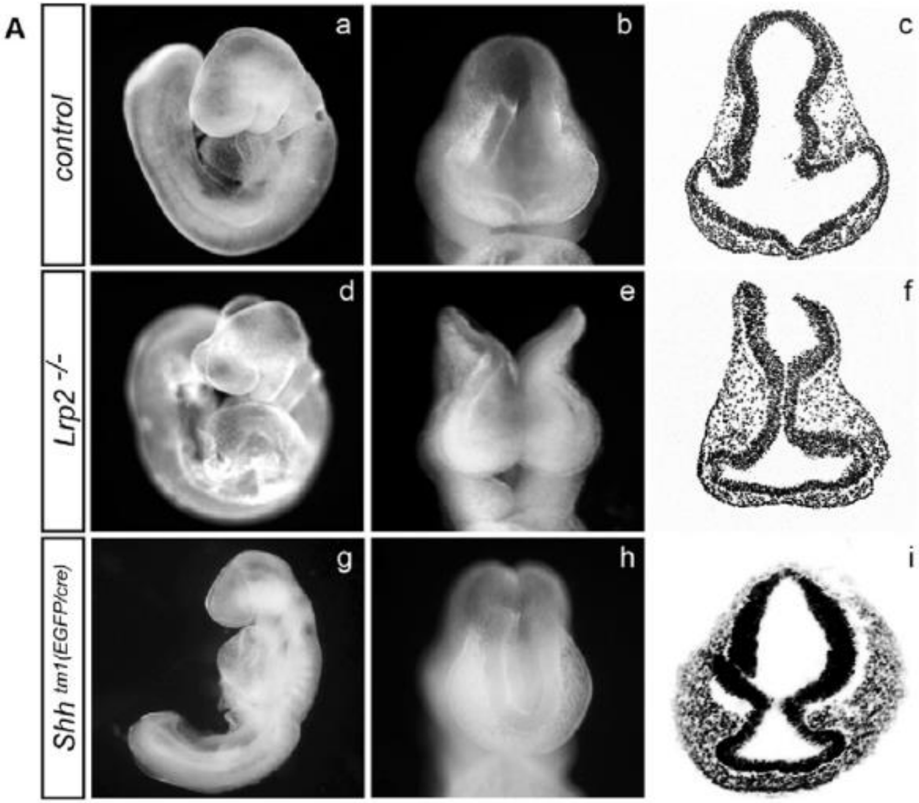


Neural tube formation

RESEARCH ARTICLE

LRP2 mediates folate uptake in the developing neural tube

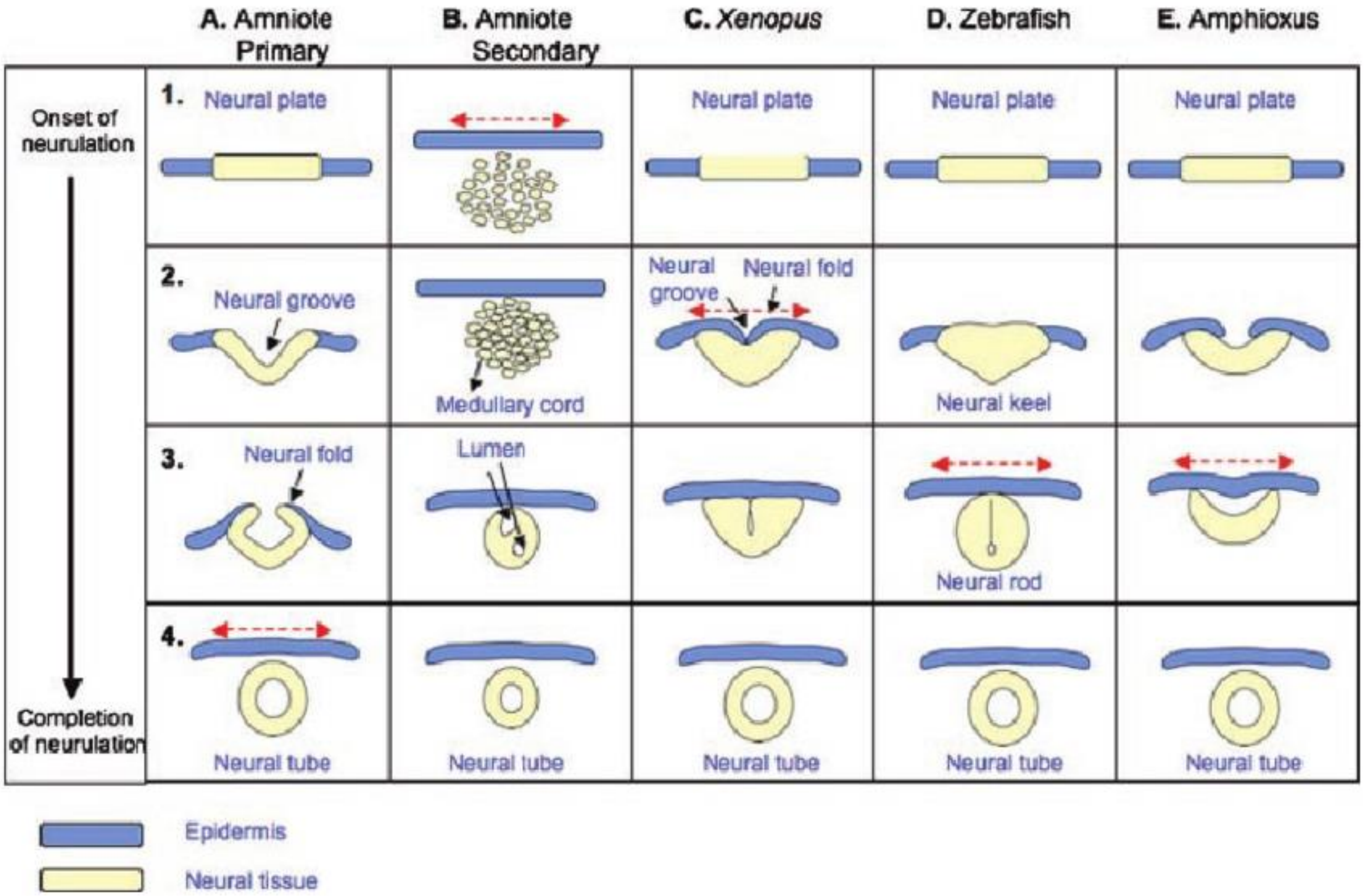
Esther Kur[1,*,‡], Nora Mecklenburg[1,‡], Robert M. Cabrera[2], Thomas E. Willnow[1] and Annette Hammes[1,§]



Kur, Mecklenburg et al., 2014

mouse

Neural tube formation



Neural tube formation

In Cephalochordates

Lateral borders of neural groove separate from general body ectoderm.
Continuous ectodermal layer, beneath which the neural groove transforms secondarily into a tube

In Birds and Mammals

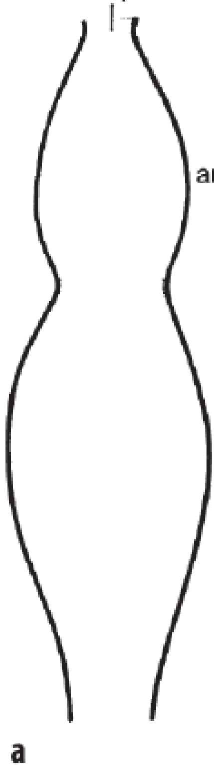
Most caudal part of the spinal cord develops from a solid cord of cells→ then transformed into a hollow tube by **cavitation**.

In Lampreys and Teleosts

- Entire CNS is developed from a solid cord of neuroectoderm, that secondarily form a tube by **cavitation.**
- In teleosts, during neurulation the neuroectodem is tightly folded → **narrow** neural groove and narrow cleft as future ventricle.

Formation of Brain Regions

Rostral part becomes wider than the caudal part.



Archencephalo
n

Deuterencephalon

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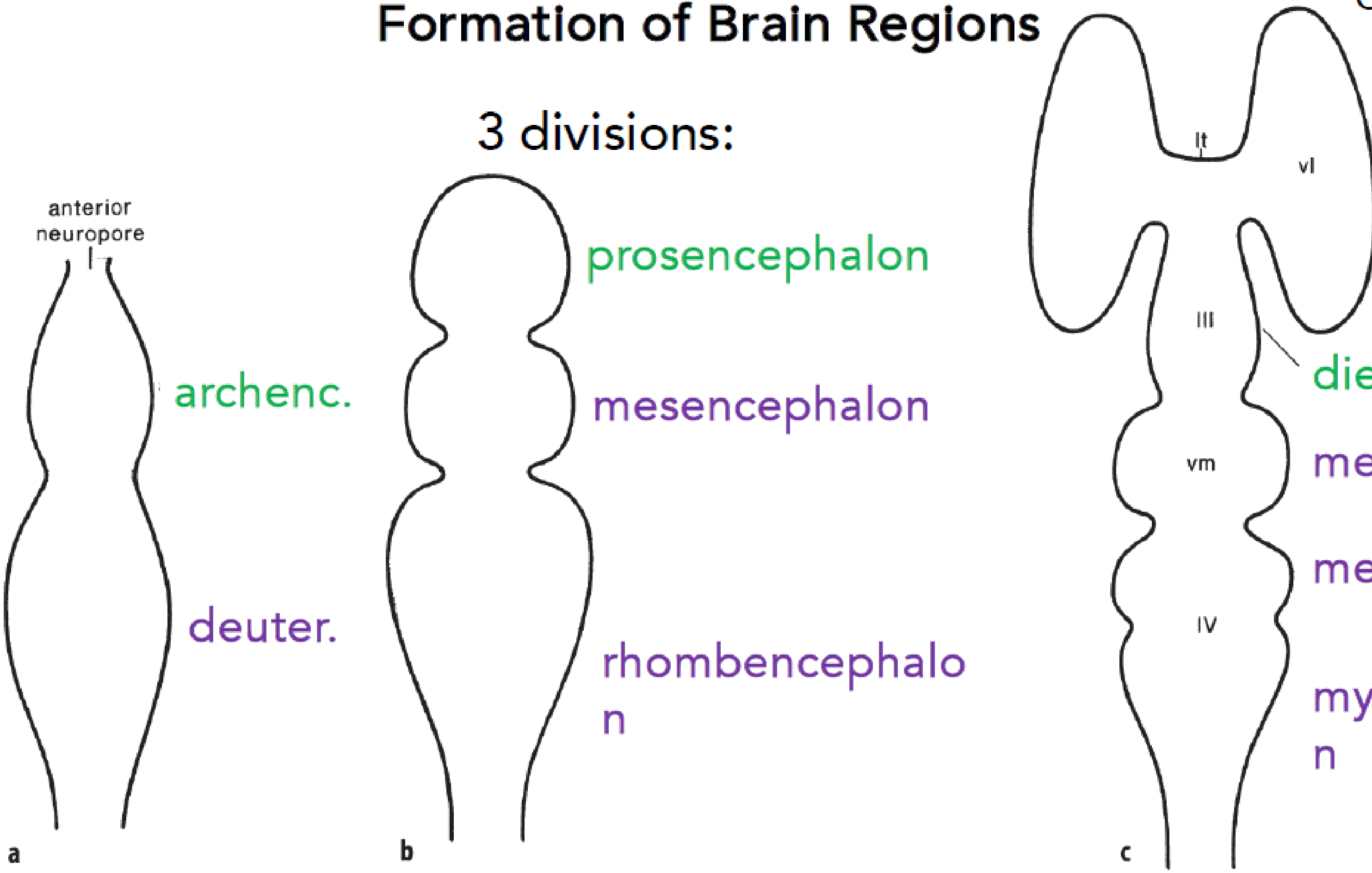
Formation of Brain Regions

3 divisions:

common to all vertebrates:



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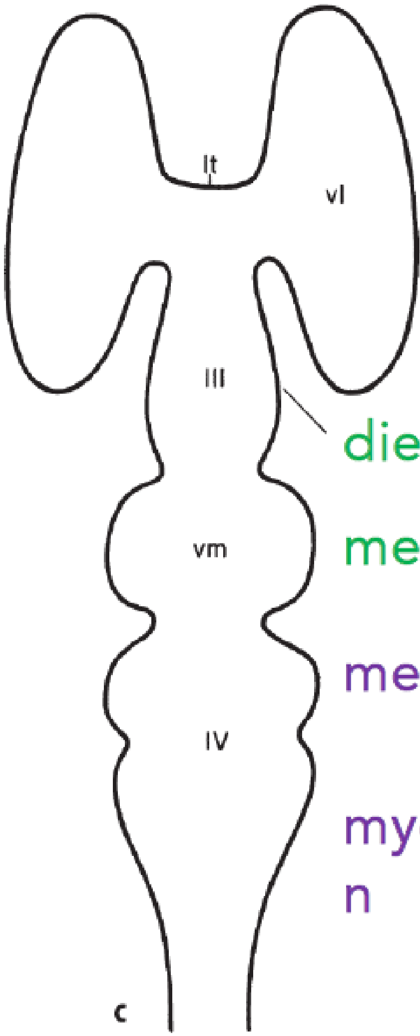
Formation of Brain Regions



telencephalon

Prosencephalon (forebrain)

diencephalon

mesencephalon

Mesencephalon (midbrain)

metencephalon

Rhombencephalon (hindbrain)

myelencephalo
n

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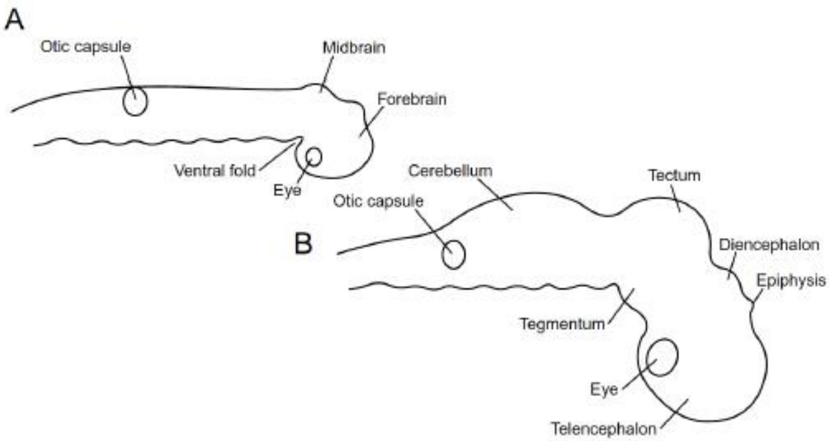
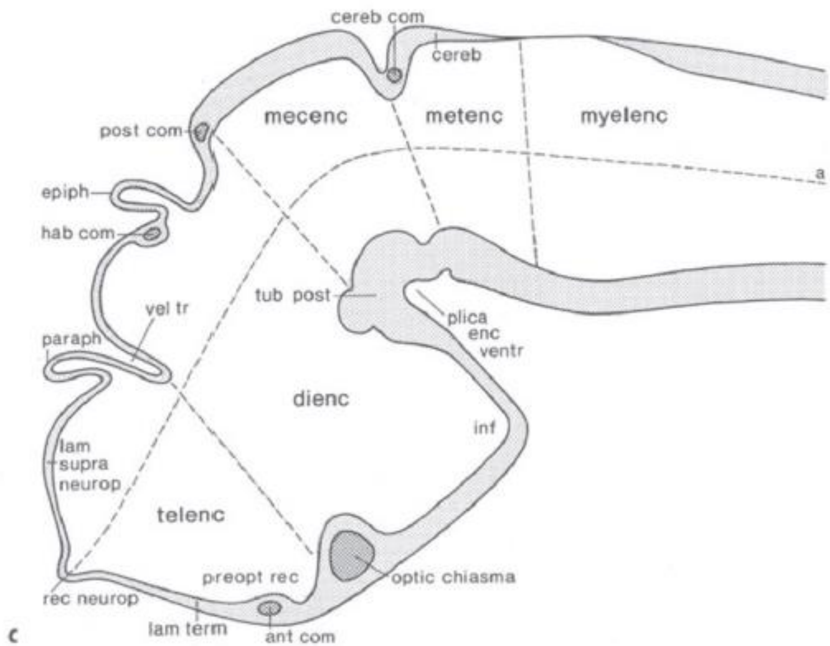
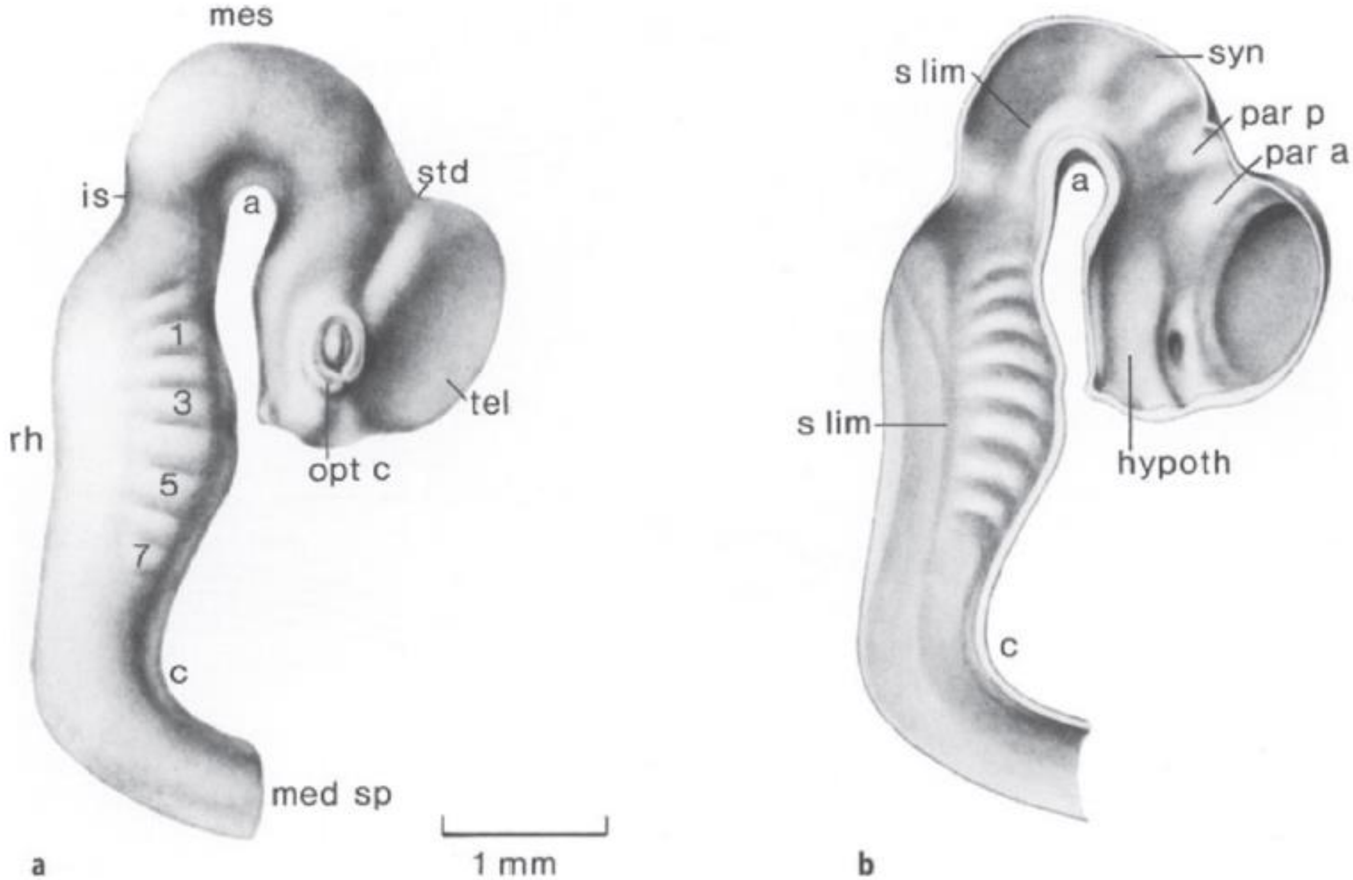
Flexures in rostro-caudal direction

All brain regions grow unequally → appearance of flexures



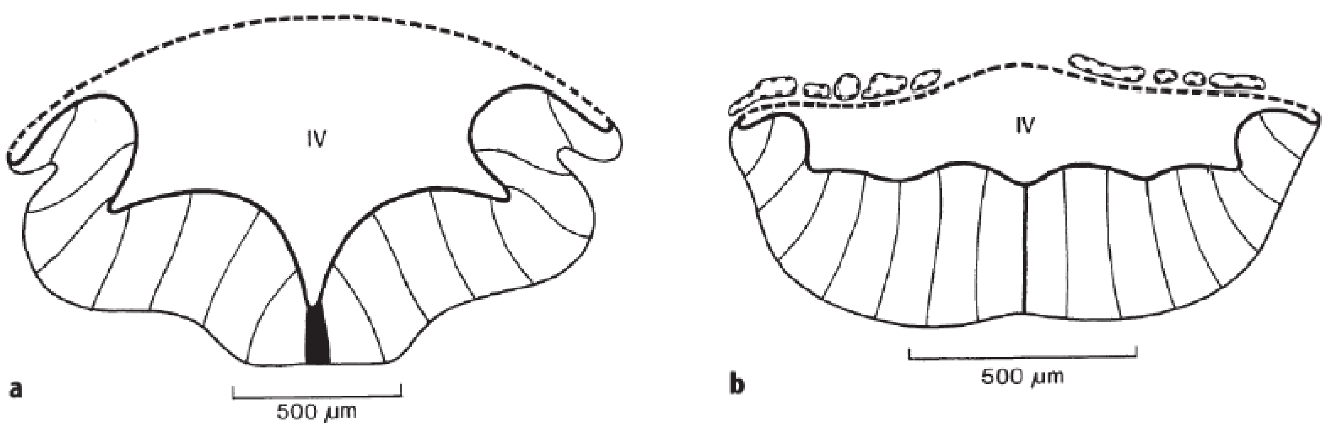




3-D reconstruction of Rhesus macaque embryo

Different morphogenic events:
Modifications of the neural tube in Vertebrates

1. Divergence of lateral plates



Rhombencephalon in human In sharks

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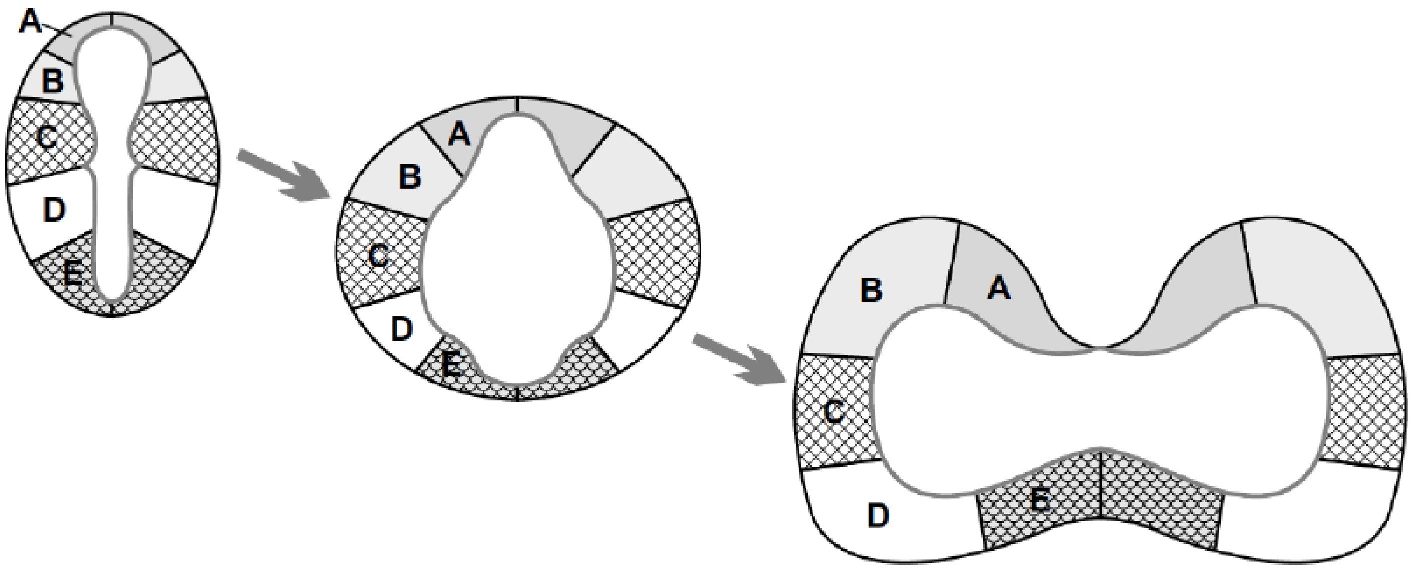
2. Evagination of the lateral plates



- in most vertebrates (lampreys, cartilaginous fishes, amphibians, amniotes)

- Central lumen enlarges → telencephalic ventricles → telencephalon bulges outwards and expands (=evaginates)

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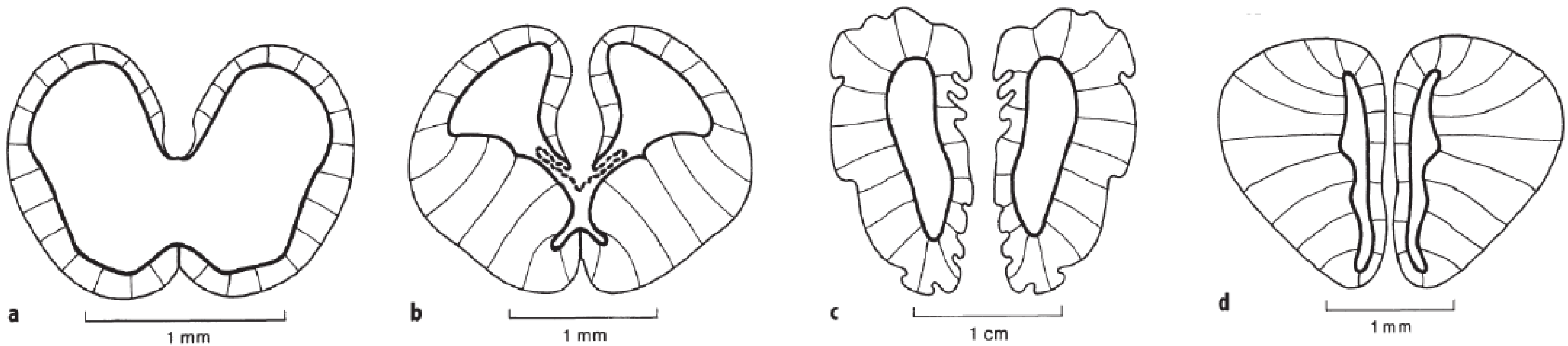
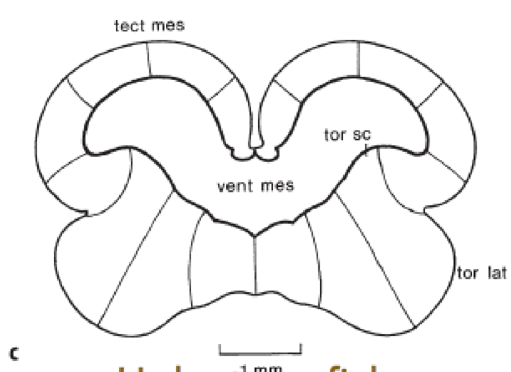
2. Evagination of the lateral plates: EXAMPLES

Telencephalo



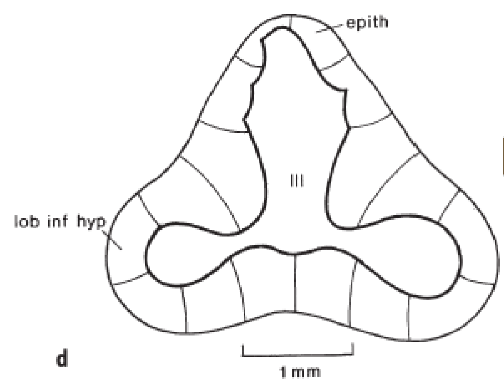
Hamster (E13) Hamster (E15) Blue whale fetus Pigeon

Mesencephalon



Holostean fish
Amia

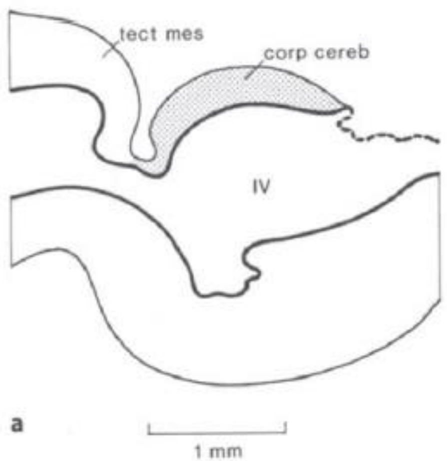
Diencephalon



Chondrostean fish

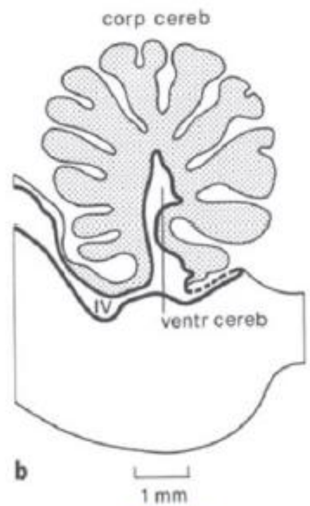
2. Evagination of the lateral plates (Cerebellum development)

In all vertebrates: originates from rostral &dorsal part of Rhomb. (lateral walls fuse dorsally → cerebellar plate)

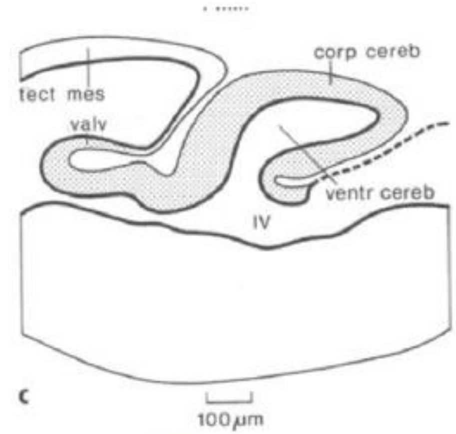


Alligator embryo

In amphibians and chelonians, Single plate-like config.



Chick



Trout

In chondrichtyans, teleosts, crosspterygians, birds, mammals, cerebellum evaginates dorsally.

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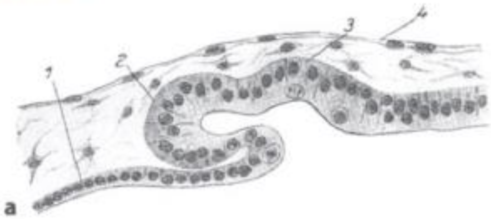
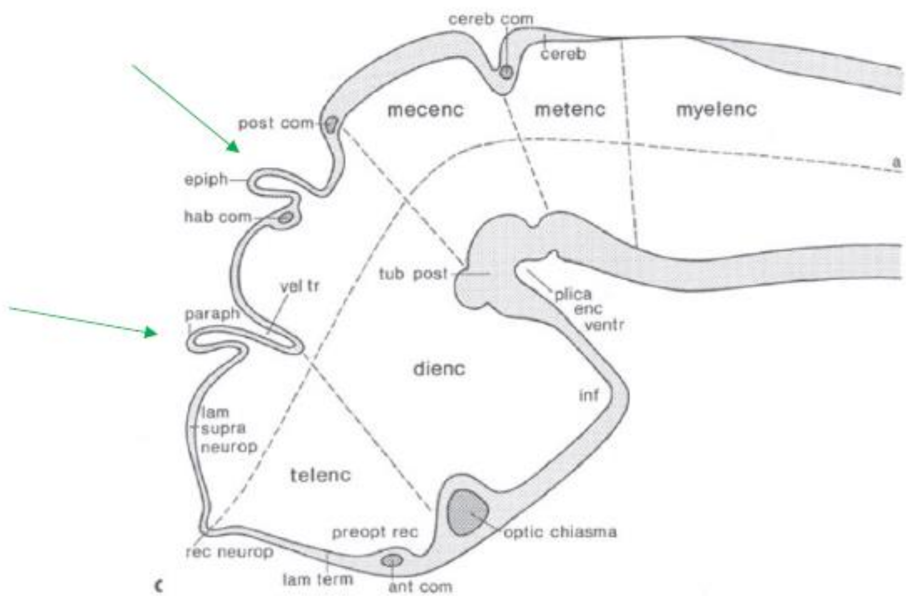
3. Median evaginations of the prosencephalic roof plate

Prosenc. Roof plate expands dorsally at specific spots.





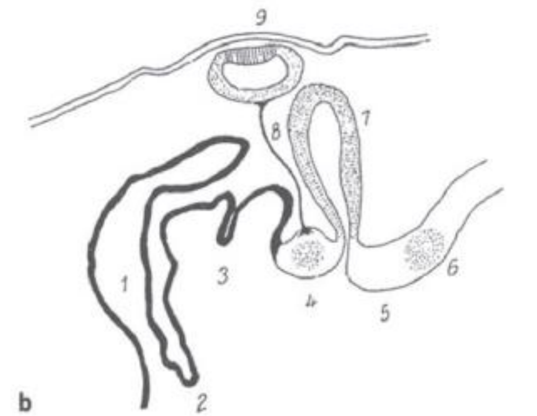
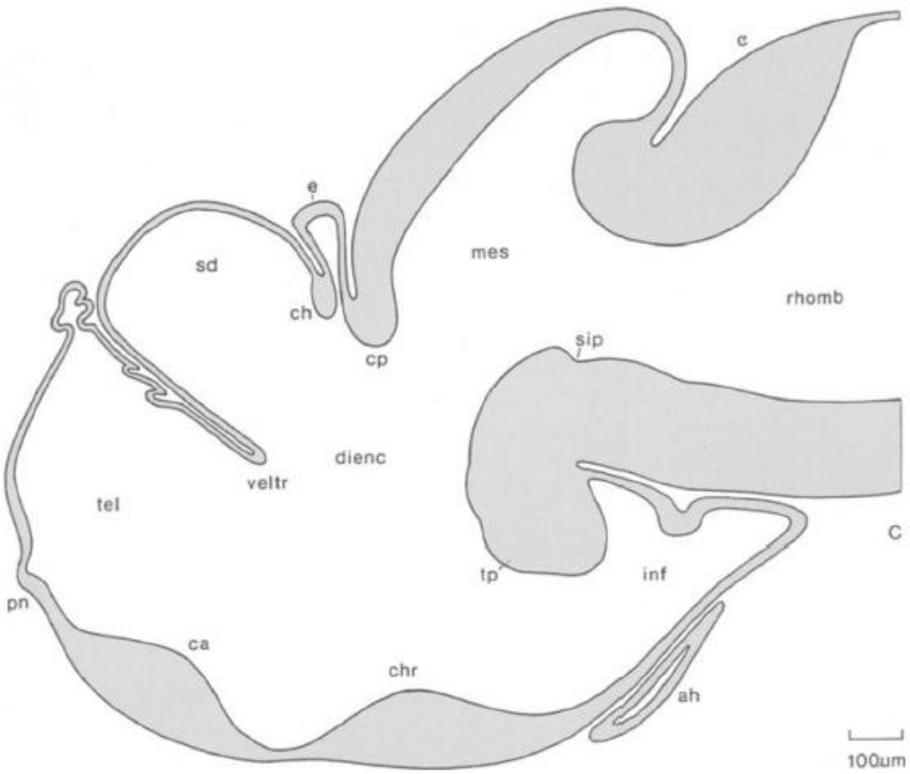


Fig. 4.12a,b. Median sections through dorsal part of the diencephalon of embryonic reptiles, showing development of the pineal complex. **a** The lizard *Lacerta vivipera*, 4-mm-embryo; *1*, diencephalic roof; *2*, anlage of the parapineal organ, which will become the parietal eye; *3*, anlage of the pineal organ, which will differentiate into the epiphysis; *4*, ectoderm. **b** An older embryo of the blindworm *Anguis fragilis*; *1*, paraphysis; *2*, velum transversum; *3*, saccus vasculosus; *4*, commissura habenulae; *5*, pretectum; *6*, commissura posterior; *7*, epiphysis; *8*, parietal nerve; *9*, parietal eye (reproduced from Becarri 1943, Figs. 241, 242)

4. Median evaginations of the diencephalic floor



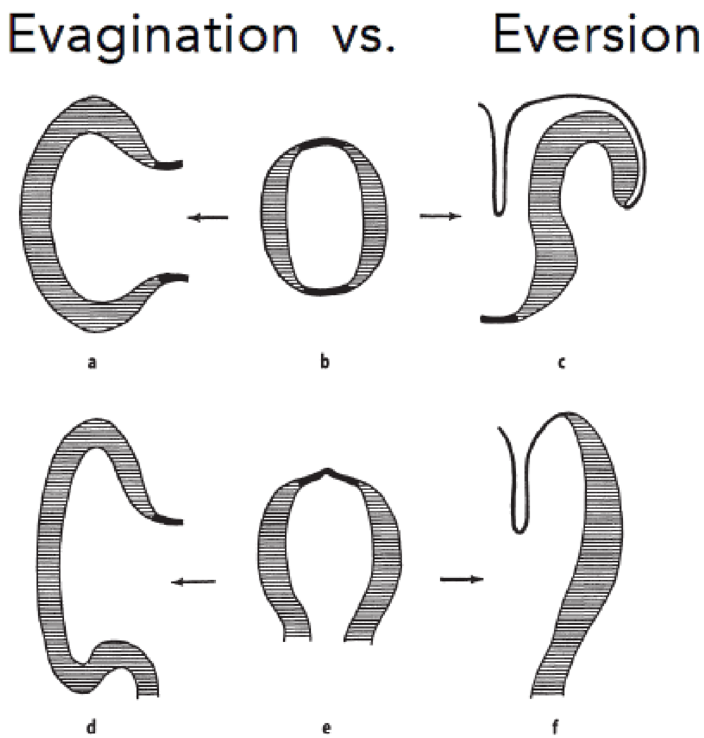
Sturgeon larva (4w)

Thin floor of diencephalon is formed by lateral plates of the 2 sides.

Ventrocaudal evagination of diencephalic floor.

It leads to infundibulum and to the saccus vasculosus.

5. Eversion of the lateral plates



Eversion: rolling outward

The side walls recurve laterally and the roof plate is transformed in an expanded tela.

Branchiopterygians & Actinopterygians

Lacerts and rhynchocephalis

Sharks

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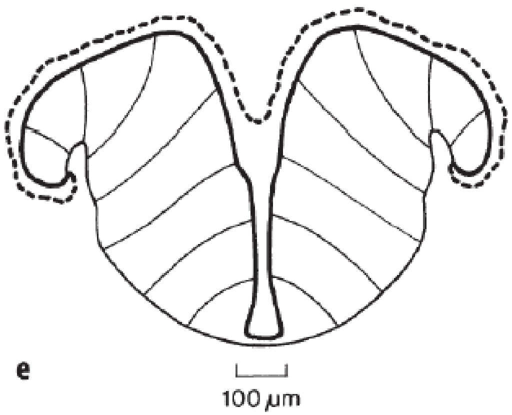
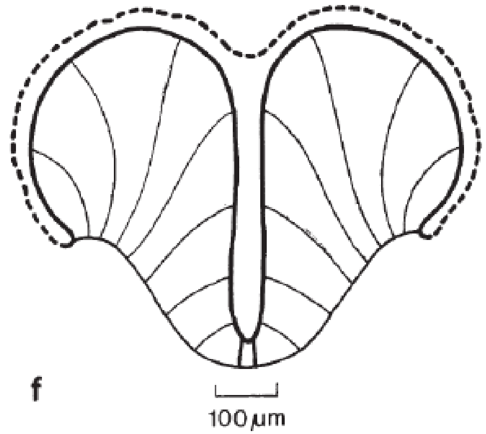
5. Eversion of the lateral plates



Branchiopterygians & Actinopterygians

Eversion in telenc. Combined with thickening of the dorsal part of the lateral telenc. walls



Teleosts
(Actinopterygian=ray-finned fish)

Lacerts and rhynchocephalis — Eversion in the cerebellum

Sharks — Eversion in the rhombencephalon

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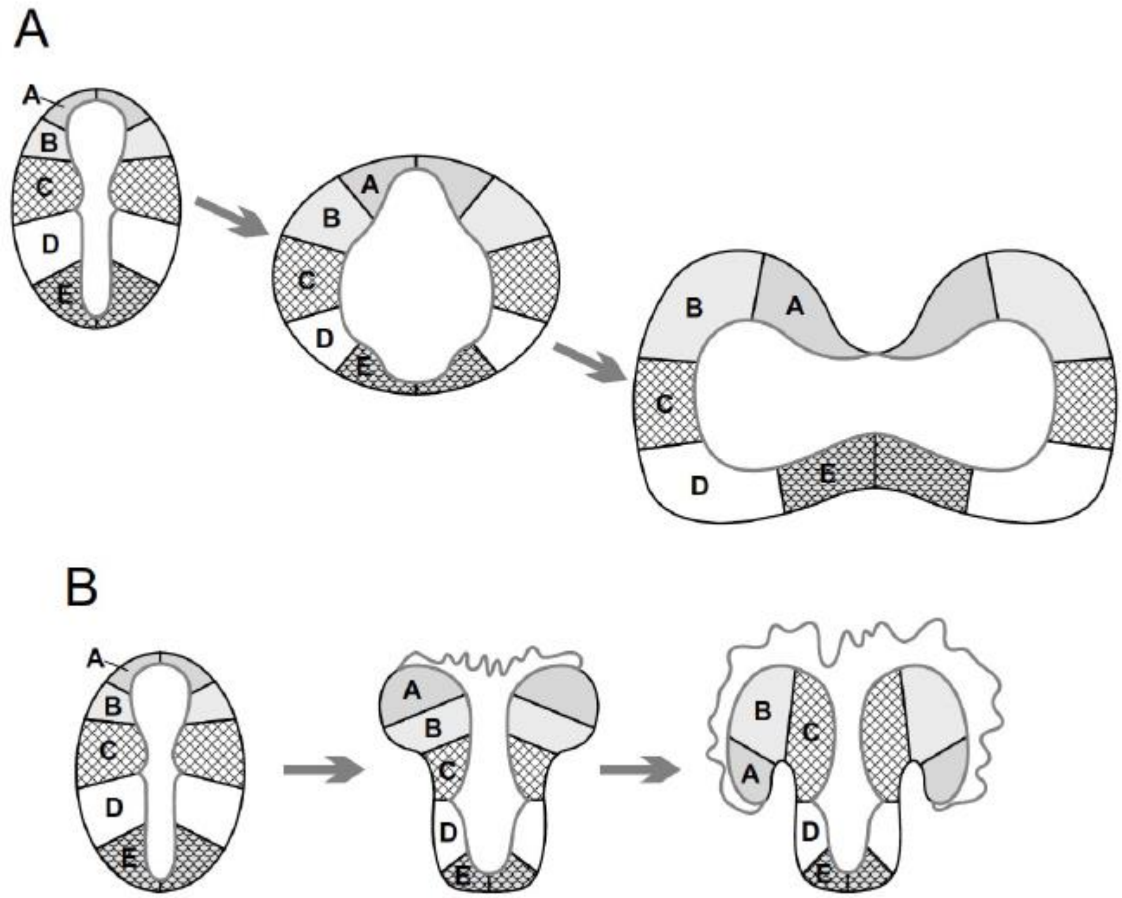
Evagination vs. Eversion

Evagination

Eversion



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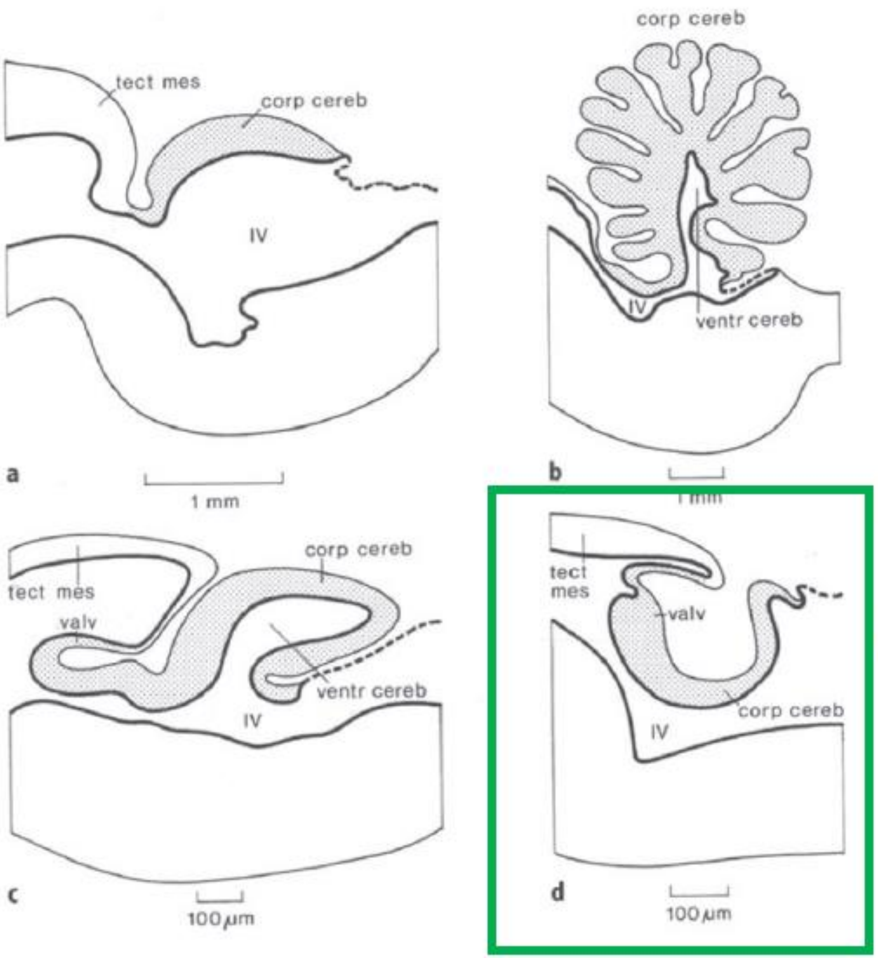
6. Invagination of the nervous and membranous part of the neural tube



It occurs in both cerebellum and telencephalon

Brachiopterygian fish

The whole cerebellum invaginates into the mesencephalic and rhomb. ventricular cavities

Mammals

hippocampus invaginates into the lateral ventricles.

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7. Local widening of the wall

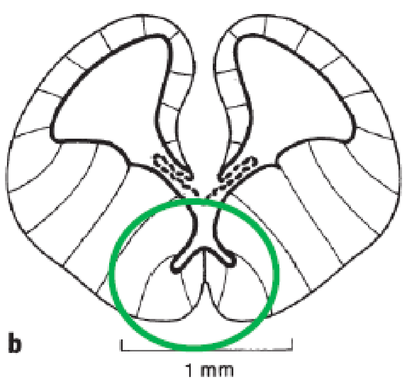
Development → formation of internal or external protrusions

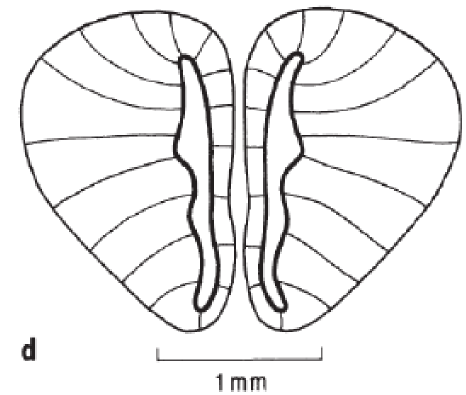
Dinoi, Crossopterygian

Dorsal thalami protrude into the third ventricle

Mammals

Large ridge-like protuberances from primordia of strio-amygdaloid complex





Birds

Thickening of telencephalic walls, reduces the ventricular cavities

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8. Fusion (coarctation) of the ventricular wall

Fusion of the ventricular walls is **common** (occurs in many parts of the brain).

Holostean & Teleostean

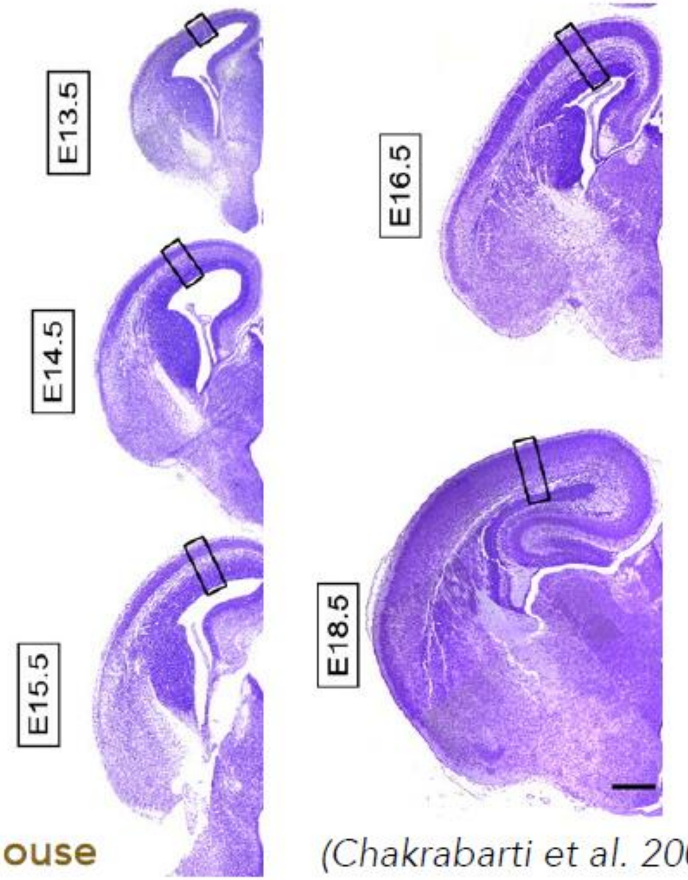
Granular layer of cerebellum develop from bilateral protrusions (that fuse along the medial plate).

Gymnotied teleosts & Anuran amphibians

Median surfaces of right/left tori semicirculares fuse almost completely.

Mammals

In telencephalon: coarctation between ganglionic eminences & septal/pallial parts of the cerebral hemispheres.



mouse

(Chakrabarti et al. 2007)

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8. Fusion (coarctation) of the ventricular wall

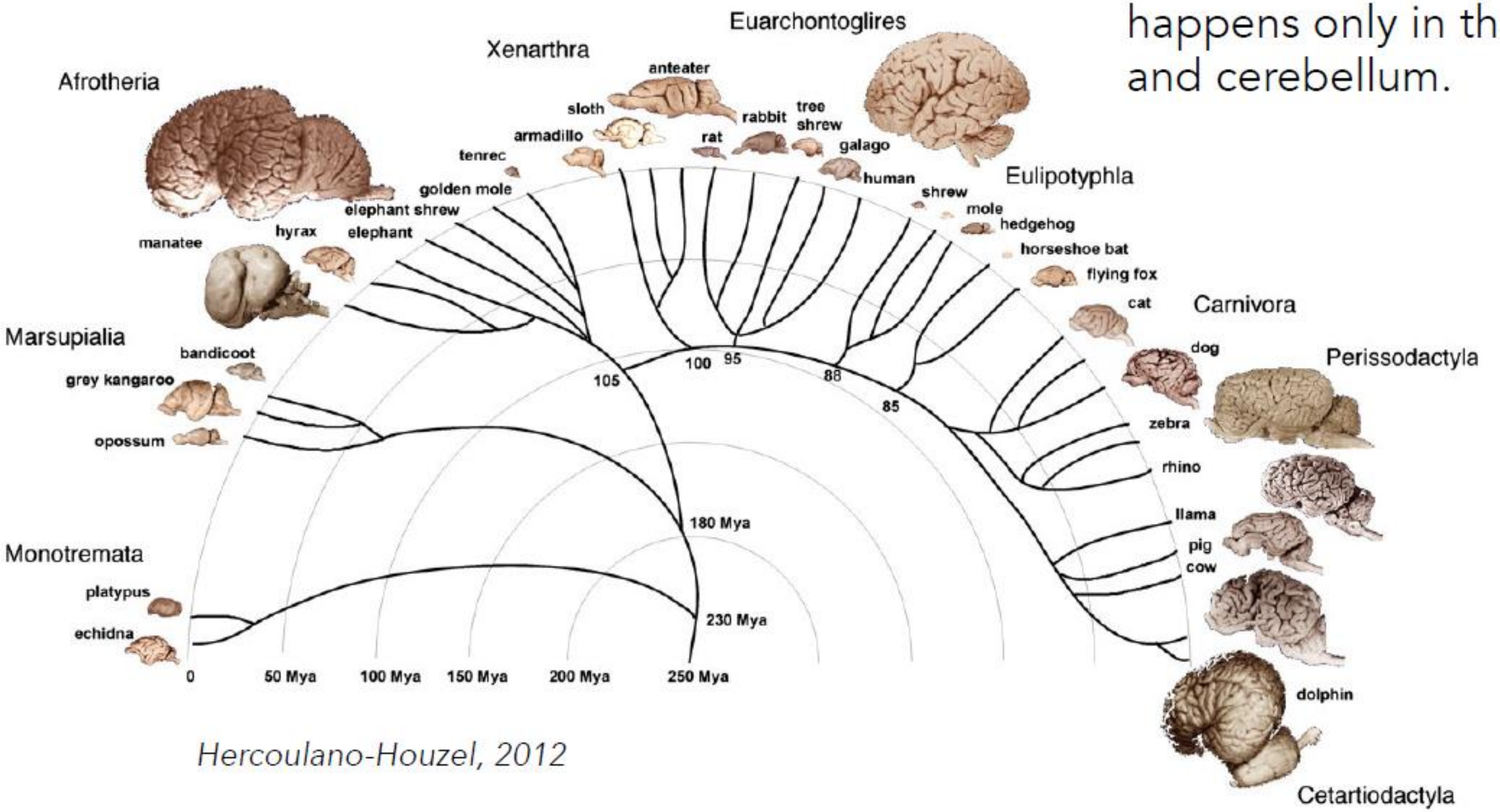
Fusion of the ventricular walls is **common** (occurs in many parts of the brain).

Reduction of the size of the ventricular cavity is not walways due to coarctation.

- In the **spinal cord**: decrease of the central canal due to loss of ependymal cells.

9. Surface enlargement, gyrification and folding

Always connected with cortex formation, so it happens only in the pallium and cerebellum.



Hercoulano-Houzel, 2012

Summary

Neural plate

↓

Neural groove

↓

Neural tube

→ Common to all vertebrates

↓

Modifications of neural tube

- Evagination
- Eversion
- Invagination
- Widening of lateral walls
- Local widening of roof plate
- Fusion of the walls
- Gyrification

→ Different in diff. species and diff. parts of the CNS

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