

Jonas Rose  
bird brains

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Te Whare Wānanga o Ōtāgo  
NEW ZEALAND

## BIRDS ?

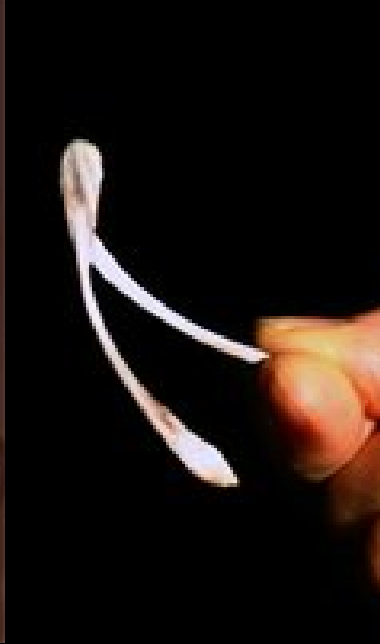


- Who are they
- What tricks can they do
- What do their brains look like
- What don't we know yet
- What are the implications

## Bird evolution

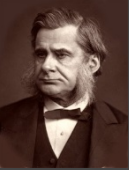


### Birds are dinosaurs



Henry Huxley ("Darwin's Bulldog") 1868  
Described *Archaeopteryx* as a transitional  
fossil between birds and reptiles and  
compared it to several dinosaurs.


# Bird evolution



## Birds are dinosaurs

**EARLY BIRD**

A fossil of a two-footed dinosaur discovered in China and lived 160 million years ago, is believed by experts to be the oldest known ancestor of birds



Beijing  
CHINA

Found in deposits in the Junggar Basin of Xinjiang

Belongs to group of long-legged stubby-armed carnivorous dinosaurs called Alvarezsaurids

63 million years older than any known members of the group

**Haplocheirus solers**

Three-fingered hands

Single massive claw on each hand

Pronounced keel

SIZE (by height)

4.6 to 6 m

1.8 m

0.8 m

0.7 m

Human

Velociraptor

T-Rex

Haplocheirus

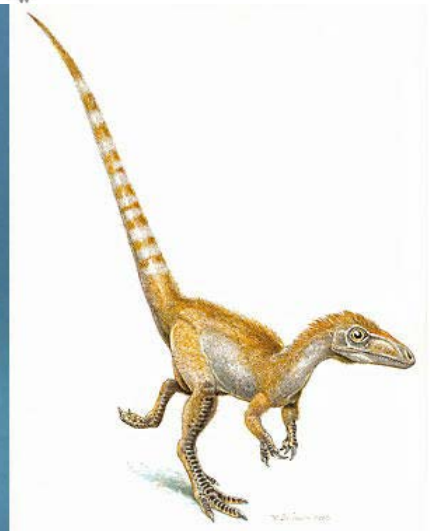
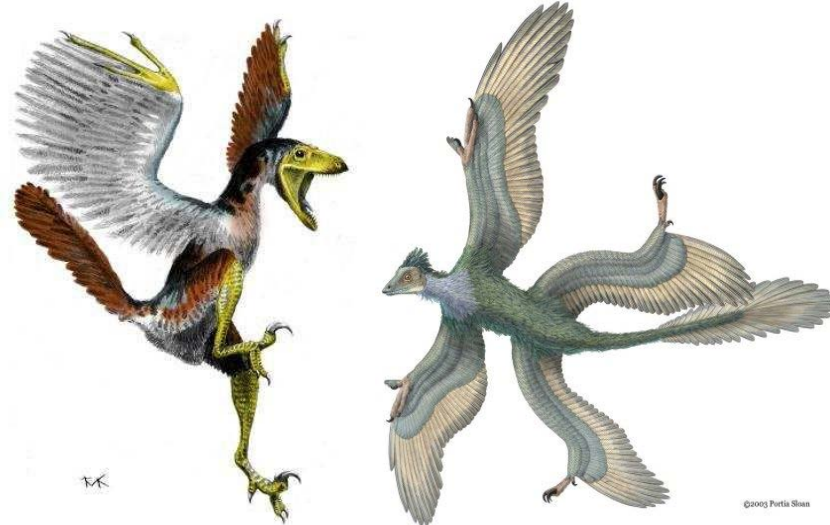
\*Artist's impression

**APPEARANCE TIMELINE (Million years ago)**

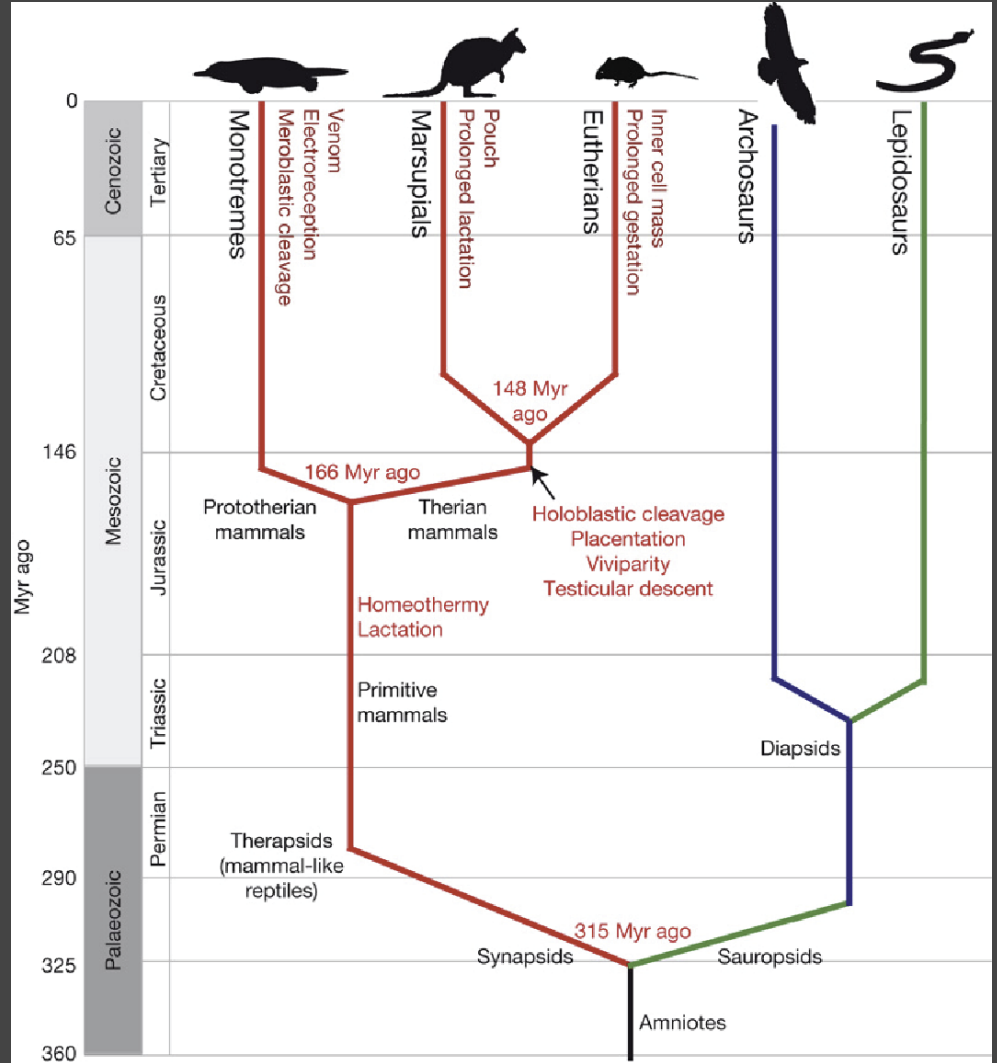
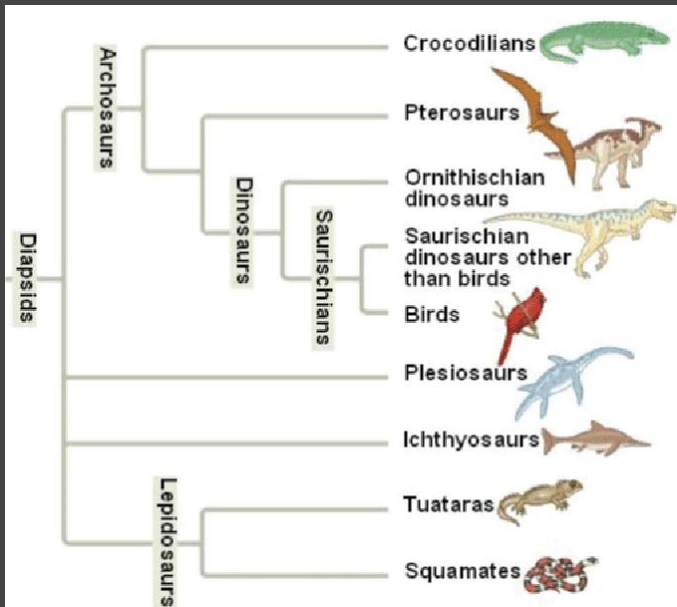
M. Jurassic	L. Jurassic	Early Cretaceous	Late Cretaceous
	<ul style="list-style-type: none"> <li>Archaeopteryx (150-145)</li> </ul>	<ul style="list-style-type: none"> <li>Microraptor (120)</li> </ul>	<ul style="list-style-type: none"> <li>T-Rex (68-65)</li> <li>Velociraptor (75-71)</li> </ul>
	<ul style="list-style-type: none"> <li>Haplocheirus (160)</li> </ul>		<ul style="list-style-type: none"> <li>Alvarezsaurus (86-83)</li> </ul>

Source: Science Journal

REUTERS



# Bird evolution



# New view on the avian brain



## Scala naturae, Ludwig Edinger (1855-1918)



- With each new class of vertebrates, a new brain-structure is added
- Cognitive abilities are scaled accordingly

**HISTORIC VIEW – WE DO NOT LIKE IT !**

Humans



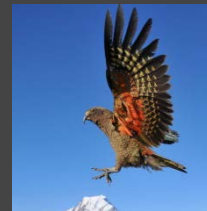
Neocortex  
(dorsal pallium)

Mammals



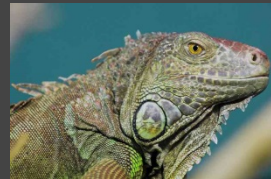
Enlarged striatum

Birds



Enlarged pallium

Reptiles



Striatum

Amphibia



Primordial vertebrate brain, no dorsal pallium,  
Small basal ganglia (pallidum but no striatum)

Fish



## New view on the avian brain

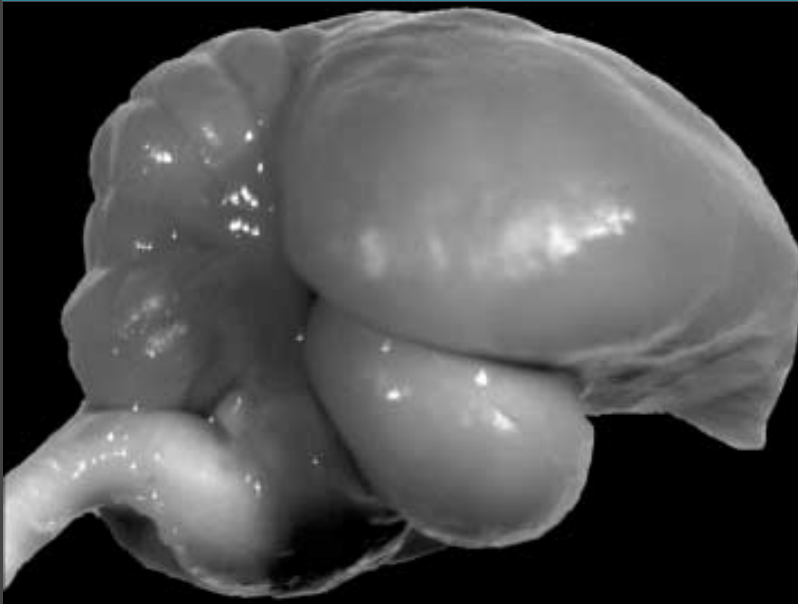
Edinger's scala naturae is contradicted by birds (amongst others).



# New view on the avian brain



Songbird

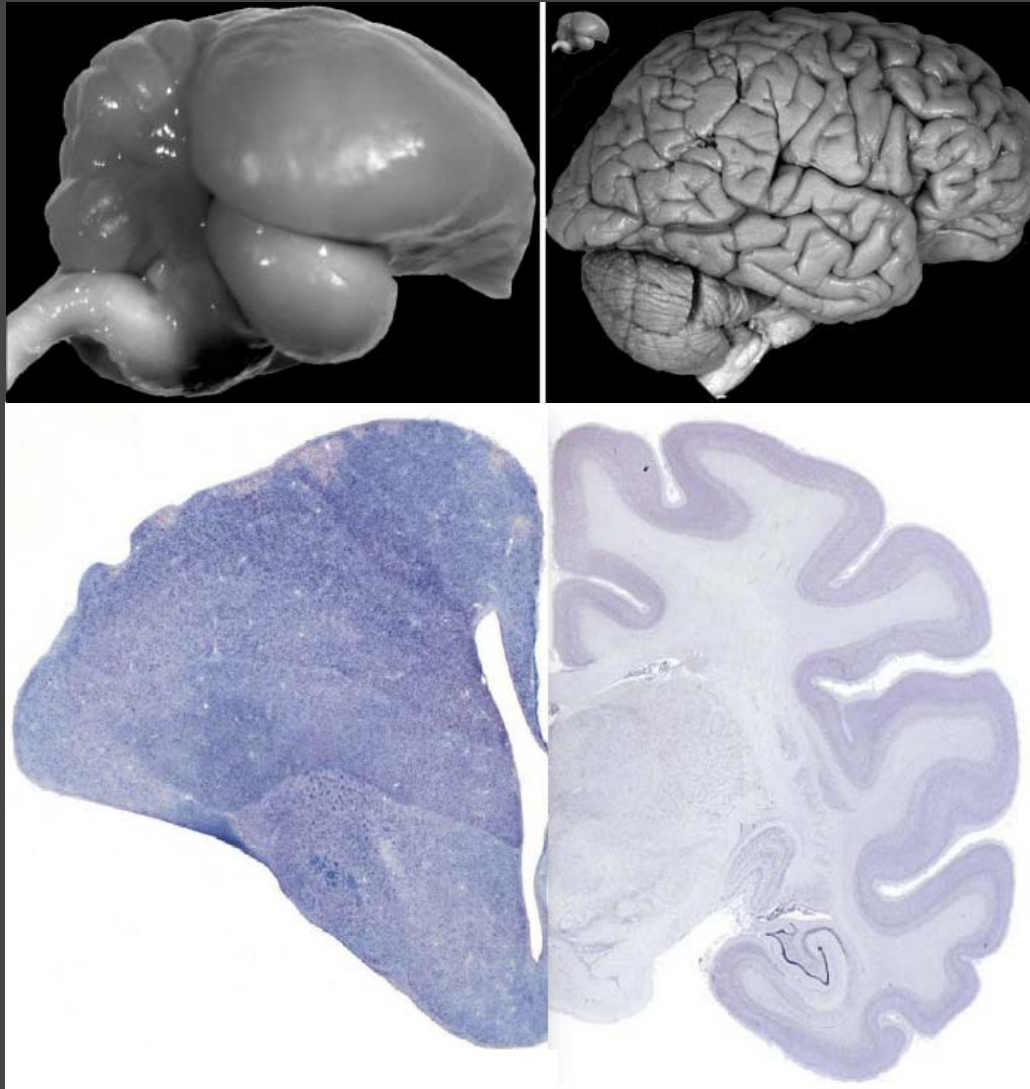


Human

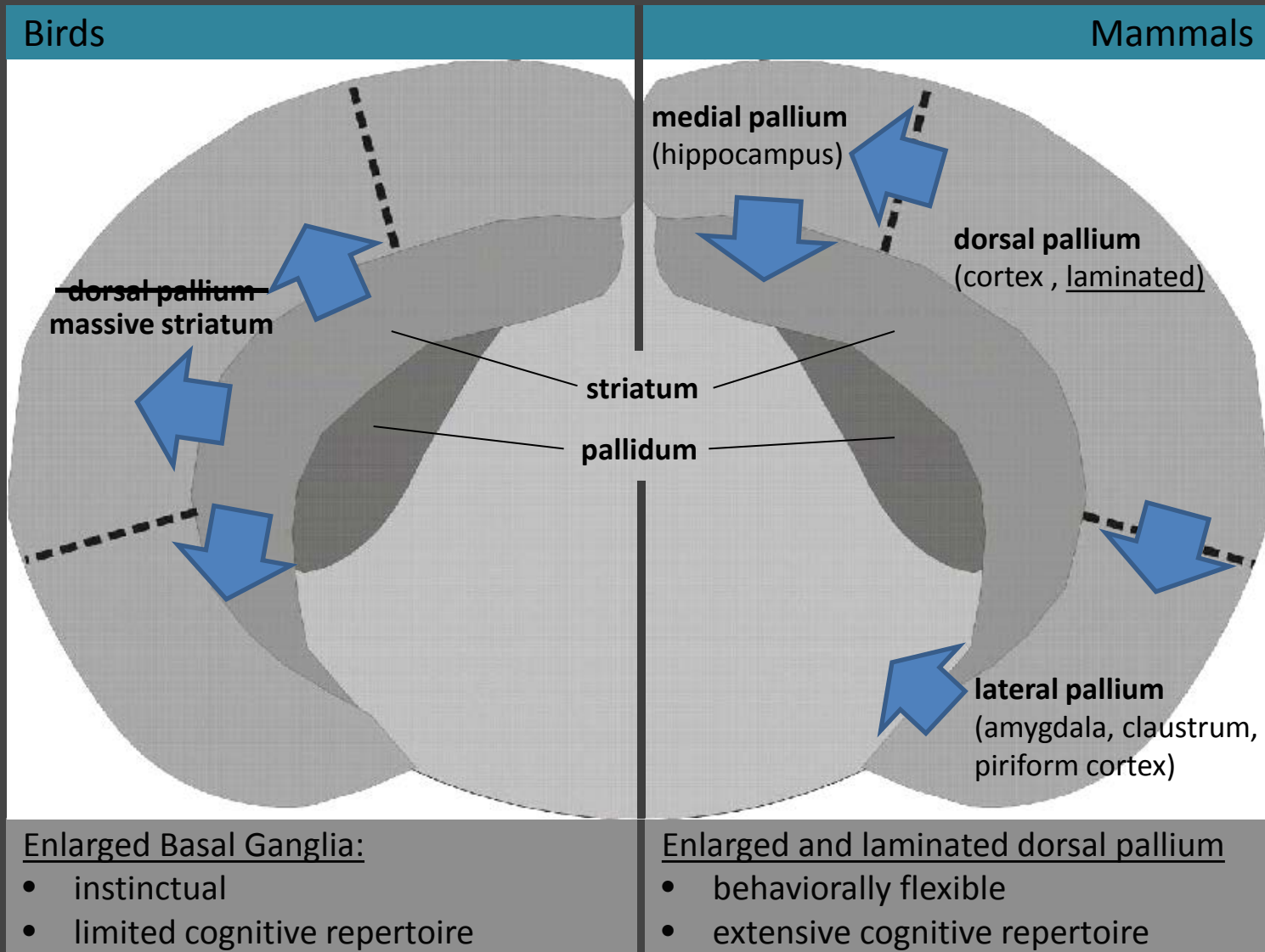




# New view on the avian brain



# New view on the avian brain

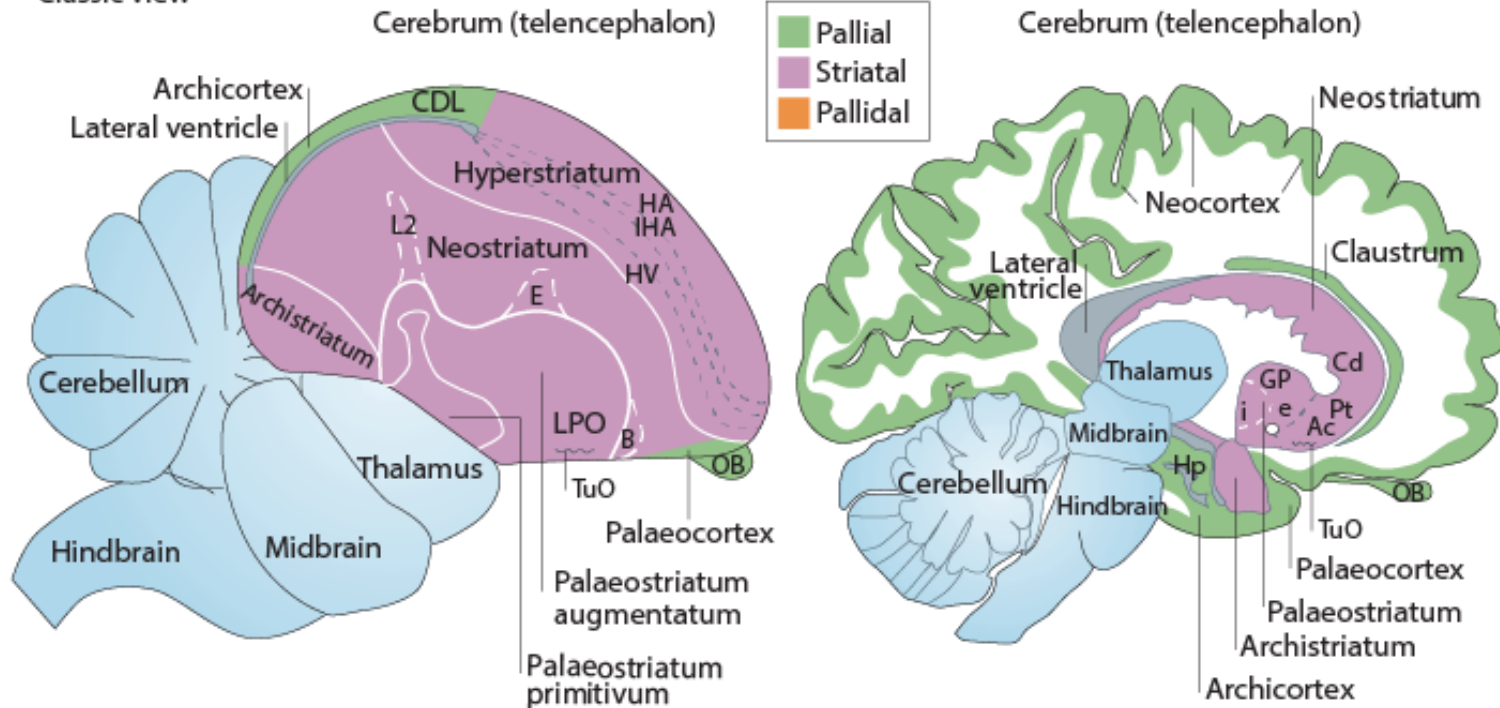


# New view on the avian brain



## Outdated view

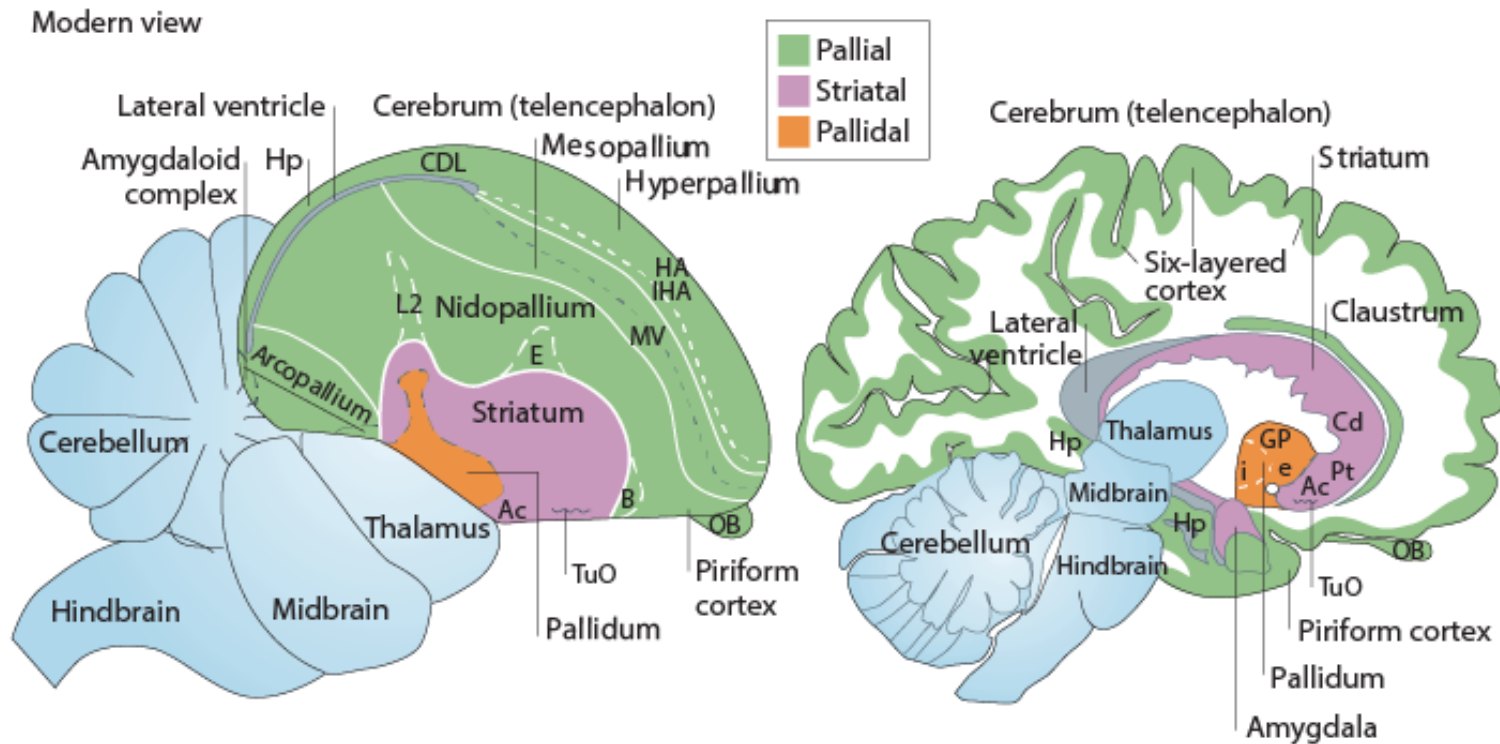
Classic view



# New view on the avian brain



## Modern view

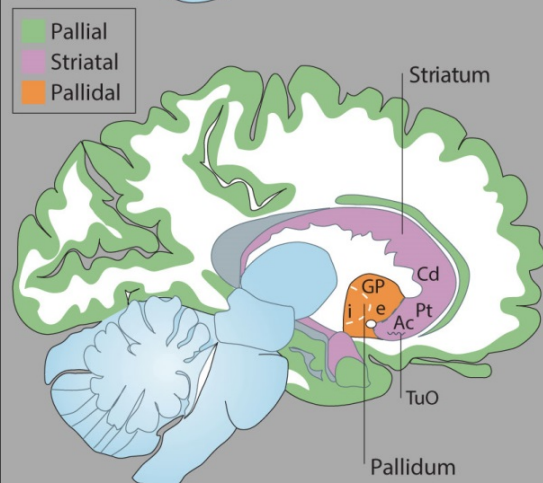
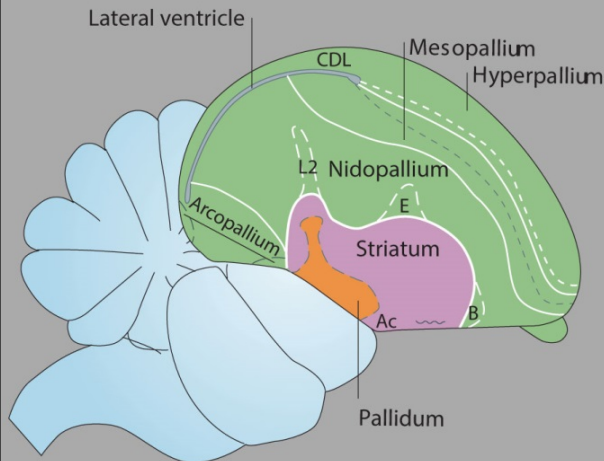


Birds have a large pallium, it is homologous to the mammalian pallium. The pallium-striatum ratio is comparable between birds and mammals.



## Why the modern view?

Modern view



## 1. Anatomic evidence

### Avian telencephalon is not predominantly striatal

- Striatum but not pallium of birds and mammals is rich in acetylcholinesterase and is the major target of dopaminergic projections
- Different types of cells (substance P/ enkephalin) serve distinct functions (movement promotion/ inhibition) and project to distinct cell populations (in mammals SNR & GPi/ GPe, in birds distinct populations of pallidal neurons)

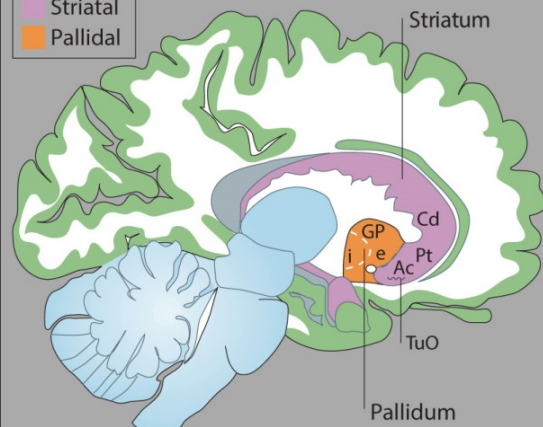
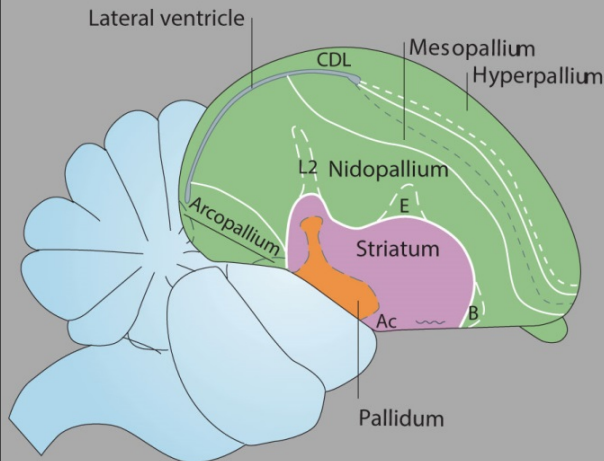
### Avian telencephalon has large pallial region

- pallium of birds and mammals receives visual, somatosensory and auditory input from thalamus
- The avian pallium (A, HA) gives rise to motor-pathways that resemble mammalian motor-projections (cortico-bulbar, cortico-spinal)



## Why the modern view?

Modern view



## 2. Embryonic/ molecular evidence

### Avian telencephalon is not predominantly striatal

- In birds and mammals the developing subpallium consists of two separate zones that express separate transcription factors (dorsal: DLX1 & DLX2 / ventral: DLX1 & DLX2 & NKX2.1)
- these zones give rise to different parts of the basal ganglia (dorsal striatum & ventral striatum & olfactory tubercle / dorsal pallidum & ventral pallidum) but not to pallial structures

### Avian telencephalon has large pallial region

- Transcription factors (EMX1, PAX6, TBR1), in mammals specific to the pallium are also found in avian pallium (nido-, meso- and hyperpallium)
- Uncertainty about the archopallium was resolved with the help of pallium specific mRNAs (BDNF, mGluR2)



Why the modern view?

4. Behavioral evidence

Planning



Tool Use



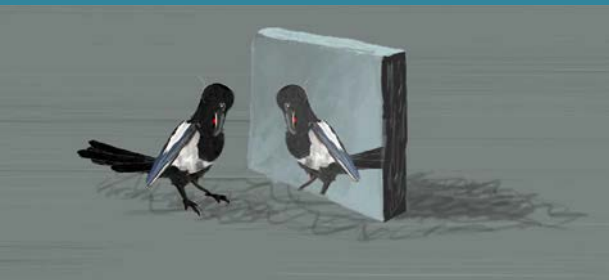
Theory of Mind'



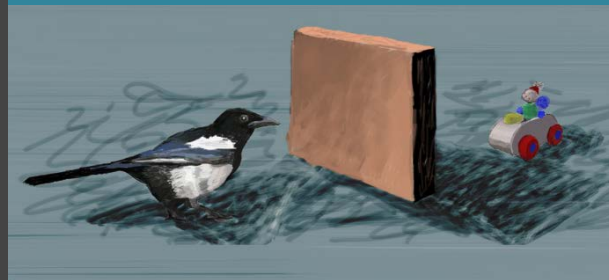
Executive Control



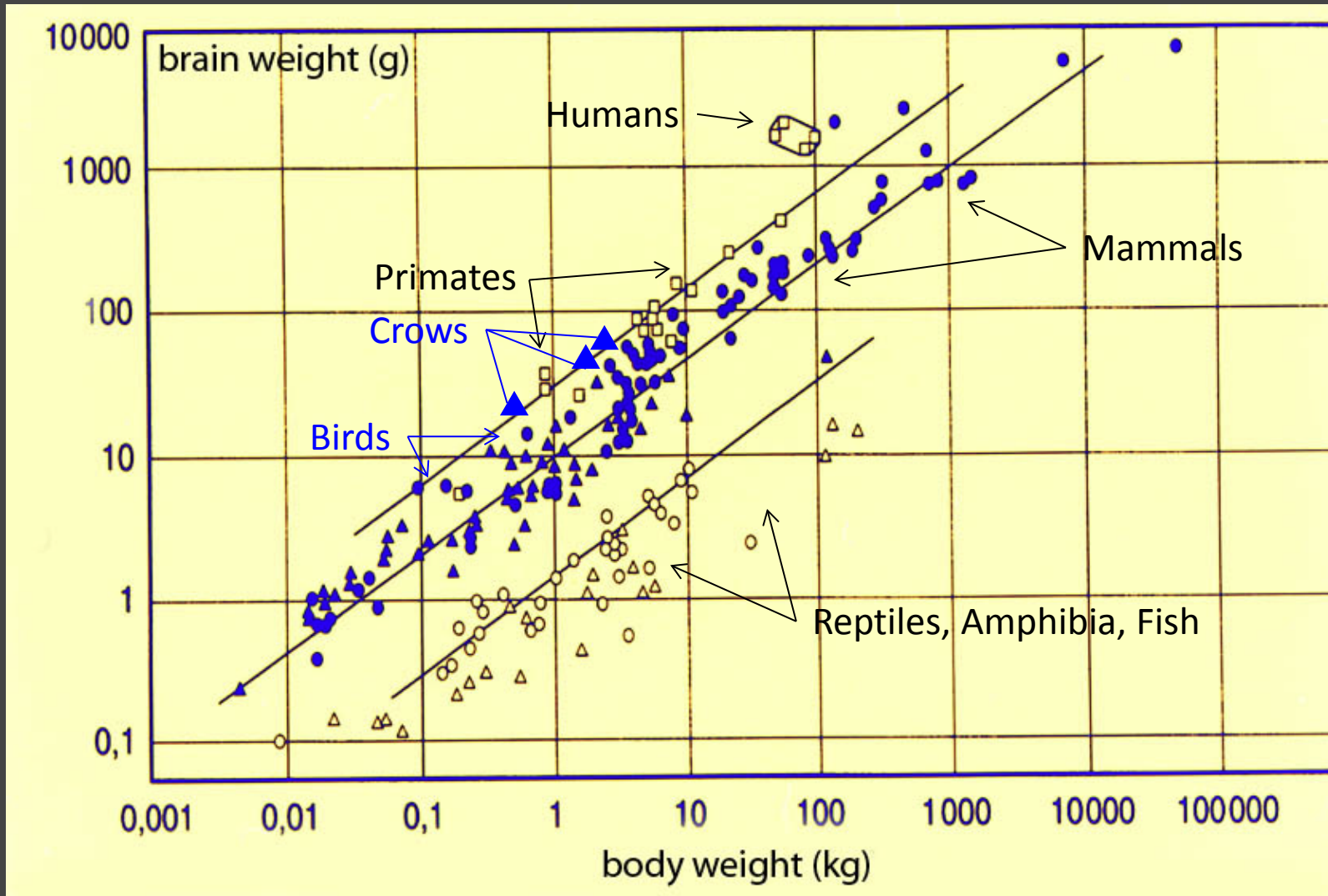
Mirror Self-Recognition



Object Permanence



# Convergent evolution of cognition





## Convergent evolution of cognition



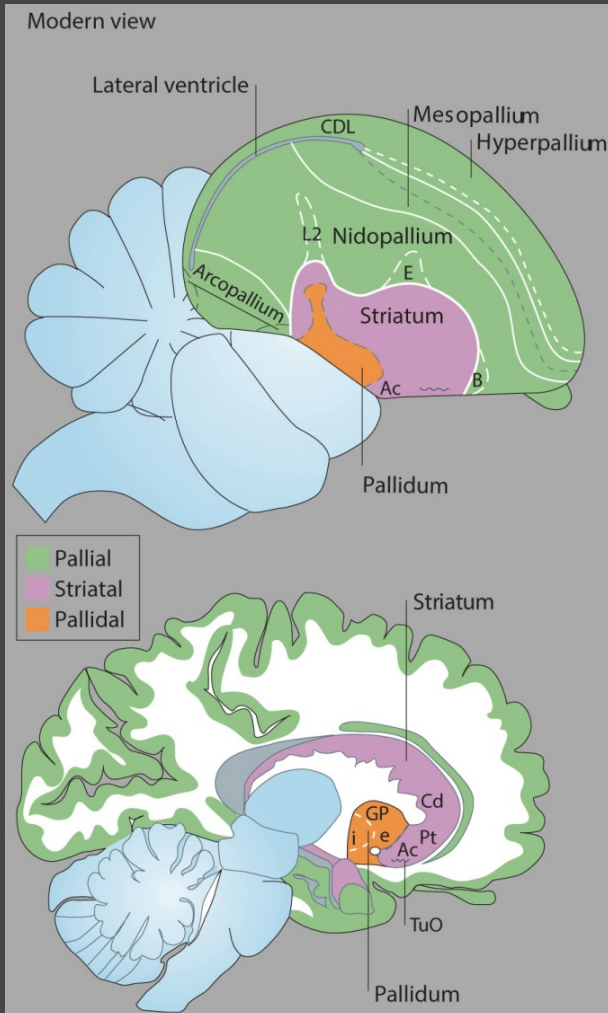
Songbird

Crow



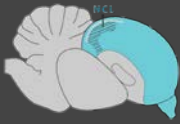
In corvids (read: smart birds) the size of the pallium is enlarged relative to the size of the subpallium. This enlargement is comparable to that in primates.

# New view on the avian brain



The modern nomenclature/ view is fully accepted in the field.

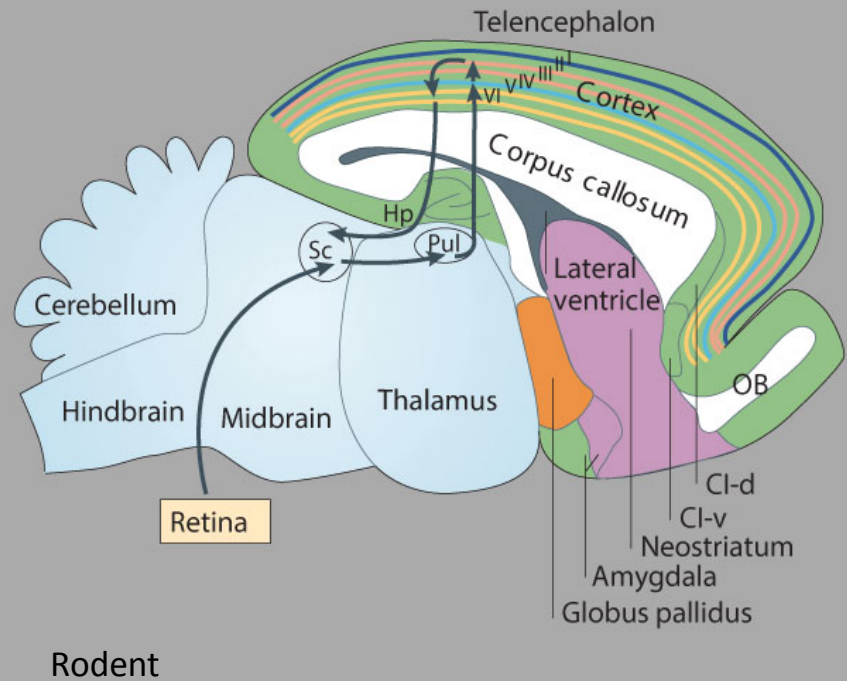
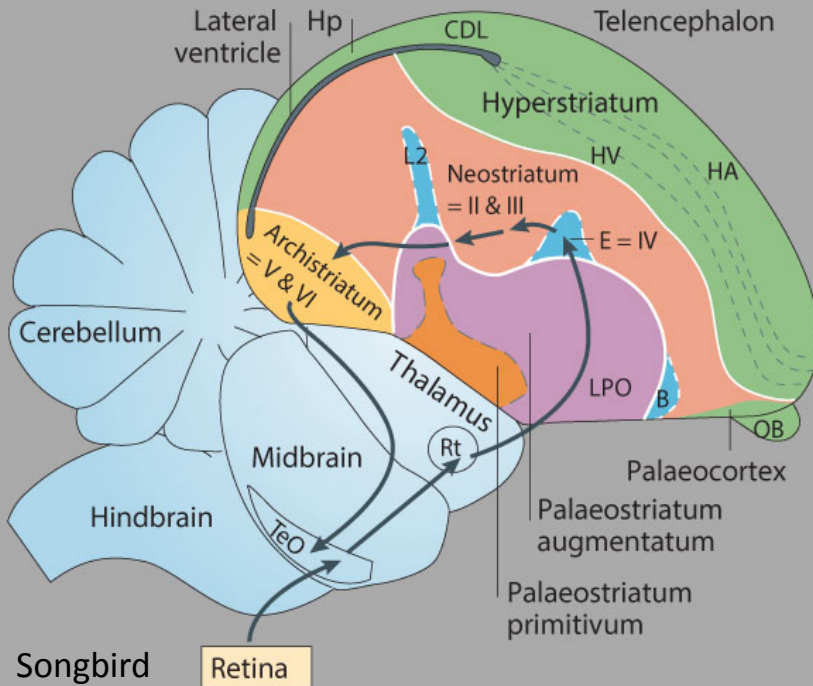
There is a dispute regarding homologies of pallial subdivisions



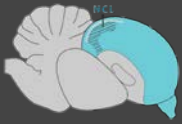
# Convergent evolution of cognition, pallial homologies

## Hypothesis on areas of the pallium: Nuclear-to-layered

Nuclear-to-layered hypothesis

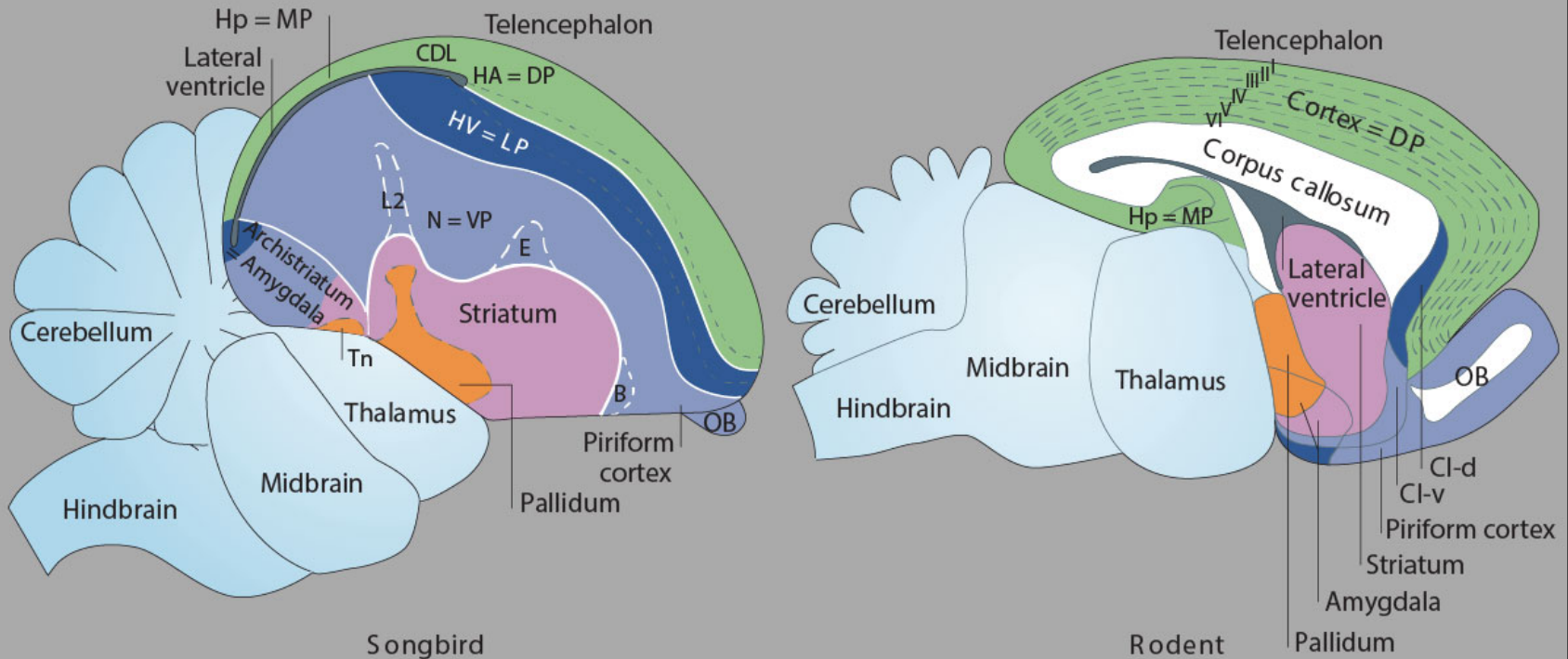


The common ancestor of birds, mammals and reptiles had a nuclear pallium. During the evolution of mammals, it was transformed (layered) but maintained the general connectivity. Thus, the pallial connectivity in birds and mammals is homologous.

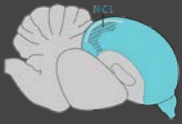


## Hypothesis on areas of the pallium: Nuclear-to-claustrum/ amygdala

Nuclear-to-claustrum/amygdala hypothesis

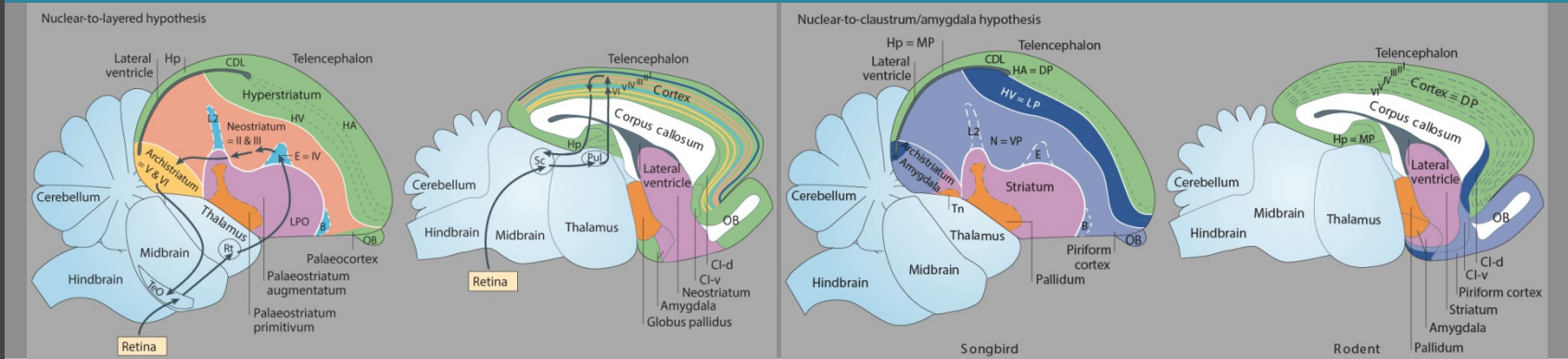


Most of the pallium is an elaboration of parts of the amygdala/ claustrum.  
 Shared connectivity between neocortex and avian pallium evolved independently.  
 Evidence from development/ expression factors.



# Convergent evolution of cognition, pallial homologies

## Unresolved, both hypotheses have limitations

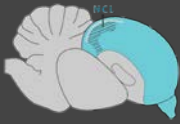


### Nuclear-to-layered

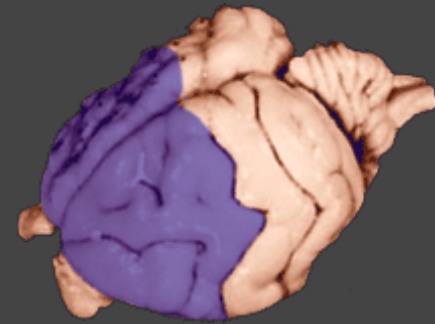
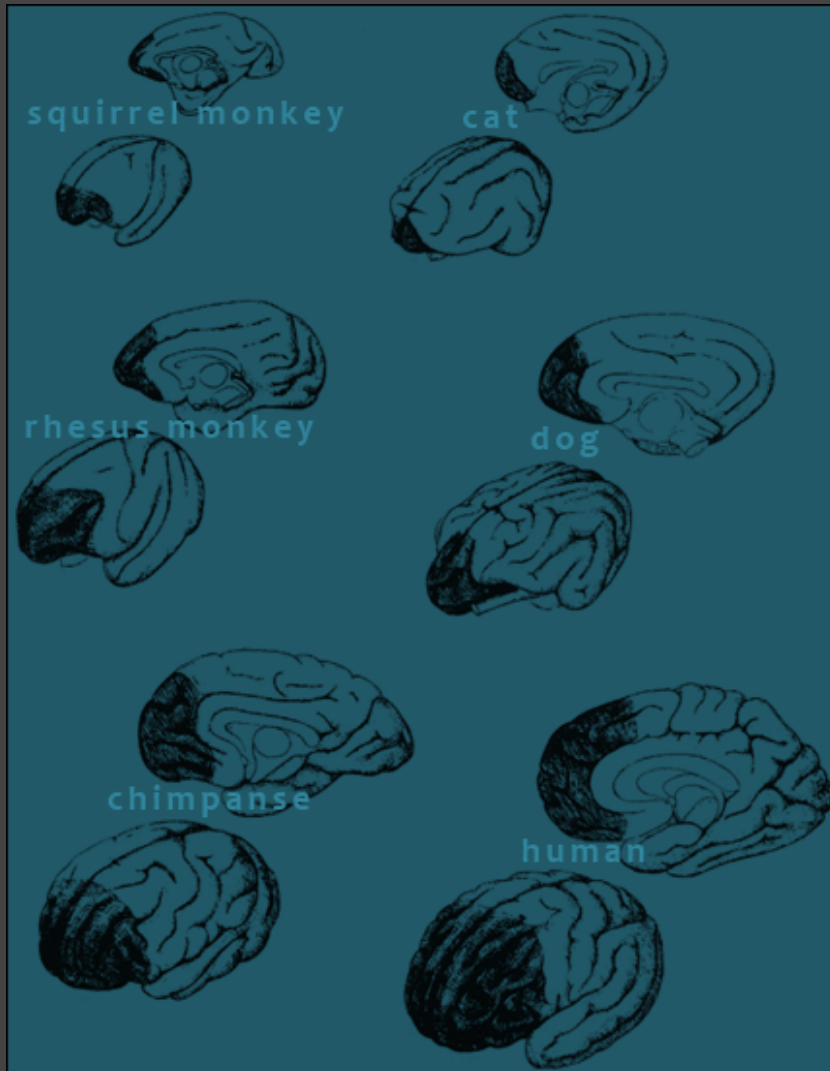
- No developmental data to demonstrate similarity between the cell types giving rise to cortical layers/ avian nuclei
- Gene-expression evidence shows some ambiguity

### Nuclear to claustrum/ amygdala

- The claustrum may not be an ancestral trait
- Gene-expression evidence is ambiguous

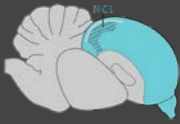


# Convergent evolution of cognition, the PFC



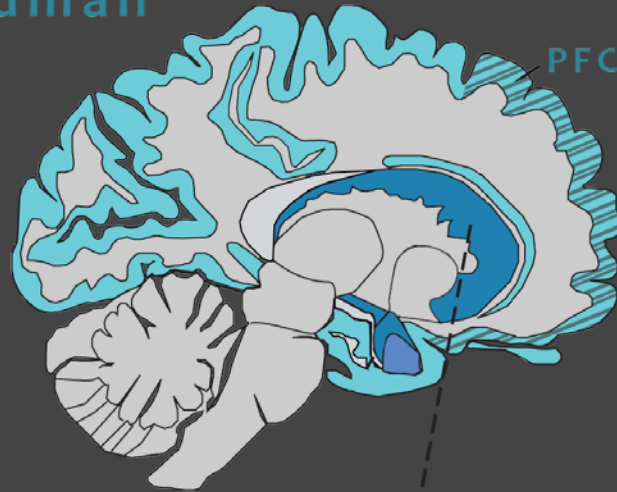
Echidna



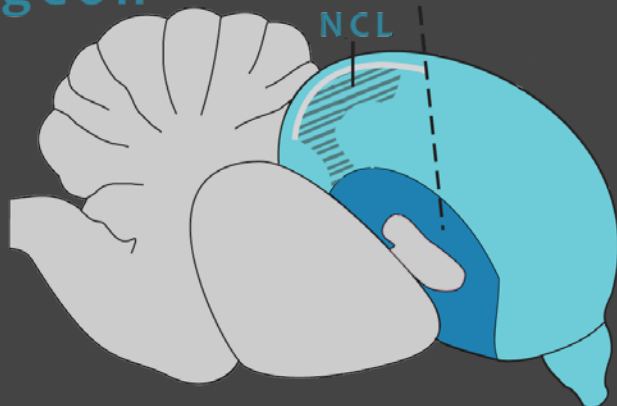


# Convergent evolution of cognition, the PFC

## Human

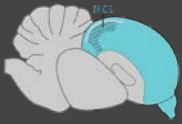


## Pigeon

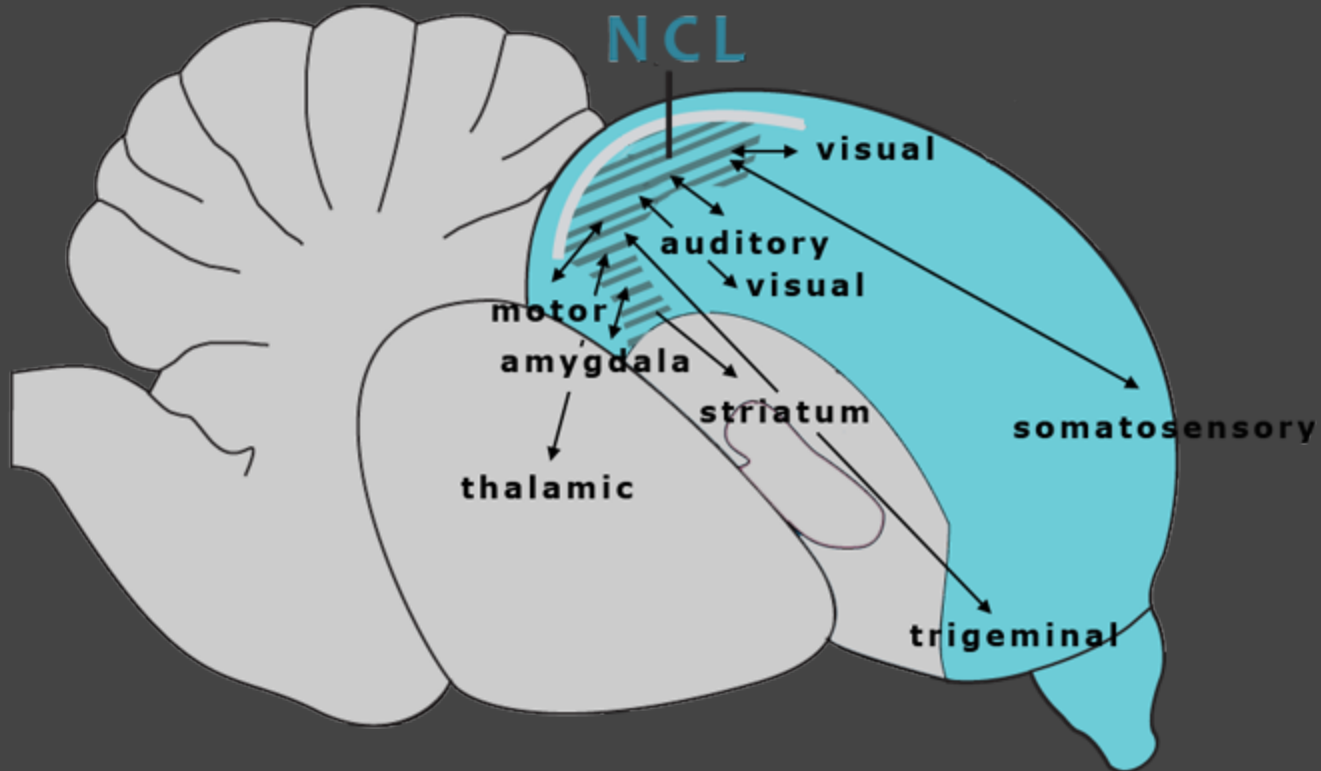


### Nidopallium caudolaterale (NCL)

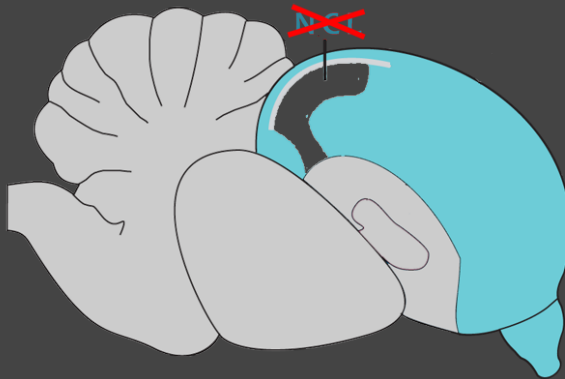
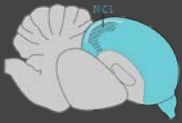
- Functional analog of the PFC
- Product of convergent evolution
- Not laminated (!)
- Similarities/ differences might help understanding neural constraints of working memory and executive control



# Convergent evolution of cognition, the PFC

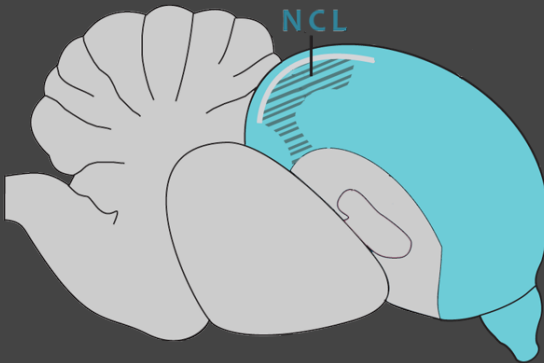






## NCL-lesions

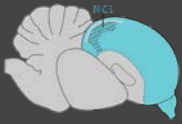
- disrupt working memory
- disrupt reversal learning
- disrupt integration of complex reward information
- don't affect simple discrimination



## NCL-recordings

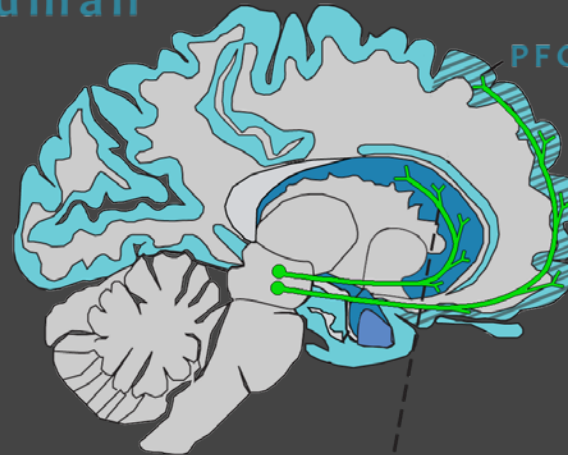
- delay cells
- representation of value  
(time-to- and amount-of- reward)

# Convergent evolution of cognition, the PFC

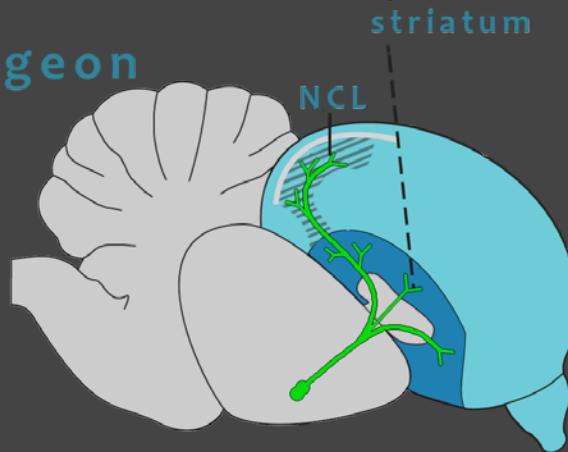


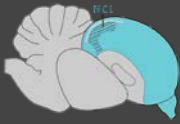
Dopamine

Human



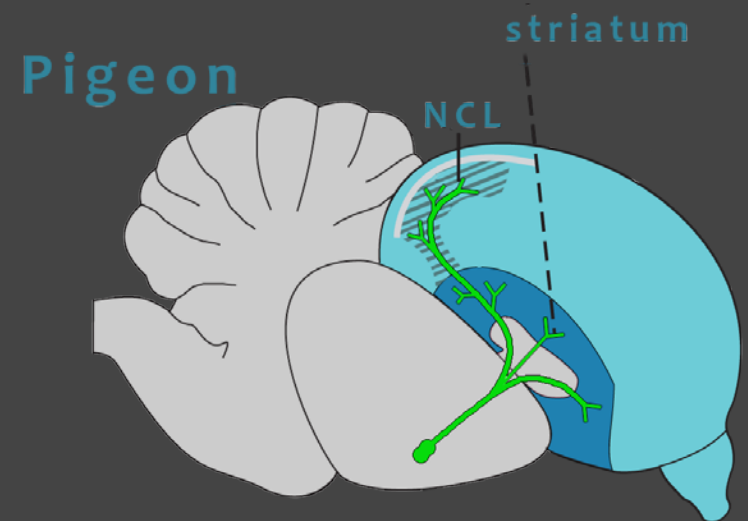
Pigeon





## Dopamine in the NCL

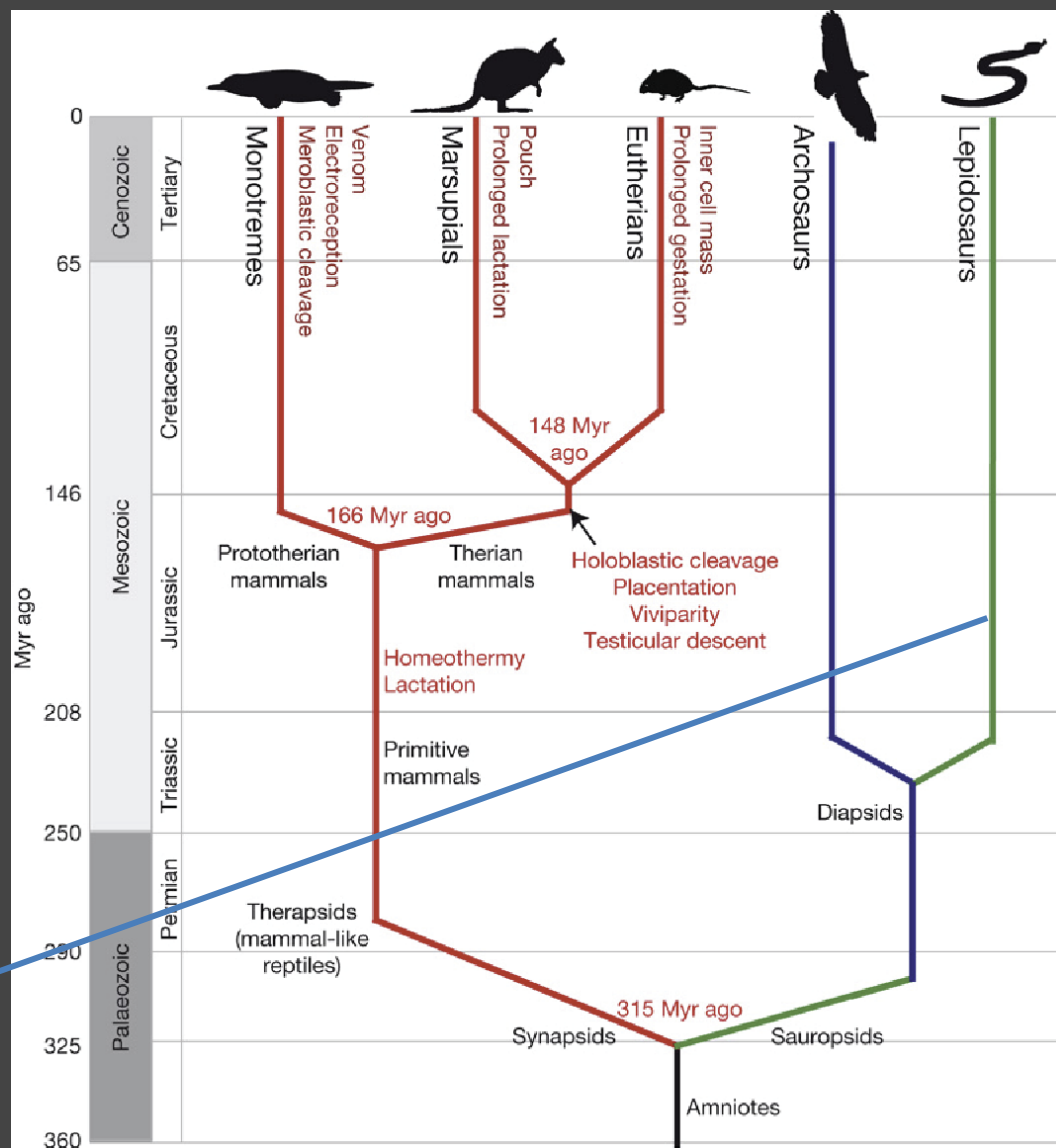
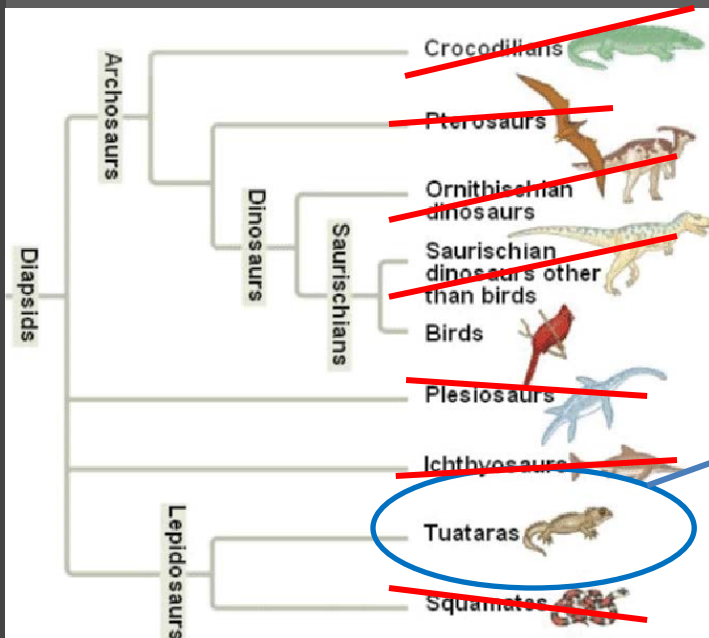
- DA-neurons found only in SNr/ VTA
- Mainly ipsilateral projections to striatum and NCL/ PFC
- Birds have different D2-D1 ratio than mammals
- Pattern of DA-terminals is similar (dendritic shafts and spines, close to excitatory synapses)
- Baskets of DA terminals encase large projection-neurons in the avian pallium, this may (functionally) correspond to the dense innervation of the deep layers in the mammalian cortex
- Intact DA in NCL is required for attention and working memory





# Is lamination really a mammalian 'invention' ?

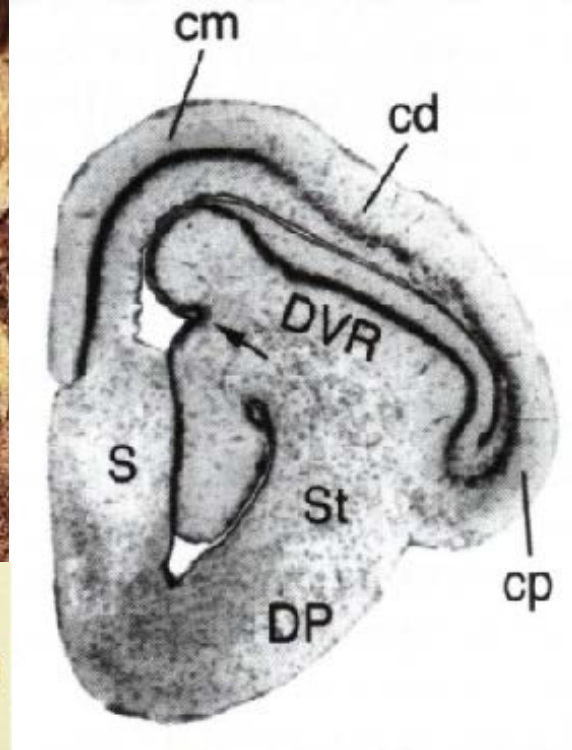
- Through convergent evolution, birds evolved a set of cognitive abilities that are comparable to the abilities of mammals.
- The avian brain has a large pallium but it is not laminated.
- There seem to be clear constraints on the neural implementation of cognitive operations.



# Is lamination really a mammalian 'invention' ?



## Sphenodon punctatus



Hypothesis: Eventually, even lamination was not newly 'invented' by early mammals but existed in stem amniotes and was later abandoned in reptiles and birds.