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Visual working memory and motor inhibition across ectotherms and endotherms

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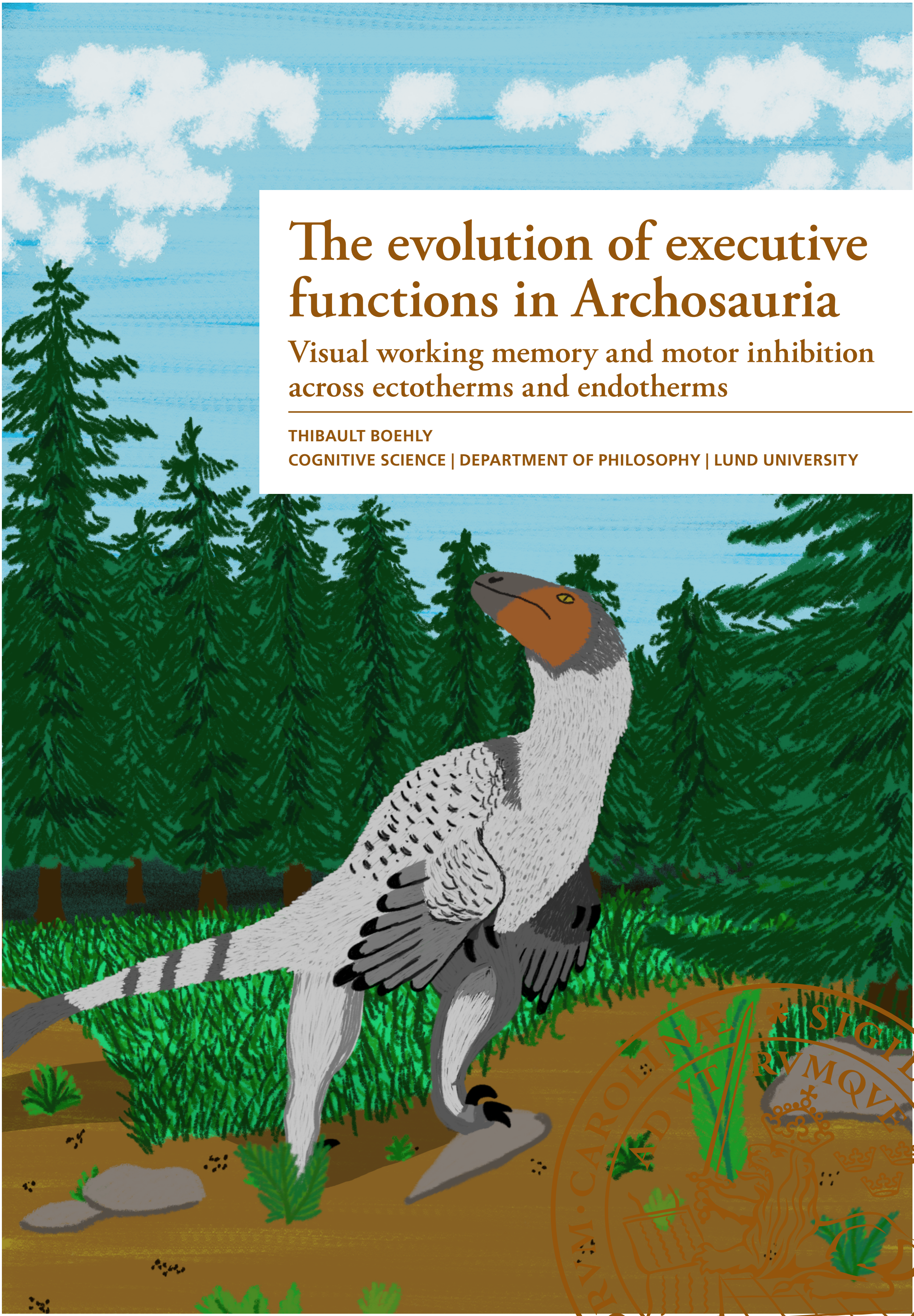

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Visual working memory and motor inhibition across ectotherms and endotherms

Thibault Boehly

DOCTORAL DISSERTATION

Doctoral dissertation for the degree of Doctor of Philosophy (PhD) at the Joint Faculties of Humanities and Theology at Lund University to be publicly defended on the 28th of November at 09.00 in Room C126 at LUX, Department of Philosophy, Helgonavägen 3, 223 62 Lund

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Abstract:

Executive functions are a set of cognitive skills enabling goal-directed behaviours. Both mammals and birds have highly proficient executive functions, despite diverging from each other around 360 million years ago. This cognitive convergence is due to both taxa being tachymetabolic endotherms. They can maintain a stable and elevated body temperature with a high metabolism. However, in order to sustain this physiology, they also require substantial amounts of food compared to ectotherms. Thus, mammals and birds evolved larger brains and higher neuron densities, leading to improved executive functions.

Archosauria is the taxon including crocodylians and birds, which are respectively ectotherms and endotherms. Moreover, they possess a nidopallium caudolaterale (NCL), a brain region functionally equivalent to the mammalian prefrontal cortex and mediating executive functions. However, the crocodylian NCL is more rudimentary than the avian NCL. Thus, modern archosaurs show a diversity of thermal physiology, neuron density, and brain anatomy, making them an ideal taxon to study the evolution of executive functions.

In this thesis, we examined the visual working memory and motor inhibitory control of American alligators, emus, domestic chickens, ring doves, and common ravens. We studied self-control, interference control of visual working memory, memory retention, and the interaction between visual memory and motor inhibitory control. Overall, the results show that alligators can perform on par with emus and chickens when having to choose between two visual stimuli of different values in a self-control test. However, they have a less robust visual working memory compared to birds. Even though they retain the presence of hidden food items, they are more susceptible to interference. Finally, in the context of a motor inhibitory control task, the use of memory instead of a visual stimulus improves their ability to override a motor impulse.

Key words: executive functions, evolution of cognition, archosaurs, ectothermy, endothermy, visual working memory, motor inhibitory control

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To my parents and my sisters

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List of original papers

Paper I

Boehly, T., Grendéus, S., Lalić, L., Osvath, M., Reber, S. A. (in prep). Parallel performance in a minimal self-control task by endothermic and ectothermic archosaurs.

Paper II

Boehly, T., Grendéus, S., Lalić, L., Reber, S. A., Osvath, M. (in prep). Interference control of visual working memory across ectothermic and endothermic archosaurs.

Paper III

Boehly, T., Lalić, L., Reber, S. A., Osvath, M. (in prep). Out of sight, still in mind? Visual memory retention in ectothermic and endothermic archosaurs.

Paper IV

Boehly, T., Lalić, L., Grendéus, S., Reber, S. A., Osvath, M. (in prep). Alligators show enhanced motor inhibitory control with visual memory over direct perception.

Structure of the thesis

This thesis compiles comparative cognitive studies across crocodylians and birds. It consists of four empirical studies on executive functions, with a focus on visual working memory (Papers II, III and IV) and its connection to motor inhibitory control (Papers I and IV). The four studies are interconnected and can be considered follow-ups to a large comparative study, whose publication is currently in preparation (Osvath et al., in prep.). Thus, the papers regularly cite each other

Due to the time required to conduct cognitive studies on American alligators, an ectotherm species with a low metabolism and little care about theses deadlines, the papers are still in preparation and have not been submitted for publication yet.

Chapter 1 introduces executive functions as well as the endothermic brain hypothesis, which serves as a theoretical background for the thesis.

Chapter 2 introduces the phylogeny of archosaurs, both within the taxon and in the context of amniotes. It explains why archosaurs constitute an ideal taxon to study the evolution of executive functions in the context of the endothermic brain hypothesis. It also contains a short introduction to the species studied in the thesis.

Chapter 3 provides a primer of the neuroanatomy of archosaurs, and more broadly of sauropsids. It begins with an overview of the evolution of the brain and neurons, before focusing on the nidopallium caudolaterale.

Chapter 4 describes the executive functions studied in this thesis and summarises the results of each study. Paper I is a comparative study of self-control between three species of archosaurs, representing ectotherms and endotherms, and focusing on species with plesiomorphic neurocognition. Paper II is a comparative study of interference control in visual working memory across five species of archosaurs, representing ectotherms and endotherms, as well as plesiomorphic and highly derived forms of neurocognition. Paper III compares American alligators and common ravens, investigating whether alligators retain the memory of a hidden food item even after choosing to approach a visible one of equal value. Finally, Paper IV focuses on American alligators and investigates how motor inhibitory control is impacted when guided by visual memory instead of direct perception.

Finally, *Chapter 5* provides concluding remarks and proposes some future lines of inquiry to study the evolution of goal-oriented behaviours in archosaurs.

1 Introduction

Most of our everyday behaviours are directed toward the achievement of a goal. However, not all objectives are equally easy to reach. We can readily eat a cookie to satisfy a desire for sweets, but it requires some will to refuse it so to avoid snacking between meals. *Executive functions* is an umbrella term to designate an ensemble of cognitive skills which help us to deal with situations of this latter kind. They are classically defined as top-down mental processes which enable us to identify and maintain a goal, and guide our behaviour despite challenges like new, hidden, or conflicting information. We resort to executive functions in situations where following prepotent behaviours, like habits or impulses, would be counterproductive, because they would not lead to the intended outcome. For example, when we do not want to snack, even though a cookie looks delicious and is very tempting (Diamond, 2013; Goldstein et al., 2014).

Executive functions are a set of cognitive skills ranging from fundamental capacities, like motor self-regulation, to more complex behaviours, like planning for the future. Usually, three core functions are identified: inhibitory control, working memory, and cognitive flexibility (Diamond, 2013; Miyake et al., 2000). Inhibitory control refers to the capacity to inhibit an impulse or habit in favour of a more appropriate behaviour (Loyant et al., 2025). Working memory maintains a limited amount of information accessible for a short duration, and protects it from interferences, as well as manipulates it to guide goal-directed behaviour (Cowan, 2017). Finally, cognitive flexibility refers to the ability to dynamically adjust behaviour by integrating new information from the environment and to switch between perspectives (Cantwell et al., 2022). In humans, and other mammals, these skills are mediated by a network of brain regions with the prefrontal cortex as a central element (Cristofori et al., 2019; Diamond, 2013).

How these capacities evolved is currently not well understood. Nonetheless, this can be studied with comparative research, i.e., investigating executive function-like behaviour in multiple species at key phylogenetic positions. Many studies have investigated executive functions in non-human animals (for some reviews, see: Kabadayi et al., 2018; Miller et al., 2019), and what emerges from them is that mammals and birds (particularly primates, corvids, and parrots) show an outstanding cognitive convergence (e.g., Güntürkün & Bugnyar, 2016; Lambert et al., 2019). This may seem odd, as birds and mammals come from two different branches of the amniote taxon, the Synapsida for mammals and the Sauropsida for birds, which diverged from each other around 360 million years ago (Long et al.,

2025) and consequently evolved very different brains (Striedter & Northcutt, 2020). Thus, there must have been a common factor that drove the evolution of cognition towards this convergence between mammals and birds.

1.1 The endothermic brain hypothesis

The endothermic brain hypothesis postulates that the cognitive convergence observed between mammals and birds is due to their common thermal physiology (Osvath et al., 2024). Both taxa are so-called tachymetabolic endotherms: they can produce internal heat via a molecular innovation enabling them to burn energy without muscle contraction, leading them to keep a stable and elevated body temperature and a high metabolism (Benton, 2021; Grigg et al., 2022). On the opposite, reptiles (the closest relatives of birds) are ectotherms and do not produce internal heat. They must behaviourally regulate their body temperature and their metabolism by using the environmental temperature. To achieve this, they must spend a significant amount of time basking in warm places to heat up their body, and sometimes to cool it down at other spots (Grigg et al., 2022). Endothermy provides many advantages, like enhanced locomotion, faster growth rate, more quickly reached sexual maturity, and the ability to spread into ecological niches inaccessible to ectotherms (Lovegrove, 2019; Rosslenbroich, 2014). However, it also comes with a high cost. Over time, mammals and birds must eat around 30 times more food than reptiles of the same body mass in order to sustain their lifestyle (Nagy, 2001, 2005).

Moreover, mammals and birds increased their relative brain sizes, which are around 10 times larger than reptile brains (Ksepka et al., 2020; Smaers et al., 2021; Striedter & Northcutt, 2020), and evolved higher neuron densities, having from 20 to 75 times more neurons than reptiles of the same body size (Kverková et al., 2022; Olkowicz et al., 2016). At first glance, this might look like a paradox, because neural tissue is one of the most expensive tissues to maintain and would just add an even higher energetic pressure on endotherms (Heldstab et al., 2022; Isler & van Schaik, 2006). However, because neurons can be thought of as the computational units of brains, their increased number would also improve the cognitive capacities of the animal, enabling it to forage for enough food to sustain both its higher metabolism and larger brain (Osvath et al., 2024).

This causal relationship between metabolism and cognition makes sense in light of the nature of cognition. From a biological perspective, it can be considered an intrinsic function of life, like respiration or photosynthesis, but ubiquitous in all organisms (e.g., Lyon, 2006). Thus, in all living organisms, cognition is the continuous sensorimotor (in its widest meaning) loop that connects the internal state with the external world. Cognition lies in the process that enables interaction with the environment that identifies values for the organism in relation to its embodiment and current state, which makes the organism capable of upholding itself and sometimes reproducing (e.g., Buzsáki, 2021; Lyon, 2020; Pezzulo et al., 2024). With “values” defined in this context as something that can induce changes in the physiology or behavioural opportunities of the organisms (e.g., Lyon et al., 2021, who uses the term "information"). Therefore, cognition is mostly an allostatic process: it regulates physiology and behaviour in an anticipatory manner, often preceding the actual disruption of homeostasis (e.g., Maturana & Varela, 1980; Schulkin & Sterling, 2019; Thompson, 2007). Because of this interwovenness of life and cognition, major biological transitions are naturally accompanied by cognitive innovations. For example, brains and central nervous systems appeared with the emergence of large, mobile, multicellular and bilateral organisms. This enabled the communication and coordination between different body parts and resulted in the emergence of smooth and unidirectional locomotion towards objects of interest or away from danger (Sterling & Laughlin, 2023). Similarly, the transition to tachymetabolic endothermy created new challenges for the regulation of metabolism, because of the amount of food required to sustain it. Consequently, it must have been accompanied by an elaboration of cognition which increased foraging efficiency.

Animals can maximize their food intake by using goal-oriented behaviours (Osvath et al., 2024), which are behaviours sensitive to the current value of the outcome resulting from the animal’s action (Pezzulo et al., 2014). For example, a rat trained to pull a lever to get a desirable food reward will do so if hungry, but not if it just had the opportunity to eat until satiation, a phenomenon known as reward devaluation (Balleine & Dickinson, 1998). The opposite of this are behaviours which are insensitive to the current value of the outcome – these are called habits. A rat pulling a lever out of habit will do so whether it has just eaten or not, and it will take several non-rewarding events to learn to stop pulling the lever. Wild animals show goal-oriented behaviours when they navigate their environment. For example, if they come across a water source without being thirsty, they can memorise its location and visit it later when they need to drink.

Goal-directed behaviours are enabled by model-based cognition. This cognition relies on internal models of the environment, which are mediated by the hippocampus and its interaction with other pallial areas (Bennett, 2021). These models – sometimes equated with cognitive maps – include memories of abstract relations between spatial locations, temporal events, and objects, which are organized sequentially (Murray et al., 2017; Pezzulo et al., 2014). They enable the animal to generalize knowledge across contexts, so to find the best possible action to reach a desired outcome (Behrens et al., 2018; Whittington et al., 2022). Notably, cognitive maps can be used to simulate possible futures, and through these simulations, evaluate the outcomes of different possible actions. Results from these simulations reach the basal ganglia, which execute action selection (Bennett, 2021). A famous example of the use of these simulations is the vicarious trial and error behaviour in rats. When reaching a bifurcation in a maze, rats often hesitate, repeatedly looking at both options. During this behaviour, the firing of their hippocampal place cells corresponds to the ones observed when they walk down each path, suggesting they mentally “stroll down” these paths and predict their outcomes before making a choice (Redish, 2016; Tolman, 1948). Compared to model-free cognition – which relies on habits – model-based cognition is slower and computationally more complex (Dolan & Dayan, 2013). However, it enables quick learning and high behavioural flexibility, which are crucial elements for efficient foraging behaviours able to sustain the endothermic lifestyle (Osvath et al., 2024).

2 The archosaurs

The archosaurs are a monophyletic group that emerged around 250 million years ago during the Early Triassic. Today, their only living representatives are the modern crocodylians and birds. But extinct lineages include various terrestrial and marine pseudosuchians, flying pterosaurs, and non-avian dinosaurs (e.g. Brusatte, Benton, Desojo, et al., 2010; Fastovsky & Weishampel, 2021; Nesbitt, 2011). Because of their thermal physiology and neuroanatomy, they are ideal models to study the evolution of executive functions in the context of the endothermic brain hypothesis (Osvath et al., 2024). This chapter provides an overview of their phylogeny, explains the reasons to use them as models for cognitive studies, and introduces the species that have been tested in this thesis.

2.1 Phylogeny of the archosaurs

The archosaurs are part of the larger taxon Amniota, which appeared between perhaps 380 and 360 million years ago (hereafter mya) during the Devonian (Long et al., 2025). Their distinctive features are the presence of three extraembryonic membranes which allow for gas exchange without losing water: the amnion (hence their name), the chorion, and the allantois. They also evolved keratinized skin protecting from desiccation, costal respiration improving breathing, and enhanced locomotion facilitating movements on land. With these adaptations, amniotes gained a greater independence from water sources and could disperse into the mainland (e.g., Shedlock & Edwards, 2009). Around possibly 360 mya, during the Carboniferous, they diverged into two main lineages: the Synapsida, whose only extant members are the mammals, and the Sauropsida, whose extant members are reptiles and birds (e.g., Long et al., 2025).

Around 270 mya, during the Permian, the sauropsids diverged twice in quick succession, giving rise to three lineages. The Lepidosauria include squamate reptiles (lizards and snakes) and the tuatara, the only remaining species of the once diverse order of Rhynchocephalia. The Testudinata includes all turtles. And the Archosauria include crocodylians and birds (e.g., Simões et al., 2022).

The archosaurs appeared around 250 mya during the Early Triassic, following the Permian-Triassic extinction event which occurred around 252 mya. Their diagnostic features are the presence of antorbital fenestrae (a pair of openings in the skull anterior to the eye orbits), the loss of teeth on the palate, and a new shape of the calcaneum (the bone articulating the ankle) (e.g., Fastovsky & Weishampel, 2021). They split into two lineages: the Pseudosuchia, which include modern crocodylians, and the Avemetatarsalia, which include modern birds. Both taxa diversified progressively during the Early and Middle Triassic, taking advantage of the ecological niches freed by the extinction event (e.g., Chen & Benton, 2012). By the Late Triassic, pseudosuchians diversified into several taxa, like the ornithosuchids, the poposaurids, the rauisuchians, the aetosaurs, and the sphenosuchians (e.g., Brusatte, Benton, Lloyd, et al., 2010; Grigg & Kirshner, 2015). They also produced a large variety of body types, sometimes preceding what will appear later in dinosaurs (Nesbitt & Norell, 2006). The Late Triassic ended with the Triassic-Jurassic extinction event around 201 mya, which caused a crash in the species diversity of pseudosuchians, leaving the crocodylomorphs as the sole survivors (Brusatte, Benton, Lloyd, et al., 2010).

The Dinosauria are avemetatarsalians and appeared during the Late Triassic. They became the dominant terrestrial vertebrates during the Jurassic by filling the newly opened ecological niches following the extinction event. One of the oldest and most consistent diagnostic characters of dinosaurs is the perforated acetabulum, meaning the hip socket of the pelvis, the part that articulates with the femur, is open instead of having a bounding wall. Moreover, based on the pelvis morphology, dinosaurs can be split into two main lineages. The ornithischians are diagnosed by an opisthopubic pelvis, meaning that at least a part of the pubis is oriented posteriorly along the ischium. They are a diverse group of herbivores with taxa such as the ceratopsians (e.g., *Protoceratops andrewsi*), the thyreophorans (e.g., *Stegosaurus armatus*), and the ornithopods (e.g., *Iguanodon bernissartensis*). The saurischians are diagnosed by a pubis oriented anteriorly and can be further subdivided into the sauropodomorphs and the theropods. The sauropodomorphs are a group of giants, long-necked herbivores (e.g., *Brachiosaurus altithorax*), while the theropods are a group of mostly bipedal carnivores (e.g., *Dilophosaurus wetherilli*) (e.g., Fastovsky & Weishampel, 2021).

Birds are theropod dinosaurs and are part of the taxa Coelurosauria (e.g., *Tyrannosaurus rex*), Maniraptora (e.g., *Oviraptor philoceratops*), Paraves (e.g., *Velociraptor mongoliensis*), and Avialae (e.g., *Archaeopteryx lithographica*). Maniraptorans are characterised by true pneumaticity with extensive air sacs, a highly efficient breathing with unidirectional air flow, and hollow bones, while avialans show increased flight proficiency through a rigid trunk, flight feathers, and specialized flight musculature (e.g., Fastovsky & Weishampel, 2021).

Aves, the modern birds, appeared between 165 and 150 mya during the Late Jurassic (e.g., Brusatte et al., 2015). They diversified during the Cretaceous, with the Palaeognathae (e.g., emus, tinamous) diverging from all other extant birds around 110 mya, and the Galloanserae (e.g., ducks, quails) diverging from other neognaths around 90 mya (Yonezawa et al., 2017). Meanwhile, crocodylians emerged around 100 mya (Grigg & Kirshner, 2015). The Cretaceous ended with the

Cretaceous-Paleogene extinction event around 66 mya, leaving the crocodylians and birds as the only surviving archosaurs. Following this event, birds underwent an intense evolutionary radiation, with most of the modern taxa diversifying during the Paleogene. Among them were the Columbimorphae (e.g., pigeons, doves), which emerged around 66 mya. The Telluraves, a large taxon that includes 13 orders of birds (e.g., eagles, woodpeckers, parrots), appeared around 65 mya. Within this taxon, the Passeriformes (e.g., finches, ravens) emerged around 56 mya (Prum et al., 2015; Figure 1).

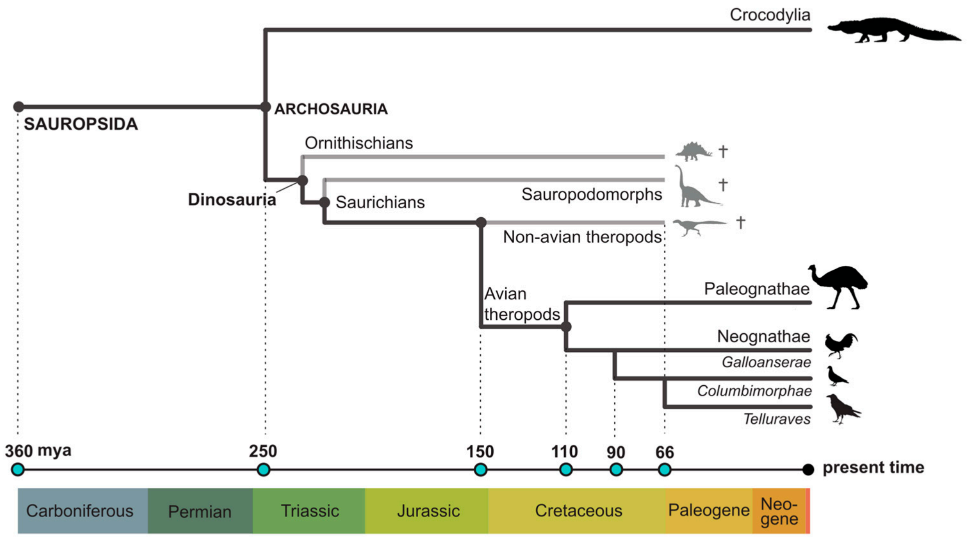

Figure 1. A simplified phylogenetic tree of archosaurs based on Brusatte et al. (2015), Long et al. (2025), Prum et al. (2015), and Yonezawa et al. (2017). Illustration by Helena Osvath. Silhouettes are sourced from Phylopic.org.

2.2 The archosaurs as models for cognitive studies

There are two reasons why the archosaurs are an ideal taxon to study the evolution of executive functions in the context of the endothermic brain hypothesis. First, they are a taxon that still contains both ectothermic and endothermic species alive today. Crocodylians are ectotherms and regulate their body temperature and metabolism through bouts of basking behaviour on land. In addition to this behavioural thermoregulation, large individuals can also maintain relatively stable body temperatures through gigantothermy. This phenomenon has been observed in large crocodylians, such as saltwater crocodiles (*Crocodylus porosus*) weighing more than a tonne. Body temperature becomes both stable and higher than the surrounding environment due to a large body mass that reduces heat loss and favours thermal inertia. Interestingly, crocodylians also have several “pre-adaptations” to tachymetabolic endothermy, such as a four-chambered heart and a unidirectional air flow within their lungs, both aiding blood oxygenation (e.g., Grigg & Kirshner, 2015). Birds, on the other hand, are tachymetabolic endotherms with body temperatures ranging from 37-39°C in flightless palaeognaths to 43°C in resting passerines (e.g., Grigg et al., 2004; Prinzinger et al., 1991). Within sauropsids, endothermy likely first emerged in non-avian dinosaurs, starting with a combination of intermediate metabolic rate and gigantothermy (e.g., Benton, 2021; Grady et al., 2014; Rezende et al., 2020). Metabolism progressively increased in parallel with the reduction of body size in the lineage leading to birds, probably to counteract the higher heat loss due to small bodies. Moreover, feathers helped to reduce heat loss by insulating the body (e.g., Rezende et al., 2020). Body temperatures of extinct non-avian dinosaurs have been estimated using carbonate clumped isotope palaeothermometry on eggshells. Since eggs are formed within the body, the isotopic distribution of carbonates within the shells – which is sensitive to temperature – can be used to infer the core body temperature. This method made it possible to determine that a species of abelisaurid had a body temperature estimated at 37-40°C (Laskar et al., 2020), an oviraptorid at 30°C (Eagle et al., 2015), and troodontids at temperatures ranging from 29 to 42°C, suggesting heterothermy (Dawson et al., 2020; Tagliavento et al., 2023). Heterothermy is the ability to lower body temperature to reduce energy expenditure. It was likely a transitional step toward full tachymetabolic homeothermic endothermy, characterized by the high and stable body temperatures observed in many birds and mammals (Lovegrove, 2019). Heterothermy is still present in modern birds and mammals, with some species entering bouts of torpor to conserve energy (e.g., Schleucher, 2004).

The second reason why archosaurs are ideal models is that both crocodylians and birds possess a nidopallium caudolaterale (hereafter NCL) – not yet found in any other sauropsids – a brain region functionally equivalent to the prefrontal cortex, notably because it also mediates executive functions (e.g., Güntürkün & Bugnyar, 2016; Nieder, 2023). The crocodylian NCL has been discovered in the Nile crocodile (*Crocodylus niloticus*) and was initially termed the caudolateral anterior dorsal ventricular ridge (Billings et al., 2020). Interestingly, it is much smaller in size compared to the avian NCL (Güntürkün et al., 2021), indicating that this region expanded during the transition to tachymetabolic endothermy. Moreover, the NCL continued to expand during the evolutionary radiation of birds. Thus, the taxon Galloanserae, which diverged from other birds around 90 mya during the Cretaceous, has the smallest NCL relative to brain size (hereafter relative NCL size) among neognaths. The taxon Columbimorphae, which diverged around 66 mya, shortly after the Cretaceous-Paleogene extinction event, has a larger relative NCL size than Galloanserae. Finally, the taxon Passeriformes, which appeared around 56 mya during the Paleocene, has a relatively large and parcellated NCL with three distinct regions: a medial, a dorsal, and a ventral area (Prum et al., 2015; von Eugen et al., 2020). This anatomy is very similar to the primate prefrontal cortex and is assumed to be a key factor in the complex cognition exhibited by highly derived avian taxa like the corvids and parrots (Güntürkün et al., 2024). The Passeriformes are also part of the larger taxon Telluraves, which has the highest neuron densities of all birds. In contrast, crocodylians have much lower neuron densities than any bird (Kverková et al., 2022).

In summary, living archosaurs possess varying thermal physiology, neuron densities, and NCL sizes and structures. Put simply, crocodylians are ectotherms with low neuron densities and small NCLs, while birds are tachymetabolic endotherms with high neuron densities and large NCLs. Moreover, there is also heterogeneity within birds, with some highly derived taxa possessing even higher neuron densities and larger NCLs than taxa with more plesiomorphic neuroanatomy. Therefore, comparative studies across crocodylians and birds are informative about the evolution of executive functions in the context of the endothermic brain hypothesis (Osvath et al., 2024).

2.3 Species in this thesis

This thesis compiles studies done with five species of archosaurs: one crocodylian and four avian species. The American alligator (*Alligator mississippiensis*) represents the crocodylians and serves as a model for the ancestral condition of the archosaurs' neuroanatomy. The emu (*Dromaius novaehollandiae*), the domestic chicken (*Gallus gallus domesticus*), and the ring dove (*Streptopelia risoria*) each represent different gradations in the evolution of the avian brain during the evolutionary radiation that happened during the Cretaceous and shortly after the Cretaceous-Paleogene extinction event. Finally, the common raven (*Corvus corax*) represents the more recent clade of Telluraves and their more derived neuroanatomy (for pictures of each species, see Figure 2).

The American alligator is one of the 28 extant species of crocodylians and one of the only two remaining species from the genus *Alligator*, the other one being the Chinese alligator (*Alligator sinensis*). They live in freshwater marshes, swamps, rivers, and lakes of the southern and eastern parts of the United States of America. They are opportunistic predators with a broad diet that includes invertebrates, fish, amphibians, reptiles, birds, mammals, and various fruits. Alligators are socially tolerant and can gather in groups for basking or breeding. Like all crocodylians, they show parental behaviours with females protecting their nest, carrying the hatchlings to the water, and guarding them against potential predators for up to a year (e.g., Grigg & Kirshner, 2015).

The emu is a large and flightless bird from the taxon Palaeognathae. It is the second largest extant bird in the world after the ostrich (genus *Struthio*). Emus live in various habitats over a large part of mainland Australia, except for sandy deserts and dense forests. Their diet consists of fruits, seeds, growing shoots of plants, and arthropods. In the wild, emus can be solitary, move in pairs, or in small groups. Emus are communal breeders; one male breeds with several females, which lay their eggs in a single nest. Males incubate the eggs and guard the chicks for several months (e.g., Folch et al., 2020).

The domestic chicken is a flightless and ground-feeding bird from the order Galliformes. It is a domesticated form of the red junglefowl (*Gallus gallus*). Red junglefowls live in most of Southeast Asia and parts of South Asia. Their diet includes fruits, seeds, plant materials, arthropods, other invertebrates, and small vertebrates. They usually live in flocks of one or a few roosters with several females. Females incubate the eggs and rear the chicks (e.g., McGowan & Kirwan, 2020).

The ring dove is a medium-sized, flighted bird from the order Columbiformes. It is a domesticated form of the African collared dove (*Streptopelia roseogrisea*). African collared doves live around water sources in the Sahel region, the northern parts of the Horn of Africa, and southwestern Arabia. Their diet includes fruits, seeds, plant materials, arthropods, and other invertebrates (e.g., Baptista et al., 2020).

The common raven is a flighted bird from the order Passeriformes, and a member of the family Corvidae. They live in various habitats all over the Northern Hemisphere. They are omnivorous and highly opportunistic. Subadults live in large and vagrant fission-fusion flocks, while sexually mature individuals form long-term monogamous pairs and are territorial. The pair raises their offspring together, and raven chicks can stay with their parents for up to six months (e.g., Boarman & Heinrich, 2020).

Figure 2. Species in this thesis. From top to bottom and left to right: American alligators, emu, domestic chicken, ring dove, and common raven. Photo credit: Helena Osvath for the domestic chicken and Ivo Jacobs for the common raven.

3 Neuroanatomy of archosaurs

Goal-directed behaviours are mediated by networks of brain regions present in the telencephalon. In mammals, these networks involve the prefrontal cortex (PFC), the hippocampus, the basal ganglia, and the amygdala. The PFC keeps information about the current goals and task rules. The hippocampus mediates cognitive maps, which are a system of relational knowledge. The amygdala forms stimulus-outcome associations. Finally, the basal ganglia integrate prefrontal, hippocampal, amygdalar, and thalamic information to construct outcome predictions that support action selection (Bennett, 2021; Pezzulo et al., 2014).

This chapter provides a brief description of the brain evolution in archosaurs, and more broadly in sauropsids. It starts with an overview of the brain evolution before focusing on the nidopallium caudolaterale (NCL), a region of interest for executive functions.

3.1 Brain evolution

The reptilian brain displays a linear organization. From the rostral to the caudal end, there are the olfactory bulbs, the cerebral hemispheres, the optic lobes, and the cerebellum. The relative brain size of sauropsids did not drastically increase and is comparable to anuran amphibians. However, it independently increased in several lizard lineages, like the tegus and the varanids. mostly due to an expansion of the forebrain. Interestingly, these clades also have higher metabolisms than other lepidosaurs, reminiscent of the link between the two. Generally, sauropsids also have a larger and more complex optic tectum than amphibians. The crocodylian brain follows the reptilian pattern, with the same linearly arranged brain structures and the same relative brain sizes. However, they have much larger absolute brain sizes. They also have a clearly larger cerebellum, probably because of the evolution of the semi-erect stance and high-walking behaviour, which require finer motor control than the sprawling gait of other reptiles (Striedter & Northcutt, 2020).

Soft tissues like the brain rarely fossilize (see Brasier et al., 2017 for an exception). Thus, to study the neuroanatomy of extinct species, palaeontologists must use fossilized skulls and their endocranial cavity, the cavity that housed the brain. In earlier times, this technique required one to fill the brain case with latex and involved the destruction of the specimen (Hurlburt et al., 2013). However, with the development of X-ray computed tomography, it is now possible to create 3D models of the endocast in a non-destructive manner. The endocasts are a proxy for the actual brain shape. The amount of information we can obtain from them depends on the brain-to-endocranial cavity index, which indicates to what extent the brain fills the brain cavity (e.g., Balanoff & Bever, 2017). Indeed, only mammals and birds possess brains that almost fill the brain cavity when they're adults. In contrast, most adult extant reptiles only fill around 30% to 50% (Hurlburt et al., 2013). However, juveniles have a much closer correspondence between the brain and the cavity (e.g., Hu et al., 2021).

Studies of endocasts are important for understanding the evolution of brains. The endocast of the archosauriform *Euparkeria capensis*, a species closely related to archosaurs, shows they already had a very similar brain compared to modern crocodylians. This suggests that Crocodylia retained a plesiomorphic neuroanatomy very close to the last common ancestor of all archosaurs (Fabbri & Bhullar, 2022). Similarly, endocasts of extinct non-avian dinosaurs show that early theropods like *Allosaurus fragilis* did not diverge significantly from the ancestral condition (Beyrand et al., 2019; Rogers, 1998). However, some changes can be observed with the emergence of coelurosaurs. Indeed, the endocast of *Alioramus altai*, a tyrannosaurid from the Late Cretaceous, shows a significant expansion of the telencephalon, accompanied by a caudolateral displacement of the optic lobes (Bever et al., 2011, 2013). More recently, a study looked at the ontogenetic changes in the endocast of *Gorgosaurus libratus*. It notably included endocasts of juveniles, which provided detailed insights into the tyrannosaurid brain. There, the endocast clearly showed an enlarged telencephalon compared to the more ancestral condition (Voris et al., 2025).

Fossils of ornithomimosaurs (*Dromiceiomimus brevitertius*) and oviraptorosaurs (*Ingenia yanshini*) show imprints of the vascular system on the internal surface of the brain case in areas corresponding to the cerebellum and the cerebral hemispheres. This suggests that their brains filled the endocranial cavity (Osmólska, 2004; Russell, 1972). This new feature probably resulted from a synergy between the reduced body sizes and the inflation of the forebrain. Moreover, this inflation also caused further lateral displacement of the optic lobes and the emergence of the sigmoidal brain shape that is still observed in modern birds (Balanoff et al., 2013, 2014). In avialans, the brain expansion continued the same trend. *Archeopteryx lithographica* possessed large cerebral hemispheres, large optic lobes, and a broad cerebellum. Thus, the telencephalon and cerebellum came into contact, resulting in a full displacement of the optic lobes in a lateral position. However, they are still more anteriorly positioned than in modern birds (Alonso et al., 2004). Finally, the clade of extant birds appeared during the Late Jurassic with modern avian brains that show fully ventrolaterally displaced optic lobes and the hyperpallium (Medina & Reiner, 2000). The expansion of the telencephalon is mostly complete by the end of the Mesozoic, and the brain of birds from the Early Eocene (e.g., *Halcyornis* *toliapicus*) is very close to what can be observed in living birds today (Milner & Walsh, 2009; Walsh & Milner, 2011).

In summary, there have been four evolutionary steps from the ancestral brain arrangement still present in crocodylians to the derived brain of birds (Larsson et al., 2000; Torres et al., 2021). A first expansion of the telencephalon happened with the emergence of coelurosaurs, with some displacement of the optic lobes (Bever et al., 2011, 2013; Voris et al., 2025). With maniraptorans, the brain expansion reached a point where it mostly filled the endocranial cavity. This came along with the sigmoidal brain shape due to the ventral deflection of the midbrain and the dorsal deflection of the cerebrum (Balanoff et al., 2014; Osmólska, 2004). With avialae, the cerebellum expansion resulted in the contact between the cerebrum and cerebellum. This also excluded the midbrain from the dorsal margin (Alonso et al., 2004; Balanoff et al., 2013). And finally, an expansion of the whole brain and the cerebrum after the divergence of avialans, with optic lobes entirely ventral to the cerebrum (Balanoff et al., 2013).

In parallel with these modifications, the neuron density also considerably increased. There have been four allometric shifts in the neuron–brain scaling in amniotes (Kverková et al., 2022). Two of them happened in archosaurs. The first one occurred in the stem-bird lineage, with the transition to tachymetabolic endothermy. This results in much higher neuron numbers in extant birds compared to crocodylians. Thus, a red junglefowl (*Gallus gallus*) has around 2.5 times more neurons in its telencephalon than a Nile crocodile (*Crocodylus niloticus*), while having a brain that is only half the size. The second shift happened during the avian evolutionary radiation following the Cretaceous-Paleogene extinction event. This results in much higher neuron numbers in Telluraves, the core landbirds, compared to taxa with a more ancestral neuroanatomy. Therefore, a common raven (*Corvus corax*) has around 2.9 times more neurons in its telencephalon than an emu (*Dromaius novaehollandiae*), while an emu has a brain 1.5 times larger than the brain of a raven (Kverková et al., 2022).

A comparison of neuronal numbers between each species studied in this thesis is available in Table 1. The only crocodylian species with available data on neuronal numbers is the Nile crocodile (*Crocodylus niloticus*), which is used as a representative for crocodylians (however, the Cognitive Zoology Group has access to unpublished data of dwarf crocodiles, which corroborates that the numbers of the published Nile crocodile are likely ubiquitous among all crocodylians). The data on neuronal numbers for the domestic chicken comes from the red junglefowl, while the one for the ring dove comes from the African collared dove, their wild ancestors.

Table 1. Neuronal numbers for the species in this thesis, the numbers are from Kverková et al. (2022) and Olkowicz et al. (2016).

Species	Brain mass (g)	# Neurons total [$\times 10^6$]	# Neurons telencephalon [$\times 10^6$]	# Neurons cerebellum [$\times 10^6$]
Nile crocodile	5.8	81.54	29.95	39.86
Emu	21.8	1,335.40	471.57	814.61
Red junglefowl	2.8	220.84	73.79	114.45
African collared dove	1.1	139.27	47.55	72.38
Common raven	14.1	2,170.68	1,355.34	753.64

3.2 The nidopallium caudolaterale

Archosaurs do not possess a prefrontal cortex. However, birds evolved a functionally equivalent region called the nidopallium caudolaterale. This region is in the caudal part of the nidopallium, a region of the ventral pallium (Güntürkün et al., 2020). Thus, the NCL is analogous to the PFC and is an important region mediating executive functions (Nieder, 2023; Pezzulo et al., 2014).

It has been recognised very early that the NCL is histochemically, biochemically, functionally, and hodologically similar to the PFC (Divac & Mogensen, 1985). This region is highly densely innervated by dopaminergic fibres projecting from the ventral tegmental area (VTA) and the substantia nigra pars compacta (SNc), two brain regions from the midbrain. These dopaminergic projections innervate NCL neurons either by boutons-en-passant or by creating dense baskets where they coil up around single neurons, establishing synapses with both the dendrites and the soma of the target neurons. Thus, the NCL neurons are under tight dopaminergic control (Güntürkün et al., 2020; Waldmann & Güntürkün, 1993; Wynne & Güntürkün, 1995). The NCL is a key integrative hub of secondary sensory information and receives projections from visual, auditory, somatosensory, and olfactory regions of the telencephalon. This integrated sensory information is further combined with information from the limbic and premotor structures, before being projected to the arcopallium, the hyperpallium, and the basal ganglia. Thus, the NCL represents a convergence area between the ascending sensory system and the descending motor system, like the PFC (Güntürkün et al., 2020; Kirsch et al., 2008).

However, several divergences distinguish the NCL from the PFC. First, contrary to the mammalian PFC, the avian NCL does not receive projections from the mediodorsal thalamic nucleus. Instead, it receives projections from the dorsolateral posterior thalamic nucleus (Kröner & Güntürkün, 1999). Second, NCL neurons exhibit high firing rates and are selective for highly familiar stimuli (Veit et al., 2015), features which are similar to association cortices posterior to the PFC in primates (Güntürkün et al., 2020). Third, there are no direct connections between the NCL and the hippocampus (Rattenborg & Martinez-Gonzalez, 2011; Shanahan et al., 2013). The exception is the highly neurocognitively derived carrion crow (*Corvus corone*), in which direct projections from the hippocampus to the dorsal NCL have been described (Kersten et al., 2024). This connection does not seem to be present in the zebra finch (*Taeniopygia guttata*), another Passeriformes (Paterson & Bottjer, 2017), which suggests convergent evolution between mammals and corvids.

As previously mentioned (see section 2.2), the NCL has recently been described in the Nile crocodile (*Crocodylus niloticus*). Dense dopaminergic innervations forming pericellular baskets have been observed in the caudolateral area of the anterior dorsal ventricular ridge (ADVR) (Billings et al., 2020). At discovery, this region has been termed the caudolateral ADVR (ADVRcl). However, it is most likely a homologue of the avian NCL. This indicates that both crocodylians and birds inherited this brain region from the last common ancestor of archosaurs (Güntürkün et al., 2021). However, the NCL enlarged along the avian lineage (see section 2.2; von Eugen et al., 2020). An NCL-like structure has not been described in lepidosaurs or testudines. However, Striedter and Northcutt suggest the presence of a possible homologue in the lizard brain (Striedter & Northcutt, 2020). This suggestion is based on a paper by Andreu and colleagues, which examined the intrinsic connections of the ADVR in the lacertid lizard *Psammodromus algirus*. This study describes the presence of specific areas in the caudal region of the ADVR receiving projections from rostrally distant neurons throughout the ridge. These neurons themselves receive sensory projections from the thalamus. Thus, it suggests the presence of secondary sensory integration in the caudal area of the ADVR of lepidosaurs (Andreu et al., 1996).

In summary, the NCL probably emerged with early archosaurs. Crocodylians retained a small and simpler NCL compared to birds. This suggests an elaboration of this region with the transition to tachymetabolic endothermy.

4 Executive functions

Executive functions are a set of cognitive skills that enable goal-directed behaviours, like working memory or motor inhibition. They are classically defined as top-down mental processes used to guide behaviours in situations where following habits or impulses would not lead to the intended outcome (Diamond, 2013).

The Cognitive Zoology Group at Lund University has previously investigated various aspects of visual working memory and motor self-regulation in archosaurs, with comparative studies testing American alligators (*Alligator mississippiensis*), emus (*Dromaius novaehollandiae*), greater rheas (*Rhea americana*), Tataupa tinamous (*Crypturellus tataupa*), elegant-crested tinamous (*Eudromia elegans*), and red junglefowls (*Gallus gallus*) (Osvath et al., in prep.). Concerning visual working memory, all species were able to keep track of one food item in various tests, or two different food items (one desirable and one less-preferred) hidden behind opaque barriers. Moreover, in a mnemonic-vision competition task, all species were able to choose a desirable food item placed behind an opaque barrier over a less-preferred food item visible behind a transparent barrier. However, results diverged in a follow-up task. In the mnemonic-vision priority task, they could choose between two food items equal in quality, one hidden behind an opaque barrier and one visually accessible. Alligators showed an extreme preference for the visible food (119 out of 120 trials across six subjects). However, emus choose at random, and all other bird species selected the hidden food significantly more often than the alligators. The motor self-regulation task compared species in their ability to suppress a prepotent response of reaching for a food reward through a transparent barrier. An animal had to detour the barrier and retrieve the food item for the trial to be finished, and it was considered a pass if the animal did so without touching the barrier. They were tested in two conditions, one with a wire mesh barrier and one with a transparent barrier. Alligators showed the poorest performance among all tested species, both in the mesh condition (19 passed out of 120 trials across six subjects) and in the transparent condition (5 passed out of 120 trials). Furthermore, they attempted to reach for the reward significantly more compared to other species in failed trials. This was true with the mesh barrier (8.97 touches for alligators versus 2.55 for birds) and with the transparent barrier (10.71 touches for alligators versus 4.56 for birds).

This thesis contains four studies that build on the results from these original comparative studies in archosaurs. The first study compared self-control behaviour using a spatial discounting task (see section 4.1 and Paper I). The second study comparatively investigated interference control and tested whether several archosaur species can uphold visual information in their working memory when challenged by interferences (section 4.2 and Paper II). The third study investigated memory retention and whether alligators retain the memory of a hidden food item even after choosing the visible one during the mnemonic-vision priority task (section 4.3 and Paper III). Finally, the fourth study investigated whether American alligators improve their motor self-regulation when guided by memory rather than visual stimuli (see section 4.4 and Paper IV).

4.1 Self-control

Self-control is a psychological term that is operationally defined as the capacity to obtain a subjectively more valuable outcome rather than a less valuable one, by accepting a greater effort or a longer delay (Beran, 2018). It is an important skill that is useful in a wide range of contexts, such as foraging (Should I forage here or search for a better patch?), mate selection (Should I mate with this individual now or wait for a better one?), and building social relationships (Should I eat this food by myself or share it and strengthen my bonds?) (Stevens & Stephens, 2010). This diversity reflects the fact that it is not a unitary construct, but rather a collection of behaviours which can differ greatly in terms of effort and function. For example, delays can range from seconds to several years, and outcomes can be directly perceived or currently outside of the sensory field. Thus, self-control behaviours rely on various neural mechanisms, each mediating different memory systems and inhibitory functions. Consequently, to understand how these behaviours emerged, it is necessary to use a battery of tests.

Classically, self-control is studied through delay of gratification tasks, where the subjects are confronted with a choice between a smaller reward available immediately and a larger reward available after a delay. Thus, they demonstrate self-control by inhibiting their impulse to go for the small and immediate reward until the larger reward is available (Beran, 2018). These tasks have mostly been used on mammals and birds, with a high focus on primates, rodents, passerines, and parrots (see Miller et al., 2019; Susini et al., 2021 for reviews). Moreover, direct comparative studies have been done only in primates, corvids, and parrots (e.g., Brucks et al., 2021; Pelé et al., 2011). In recent years, more diverse species have been tested with delay of gratification tasks, like the cleaner wrasse (*Labroides dimidiatus*) (Aellen et al., 2021), the cuttlefish (*Sepia officinalis*) (Schnell et al., 2021), and the honeybee (Cheng et al., 2002). All showed self-control abilities. However, despite their key phylogenetic position, no studies have yet been conducted on reptile species (Susini et al., 2021; Szabo et al., 2021). An obstacle to a broader diversity of species tested in delay of gratification tasks may be their complexity. They require the subject to wait for a food item that is usually out of sight while another one is immediately available. Thus, extensive training is necessary for the subject to understand – if at all – that the desired option will be made available after a delay. This prompted the development of alternative methodologies. For example, the rotating tray task. There, both food options are moving at the same speed towards the subject, but from different distances, making the desired food option arrive later (Bramlett et al., 2012; Miller et al., 2020).

The spatial discounting task is a test of self-control where both food options are placed at different locations, more or less distant from the subject (Stevens et al., 2005). Here, the delay is integrated into a spatial factor: the subject must move over a longer distance, and thus for a longer period of time, to get the higher valued option (Mallpress, 2021). It diverges from other self-control tasks because in this situation, both food options are visible and immediately available. This means the subject does not have to rely on its memory and does not have to inhibit an impulsive action until the alternative is available. The task requires little training compared to more traditional delay of gratification tasks (Brady et al., 2018). Hence, it has also been successfully used to test wild animals (Kralik & Sampson, 2012; McCallum & Shaw, 2024). The spatial discounting task has been applied to several taxa like primates (Kralik & Sampson, 2012; Stevens et al., 2005), songbirds (McCallum & Shaw, 2024), canids (Brady et al., 2018; Jordan et al., 2023), fish (Mühlhoff et al., 2011), and insects (Ohkubo et al., 2018; Wendt & Czaczkes, 2017). The simplicity of the task makes it an ideal methodology to investigate minimal self-control behaviours.

In Paper I, we conducted a comparative study investigating self-control abilities with a spatial discounting task. We tested three archosaur species: the American alligator, the emu, and the domestic chicken (*Gallus gallus domesticus*). We conducted two experiments. In Experiment 1, we did a food preference test by presenting two food options at equal distances from the subjects, which were free to choose one. In Experiment 2, we tested self-control by presenting the two food options at different distances. In half of the trials, the preferred option was closer to the subject (to serve as a control), while in the other half, the preferred option was farther away (requiring self-control). Moreover, both experiments had two conditions. In the quality condition, the options were between a preferred food item and a less-preferred food item. In the quantity condition, the choice was between five preferred food items and one preferred food item.

In Experiment 1, all three species had a clear preference for the preferred food item in the quality condition. However, only the alligators and the emus preferred the higher quantity in the quantity condition, while chickens chose at random. Consequently, we did not test chickens in the quantity condition of the self-control test. In Experiment 2, all species could exert self-control in the spatial discounting task, with no significant difference between species. However, there was a significant difference between conditions. Alligators and emus more often chose the preferred option farther away in the quality condition compared to the quantity condition. This stronger effect of quality over quantity is consistent with delay of gratification studies done in corvids, parrots (e.g., Dufour et al., 2011; Schwing et al., 2017), and monkeys (e.g., De Petrillo et al., 2015; Drapier et al., 2005). This may reflect a cognitive bias favouring food quality over quantity during foraging in amniotes.

The size difference of the NCL between alligators and birds had no obvious effect on self-control performance in this spatial discounting task. This is in contrast with results from delay of gratification studies, where avian species with more plesiomorphic neuroanatomy, like chickens and pigeons (Abeyesinghe et al., 2005; Kalenscher et al., 2005; Mohell Malinen, 2016), cannot sustain delays as long as the neurocognitively derived corvids and parrots (e.g., Auersperg et al., 2013; Hillemann et al., 2014; Koepke et al., 2015). These results are in agreement with the idea that self-control is a collection of behaviours with different neurological underpinnings. The apparent lack of involvement of the NCL might indicate that decisions involving two visible food options immediately accessible are primarily mediated by the visual regions instead. For example, the optic tectum, a brain structure that differs markedly between mammals and sauropsids (Knudsen, 2020). However, our understanding of its neurocognitive functions remains limited. Alternatively, this result could be due to our limited number of species. Inter-species differences could have been present if we had included a more neurocognitively derived bird in our sample, like the common ravens (*Corvus corax*). Indeed, in our interference control study, ravens' performance was the only one that differed significantly from the other species (see section 4.2, Paper II).

In summary, our findings suggest that the elaboration of the pallium observed in birds probably did not evolve mainly for foraging situations involving directly accessible visual information. The presumably enhanced cognitive maps of endothermic species may have conferred advantages in situations where options are spatio-temporally distant and rely on memories.

4.2 Interference control

Visual working memory refers to the capacity to remember visual information about something that has moved out of sight, and to protect it against interferences (Lorenc et al., 2021; Schurgin, 2018). This memory is limited by time and the amount of information it can uphold, which are two characteristics that can be used for comparative studies (e.g., Hahn & Rose, 2020). Notably, despite protecting the information from interferences, it remains sensitive to it. This can provoke impaired memory performance (Lorenc et al., 2021). Visual working memory and interference control are regulated by selective attention. This basic process is present in all organisms moving through noisy sensory environments. It enables them to prioritize objects, locations, or events when confronted with multiple simultaneously arising possibilities (Lev-Ari et al., 2022). Thus, the role of selective attention is to bring relevant information into working memory and to keep it active, while preventing irrelevant information from entering.

An interference is a stimulus encountered by the animal while it is keeping information in working memory. We can distinguish two types of interferences. *Interruptions* are interferences involving relevant stimuli that require attention and might necessitate a behavioural response. While *distractions* are interferences involving irrelevant stimuli that should be ignored (Clapp et al., 2010). This categorical division is contextual, and the same stimulus can be considered an interruption or a distraction depending on the task in which the animal is currently engaged. Several studies done on corvids, humans, and other primates have shown that interferences can impair performance in visual working memory tasks (e.g., Völter et al., 2019; Wagener et al., 2023), with interruptions having a greater effect than distractions (e.g., Dolcos et al., 2007; Yoon et al., 2006).

Primates and corvids evolved similarly functioning visual working memory, both in terms of behavioural capacity and neural mechanisms (Balakhonov & Rose, 2017; Hahn et al., 2021, 2022). In primates, visual working memory and the ability to protect it from interferences are mediated by the prefrontal cortex (PFC), the parietal cortex, and the visual areas (e.g., Jacob & Nieder, 2014; Jha et al., 2004). In birds, they have been associated with the NCL (e.g., Veit et al., 2014; Wagener et al., 2023), but we lack studies investigating the possible involvement of other brain regions. However, the optic tectum is likely important due to its involvement in the processing of visual information and the regulation of attention in sauropsids (Knudsen, 2020; Krauzlis et al., 2018).

In Paper II, we conducted a comparative study to investigate the ability of archosaurs to protect information stored in visual working memory. We used five species of archosaurs: the American alligator, the emu, the domestic chicken, the ring dove (*Streptopelia risoria*), and the common raven.

We used a new and ecologically relevant task based on an object permanence setup with a choice between two opaque barriers. A trial began with a food item placed at one location. Once the subject started to approach, the food item was hidden. From then, four different things could happen depending on the experiment: (1) in the baseline, after the food had been hidden, the subject was free to select a barrier; (2) in the one-food interruption experiment, the experimenter gently tossed another food item (of the same type as the hidden food) in reaching distance of the subject, which had to eat it before choosing one of the barrier; (3) in the two-food interruptions experiment, the experimenter tossed two such food items consecutively and the subject had to eat both of them before selecting; (4) in the irrelevant distraction experiment, the experimenter tossed a known and non-valuable object in reaching distance of the subject, who was free to interact with it or not, before choosing one of the barriers. This methodology aimed to mimic a foraging context where the animal is confronted with new and immediately accessible food sources while trying to reach a known food location guided by its visual working memory. Thus, the interruptions represent opportunities to maximize food intake, which will be highest if the animals integrate these new opportunities as sub-goals while remembering the location of the initial goal. This skill would rely on a sufficiently strong visual working memory.

Results showed that all species could, to various degrees, protect the visual working memory from interferences. Alligators, emus, chickens, and ring doves had an impaired performance during the food interruptions experiments, but all of them except the ring doves could still find the hidden food above chance level. No species had an impaired performance during the irrelevant distraction experiment. This suggests that the performance was impaired by the need to adjust behaviour to integrate new goals, and not by the mere appearance of objects in proximity. This mirrors results from previous studies that have shown that interruptions have a higher effect than distractions during visual working memory tasks in humans (e.g., Clapp et al., 2010; Jha et al., 2004) and carrion crows (*Corvus corone*) (Wagener et al., 2023).

Ravens stood out compared to other species because they were not impaired by the food interruptions but maintained very high performance across all conditions. Ravens have a particularly large and parcellated NCL and a very high neuron density compared to the other species tested in this study (Kverková et al., 2022; von Eugen et al., 2020). Thus, their performance is consistent with the idea that their derived neuroanatomy enhances their goal-directed cognition.

Ring doves also stood out compared to other species because their performance was particularly low during the food interruptions conditions. They found the hidden food at chance level. This could be due to the sample of ring doves that we tested. All of them were subadult individuals which had no prior experience with cognitive experiments. Thus, their results could be explained either by cognitive immaturity or lack of experience. During testing, the doves could easily be distracted by events happening outside of the testing aviary. For example, social interactions that were happening between two conspecifics in the housing aviary. In these situations, they often did not finish the trial they were currently engaged in. This suggests they had a low attention level for the task.

Moreover, we also examined the number of abandoned trials, which are trials where subjects refused to choose any barrier and returned to the starting position. These trials were not used to determine the performance in the task. However, they suggest that the subject forgot the location of the initial food item, or the hiding event itself, and preferred to start anew. This is also indicative of less robust visual working memory. Generally, alligators abandoned more trials compared to emus, chickens, and ravens. Additionally, alligators, emus, and chickens abandoned more frequently in food interruptions experiments compared to the baseline and irrelevant distraction experiments.

Alligators' performance was comparable to that of emus and chickens; however, they also abandoned many more trials. This suggests that alligators have a less robust visual working memory, which is more susceptible to interferences. In order to keep memories active, populations of excitatory neurons in the NCL fire throughout the delay period between the acquisition of relevant information and its use (Moll & Nieder, 2015; Rose & Colombo, 2005; Veit et al., 2014). The smaller NCL and the lower number of pallial neurons of the crocodylian brain suggest that cognitive processes mediated by this region can more easily compete with each other. Thus, a visual working memory task could represent a high cognitive load for crocodylians. On the other side, ravens had the best performance of all tested species. They are also the most neurocognitively derived species in our sample, with a large NCL and high pallial neuron numbers. Overall, these results suggest that the expansion of the NCL and the increased pallial neuron densities have enhanced visual working memory by reducing the cognitive load represented by single elements of information. Previous studies have shown that concurrent cognitive loads lead to reduced performance in visual working memory tasks in primates (Basile & Hampton, 2013; Brady & Hampton, 2018; Völter et al., 2019) and corvids (Apostel et al., 2023; Wagener et al., 2023). Thus, it would be interesting to expand the study by examining how archosaurs, and especially alligators, perform when the cognitive load of the task is further increased. For example, by increasing the number of hidden food items and locations.

4.3 Memory retention

We know from a previous study that American alligators diverge from birds in the mnemonic-vision priority task. When they are free to choose between two food items of equal quality – where one is placed behind an opaque screen and the other one is visible – alligators clearly prefer the visible one over the hidden one (Osvath et al., in prep.). A possible explanation is that alligators' visual working memory is more vulnerable when two equally valued options compete. In this situation, their limited NCL resources might bias their neural representation towards the most salient stimulus, the one visually available. This would be optimal in situations where only one goal can be reached. Consequently, they would have no retention of the other, hidden option. This is supported by some of the results in our interference control study, which suggest that maintaining information in visual working memory represents a higher cognitive load for alligators (see section 4.2 and Paper II). Thus, they could be more prone to reduce this cognitive load when the opportunity arises and forget redundant information.

In Paper III, we conducted a study to determine whether alligators had a memory retention of a hidden food item. Within the context of this thesis, memory retention refers to the ability to retain visual information in working memory, despite not using this information to orient behaviour. We used the original mnemonic-vision priority task as a control experiment and interspersed control trials with the test trials of the new experiment. The new task introduced the removal of the food item that was previously behind the transparent barrier after the subjects started to approach.

The task was designed to test whether the animal would reverse their choice and retrieve the food from the opaque barrier after the visible food had been removed. This behavioural adjustment would suggest the presence of memory retention about the hidden food item. We compared American alligators with common ravens. Ravens consistently show high performance in cognitive studies investigating their executive functions, notably their visual working memory (e.g., Apostel et al., 2023; Balakhonov & Rose, 2017; Paper II). Therefore, we tested them as a comparative benchmark.

Our results showed that during the control experiment, alligators preferred the visible food item while ravens had no preference, which supports the results previously obtained with the alligators and the emus (Osvath et al., in prep.). When the visible food item was removed in the test experiment, both species significantly increased their preference for the hidden food item. These results support the idea that alligators retain memory of hidden food items. They can use this knowledge to flexibly adjust their behaviour when the features of the trial change.

4.4 Motor self-regulation

Motor self-regulation refers to the capacity to inhibit an impulsive or habitual motor movement in favour of a more appropriate goal-oriented one (Kabadayi et al., 2018). This capacity has been studied in animal psychology for around a century through many iterations of the detour task (Hobhouse, 1901; Kabadayi et al., 2018). The basic principle of the task is as follows: a desirable food item is placed behind a see-through barrier; to pass the test, the animal must hinder its impulse to directly reach for the food item and instead detour the barrier. Many variations of the task exist, which can broadly be classified into two categories: continuously visible goal detours and initially visible goal detours. The continuously visible goal detours generally involve simple barriers that allow the animal to keep the goal in view during the whole detour. The initially visible goal detours involve apparatuses that break the animal's line of sight to the goal during the detour, either with the use of opaque walls or by requiring the subject to move away from the goal. The latter tasks are often used to test different aspects of working memory (Kabadayi et al., 2018). Moreover, the shape of the barrier (e.g., V-shaped, cylinder), or its transparency (e.g., Plexiglas, wire mesh) can be manipulated in both categories. All such features can affect the ability to pass the test, because they require different motor movements or engage different sensory modalities (Kabadayi et al., 2018). For example, performance on locomotor detours with V-shaped barriers does not correlate with performance on reaching detours (using only paws or head movement) with cylinder barriers in wolves and dogs (Marshall-Pescini et al., 2015). Detour studies have focused mostly on mammals and birds (see Kabadayi et al., 2018; Loyant et al., 2025 for reviews), but more diverse model species have recently been added, like reptiles (e.g., Szabo et al., 2020) and fish (e.g., Sovrano et al., 2018).

The neurological underpinnings of detour behaviours are still not well understood. However, several lesion studies in primates show the importance of the PFC (e.g., Wallis et al., 2001). No studies have associated the NCL with detour behaviours, but this brain region has been shown to mediate motor inhibition in birds (Kalt et al., 1999).

A large comparative study used the cylinder task to measure motor self-regulation in mammals and birds (MacLean et al., 2014). Even though they mistakenly called it self-control (Beran, 2015). In this task, the reward is placed inside a transparent cylinder open at both ends. The test has been applied in broad comparative studies of birds, mammals, fish, and reptiles (Lucon-Xiccato et al., 2017; Szabo et al., 2020). The MacLean study concluded that absolute brain size was the best predictor of the species differences in performance. Another study found that both absolute and relative brain size well predicted the performance of different corvid species (Kabadayi et al., 2016). However, these results should be interpreted with caution, as the cylinder task required some animals to reach into the cylinder while others had to enter it with their whole bodies, effectively making it a different task (Kabadayi et al., 2017). For example, a study on cats systematically evaluated how cylinder dimensions affected performance and found that results varied greatly with changes in length and hole size (Bobrowicz & Osvath, 2018). These results are likely best explained by differences in neuron numbers, but only within clades, as avian neuroanatomy allows for a more efficient brain capable of performing similar functions with fewer neurons. This is partly due to a different distribution of neurons across the brain regions in birds compared to mammals (Stacho et al., 2020; von Eugen et al., 2022).

A previous study conducted by the Cognitive Zoology Group investigated motor self-regulation in archosaurs. The task consisted of detouring a single see-through barrier, made either of wire mesh or of completely transparent acrylic. It showed that American alligators' performance in motor self-regulation is poorer compared to palaeognaths and galliforms (Osvath et al., in prep.). Moreover, the study showed that visible food items act as strong lures that alligators consistently choose over hidden ones when they are of the same value (mnemonic-vision priority task; Osvath et al., in prep.; Boehly et al., Paper III). However, it also showed that alligators can choose hidden food items over visible ones when the two differ in values (mnemonic-vision competition task; Osvath et al., in prep.). In other words, visible stimuli evoke stronger impulses than memory, but memory can still override weak impulses. Thus, alligators' performance in the detour task could improve when the visible food is replaced by a memory of it.

In Paper IV, we tested American alligators in a modified version of the detour task. We compared their performance between two conditions. The control condition corresponded to the original detour task, with a food item visible behind a transparent barrier. In the test condition, we additionally introduced a small opaque barrier to hide the food item. Thus, we reduced the impulse evoked by the food item.

The results showed that alligators were better at detouring the transparent barrier when the food item was hidden. Archosaurs are visually oriented animals. Thus, visual stimuli probably provoke strong activation of the sensorimotor pathways. In these situations, the crocodylian's small NCL is likely overwhelmed by strong bottom-up signals that override motor planning. On the contrary, memories likely provoke reduced activation of these pathways. This enables the crocodylian's NCL to exert top-down motor control.

5 Concluding remarks

This thesis represents an attempt at understanding how executive functions have changed in the transition from ectothermy to tachymetabolic endothermy. I studied archosaurs, the taxon including crocodylians and birds. They are ideal models because of their diversity in thermal physiology, neuron density, and neuroanatomy.

Interestingly, the alligators performed on par with the least neurocognitively derived bird species in our self-control study. However, the results from the interference control study brought more evidence that alligators have a less robust visual working memory compared to birds. This mosaic pattern of results shows that endothermy likely did not cause an overall improvement of goal-oriented behaviours but affected specific features of model-based cognition. One change that we could identify is the likely reduced cognitive load during decision-making involving invisible stimuli. This likely improved the ability to make goal-oriented decisions about food opportunities that are outside of the sensory field.

Neuroanatomy studies show that crocodylians already possess bird-like features compared to other reptiles, like the presence of an NCL or of a mesopallium (Billings et al., 2020; Striedter & Northcutt, 2020). This might explain why alligators can be on par with the neuroanatomically most plesiomorphic birds in some tasks. This also suggests that some of these adaptations were not the consequence of endothermy, but maybe rather "pre-adaptations" which later enabled this transition in the bird lineage. Thus, the archosaur brain was "ready" for the transition to happen. Neuroanatomy studies on crocodylians are still rare, but it would be interesting to verify whether other adaptations which have currently only been observed in birds (and mammals) are also present in crocodylians, like the pallido-thalamo-pallial loops, for example (Güntürkün et al., 2020). Moreover, this calls for including more non-archosaur reptiles in cognitive studies to better understand the effect of these features on archosaurs' cognition. This could also help to explain how, among all reptiles, the archosaurs became the dominant terrestrial vertebrates of the Mesozoic.

The fossil record of non-avian dinosaurs shows a constant expansion of the telencephalon from the coelurosaurs up to the emergence of birds (Balanoff et al., 2013; Torres et al., 2021). This may suggest a progressive improvement of model-based cognition. Unfortunately, because brains do not fossilize, it is not possible to know about more specific features that would be more informative, like the size of the NCL. We can only hope that some osteological correlates in fossils will be identified in the future, shedding more light on extinct cognition.

Within birds, ravens stand out among the other species. Their neuroanatomy has several peculiarities. Their neuron density is extremely high due to being core landbirds (Kverková et al., 2022). Their NCL is very large and parcellated into three regions due to being Passeriformes (von Eugen et al., 2020). And due to being corvids, they have a high proportion of pallial neurons in the associative areas (Ströckens et al., 2022), as well as direct projections from their hippocampus to their NCL (Kersten et al., 2024). This could help explain their outstanding performance in goal-oriented behaviours. Future cognitive studies should include more diverse species of Telluraves to disentangle the effects that each of these features has on cognition. Moreover, neuroanatomical studies should examine whether the parcellation of the NCL is passerine specific or a shared feature with other Telluravians. It could be that it emerged with the higher neuron density of Telluraves. Finally, we already have some evidence that among passerines, the hippocampus–NCL projections are a corvid innovation. But it would be interesting to know whether parrots convergently evolved this connection. Indeed, parrots are another taxon of core landbirds, with some species being on par with corvids in some cognitive studies. If confirmed, this could be a crucial finding to explain how these two clades of birds display such sophisticated cognitive abilities.

To conclude, I would like to encourage future cognitive studies to carefully choose their model species via informed decisions based on the neuroanatomical data and phylogenetic rigor, and to design their experiments with the aim of revealing the crucial cognitive differences existing between species. Due to perhaps an implicit anthropocentric bias, the animal cognition field has been focused on species showing outstanding cognition and has been seeking for human-like features in non-human animals. However, this provides only limited data to understand the evolutionary history of this fascinating biological function and tends to erase the cognitive diversity existing across the tree of life. I hope that the content of this thesis provides a good argument for embracing this diversity and seeing the value in these differences.

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EXECUTIVE FUNCTIONS are a set of cognitive skills enabling goal-directed behaviours. This thesis is about the evolution of these functions in Archosauria, a group of animals including extant crocodylians and birds. It compiles four studies on visual working memory and motor inhibitory control. Moreover, these studies used one crocodylian and four avian species as models. Thus, the findings shed light on the evolution of cognition during the transition from reptiles to birds.

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