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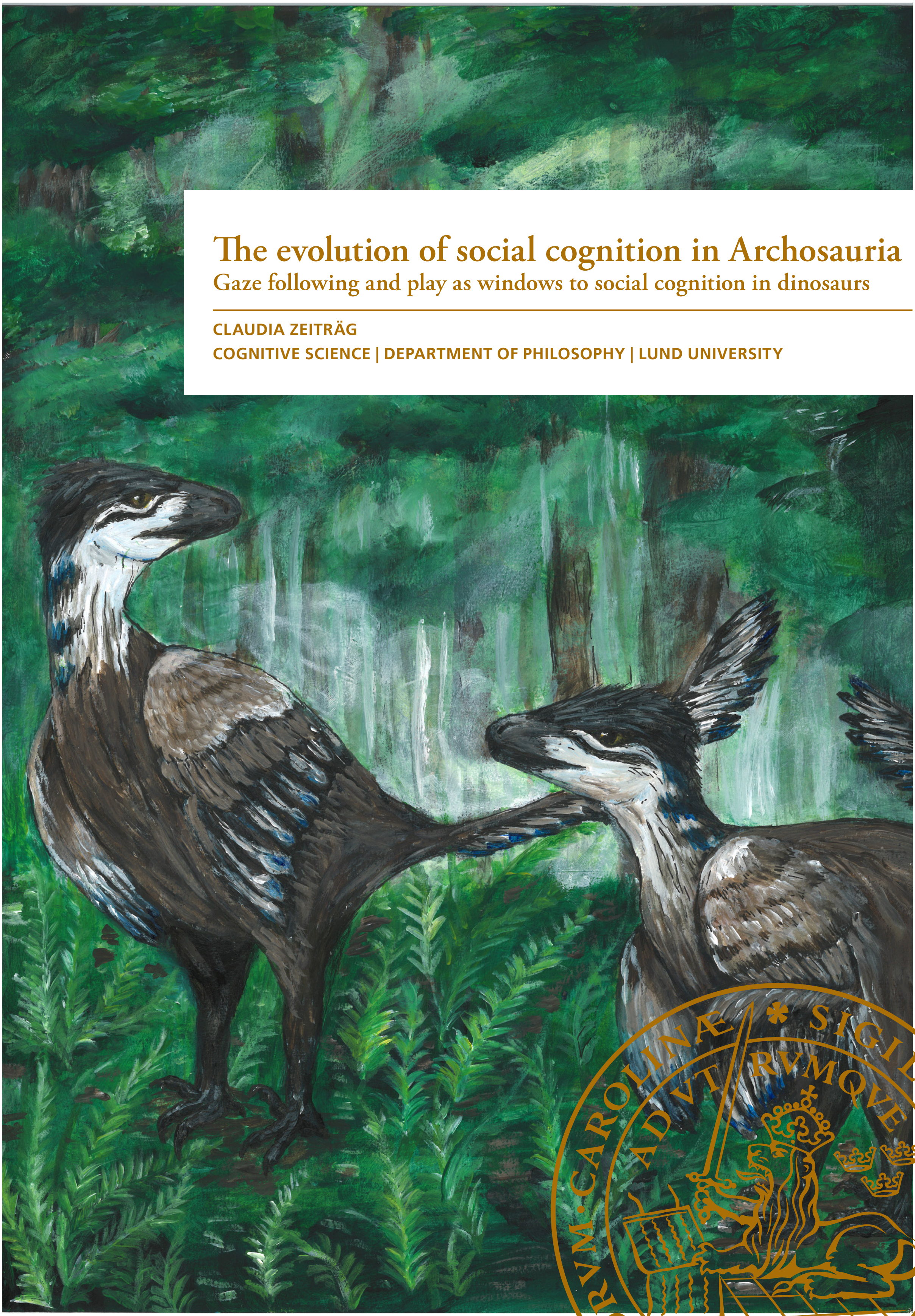

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Gaze following and play as windows to social cognition in dinosaurs

Claudia Zeiträg

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 25th of November at 10.00 in the Upper Auditorium at LUX, Department of Philosophy, Helgonavägen 3, 223 62 Lund

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Abstract

Social cognition entails all cognitive processes involved in social interactions. To study the evolution of social cognition, it is crucial to investigate several distantly related lineages. Studies in comparative cognition have traditionally been biased towards primates and a few social mammalian species, limiting evolutionary interpretations to few and closely related lineages.

To obtain a better understanding of the evolution of social cognition in the avian lineage, this thesis investigates species phylogenetically bracketing the lineage of dinosaurs from which the birds derived. Crocodylians and modern birds form the clade Archosauria that also comprises the extinct dinosaurs. Through studying socio-cognitive capacities in extant archosaurs, it is possible to draw inferences on the social cognition of non-avian dinosaurs. In this light, two topics are covered in this thesis: gaze following and play.

We found shared low-level gaze following skills in birds and alligators, while only birds demonstrated visual perspective taking. The more sophisticated gaze following repertoire of birds is likely caused by their dramatic increase of neurons in the cerebellum. This structure has been proposed to be involved in the formation of so-called internal forward models that allow for the formation of social predictions. We moreover studied the development of gaze following skills in ravens and found an extraordinarily early ontogenetic onset of such predictive capacities.

Furthermore, we regarded socio-cognitive skills and their development through the lense of play. We studied play behaviours of greater rheas and found a pronounced aspect of sociality in their play repertoire early in their ontogeny.

Finally, we used our findings to hypothesize about social cognition in extinct dinosaurs. Our findings are indicative of an earlier evolution of visual perspective taking in dinosaurs than in mammals. This is probably linked to the evolution of refined visual senses in this lineage. Non-avian paravian dinosaurs likely followed each other's gazes and might have been capable of generating social predictions based on observed gaze. Moreover, they most likely played, and their play probably contained a pronounced aspect of sociality. Taken together, the findings of this thesis suggest that non-avian paravians possessed a variety of socio-cognitive skills surpassing those of mammals living at the same time.

Key words social cognition, evolution of cognition, gaze following, play, development, dinosaurs

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List of original papers

PAPER I:

Zeiträg, C, Reber, S.A., Osvath, M. (submitted): Gaze-following in Archosauria – alligators and palaeognath birds suggest dinosaur origin of visual perspective taking.

PAPER II:

Zeiträg, C., Jensen, T.R., Osvath, M. (in review): Gaze following: A socio-cognitive skill rooted in deep time.

PAPER III:

Zeiträg, C., Osvath, M. (submitted): Differential responses to con- and allospecific visual cues in juvenile ravens (*Corvus corax*): The ontogeny of gaze following and social predictions.

PAPER IV:

Zeiträg, C., Jensen, T.R., Osvath, M. (accepted): Play in juvenile greater rheas – Different modes and their evolutionary and socio-cognitive implications.

1 Introduction

Just imagine standing in a crowd at St Mark's square in Venice. You are queuing together with hundreds of other tourists to be let into the famous Basilica. Suddenly, the person in front of you lifts their head and starts to scan the sky. What will you do? Most likely, and without thinking about it, you will copy the movement and start looking up yourself.

This phenomenon is called *gaze following* – a socio-cognitive skill central to this thesis. The focus, however, will not lie on human gaze following, even though we are skilled gaze followers. This thesis concerns gaze following in non-human animals (hereafter "animals").

In the last decades, many animal species have proven their skills in gaze following experiments, ranging from chimpanzees to lizards (e.g. Povinelli & Eddy, 1996; Simpson & O'Hara, 2019). However, these studies have primarily described gaze following skills of one or few closely related species. Moreover, like most studies in animal cognition, gaze following experiments have traditionally focused on our own closest relatives, the non-human primates, and few other social mammalian species. This led to a sound understanding of the distribution of gaze following in some lineages, while others have been left unexplored for the most part. By largely disregarding some taxa, we are left with a patchy understanding of the evolution of this fundamental socio-cognitive skill. To better grasp the evolutionary roots of gaze following, and the evolution of social cognition in general, it is crucial to study it in distantly related lineages.

When thinking about animals exhibiting complex cognition, primates come to mind naturally. However, the field of comparative psychology by now commonly acknowledges that at least some bird species, such as corvids and parrots, exhibit striking cognitive capacities, paralleling great apes in several domains (e.g. Emery & Clayton, 2004; Seed et al., 2009; Kabadayi & Osvath, 2017; Pika et al., 2020).

What is remarkable about these cognitive parallels is the fact that the lineages leading to modern mammals (Synapsida) and birds (Sauropsida) split around 325 million years ago (Ford & Benson, 2020) and have during that period evolved vastly differing neuroanatomies. Nevertheless, both ended up with comparable cognitive skillsets. It is through studying representatives of distantly related lineages, such as mammals and birds, that we can gain an understanding of the evolutionary pressures and patterns shaping complex cognition.

Birds are, however, also interesting for a different reason. They are living dinosaurs. Accordingly, through studying social cognition in birds, we can peer through a window to the cognition of non-avian dinosaurs (hereafter "dinosaurs"). This allows for even deeper insights into the cognitive evolution of birds.

Palaeontologists have been fascinated with the social lives of dinosaurs ever since the first discovery of an accumulation of 31 *Iguanodon* skeletons in 1878. This was the first indication of herding behaviour in these creatures and sparked interest in the topic of sociality in dinosaurs. By now, evidence of gregariousness in dinosaurs has been well established through communal bonebeds (e.g. Funston et al., 2016), trackways (e.g. Lockley & Matsukawa, 1999) and nesting sites (e.g. Horner & Makela, 1979). However, this evidence is exclusively based on trace records that fail to provide insights into dinosaurs' cognitive abilities to navigate their social lives.

By studying fundamental socio-cognitive skills, such as gaze following, in extant representatives of Archosauria, the clade containing crocodylians, birds, and dinosaurs, this thesis will begin to explore social cognition in extinct dinosaurs with the objective of uncovering the evolutionary roots of such skills.

The second behaviour that will be covered in this light is *play*. Play represents a behavioural state that appears to be – just like gaze following - phylogenetically widespread. Despite this, its functions and evolutionary roots remain elusive. Play is moreover an interesting topic when studying the sociality of dinosaurs. The frequency, contagion, and categories of play are informative about a species' social repertoire. Thus, through studying play in extant descendants of dinosaurs we will obtain an understanding of the level of sociality and the associated socio-cognition of their extinct ancestors.

1.1 Structure of the thesis

This thesis revolves around two topics with implication for the social cognition of dinosaurs: gaze following and play. These subjects are covered over the course of four scientific papers – three empirical studies (PAPER I, III and IV) and one review paper (PAPER II). These papers will be introduced, explained, and discussed throughout five chapters.

Chapter 2 introduces dinosaurs, why they are interesting for studying the evolution of cognition, what is known about their brains, and how it is possible to study cognition in extinct species.

Chapter 3 describes how and why animals transfer and use social information. It moreover discusses different hypotheses about the role of social group living in the evolution of complex cognition and large brains.

Chapter 4 focusses on the central topic of this thesis: gaze following. This chapter presents the background of this research field in human developmental psychology. It moreover explains neurocognitive mechanisms involved in the processing of social gaze. PAPER I is an empirical study investigating gaze following skills in five archosaur species. Additionally, it proposes internal forward models as a possible mechanism for refined visual socio-cognitive skills of birds and possibly dinosaurs. PAPER II reviews the current state of knowledge of gaze following in animals and introduces general ideas and methods of this field. In the same chapter, the development of gaze following in humans and animals is explained. PAPER III investigates the development of gaze following in juvenile ravens with human and conspecific demonstrators.

Play is a behavioural state closely linked to ontogeny and cognitive development. *Chapter 5* introduces the study of animal play and its definitions. PAPER IV is the first systematic description of play and its ontogeny in a palaeognath bird. A novel theoretical framework for the functions of play – predictive processing – is introduced and connected to the findings of PAPER IV.

Finally, *Chapter 6* discusses the implications of the results of this thesis for dinosaur cognition. It hypothesizes about the socio-cognitive skills of non-avian paravian dinosaurs and their differences to mammals living at the same time. Finally, it discusses the impact of these findings on our knowledge about the evolution of social cognition and predictive brains.

1.2 Phylogeny

To be able to study evolutionary processes, an understanding of the phylogeny of the animals in question is required. The phylogeny underlying this work is depicted in Figure 1.

Amniota are tetrapod vertebrates that evolved a specific extraembryonic membrane – the amnion. This membrane is considered a key adaptation to terrestrial life, as it allows for egg-laying on land and thereby led to reproductive independence from water. This clade emerged around 325 million years ago (from here on MYA) and includes mammals, non-avian reptiles, and birds (e.g. Shedlock & Edwards, 2009).

Amniota further split into Synapsida, that today only contains mammals, and Sauropsida, including all non-avian reptiles and archosaurs. Archosauria comprises crocodylians, birds, and dinosaurs. Birds are living dinosaurs and form, together with the extinct dinosaurs, the clade Dinosauria.

Archosauria originated around 250 MYA. During the Late Triassic, crocodile-line archosaurs (crurotarsans) were dominant over bird-line archosaurs including dinosaurs (avemetatarsalians) in diversity and abundance. However, in the Early Jurassic, dinosaurs achieved their role as dominant terrestrial vertebrates (Brusatte, Benton, et al., 2010). Dinosaurs were inhabiting the Earth for approximately 163 MY throughout the Mesozoic (Fastovsky & Weishampel, 2016)) until going extinct during the Late Cretaceous, around 66 MYA (Renne et al., 2013).

Within Dinosauria, one generally distinguishes between Ornithischia and Saurischia. These two groups differ from each other regarding their pelvis structures. In ornithischian ("bird-hipped") dinosaurs, at least a part of the pubis is rotated backwards, lying parallel to the ischium. In saurischian ("lizard-hipped") dinosaurs, on the other hand, the pubis is directed anteriorly. Ornithischia comprises a variety of herbivorous dinosaurs, such as *Triceratops* and *Stegosaurus*. Saurischia consists of Sauropodomorpha and Theropoda - the latter including modern birds (Fastovsky & Weishampel, 2016).

Within the theropod dinosaurs, Maniraptora includes the closest relatives to modern birds. Maniraptoran theropods exhibited true pneumaticity with extensive air sacs, highly efficient unidirectional breathing, and hollowed bones. Maniraptora comprises the oviraptorosaurs, deinonychosaurs, and Avialae. Deinonychosaurs and avialans together represent Paraves. The non-avian paravians will be mentioned frequently throughout this thesis as this group includes the most "bird-like" dinosaurs.

Finally, Avialae includes *Archaeopteryx*, Aves (the extant birds), and all the evolutionary steps in between. These steps led towards increased flight proficiency through for example flight feathers, a rigid trunk, increased encephalization and flight musculature. The extant representatives of Aves still inhabit this planet today in form of modern birds (Fastovsky & Weishampel, 2016).

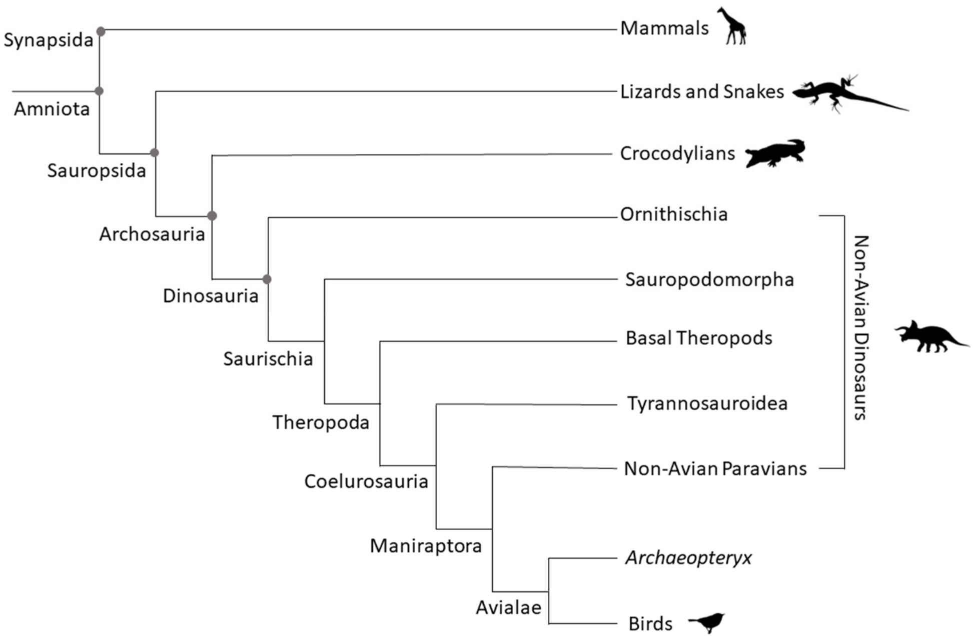

Figure 1: A phylogenetic tree of amniotes (drawn by CZ, silhouettes from PhyloPic, based on Brusatte, Nesbitt, et al., 2010).

2 Dinosaurs

2.1 Why study dinosaurs?

According to the most recent estimate, there are currently around 8.7 million eukaryote species inhabiting the Earth (Mora et al., 2011). However, to obtain a better understanding of the principles of cognitive evolution, it is of special interest to study extinct species to gain insights into the emergence of cognitive traits, the selective pressures they are underlying, and possible relaxations of evolutionary constraints.

Comparative psychologists have for the longest time focused their research predominantly on primates, primarily with the aim of uncovering the origins of our own cognitive capacities. The field has since broadened, but studies are still biased towards mammals and some large-brained bird species, such as corvids and parrots.

However, when trying to unveil the evolution of cognition, it is crucial to study a wide variety of distantly related species (Matsubara et al., 2017). Comparisons of performances on the same task of species occupying key phylogenetic positions are needed to trace how specific traits have changed in evolutionary time. Further knowledge is gained if the results of such studies are subsequently correlated with species' socio-ecologies, brain anatomies, and various other factors.

Birds are of special interest when trying to understand evolutionary trends in cognition for two reasons. Firstly, birds have demonstrated cognitive capacities matching or even surpassing that of many mammals. Corvids and parrots even appear to exhibit cognitive levels on par with great apes. They have among other things been shown to possess complex problem-solving skills (Huber & Gajdon, 2006), manufacture and use tools (Auersperg et al., 2012), pass a mirror-self-recognition test (Prior et al., 2008), and plan for the future (Kabadayi & Osvath, 2017).

Despite their similarities in cognitive output, avian brain morphology differs drastically from that of mammals. Birds lack a neocortex – the brain region commonly associated with higher cognitive functions in mammals. Instead, the avian cerebrum is organized in pallial aggregations. Additionally, birds have evolved an equivalent to the mammalian prefrontal cortex – a part of the neocortex associated with executive functions, such as working memory and planning. The functional equivalent in the avian brain is called the nidopallium caudolaterale (Güntürkün & Bugnyar, 2016).

Mammals and birds shared their last common ancestor around 325 MYA, possibly even further in the past (Ford & Benson, 2020). Despite their long, separate evolutionary paths and their different neuroanatomical outcomes, the achieved cognitive output appears to be very similar. This is one reason why it is important to compare avian and mammalian cognitive capacities: to find functional similarities, but also uncover differences and limitations of different neuroanatomies.

The second motive to study avian cognition is that they represent a direct window to extinct species – the dinosaurs. We know today that birds are not descendants of the dinosaurs; they are in fact living theropod dinosaurs. This, in combination with extensive palaeontological research providing a wealth of knowledge about dinosaurs, allows for glimpses into the behaviour and cognition of early birds and to an extent dinosaurs. Through studying cognition in extinct species, we can draw inferences on the cognitive capacities of animals living at that time and can trace back the emergence of certain cognitive traits.

In the following, the current state of knowledge regarding dinosaur brains and their evolution will be explained together with methods of studying cognition in extinct species.

2.2 Dinosaur brains

Due to advances in the field of palaeontology and the extensive fossil record of dinosaurs, we today know a great deal about the brains of these extinct animals. As this thesis concerns the evolution of avian cognition, we will focus here on theropod brains.

One might ask how it is possible to gain information about the brains of extinct species, as soft tissue rarely fossilizes (but see for example Brasier et al., 2017). Fossilized skulls, however, can shed light on brain anatomies. Palaeontologists create 3D-models of dinosaur brains through generating endocasts of the endocranial cavity - the cavity in the skull that houses the brain. In earlier times, the braincase of a fossil specimen was for that purpose filled with successive layers of latex (Hurlburt et al., 2013). New technological advances allow for the generation of digital endocasts through high-resolution X-Ray Computed Tomography (HRCT), a completely non-destructive method. The endocasts represent a proxy for the actual brain shape depending on its brain-to-endocranial cavity (BEC) index of the respective specimen, i.e.,to which extent the brain was filling the braincase (Balanoff & Bever, 2017).

BEC differs significantly between animal species. The brains of ancestral vertebrates only filled a very small proportion of the braincase and even those of extant reptiles only fill about half of their braincase (Hurlburt et al., 2013). Consequently, endocasts from such species are poor estimates for their brain morphology.

Nevertheless, they can be used to estimate the relative size of the brain. Hurlburt and colleagues (2013) compared the encephalization quotients (brain mass to body mass ratio; EQ) of several theropod species, including tyrannosaurids, allosaurids, and *Archaeopteryx* to extant bird and non-avian reptile species. They thereby differentiated between bird EQs (BEQs) and reptile EQs (REQs). The authors found that the relative brain size of most theropod dinosaurs falls well within the range of extant non-avian reptiles of their body-mass, with the highest value for *Tyrannosaurus rex* with an EQ comparable to that of extant crocodylians. The EQ of *Archaeopteryx lithographica* was found to lie above the mean REQ, placing it at the lower end of the BEQ range. The only theropod dinosaurs falling within the bird EQ-range were late Cretaceous small theropods (*Bambiraptor*, *Ornithomimus*, *Troodon*). This indicates an evolutionary shift in relative brain size from earlier theropod dinosaurs to theropods from the late Cretaceous, such as the coelurosaurs and maniraptorans.

In fact, Osmólska (2004) discovered imprints of intracranial vascular channels on the skull roof of an oviraptorid theropod (*Ingenia yanshini*). It was inferred from this finding that the brain surface must have been closely appressed to the bone, indicating that the brain was filling the braincase to a high degree in this species. This, combined with similar observations in ornithomimids, troodontids and dromaeosaurids (Russell, 1972; Osmólska, 2004) led to the conclusion that all maniraptoran theropods exhibited this feature.

Oviraptorosaur brains were later shown to not only have filled the braincase, but were moreover the first ones to exhibit an inflation of the forebrain, resulting in a sigmoidal shape of the brain and a lateral displacement of the optic lobes (Balanoff et al., 2014). Despite this, their forebrain was not yet large enough to close the gap to the cerebellum, as found in extant birds. Furthermore, oviraptorosaur brains exhibited a reduction of olfactory tracts and bulbs.

Finally, the Neornithes - the clade containing the extant bird groups Neognathae and Palaeognathae – diverged. Neornithes established during the Cretaceous but experienced an explosive radiation after the end-Cretaceous extinction (K-Pg boundary). Mesozoic birds from the Lower Eocene have been found to already have possessed essentially modern avian brains, with ventrolaterally displaced optic lobes due to an expanded telencephalon (to a much higher degree than in *Archaeopteryx*), and a hyperpallium (formerly called “Wulst”) that is commonly regarded as the primary visual processing area of the avian brain (Medina & Reiner, 2000).

However, some features of these early birds were differing from modern avian brains. Their olfactory lobes were relatively large, and their hearing sensibility was increased due to a long cochlear duct. These features represent a sensory adaptation that paralleled and even exceeded that of extant birds. Moreover, the cerebellar expansion of these early birds had not reached the extent of modern birds (Milner & Walsh, 2009; Walsh & Milner, 2011)

In general, four evolutionary steps can be identified from the brains of non-maniraptoran theropods to that of extant birds (Torres et al., 2021). Basal non-maniraptoran theropods, such as *Tyrannosaurus*, retained the ancestral, linear arrangement of neuroanatomical regions (Bever et al., 2011). The brains of non-avialan maniraptorans, such as *Zanabazar*, showed first expansions of both the cerebrum and the cerebellum, causing a ventral displacement of the midbrain (Balanoff et al., 2014). Shortly after the divergence of Avialae, for example in *Archaeopteryx,* the cerebrum and cerebellum further expanded until they pushed into contact. This caused a complete ventral displacement of the midbrain. Finally, extant birds have further increased relative brain size and cerebrum size (Balanoff et al., 2013).

2.3 Avian brain evolution

While palaeontological studies have mainly used relative brain sizes estimated through endocasts as measures for the cognitive capacities of extinct dinosaurs, more recent approaches have shed new light on avian brain evolution. These new studies have increasingly focused on neuronal numbers as measures of cognitive performance rather than relative brain size. This approach has various advantages over more conservative methods. Firstly, distantly related brains can have vastly differing numbers of neurons in the entire brain, as well as in specific brain areas of the same mass (Herculano-Houzel, 2017; Němec & Osten, 2020). Macaques, for example, have similar numbers of pallial neurons compared to corvids, despite them having an almost seven times larger brain than their avian counterparts (Olkowicz et al., 2016).

Moreover, the causal relationship between relative brain size and cognitive capacity has been challenged. Evidence is accumulating suggesting that number of neurons – the computational units of the brain – is a better predictor of cognitive performance than relative brain size (Striedter, 2004; Roth & Dicke, 2005; Herculano-Houzel, 2011; Dicke & Roth, 2016).

Through collecting a comprehensive dataset of neuronal numbers of extant species, Kverková and colleagues (2022) recently shed new light on avian brain evolution. This study found that over time, both mammals and birds have convergently evolved towards increased total and relative brain sizes, as well as higher neuronal numbers. This increase is disproportionately bigger than in reptiles, resulting in significantly lower neuronal numbers for a given body size in this group compared to mammals and birds. Within the overall increase of neuronal numbers, primates and core land birds (hawks and eagles, owls, falcons, songbirds, and parrots) subsequently experienced an additional increase in telencephalic neurons compared to other mammal and bird species.

Interestingly, this study found that proportionally, the biggest increase of neurons in the avian brain is accounted for by the cerebellum. Until now, the telencephalon has been regarded as the centre of higher cognitive function. These new findings, however, indicate a bigger role of the cerebellum in the evolution of complex cognition than previously thought. This is in line with accumulating evidence of an involvement of the cerebellum in various cognitive functions, such as executive control, language, working memory, learning, pain, emotion, and addiction (e.g. Strick et al., 2009; Barton, 2012; Smaers et al., 2018).

Kverková and colleagues (2022) moreover argued that the transition to endothermy was key to enabling the dramatic increase of neuronal numbers. This has new implications for dinosaur brains. A recent study (Wiemann et al., 2022) argued for a dinosaur-origin of endothermy. The authors investigated traces of advanced lipoxidation end-products (ALEs) in the bones, teeth, and eggshells from all major amniote radiations. ALEs are a by-product of metabolic stress caused by the physiological heat underlying endothermy. Based on this method, the authors determined that stem archosaurs were ectothermic, but that all ornithodirans (pterosaurs, dinosaurs, and their last common ancestor) were endothermic with increasing rates along the avian lineage. According to this study, ornithischian dinosaurs secondarily reduced their metabolic rate back to ectothermy.

Though very interesting, the results of this study should be handled carefully. The authors made inferences for all extinct amniote species based on data from 30 fossil specimens, of which only six were ornithischian and seven saurischian dinosaurs. These are quite small sample sizes to make broad phylogenetic assumptions. Nevertheless, it is today commonly accepted that at least the non-avian paravian dinosaurs were endothermic (e.g. Legendre et al., 2016; Rezende et al., 2020).

As noted above, endothermy is closely related to increases in neuronal numbers (Kverková et al., 2022). Endothermy is metabolically costly (Else & Hulbert, 1981; Nagy et al., 1999), as are neurons (Hyder et al., 2013). Through shifting to endothermy, the cost of neurons might have relatively decreased, while simultaneously paying off through improved cognitive capacities. Endothermy in non-avian paravian dinosaurs thus suggests that these dinosaurs might already have had increased neuronal numbers. What cognitive capacities these neuronal numbers brought about remains, however, unclear to date. How it is possible to study the cognition of extinct dinosaurs will be explained in the following.

2.4 How to study social cognition in dinosaurs

Social behaviours are inherently difficult to preserve in the fossil record. Consequently, gregariousness in dinosaurs can only be inferred from communal bonebeds (e.g. Funston et al., 2016), trackways (e.g. Lockley & Matsukawa, 1999) and nesting sites (e.g. Horner & Makela, 1979). While such trace records can stimulate hypotheses about sociality in dinosaurs, they can often be explained in alternative ways.

An assembly of animals in one area is commonly the result of other circumstances than sociality. Firstly, members of a species are expected to be found in similar environments as they are foraging for the same food sources and have the same ecological requirements to their habitats. Even group movements, that have been proven through trackways of many members of the same dinosaur species moving in the same direction, can be explained by migrations, or simply the lack of an alternative route. Moreover, seasonal abundances of food can lure many individuals to the same location, as can for example be seen in extant grizzly bears (*Ursus arctos horribilis*) that assemble during periods of salmon migration. If these animals were to suddenly die in this location, it would likely be assumed from the fossil record that they were representatives of a social species. For these reasons, the conclusions that can be drawn on dinosaur sociality based on trace records are limited.

Even if trail records were to shed light on the sociality of extinct species, they fail to provide insights into the cognitive abilities these animals exhibited to navigate their social lives. At first glance, it might appear impossible to study non-fossilizing features of dinosaurian lives, such as cognition. However, palaeontologists commonly use a trick to overcome this issue: the so-called extant phylogenetic bracketing (Witmer, 1995).

This approach is based on the assumption that shared traits in extant members of a clade are derived from a common ancestor. Dinosaurs form, together with their extant descendants (the birds) and their closest relatives (the crocodylians) the clade Archosauria. Within this group, the lineage leading to birds, i.e., the theropod dinosaurs, can be bracketed, as closely as possible, by modern birds and crocodylians.

Crocodylians have had slow evolutionary rates (Green et al., 2014) with ancestral brain morphologies resembling those of basal archosaurs (Brown et al., 2020), and therefore represent an optimal neurocognitive model for stem archosaurs. On the other side of the phylogenetic bracket are the modern birds. Within Aves, one group is of special importance as a neurocognitive model for extinct dinosaurs: the palaeognath birds.

Paleognathae includes the flightless ratites (ostriches, rheas, kiwi, emus, and cassowaries), and the volant tinamous (Widrig & Field, 2022). Palaeognathae and Neognathae split around 110 MYA, before the end-Cretaceous extinction (Yonezawa et al., 2017). Consequently, they existed at the same time as the non-avian dinosaurs.

These birds constitute the best neurocognitive model for the closely related non-avian paravian dinosaurs, such as dromaeosaurids and troodontids. Palaeognaths exhibit the least derived number of pallial neurons (Olkowicz et al., 2016) and share numerous homologies with the non-avian paravian dinosaurs, including scaling relationships and morphology of the brain (Balanoff et al., 2013; Ksepka et al., 2020).

Moreover, maniraptoran dinosaurs – the clade including the oviraptorosaurs and paravians - displayed a variety of complex social behaviours such as paternal care and brooding of communal nests similar to reproductive strategies of palaeognath birds (Varricchio et al., 2008; Varricchio & Jackson, 2016). These findings, in combination with the above-mentioned shared brain features, suggest similar socio-cognitive capacities in non-avian paravian dinosaurs and palaeognath birds.

Taken together, by studying social cognition in extant crocodylians and palaeognath birds, it is possible to draw inferences about the cognitive abilities of early birds and the most "bird-like" dinosaurs, the non-avian paravians.

2.5 Species in this thesis

This thesis revolves around six species. To phylogenetically bracket extinct dinosaurs, we chose three representatives of Palaeognathae: emus (*Dromaius novaehollandiae*), greater rheas (*Rhea americana*), and elegant-crested tinamous (*Eudromia elegans*). These three palaeognath species occupy different phylogenetic nodes, are representatives of different socio-ecologies, and some are flightless, while others are volant (e.g. Yonezawa et al., 2017). We moreover included one plesiomorphic neognath species that served as an outgroup: red junglefowl (*Gallus gallus*). This species belongs to the lineage Galloanserae that already diverged from other large group of neognaths (Neoaves) before the end-Cretaceous extinction. As a representative of the crocodylians, we chose American alligators (*Alligator mississipiensis*). On the other hand, we studied common ravens (*Corvus corax*), one of the most large-brained avian species that has proven its complex cognitive capacities in many cognitive experiments (for pictures of each species, see Figure 2).

Emus and greater rheas are representatives of the flightless ratites. Emus are the second largest birds in the world (after ostriches), and can be found in most parts of continental Australia, except for sandy deserts and dense forest. In the wild, emus are mainly solitary, but can form pairs and small groups. Males incubates the nest by themselves and guard the chicks for five to seven months after hatching (Folch et al., 2020).

Greater rheas are one of two species of Rheidae. The other species is the Lesser rhea or Darwin's rhea (*Rhea pennata*). Greater rheas inhabit open areas in eastern and southern South America. Males are usually solitary, while females live in small flocks. During breeding season, males gather small harems around them. Like in emus, the males perform parental care including incubation of nests and chick guarding for six to eight months after hatching (Winkler et al., 2020).

Elegant-crested tinamous are representatives of the tinamous, a group of small, ground-dwelling birds of South America. Elegant-crested tinamous inhabit shrublands of southern Chile and Argentina, where they form mixed-sex flocks. Tinamous are volant, though their flight proficiency is rather poor, and they can only fly for short distances. Typically for many palaeognath species, the males incubate the eggs and rear the young (Bohl, 1970).

Red junglefowl are wild ancestors of the domestic chicken. These birds can be found in most areas of Southeast Asia and parts of South Asia. They usually live in flocks of one or a few roosters with several females. The females incubate and rear the chicks (McGowan & Kirwan, 2020).

Common ravens are found all over the Northern hemisphere in a variety of habitats. Subadult ravens live in large fission-fusion flocks, but form pair-bonds when reaching sexual maturity. The pair raises their offspring together. The chicks fledge around 35 days old, but stay with their parents for up to six months (Boarman & Heinrich, 2020).

American alligators are one of two species of alligator, the other one being the Chinese alligator (*Alligator sinensis*). American alligators can be found in freshwater marshes, swamps, rivers, and lakes of the southern and eastern US. These crocodylians are commonly tolerant and can aggregate in basking groups, during droughts, and in breeding groups. Females protect their nest, carry the young to the water after hatching, and guard them for up to one year (Grigg & Kirshner, 2015).

Figure 2: Species in this thesis: Top row (from left to right): Emu, greater rhea, elegant-crested tinamou. Bottom row: American alligator, red junglefowl, common raven. Photo credit: Ivo Jacobs, Helena Osvath.

For a comparison of neuronal numbers of these species, see Table 1. The only crocodylian species with available data on neuronal numbers is the Nile crocodile (*Crocodylus niloticus*), which will be used as a representative for other crocodylian species here.

The neuronal numbers shown in this table are in line with the above-described pattern of avian brain evolution. The birds generally have more neurons in their brains compared the Nile crocodile. The relatively biggest increase took place in the cerebellum. While an emu has approximately 15.75 times as many neurons in the telencephalon as a Nile crocodile, it has about 20.5 more neurons in the cerebellum.

Ravens have almost twice as many neurons in total compared to the larger palaeognaths (emus and rheas), though their numbers of cerebellar neurons are comparable. This reflects the secondary drastic increase in neuronal numbers in the telencephalon of core land birds. Indeed, the telencephalon of a raven houses approximately 2.8 times more neurons than that of an emu.

Table 1: Neuronal numbers of species in this thesis (numbers from Olkowicz et al., 2016; Kverková et al., 2022)

Species	Brain mass [g]	#Neurons total [x10^7]	#Neurons telencephalon [x10^7]	#Neurons cerebellum [x10^7]
Nile crocodile	5.8	8.2	3	4
Elegant-crested tinamou	2	21.8	6	13
Greater rhea	21.3	103	36.7	61.1
Emu	21.8	133.5	47.2	81.5
Red junglefowl	2.8	22.1	7.4	11.4
Common raven	14.1	217.1	135.5	75.4

3 Social information and the evolution of social cognition

Social group living has many advantages for animals. It can serve as protection against predators and provide reproductive advantages (Shettleworth, 2010). Moreover, and of special significance to this thesis, it provides animals with opportunities for receiving and transferring social information (Brown & Laland, 2003).

Sociality in animals can take many different forms, ranging from pair-bonds to fission-fusion societies. It can be argued that very few species are truly solitary, as most of them as a minimum meet to mate – at least those that are sexually reproducing. Being able to read and interpret others is thus a useful skill for many species.

This chapter explains how animals acquire and use social information and how the special challenges connected to dealing with social relationships have been suggested to have impacted brain evolution.

3.1 Social information

Animals require information about their environment to be able to make informed inferences about for example the location of food and predators, the reproductive status of possible mates, or the strength of a rival (Giraldeau et al., 2002). Such information is hence used to reduce uncertainty about variable environments (Carter et al., 2016).

Two types of information are accessible to animals: personal information - information animals acquire through interacting with their environment - and social information – information that is acquired by observing others (Dall et al., 2005). Animals can extract personal information from markers in the environment such as landmarks, the sun, or the geomagnetic field (Dall et al., 2005). Social information, on the other hand, can either be shared intentionally through visual or vocal signals, or it can be conveyed inadvertently (Morand-Ferron et al., 2010). Every choice an animal makes sends inadvertent information to others. For example, a gazelle's choice of grazing in a certain patch of grass can inform other gazelles about the abundance and quality of food in that area.

Three steps are involved in the use of social information: acquisition, application, and exploitation (Carter et al., 2016). All three steps underly different phenotypic constraints, and do not necessarily predict each other. In other words, the acquisition of social information does not predict subsequent exploitation of that information. Three-spined sticklebacks (*Gasterosteus aculeatus*), for example, have been observed to discover a foraging task quicker when observing conspecifics solving the task, but did subsequently not solve it quicker themselves (Atton et al., 2012). In chacma baboons (*Papio ursinus*), interest in the acquisition of social information, did not predict the ability to use such information. In other words, the time spent observing a demonstrator was not correlated with subsequent improvements in solving the observed task (Carter et al., 2014).

Such constraints in exploiting social information can operate on an individual level, with individuals varying, for example, in their social competencies, cognition, rank and age, but also on a species level (Carter et al., 2016). Different species undergo varying selective pressures favouring social information use and are equipped with diverse cognitive capacities. These capacities allow for increased attention towards social cues and subsequently improved processing of such information.

The first step of social information use refers to the acquisition of social information. This step requires paying attention to others and their actions. One way of gathering information is to attend to what others are looking at – gaze following. This topic will be discussed at length in *Chapter 4*.

In the next two steps, social information is applied and exploited. Such a sequence could for example look as follows: A young monkey observes a conspecific shaking a branch, which leads to fruit falling (information acquisition). The monkey then climbs up a tree and starts shaking a branch itself (information application). As the fruit falls, it collects and eats it (information exploitation).

This example represents a classic social learning scenario. Other areas of social information use are public information use and social eavesdropping (Bonnie & Earley, 2007). Public information use refers to the use of inadvertently conveyed information such as resource quality, while social eavesdropping informs animals about others' relationships through witnessing their interactions.

Social information has many advantages over personal information, as it allows for quicker, and less costly gathering of information compared to personal information gathering based on trial-and-error (Clark & Mangel, 1984, 1986; Giraldeau et al., 1994; Giraldeau, 1997; Galef & Giraldeau, 2001). It moreover enables the receiver to optimize decisions beyond their personal knowledge, making the ability to use such information adaptive (Morand-Ferron et al., 2010). However, social information can also be unreliable, especially when observed individuals are misinformative, or when information is quickly outdated (Dall et al., 2005).

Nevertheless, the use of social information is generally adaptive, and has therefore been favoured by selective forces throughout evolution. The complex challenges animals face when living in social groups have even been hypothesized to be one of the main drivers of the evolution of large brains and complex cognition. This is called the social intelligence or social brain hypothesis (Jolly, 1966; Humphrey, 1976). These hypotheses will be explained in the next section.

3.2 The social intelligence hypothesis

The social intelligence hypothesis (SIH) has first been proposed by Jolly (1966), and later brought forth again by Humphrey (1976). This hypothesis suggests that the complex cognitive demands of social group living are the main drivers of the evolution of complex cognition in primates and consequently the evolution of large brains (social brain hypothesis; Shettleworth, 2013).

This hypothesis has been inspired by two observations. Humans and non-human primates have larger brains than expected for their body size (Byrne, 1994). They moreover exhibit a number of exceptionally complex cognitive skills. For these reasons, the SIH proposes that these traits have evolved to better anticipate, understand, and manipulate others' behaviour in the complex social groups of primates (Humphrey, 1976). Alternatively, but closely related, the "Machiavellian" intelligence hypothesis (Whiten & Byrne, 1988) suggests that the roots of primate intelligence lie in tactical deception and manipulation of others.

The SIH has found a lot of support by researchers working on primate cognition. Indeed, a correlation between relative brain size and social complexity measured by group size has been identified for many primate species (Dunbar, 1998).

However, the SIH has also received a lot of criticism over time. Firstly, the parameters it is based on are problematic. Some ungulates, for example, live in enormous herds, but they are predominantly anonymous and don't engage in complex social behaviours (Pérez-Barbería et al., 2007). Consequently, group size is not an ideal measure for social complexity. Moreover, the relationship between brain size and cognitive complexity is not fully understood and thus speculative (e.g. Logan et al., 2018).

Additionally, there are a range of phenomena that the SIH cannot account for. Its original formulation disregards non-primate species. However, distantly related groups, such as corvids have demonstrated complex cognitive capacities on par with apes in many cognitive experiments (e.g. Kabadayi et al., 2016; Kabadayi & Osvath, 2017; Pika et al., 2020), even though their brain morphologies differ substantially from those of primates (Güntürkün & Bugnyar, 2016). Birds moreover do not appear to exhibit the same correlational relationship between group size and relative brain size as primates. On the contrary, avian species forming monogamous pair-bonds have larger brains than those with complex mating systems (Emery et al., 2007).

On the other hand, there are species living in similarly complex social structures as primates that have not evolved comparable cognitive skills. Spotted hyenas (*Crocuta crocuta*), for example, live in so-called clans – a social system comparable to troops in baboons. Nevertheless, they have not evolved the same cognitive capacities as primates (Holekamp, 2007).

Finally, even within primates, innovation, tool use, and frequency and sophistication of social learning vary between species independent of their group size (e.g. Reader & Laland, 2002).

For these reasons, alternative explanations for the increase in brain size of primates have been put forth. In fact, a number of other, non-social factors, such as feeding ecologies and foraging techniques could explain brain expansion just as well (Whiten, 2000). The so-called foraging theory of intellect proposes that challenges animals encounter during foraging select for higher cognitive skills (Shettleworth, 2010). Similarly, the ecological intelligence hypothesis states that challenges caused by variable environments such as changing climatic conditions and food sources have driven the evolution of cognition (e.g. Barton, 1996).

A recent study (Hooper et al., 2022) brought up criticism for both the social and the ecological intelligence hypothesis. The authors found several problems in correlational studies of this kind. Estimates of a species' brain size vary significantly between datasets. The same applies to body size estimates used to calculate relative brain sizes. Brain and body size measures are either estimated from one individual or averaged across several individuals. Nevertheless, depending on the sample, this might yield different results in various datasets due to large intraspecific variation. They moreover showed that model specifications, such as the combination of variables included in statistical models and their source significantly impact the results of such correlational studies. The authors found, depending on the models they were choosing, evidence supporting several contradicting theories. Basing entire evolutionary hypotheses on correlational analyses that are susceptible to variation depending on the used dataset or model specification is hence a problematic method.

The ultimate causes of the evolution of complex cognition remain elusive. While some support has been found for both the social and the ecological intelligence hypothesis, it is not fruitful to regard the two as contradictory. The drivers of cognitive evolution are likely variable environmental conditions – which include both the social *and* the ecological environment. The challenges animals are facing due to their social environment are undoubtedly numerous, complex, and extremely important for the survival of a species. Just imagine animals that are not capable of recognizing suitable mating partners or maintaining good relationships with other group members. Such individuals would likely not be able to reproduce successfully. The social environment is thus expected to be an important driver for the evolution of cognition, but most likely not – as stated by the social intelligence hypothesis – the only one.

4 Gaze following

Animals have evolved various mechanisms of gathering social information. One effective way of acquiring such information is by attending to what others are looking at. Co-orienting with others' gaze directions – gaze following - is a fast, easy, and effective way of gathering information about the location of food, predators and third-party relationships (Tomasello et al., 1998; Emery, 2000).

Gaze following is a fundamental socio-cognitive skill due to the many benefits of utilizing social gaze as a source of social information. It moreover has direct implications for the development and evolution of other socio-cognitive components in humans as well as animals. The fundamental character of gaze following becomes apparent in its phylogenetic ubiquity.

65 species across 4 vertebrate classes have been tested for their ability to either co-orient with observed gaze or to find hidden food based on gaze cues. Traditionally, the study of gaze following has focused on primates and some social mammals, limiting evolutionary interpretations to few and closely related lineages. However, in recent years, new studies have emerged, trying to broaden the understanding of gaze following skills in the animal kingdom. These new studies have mainly focused on birds, but also on some reptiles, and fishes. Nevertheless, over time, many different methodologies have been introduced, once again hampering phylogenetic comparisons. Moreover, gaze following studies have often disregarded a number of factors potentially influencing the results of such studies. We have reviewed methodologies, limitations, and new advances in the field of gaze following in PAPER II.

4.1 Gaze following and its implications for human infants

Gaze following was first studied in 1975, when Scaife and Bruner tested co-orientation of human infants with an experimenter's gaze direction. Human infants start to spontaneously follow gaze between three and six months (Butterworth & Jarrett, 1991), but are sensitive to others' gaze directions already as new-borns (Batki et al., 2000; Farroni et al., 2002). A more detailed description of the development of gaze following skills in humans can be found in PAPER II.

The development of gaze following has direct implications for the development of other socio-cognitive skills of humans, such as theory of mind (Brooks & Meltzoff, 2015), joint attention (Carpenter et al., 1998), and language acquisition (Baldwin, 1991; Schafer & Plunkett, 1998; Houston-Price et al., 2006). These developmental connections demonstrate the fundamental role of gaze following in the development of human social cognition.

This becomes even clearer when investigating children with deficiencies in their socio-cognitive skillsets such as individuals with autism spectrum disorder (ASD). Children with ASD are impaired in their ability to detect and attend to social stimuli, such as gaze (Dawson et al., 1998; Dawson et al., 2004), and in initiating joint attention (Mundy et al., 1986; Mundy & Sigman, 1989).

Though delayed, children with ASD develop a sensitivity to directional cues conveyed through gaze at two years old (Chawarska et al., 2003). The absence of gaze following in early developmental stages could according to the authors of this study be explained by difficulties in disengaging attention from their current fixation point or by a lack of salience of social cues to these children. Indeed, studies have found that children with ASD respond better when combining multiple cues, instead of exclusively using gaze cues to redirect the children's attention (Presmanes et al., 2007; Thorup et al., 2016).

Children with ASD are moreover often impaired in their language acquisition (e.g. Charman et al., 2011) and about 25% of autistic children remain completely non-verbal (Kim et al., 2014). Children with ASD produce their first words on average at 38 months, while neurotypical children start talking between 8 and 14 months (Howlin, 2003).

When combining the early development of gaze following in human infants with its connection to the development of other socio-cognitive skills and the deficits in children with impairments in joint attention, including the use of gaze cues, it becomes clear that gaze following is a fundamental part of the socio-cognitive repertoire of humans. It is thus a skill that is also expected to be central to animals.

4.2 Modes of gaze following

The comparative cognition literature commonly distinguishes between two levels of gaze following. This dichotomy has been introduced by Povinelli and Eddy (1996) that proposed a high- and low-level interpretation of gaze following. According to this theoretical framework, low-level gaze following entails reflexive co-orientations with observed gazes that do not involve an attribution of mental states. High-level gaze following, on the other hand, requires the representation of others' visual perspectives.

These two modes are tested in two distinct experimental paradigms: gaze following into the distance and geometrical gaze following. Gaze following into the distance tests for low-level gaze following skills. In this experimental setup, a demonstrator is gazing either up or to the side. An observer with low-level gaze following skills is expected to co-orient with the observed gaze direction. In geometrical gaze following experiments, a demonstrator is lured to gaze to a location that is concealed by a barrier from the observer's viewpoint. A subject capable of high-level gaze following is expected to relocate itself around the barrier to identify the gaze target. This requires a representation of others' visual perspectives through generalising between allo- and egocentric space.

Geometrical gaze following is thus diagnostic of visual perspective taking, i.e., the ability to predict others' visual experience (Michelon & Zacks, 2006). In this context one traditionally distinguishes between level I and level II knowledge, that allow for the prediction of two different types of information (Flavell et al., 1981). Level I refers to an understanding of *what* the other can see, i.e., which objects are visible from the other's viewpoint. Level II includes an understanding of the visual aspects from the predicted viewpoint, i.e., *how* the scene looks to the other.

Geometrical gaze following can only reveal level I knowledge of others' visual perspectives, while it does not signify level II perspective taking. It has, however, been proposed as an embodied precursor for the development and evolution of such perspective taking skills (Kessler & Rutherford, 2010). Through repositioning themselves around the barrier, subjects experience the other's visual perspective, which might later be used in mental simulations of others' visual experiences.

Geometrical gaze following does hence not require an attribution of mental states, but in human children, grasping others' visual perspectives is crucial for the development of an understanding of others' mental states. Brooks and Meltzoff (2015), for example, found that children exhibiting improved gaze following skills at 10.5 months (both in speed and accuracy) were subsequently producing more mental-state words at 2.5 years, i.e., words of cognition, desire and emotion. At 4.5 years, the same children performed better on a theory of mind test battery including diverse desires, knowledge acquisition, false belief, diverse beliefs, hidden emotions, and false beliefs.

Low-level gaze following skills, i.e., gaze following into the distance, appear to be phylogenetically widespread and have to date been found in all tested amniote species including a variety of mammals (e.g. Schaffer et al., 2020) and birds (e.g. Nawroth et al., 2017), some reptile species (e.g. Wilkinson et al., 2010), and possibly even one fish species (Leadner et al., 2021). High-level gaze following, i.e., geometrical gaze following, on the other hand, appears to have evolved in parallel in mammals (e.g. Met et al., 2014) and some songbirds (e.g. Bugnyar et al., 2004; for a review see PAPER II).

Additionally, low-level gaze following has been described to precede the development of high-level gaze following skills in the ontogeny of several distantly related species (e.g. humans: Butterworth & Jarrett, 1991; ravens: Schloegl et al., 2007; wolves: Range & Virányi, 2011).

The differences in phylogenetic distribution and development of the two modes of gaze following indicate different neurocognitive underpinnings of the two behaviours. Indeed, neuroscientists have identified two distinct neurobiological pathways in line with a low- and high-level of gaze following. These pathways will be described in the following.

4.3 Neurocognitive mechanisms of gaze following

Despite the abundance of studies on gaze following in human psychology as well as comparative cognition, the underlying neurobiological processes remain puzzling. Nevertheless, neurobiological studies suggest two distinct pathways: one fast, yet crude pathway, and one more sophisticated, cortical pathway that allows for visual perspective taking. The neurocognitive mechanisms guiding gaze following have been summarized in PAPER II but will be explained in more detail below.

4.3.1 The subcortical pathway

The fast and reflexive nature of gaze following (Deaner & Platt, 2003) suggests an evolutionary old, conserved subcortical pathway (Sewards & Sewards, 2002; Johnson, 2005). This pathway allows for fast, yet unrefined gaze following responses. In the mammalian brain, it runs from the retina to the superior colliculus, the pulvinar, and to the amygdala (Morris et al., 1999; Johnson, 2005; Jiang & He, 2006). Every step of the pathway is interconnected with cortical areas responding to social stimuli, such as the fusiform gyrus (face perception and recognition: Johnson, 2005), the exastriate body area (visual processing of the body: Downing et al., 2001) and the superior temporal sulcus (functions explained in 4.3.2; Shepherd, 2010).

The superior colliculus represents the principal visual processing centre that - together with the pulivnar nucleus of the thalamus – guides attention and organizes head and eye orientation (Platt et al., 2003). The brains of fishes, amphibians, reptiles, and birds have a homologue of the superior colliculus - the optic tectum. The remaining pathway is the same as in mammals.

The amygdala is involved in emotional processing (Hoffman et al., 2007; Adolphs, 2010), and moreover controls social attention through direct connections to reward cortices involved in the initiation of social interactions (Schilbach et al., 2010; Pfeiffer et al., 2014). It has for that reason also been proposed to play a role in the development of autism (Schultz, 2005).

Several neuroimaging studies in humans and monkeys have demonstrated the involvement of the amygdala in gaze detection (Kawashima et al., 1999; Adams et al., 2003; Hoffman et al., 2007; Hadjikhani et al., 2008; Sauer et al., 2014). Lesions of the amygdala lead to a disruption of gaze responses in humans through reduced fixation of the eyes (Adolphs et al., 2005; Spezio et al., 2007; Gamer et al., 2013). A recent study on live interactions between monkeys found a dual function of the amygdala. A subset of neurons exhibits short latency responses to mutual gaze, possibly to detect eye contact. Another group of amygdala neurons were activated towards the end of eye fixations. These neurons might regulate gaze timing through disrupting fixations and initiating gaze shifts (Gilardeau et al., 2021).

4.3.2 The cortical pathway

High-level gaze following, i.e., spatially sophisticated behaviours such as geometrical gaze following, is unlikely guided by the subcortical pathway alone. The subcortical pathway is thus proposed to be interconnected with cortical networks in mammals. How more complex gaze following is processed in other vertebrates lacking cortical structures remains unclear.

The superior temporal sulcus (STS) has been found to play a central role in cortical gaze perception in humans (Puce et al., 1998; Hoffman & Haxby, 2000) and non-human primates (Tsao et al., 2003; Kamphuis et al., 2009). This cortical area is particularly active when viewing faces and following others' gazes (Tsao et al., 2006; Kamphuis et al., 2009). Transformations of the face such as changes in colour or size have no impact on the activation of face-sensitive neurons. Scrambling of facial features, however, diminishes the cells' activation (Perrett et al., 1982).

Cells reacting to different facial orientations have been identified in the anterior and middle part of the STS of rhesus macaques (Bruce et al., 1981; Perrett et al., 1982; Desimone et al., 1984; Rolls, 1984; Baylis et al., 1985; Perrett et al., 1985; Hasselmo et al., 1989; Perrett et al., 1992; Eifuku et al., 2004; De Souza et al., 2005).

Facial orientation is encoded through neurons responding differently to various views of the face. The activation of some cells decreases the more the face is rotated away, others are more reactive to profile views of a face. In the same way, some of these neurons respond stronger to vertical head movements, i.e., turning the face up or down (Perrett et al., 1985; Perrett et al., 1992). These neurons hence encode other's visual attention as they are sensitive to face orientation rather than identity (Perrett et al., 1985; Perrett et al., 1990).

Of the face-sensitive neurons in the macaque STS, a subpopulation is sensitive to the direction of eye gaze. While most of these cells respond strongest to congruent head and eye directions, some are specifically activated when head and eye direction are incongruent (Perrett et al., 1985). Again, different neurons encode different eye orientations. Some eye-sensitive neurons only respond to direct gaze, while others are activated by averted gaze (Yamane et al., 1988). Furthermore, an ablation of the banks and floor of the STS has been found to impair the ability to discriminate between direct and other angles of eye gaze (Campbell et al., 1990).

To successfully follow gaze, the detected direction of the face and eyes needs to further be processed to shift one's own attention. The upper bank of the STS projects directly onto the intraparietal cortex in macaques (Harries & Perrett, 1991). The lateral part of this structure - the lateral parietal area (LIP) - is involved in maintaining attention (Schiller & Tehovnik, 2001; Ben Hamed & Duhamel, 2002), as well as in overt (Thier & Andersen, 1998) and covert attentional shifts (Colby & Goldberg, 1999; Bisley & Goldberg, 2003).

Shepherd and colleagues (2009) even identified "gaze mirror neurons" in the LIP that might bring about attentional shifts. These neurons fire both when gazing towards a location and when observing someone else looking at the same location, similar to the functioning of motor mirror neurons (Rizzolatti et al., 2009). Simultaneously, other neurons of the LIP act inhibitory, possibly to supress other behaviours while continuing to fixate on the face. In this way, LIP neurons might contribute to shifts in attention when detecting gaze cues.

Furthermore, the LIP is part of the dorsal attention network (in humans: dorsal & ventral frontoparietal attention systems) that detects and orients attention toward stimuli in the environment (Gitelman et al., 1999; Corbetta & Shulman, 2002). Other parts of this network are the supplementary and frontal eye fields (Seltzer & Pandya, 1989) that elicit eye movement and control gaze shifts (Tehovnik et al., 2000). Together, the attention network judges the cost and benefit of attentional shifts and redirects attention based on these cost-benefit calculations (for a review see: Klein et al., 2009).

Studies on cortical gaze processing have exclusively been conducted on humans and macaques. However, social processing areas are proposed to be homologous among primates (Tootell et al., 2003; Rosa & Tweedale, 2005) and possibly other mammalian species (Kendrick et al., 2001). The neurocognitive mechanisms mediating high-level gaze following in other taxa lacking cortical structures, such as birds and reptiles, remain unclear.

4.4 Gaze following in Archosauria

Gaze following studies have traditionally lacked a phylogenetic focus, leaving a patchy picture of the distribution and evolutionary principles of this socio-cognitive skill. To partly fill this gap, in PAPER I, we studied the gaze following repertoires of five archosaur species. Subjects to this study were respectively six individuals of three palaeognath species (emus, greater rheas, and elegant-crested tinamous), one plesiomorphic neognath species (red junglefowl), and one crocodylian species (American alligators). These species were tested over the course of three experiments following the high- and low-level distinction of gaze following. Experiment 1 and 2 tested for gaze following into the distance upwards and to the side. Experiment 3 investigated geometrical gaze following, i.e., gaze following behind a barrier.

Experiment 1 and 2 revealed low-level gaze following skills in all five tested species. It should, however, be noted that alligators followed gaze at significantly lower rates than birds. Future studies are needed to address whether this discrepancy is caused by differences in the neuroanatomy or the social ecologies of the species.

The presence of low-level gaze following in all tested species in combination with evidence of gaze following into the distance from many species of various taxa suggests roots in deep evolutionary time. This is in line with the above-described conserved subcortical pathway shared among all vertebrates. The exact emergence of gaze following into the distance, though, remains unclear. It could have evolved when vertebrates moved onto land – around 365 MYA - and visual cues became more important, or possibly even earlier than that. More studies on non-amniote vertebrates such as amphibians and fishes will be needed to pinpoint the emergence of low-level gaze following skills. To date, no studies on amphibian gaze following exist, and only one study described sensitivity to directional cues of conspecifics in archerfish (Leadner et al., 2021). It is from that study, however, not clear whether this represents a species-specific adaptation to their hunting style – shooting water jets at moving objects – or whether this capacity is shared among all fishes.

Our experiments yielded different results with respect to geometrical gaze following. Alligators did not track conspecifics' gazes around barriers, while all four bird species successfully followed their conspecifics' gazes geometrically. The performance of alligators is in line with the results of a study on central bearded dragons (*Pogona vitticeps*), that were found to follow the gaze of a conspecific into the distance, but not geometrically (Siviter et al., 2017). It should, however, be noted that this is the only other study testing geometrical gaze following in a reptile. For that reason, it is not clear whether reptiles generally do not follow gaze geometrically, or if this is an artefact of the low number of studies.

With respect to birds, geometrical gaze following had to date only been reported in corvids (Bugnyar et al., 2004; Schloegl et al., 2008) and one other songbird, the European starling (*Sturnus vulgaris*; Butler & Fernández-Juricic, 2014). Our new findings suggest geometrical gaze following and the connected visual perspective taking skills as a universal socio-cognitive component of all birds. Despite this, it should be noted that one study reported negative results for geometrical gaze following in Northern bald ibises *(Geronticus eremita*; Loretto et al., 2009). In that study, the authors reported that subjects looked significantly more often *at* the barrier in test compared to control trials. This suggests that subjects detected and co-oriented with the gaze cue. The absence of relocations around the barrier could be the result of three factors. Firstly, the ibises might lack an understanding of others' visual perspectives. Secondly, birds were placed in compartments next to each other and not facing each other. This might have distorted the subjects' predictions of the demonstrator's visual perspective, i.e., the subject might have interpreted the gaze cue as a sideways look rather than a look behind the barrier. Thirdly, subjects might have understood the demonstrator's visual perspective, but might not have been willing to move around the barrier. To look behind the barrier, subjects would have had to walk through a relatively narrow space between the barrier and the mesh dividing them from the demonstrators. This could have been avoided by the subjects due to spatial confinements as well as the closeness to the demonstrator bird. The authors claim that the birds were comfortable with moving around the barrier. However, it remains unclear whether this was also tested with the mesh divider and the demonstrator bird present.

Future studies will need to establish whether Northern bald ibises are indeed not capable of geometrical gaze following. Moreover, more studies on a variety of distantly related avian species will be needed to support our hypothesis that visual perspective taking is a shared cognitive trait among all birds.

The presence of geometrical gaze following in birds, but its absence in alligators and other reptiles, suggests a later evolution of this skill compared to gaze following into the distance. This further supports the hypothesis that geometrical gaze following involves more complex neurocognitive mechanism than gaze following into the distance as suggested by Povinelli and Eddy (1996).

Our findings indicate two different evolutionary patterns of the two gaze following modes. Gaze following into the distance likely has a shared evolutionary root for all vertebrates, though the exact point of emergence of this skill is not clear without more research on other vertebrate classes. Geometrical gaze following, on the other hand, likely evolved parallelly in mammals and birds, while being absent in other groups.

4.5 Checking back and the role of the cerebellum

Apart from our findings on gaze following in PAPER I, we observed that all tested bird species, but not the alligators, were "checking back" with their demonstrators. In other words, after following the indicated gaze direction, they looked back at the demonstrator. Such gaze alternations could occur repeatedly within one trial. This is the first description of checking back in any bird species.

This behaviour has first been discovered in human infants by Scaife and Bruner (1975). The authors observed that children were looking back at the experimenter when they could not identify anything of interest in their line of sight. Children first engage in such double looks at 8 months old (Scaife & Bruner, 1975). Developmental psychologists commonly associate this behaviour with an understanding of the deictic nature of gaze, i.e., that it is pointing towards a target in the environment. This hypothesis has been strengthened by reports of infants pointing at an object after following experimenters' gazes before checking back with them (Butterworth & Cochran, 1980). This can be interpreted as a form of double-checking the correctness of the gaze target.

In animals, checking back has first been described by Call and colleagues (1998) in chimpanzees (*Pan troglodytes*). They defined it as a subject looking back to the experimenter "when there were no interesting objects in the human's line of sight" (Call et al., 1998, p. 90). Checking back has since been described in all other great ape species: bonobos (*Pan paniscus*), gorillas (*Gorilla gorilla*), and orangutans (*Pongo pygmeaus*; Bräuer et al., 2005; Okamoto-Barth et al., 2007), gibbons: pileated gibbons (*Hylobates pileatus*; Horton & Caldwell, 2006), and some Old World monkeys: Diana monkeys (*Cercopithecus diana*; Scerif et al., 2004), and long-tailed macaques (*Macaca fascicularis*; Goossens et al., 2008). No evidence of checking back has been found in two species of New World monkey: spider monkeys (*Ateles geoffroyi*) and capuchin monkeys (*Cebus apella*; Amici et al., 2009), though this might have been a methodological artefact due to two reasons.

Firstly, in that study, checking back was defined as subjects following the demonstrator's gaze direction, looking back at them, and then looking in the gaze direction again. However, the experimenter held up a piece of food while they were presenting their gaze cue. While this most likely caught the subject's attention at the beginning of the trial, it might have been problematic for checking back. When looking back at the experimenter, the food might have attracted the subject's attention and might have kept it from retracking the experimenter's gaze direction. Moreover, the authors reported that one spider monkey repeatedly checked back, suggesting the presence of this behaviour in these animals.

In primates, checking back is commonly interpreted in the same way as in human children. In line with this interpretation, several reports describe more instances of checking back in situations where gaze cue and target referred to different locations (Scerif et al., 2004; Horton & Caldwell, 2006), i.e., where the expectancy of detecting a gaze target is violated.

Okamoto-Barth and colleagues (2007) designed an experiment to test great apes' understanding of others' visual perspectives through checking back. They investigated subjects' checking back responses in a "meaningful" and "meaningless" condition. In the meaningful condition, the demonstrators' line of sight was obstructed by a barrier. Thus, their gaze had no target. Subjects were expected to check back more often in this condition, as a sign of their surprise about the lack of a gaze target. In the meaningless condition, the barrier had a window through which the demonstrator (and the subject) could see an object. The apes were expected to check back less often in this condition, as they could easily detect the gaze target in the demonstrator's line of sight. Chimpanzees and bonobos were acting according to the experimenters' predictions. Orangutans and gorillas, however, appeared insensitive to the differences in the conditions. This indicates that there are different levels in the understanding of others' visual perspectives even among closely related species. Future studies should follow similar experimental designs to obtain a better understanding of their subjects' perspective-taking skills in the presence of checking back behaviours.

Different levels of perspective-taking capacities might impact the level of surprise animals experience when facing an expectancy violation. In PAPER I, we propose an explanation for the surprise in gaze following situations causing checking back behaviours. The surprise could be caused by the violation of social predictions. Animals might check back due to a discrepancy between a social prediction – to find a target in the other's line of sight - and the sensory feedback – not finding anything interesting in the observed gaze direction.

The results of PAPER I suggest that birds can form social predictions based on social cues, while alligators, representatives of the crocodylians, failed to do so – at least they exhibit no behavioural signs of the violation of such a prediction. This difference is likely caused by differences in neuroanatomical features between birds and crocodylians. As described above (see 2.3), avian brains have evolved significantly higher numbers of neurons compared to non-avian reptiles. The biggest proportional increase in neurons thereby took place in the cerebellum (Kverková et al., 2022).

The function of the cerebellum has long been believed to primarily lie within motor control. However, the past decades have accumulated evidence that this structure is involved in a variety of cognitive processes, such as executive control, language, working memory, learning, pain, emotion, and addiction (Strick et al., 2009). The cerebellum is interconnected with the cerebral cortex through parallel loops. Through these loops, it simultaneously receives input from and sends projections to the cerebrum (Welniarz et al., 2021). This highly regular cytoarchitecture indicates one single underlying mechanism to its numerous functions (Diedrichsen et al., 2019).

One theoretical framework proposed as such a unifying mechanism are so-called internal forward models. These models are top-down processes, i.e., they anticipate behavioural outcomes based on prior information. Forward models allow for quick updating through error processing as they do not underly feedback control (Wolpert et al., 1998). A reliance on feedback would lead to time delays of 50 and 300 ms between motor command and sensorimotor feedback (Wolpert & Flanagan, 2001). Instead, forward models rely on predictions and are subsequently updated in the case of a prediction error (e.g. Roth et al., 2013). Such models continuously strive to minimize the discrepancy between prediction and feedback. This discrepancy is also called variational free energy (Friston et al., 2017).

An example of an internal forward model from a grasping situation could look as follows: the motor system generates a motor command, while the forward model receives an efference copy of this command. The motor system controls the action, while the forward model forms a prediction about the outcome of the action. The sensory feedback of the motor system is subsequently compared to the predicted sensory feedback of the forward model. In the case of a discrepancy between the two, a prediction error is detected and the forward model is updated (Nowak et al., 2013). Updating can either be achieved through changing one's beliefs about the situation, i.e., changing the prediction, or through changing the world to match the prediction. Taking action to align the world with the prediction is called active inference (Friston et al., 2017).

The theoretical framework of internal forward models can be applied to our findings on checking back in birds. When observing a demonstrator gazing towards a location in the environment, an internal forward model forms a prediction about discovering a gaze target in the observed gaze direction. A mismatch between the prediction and the sensorimotor feedback from the eyes is registered when no gaze target is detected. Checking back could thus represent an attempt to update the model through active inference by retracking the gaze direction.

Taken together, in PAPER I, we for the first time describe that birds exhibit a gaze following repertoire on par with apes, including low- and high-level gaze following, visual perspective taking and checking back. We moreover propose an explanation for the presence of these sophisticated skills in birds in light of their neuroanatomy. More nuanced studies will be needed to fully understand birds' understanding of others' visual perspectives (similar to the study by Okamoto-Barth et al., 2007), as well as the involvement of the cerebellum in social predictions of birds.

4.6 The development of gaze following

Human infants begin to follow others' gaze directions very early. Similarly, low-level gaze following has been shown to develop early in the ontogeny of mammals (e.g. rhesus macaques and chimpanzees: Tomasello et al., 2001; wolves: Range & Virányi, 2011) and birds (e.g. ravens: Bugnyar et al., 2004; rooks: Schloegl et al., 2008; greylag geese: Kehmeier et al., 2011).

Few studies have focused on the development of gaze following skills in animals, and most of these studies have used human experimenters as demonstrators. However, this practice might be problematic, as gaze following skills arguably evolved to facilitate information transfer between conspecifics. It is thus expected that young animals are initially more attuned to conspecific gaze cues. This might cause differences in the development of con- and allospecific gaze following.

Moreover, our findings on checking back in all tested bird species of PAPER I raised questions about the presence, development, and sophistication of this behaviour in other avian species. Ravens are an interesting species in the field of comparative cognition, as their cognitive skills have been shown to match those of great apes despite their significantly smaller brains (e.g. Kabadayi & Osvath, 2017; Pika et al., 2020) and vastly differing neuroanatomy (Güntürkün & Bugnyar, 2016).

In PAPER III, we compared the development of gaze following into the distance, with human and conspecific demonstrators, as well as the presence, development, and impact of different demonstrators on checking back in juvenile common ravens (*Corvus corax*).

We did not find ontogenetic differences in the onset of con- and allospecific gaze following. Both developed between 5.5 and 8 weeks and thus after fledging. However, it took ravens significantly longer to co-orient with humans compared to conspecifics. This suggests that the gaze following system is indeed attuned to conspecifics. In a follow-up study it would be interesting to investigate whether this discrepancy diminishes over time or whether the same pattern is present in adult ravens.

Additionally – and quite extraordinarily – we found checking back as early as 30 days old, when ravens first started to occasionally co-orient with their siblings. Applying the above-mentioned theoretical framework of internal forward models (see 4.5) this result implies that the capacity to form social predictions already develops prior to fledging in ravens.

In comparison, human children only start to check back at 8 months old (Scaife & Bruner, 1975). The only other account of the ontogeny of checking back stems from great apes (Bräuer et al., 2005). All four great ape species only began to check back as juveniles, between 5 and 10 years old. This implies that the ability to form social predictions develops significantly earlier in at least one bird species compared to great apes. As ravens are somewhat outstanding in their cognitive capacities, more studies will be needed to investigate the development of this behaviour in other avian species.

Additionally, ravens check back significantly more often with conspecifics than humans. This further supports our argument that the gaze following system is attuned to conspecifics and that ravens generally exhibit heightened social attention towards other ravens. It could also suggest that ravens form more robust and/or different social predictions about their conspecifics than about humans. What exactly causes the differences in social predictions about con- and allospecific demonstrators is unclear from our data. Again, it would be interesting to investigate whether this changes throughout the ontogeny of ravens.

Taken together with the findings of PAPER I, this study strengthens our argument that birds possess extraordinary visual socio-cognitive skills. We now have gathered evidence from five distantly related avian species exhibiting checking back behaviours. This suggests a shared behavioural trait among birds. Our results indicate that birds form robust social predictions about conspecifics – likely based on internal forward models. They develop this skill significantly earlier than great apes and even human infants. In other words, gaze following skills in birds are not only sophisticated, but also develop extraordinarily early.

Kehmeier and colleagues (2011), for example, found that greylag geese were following the gazes of conspecifics as early as 10 days old. This is to our knowledge the earliest account of gaze following in any animal. The authors explained this very early onset with the precociality of this species that requires early predator avoidance strategies.

Future studies would benefit from starting developmental gaze following experiments even earlier than our study in PAPER III, while birds are still in the nest. Moreover, more studies on species with different life histories, such as precocial and altricial species, are needed to understand differences in ontogenetic onsets of gaze following responses.

5 Play

While play can be a solitary behaviour, it often involves several individuals and can represent a considerable proportion of a species' social repertoire. The proclivity of a species to play socially can thus provide insights into its social behaviours and the accompanying socio-cognitive capacities.

The past century has accumulated evidence of play from all vertebrate classes. Despite this, the functions of this behaviour remain unclear. A variety of theories have been brought forward over the years, ranging from juveniles practicing "serious behaviours" (Thompson, 1998) to burning off excess energy (Spencer, 1872). While many of these theories likely explain a part of the adaptive value of play, none of them has been able to explain it fully.

To gain an understanding about the evolution of play and its functions, it is important to study species in key phylogenetic positions. As described above, palaeognath birds occupy such a position due to their shared features with early birds and to a degree dinosaurs (see 2.2). In PAPER IV, we provide the first ever systematic description of play in a palaeognath bird, the greater rhea, and use our findings to hypothesize about the evolution of play and its connected socio-cognition.

5.1 Definitions of play

Play is an unusual behavioural state. Despite its apparent lack of function, play behaviours have been observed in all vertebrate classes, including mammals (e.g. Byers, 1999; Lewis, 2000; Himmler et al., 2016), birds (e.g. O'Hara & Auersperg, 2017), reptiles (e.g. Dinets, 2015), and fishes (e.g. Burghardt, 2015).

Before the ultimate functions of play can be discussed, one needs to define what this term entails. It might seem like humans can intuitively recognize play, raising the question for the need of a definition. However, especially in those species that are not classically labelled as "playful", such as reptiles and fishes, it can be difficult to recognize play. When, for example, observing a Komodo dragon (*Varanus komodoensis*) tossing around a bucket (as described in Burghardt et al., 2002), it is not immediately clear whether this is a case of play, object exploration, or misguided aggression.

As play can take on many different forms, one single definition might be too narrow to fully capture the phenomenon. For that reason, Burghardt (2001) determined five criteria that need to be fulfilled for a behaviour to be classified as play. The first criterion of play is that the behaviour is not fully functional. Secondly, the behaviour appears spontaneously, voluntarily and is pleasurable or rewarding to the player. Thirdly, the behaviour differs structurally from the serious performance. It is, for example, exaggerated or modified. The fourth criterion is that the behaviour appears repeatedly, but not stereotypically. Finally, the fifth criterion postulates that the animal performing the behaviour must be healthy and free from stress.

Behaviours classified as play through these criteria, are additionally commonly divided into three categories: locomotor, object, and social play. Locomotor play describes all play behaviours revolving around locomotor movements. It often includes exaggerated forms of running or leaping. Object play refers to manipulations of non-novel objects, such as mouthing, pawing, or tossing. Social play describes play behaviours directed towards other individuals (Burghardt, 2005). Common forms of social play include chasing, play fighting, and nipping.

By dividing play behaviours into these three categories, some aspects of the behaviour might get oversimplified. Chimpanzees, for example, have been found to engage in object play with sticks. However, young males engage in play resembling agonistic interactions, while juvenile females interact with sticks in a “maternal” way, resembling the way human infants interact with dolls (Kahlenberg & Wrangham, 2010). To label both as object play diminishes the complexity of these behaviours. Furthermore, play categories are often combined, such as co-manipulations of an object that are both object and social play. Nevertheless, dividing play into three categories is a useful method when first describing a species’ play repertoire. To this end, in PAPER IV, we adhered to these three categories and Burghardt’s five criteria to identify and describe play in greater rheas.

5.2 Archosaurian play

All vertebrate classes, including the archosaurs, play (Burghardt, 2005). Crocodylians have been found to be surprisingly playful. All three categories of play have been described in a variety of species (Dinets, 2015). With respect to locomotor play, subadult American alligators have been observed to repeatedly slide into water (Burghardt, 2005), and a hatchling broad-snouted caiman (*Caiman latirostris*) repeatedly let itself be drifted across a pool through the current of an outflow pipe (Dinets, 2015). Accounts of social play are exclusively anecdotal, though Dinets (2015) lists personal communications and observations of behaviours indicative of chasing, play fighting, and riding on each other's backs. Object play appears to be the predominant mode of crocodylian play. A Cuban crocodile (*Crocodylus rhombifer*) has, for example, been observed pushing around a large floating ball (Burghardt, 2005), and American alligators have been seen playfully interacting with a water stream through snapping at it and moving their heads in and out of the water (Dinets, 2015).

Object play appears to generally be the predominant play category of reptiles, as described in Komodo dragons (Burghardt et al., 2002), Nile soft-shelled turtles (*Trionyx triunguis*; Burghardt et al., 1996), and sea turtles (*Caretta caretta* and *Chelonia mydas*; Mann & Mellgren, 1997). Many reptilian species are solitary for the majority of their lives, which explains the rarity of social play. Moreover, energy constraints caused by ectothermy might cause the infrequency of locomotor play. This could also explain why most of the described examples of locomotor play are predominantly passive, i.e., letting water or gravity move the body.

The other extant archosaurs – the birds – play too. Some species have even been identified as some of the most vigorous players in the animal kingdom (e.g. ravens: Ficken, 1977; Heinrich & Smolker, 1998). However, one avian group that has to date been completely overlooked in the study of play are the palaeognath birds. Though some reports suggest that palaeognaths engage in play (Franz Sauer, 1969; Bohl, 1970; Hallager, 2010; Timothy, 2019), it has never been formally studied. To partly mend this gap, in PAPER IV, we provide the first systematic study of play behaviours in a palaeognath bird, the greater rhea.

We found that juvenile rheas initiate play significantly more often than adults, which is common among animals and humans (Burghardt, 2005). In contrast to non-avian reptiles, the predominant category was locomotor play in the form of play running. Despite locomotor play being a form of solitary play, the observed play running bouts exhibited were characterized by a considerable component of sociality. The majority of play bouts were contagious, i.e., elicited play in siblings.

Moreover, during these contagious play running bouts, one third of the times, the birds did not all move in the same direction but ran into individually different directions. Osvath & Sima (2014) introduced a theoretical framework stating that if one category of play elicited a different category of play in others it is indicative of emotional contagion, i.e., a spread of a playful mood rather than behavioural synchronization. Emotional contagion is a building block of empathy as it requires the recognition and matching of emotional states (Preston & De Waal, 2002). While locomotor play in our study elicited the same category of play, the different directions suggest an involvement of processes beyond mere behavioural contagion. In the case of behavioural contagion, it would be expected that the birds all move in the same direction. Nevertheless, alternative explanations for this observation exist. Running in different directions might serve as training for anti-predatory responses through practicing unpredictable behaviours (Humphries & Driver, 1970), or might represent a form of self-handicapping (Spinka et al., 2001).

Moreover, juvenile greater rheas actively engaged in social play, though to a smaller degree as locomotor play. They pecked each other playfully, wrestled, and bumped into each other. Social play only started when the birds were around 10.5 weeks old, while locomotor play was already present at study onset around 6 weeks old. Despite this ontogenetic discrepancy, social play still developed relatively early in the rheas' ontogeny compared to the species' sexual maturity at 20 to 24 months (Sales, 2006).

Our findings about social components in the play behaviours of these birds are suggestive of the species' socio-cognition. Firstly, the presence and early ontogeny of social play indicates an important role of sociality in their lives. Indeed, greater rheas live in mixed flocks, while forming harems with one male and several females during breeding season (Sales, 2006). Consequently, it is expected that this species possesses socio-cognitive skills allowing them to navigate social group living. As shown in PAPER I, greater rheas are capable of visual perspective taking and form social predictions about their flock mates. Additionally, our observations on play suggest primitive forms of emotional contagion in these birds implying the capacity for recognition and matching of others' emotional states. Future studies on greater rheas should explicitly focus on these aspects of their social cognition to confirm our hypotheses about their cognitive capacities.

PAPER IV includes the first description of play in adult and juvenile representatives of a palaeognath species. More studies on a variety of palaeognath birds of different ecologies, such as solitary cassowaries or volant tinamous, will be needed to identify whether this is a common play pattern in this group and how it relates to the socio-cognitive capacities of different species.

5.3 Functions of play: Predictive processing

The ultimate functions of play remain unclear. The theories brought forward over the years are diverse, but many hypotheses revolve around practicing serious behaviours in the juvenile period.

Despite many attempts to test for such training effects of play, many studies have failed to empirically prove this hypothesis. For example, one study on domestic cats (*Felis silvestris catus*), that were exposed to one prey item as kittens, did not show improved predation on other prey items as adults (Caro, 1980). A different study on meerkats (*Suricata suricatta*) found no effect of play fighting in juveniles on their fighting success later in life (Sharpe, 2005).

However, it should be noted that some studies suggest an effect of play in the juvenile period on some social behaviours in adults. Blumstein and colleagues (2013), for example, found a correlation between the outcome of play fights in juveniles and later dominance relationships in yellow-bellied marmots (*Marmota flaviventris*). Maternal territorial behaviour and reproductive success of Belding's ground squirrels (*Urocitellus beldingi*) have been found to depend on juvenile social play (Nunes, 2014). Play fighting with same-sex litter mates influences reproductive success in male mouse lemurs (*Microcebus murinus*; Perret, 2021). These examples show that at least in the social domain, the so-called "practice hypothesis" has found some support. Nevertheless, no support for this hypothesis has been identified in other categories, such as object and locomotor play.

New evidence from studies on rats and hamsters suggests that play in the juvenile period positively influences the development of executive functions mediated by the prefrontal cortex (e.g. Bell et al., 2010; Baarendse et al., 2013; Burleson et al., 2016; Schneider et al., 2016; Stark & Pellis, 2020). Thus, play in the juvenile period might improve emotion regulation, attention, information tracking and decision making (Vanderschuren & Trezza, 2013; Pellis et al., 2014). This hypothesis contradicts the "practice hypothesis" of play, as it suggests that the benefits that adult animals engaging in play as juveniles experience are not caused by practice, but by improved cognitive skills.

Recently, Andersen and colleagues (2022) used a neurocognitive framework to explain the adaptive value of play, the predictive processing framework (PP). PP generally describes the brain as constantly striving to minimize the error between predictions about the environment and its actual state (Friston, 2010; Clark, 2013; Hohwy, 2013). PP can also be applied to play. Andersen and colleagues (2022) argue that when playing, agents are deliberately creating surprising situations. These situations provide players with opportunities to learn about the environment and form predictions about it. Simultaneously, play follows specific rules and constraints (Burghardt, 2005). This suggests that there is a "right" amount of surprise (the authors call it a "sweet spot") in play, that is neither too predictable, nor too chaotic. The authors moreover see an explanation for why play is perceived as pleasurable in this framework. They argue that through creating surprising situations of the "right" amount of uncertainty, agents are reducing prediction error faster than expected. This is inherently perceived as positive and thus fun. This hypothesis was backed up by AI studies that found that error reduction motivates an agent to play and explore (e.g. Oudeyer & Smith, 2016). Play can thus be interpreted as a way of niche construction where players alter their physical and social environment to generate, test and update predictions about the world.

Predictive processing is in line with the previously described internal forward models (see 4.5). Both theoretical frameworks describe top-down processes to minimize prediction errors. In play, these errors are created intentionally, which leads to fast updating of the predictions. Through play, agents can thus practice to form predictions about a variety of situations they might not have encountered naturally.

Hence, predictive processing is a neurocognitive framework that can explain play, but also applies to processes of social information gathering such as gaze following.

6 Implications for social cognition in dinosaurs

The studies in this thesis on socio-cognitive capacities in Archosauria were executed with the overarching goal of providing glimpses into the social cognition of extinct dinosaurs and thereby shedding light on principles of the evolution of social cognition.

Over the course of three empirical studies (PAPER I, III, and IV), we investigated social information gathering and perspective taking, the development of such skills and their attunement to conspecifics and play with its implications for social cognition. The final chapter will discuss what implications these findings have for the social cognition of dinosaurs.

6.1 Gaze following

In PAPER I, we compared the gaze following repertoires of five archosaur species. The findings of this study, that both alligators and all tested bird species followed gaze into the distance in combination with the wealth of studies on other amniotes capable of this skill strongly suggest that dinosaurs were at least capable of low-level gaze following.

The presence of gaze following into the distance in alligators, which represent an optimal neurocognitive model for stem archosaurs, indicate that the common ancestor of crocodylians and birds already shared this trait 325 MYA. However, the capacity to follow gaze into the distance likely emerged even earlier than this, as inferred from the shared subcortical pathway in the brains of all vertebrates mediating fast, reflexive co-orientations with observed gaze directions (for a more detailed discussion see 4.4). Experimental evidence from mammals, reptiles, and birds implies that at least all amniotes are capable of low-level gaze following. More studies on amphibians and fishes are needed to broaden this argument to all vertebrate classes. Nevertheless, it can be safely assumed that dinosaurs followed each other's gazes into the distance.

Geometrical gaze following diagnostic of level I visual perspective taking, on the other hand, was only found in birds, but not in alligators. In Chapter 4.4 we argue that this skill has likely evolved in parallel in birds and mammals but was not present in stem archosaurs. When exactly high-level gaze following skills evolved within Dinosauria is hence difficult to pinpoint. This is partly due to our lack of knowledge about brain structures mediating spatially sophisticated gaze following in birds.

Assuming from the many shared features of the brains of palaeognath birds and non-avian paravian dinosaurs, such as dromaeosaurids and troodontids (see 2.4), it is, however, likely that these dinosaurs possessed a gaze following repertoire comparable to that of palaeognath birds. That would place the evolution of such skills in the Middle Jurassic, around 174-163 MYA.

Alternatively, the evolution of the avian hyperpallium ("Wulst"), a structure central to visual and somato-sensory integration (e.g. Reiner et al., 2005; Gold et al., 2016), might have paved the way for the emergence of visual perspective taking. The timing of the evolution of this structure remains unclear. As it can be found in the brains of both palaeognaths and neognaths, it must have latest evolved before the split of these two groups around 110 MYA (e.g. Yonezawa et al., 2017). More studies on avian neuroanatomy will be needed to confirm the involvement of the hyperpallium in visual perspective taking, along with paleontological studies working on pinpointing the emergence of this structure.

Whether checking back evolved earlier or later than geometrical gaze following is at the present time unclear. It is, however, to be expected that an understanding of the referentiality of gaze is a prerequisite for visual perspective taking. If the observer did not expect to find a gaze target behind the barrier, it would not have an incentive to move around it. Indeed, in human infants, checking back develops at 8 months, and thus considerably earlier than geometrical gaze following that only emerges around 18 months (Butterworth & Cochran, 1980; Butterworth & Jarrett, 1991). PAPER I and III are the first accounts of checking back in birds, but it appears that at least in ravens, this behaviour develops, just as in humans, earlier than geometrical gaze following. In this case, checking back is expected to have evolved earlier than geometrical gaze following and the accompanying visual perspective taking skills. More studies focussing on the phylogenetic distribution, development, and complexity of checking back are needed to allow for more robust hypotheses about the evolution of this behaviour.

In mammals, visual perspective taking has only been described in some primates (apes and Old World monkeys) and canids (wolves and dogs); lineages that diverged after the end-Cretaceous extinction. This points towards an earlier evolution of such skills in Sauropsida than in Synapsida. As briefly described in PAPER I, an earlier evolution of such skills in Sauropsida would not be surprising due to the excellent visual skills of birds. Vision is a central sensory system to birds as they use it for navigation and migration, foraging, to avoid predators, and social behaviours (Shimizu & Bowers, 1999). The importance of vision is evident from birds' excellent visual acuity, colour vision, discrimination ability, and visual memory (Donovan, 1978; Hodos, 1993; Wasserman, 1995).

Many bird species are tetrachromates, i.e., they have four different types of cones in their retina. Additionally, they have coloured oil droplets that filter light before it hits the cones. This way, the number of functional spectral sensitivities could be even higher than the number of different cones (Güntürkün, 2000). In contrast, most mammals only have two types of cones, rendering most mammalian species only capable of dichromatic colour vision. Only some diurnal primates and marsupials have evolved a third cone allowing for foraging based on vision (Heesy & Ross, 2001; Arrese et al., 2002).

Birds moreover possess a fovea; some even have two. This structure contains photoreceptors enabling high visual acuity. The retina of most mammals does not contain this structure. Only some diurnal primates (tarsiers, monkeys, apes) have evolved a fovea (Bringmann et al., 2018). However, the density of ganglion cells in the avian fovea exceeds that of even the most visual mammals, such as humans and other primates (Güntürkün, 2000).

The refinement of the visual systems of primates with colour vision and fovea represent adaptations to a diurnal life, while early mammals were nocturnal and thus did not exhibit such adaptations. Simultaneously, primates have the most complex gaze following skills with visual perspective taking and checking back. These parallels suggest that a refined visual system is needed to evolve visual perspective taking skills. This offers a plausible explanation for an earlier evolution of such skills in Sauropsida.

Firstly, reliance on visual cues is more sensible in diurnal species rather than in nocturnal ones. A visual system adapted to nocturnal vision has high light sensitivity, but, as a trade-off, has a low resolution (Martin, 2017). Nocturnal species can thus not attend to as much detail in the environment as diurnal ones. Secondly, the proclivity to attend to others is higher in animals with improved visual skills, as head and eye movements are easier to detect. Lastly, the value of social information from an individual with enhanced vision is higher, as such an individual can attend to more details in the environment. An animal with poor vision cannot provide reliable information about, for example, the location of food, as it can itself not find a food source based on its vision.

Additionally, the sophistication of the primate visual system co-evolved with an increase of cerebellar neurons (Barton, 2012; Barton & Venditti, 2014), similar to the increase in avian brains (Kverková et al., 2022). This supports the connection we have earlier established between a refined gaze following repertoire and internal forward models. The improved visual skills and connected ability to extract social information likely allowed for more robust social predictions, allowing primates comparable visual socio-cognitive capacities as birds, while other mammals have not evolved such skills.

More studies on mammalian species are needed to establish the ability to generate internal forward models in this group.

6.2 Play

In PAPER IV, we found that one species of palaeognath bird, the greater rhea, plays at least in their juvenile period with a noticeable component of sociality. This was apparent in social play bouts, but also in the high rate of play contagion in locomotor play. For the sake of being able to hypothesize about extinct dinosaurs, we will in the following assume that all palaeognaths play in a comparable manner.

Play is commonly connected to parental care. Extensive postnatal parental care is widespread among the most playful species, such as humans and non-human primates, but also birds (Burghardt, 2005). Palaeognaths exhibit a relatively rare parental care system. In nearly all species, males incubate the eggs and single-handedly care for their offspring. Only in ostriches, females and males take turns in incubating the eggs – the lightly coloured females during the day, the black males during the night. After hatching, the dominant female is sometimes involved in parental care. Similarly, in kiwi, females have been observed to sometimes assist in parental care. For the rest of Palaeognathae, incubation and chick-rearing is exclusively performed by males (Valdez, 2022).

The paternal care system of palaeognath birds likely has its origins in dinosaurs. Several lines of research are supporting this hypothesis. Firstly, fossils of adult oviraptorosaurs and troodontids – both maniraptoran theropods - have been found on top of nests in brooding positions, indicating that these dinosaurs were incubating their eggs (Norell et al., 1995; Varricchio et al., 1997). Moreover, histological analyses revealed that these individuals were likely male (Varricchio et al., 2008). Female archosaurs resorb calcium and phosphorous from their skeletons during egg formation (Simkiss, 1967; Wink & Elsey, 1986). The incubating fossils, however, did not have residual medullary bone or resorption cavities, and were thus most likely male. Lastly, the clutch size of maniraptoran theropods is equivalent to that of extant species with biparental care or that of palaeognaths (Varricchio et al., 2008). Considering the above-mentioned similarities with palaeognath parental care systems, it is more plausible that these large clutch volumes are the result of several females laying their eggs into communal nests, like in some palaeognaths, such as greater rheas. It is thus likely that the parental care system observed in Palaeognathae has been retained from maniraptoran dinosaurs.

This implies that juvenile maniraptorans grew up under comparable socio-ecological circumstances as palaeognath birds, with several clutchmates and under the supervision of a male. This creates an ideal environment not only for extensive play in general, but more specifically for social play. Considering the likely presence of comparable socio-cognitive skills in these dinosaurs and palaeognath birds, it would not be surprising if juvenile maniraptorans played in a similar fashion as the juvenile greater rheas. That would entail a noticeable social component in their play, including frequent play contagion, but also social play bouts.

6.3 Evolutionary roots of predictive minds

The findings of this thesis suggest that early birds and likely non-avian paravian dinosaurs exhibited complex visual socio-cognitive skills, making them proficient social information gatherers. They moreover likely developed these skills early in their ontogeny and supported the development of executive functions through social play in the juvenile period.

What unifies these findings is the evolution of predictive power in the avian brain. We found behaviours suggestive of internal forward models and play as a means of developing predictions involved in these models. Such predictive skills were found in all tested bird species, but not alligators.

This implies an evolutionary trend towards more robust predictive processing throughout avian brain evolution. Internal forward models are suggested to be governed by the cerebellum. Avian brains have dramatically increased numbers of neurons in this brain structure compared to crocodylians. This implies that this increase and consequently the emergence of predictive processing capacities took place somewhere within Dinosauria. It is difficult to pinpoint this evolutionary step exactly, but due to at least non-avian paravian dinosaurs likely being endothermic (e.g. Rezende et al., 2020) and increases in neuronal numbers being closely related to endothermy (Kverková et al., 2022), it is possible that the brains of non-avian paravian dinosaurs already had increased numbers of cerebellar neurons.

However, predictive processing is beneficial to many different species and is most likely not an exceptional cognitive capacity only found in cognitively advanced animals. On the contrary, complex predictive processing, such as planning, most likely evolved progressively from simpler error correction circuits, such as the release of a hormone in response to the detection of a certain physiological state like hunger. These circuits likely evolved very early in the evolution of brains and cognition as they are imperative to the survival of an animal. Throughout evolutionary time, predictions and error corrections likely became more complex, allowing animals to apply predictive processing not only to physiological processes, but also to their physical and social environment (Pezzulo et al., 2021).

The gradual improvement of predictive processing underlies genetic constraints, as well as the selective forces of new challenges animals are facing. Such challenges could for example be more complex bodies and ecological niches. Arguably, one big step towards such new situations including novel environmental challenges was when vertebrates became land dwellers around 365 MYA.

A common theme in the evolution of more complex predictive models, such as internal forward models, is the duplication of simpler error correction circuits building multiple, parallel sensorimotor loops. This means that predictive models consist of several smaller models that are specialized in particular behaviours. Early brains might hence have possessed multiple, replicated sensorimotor circuits (Pezzulo et al., 2021).

This pattern can still be recognized in the ganglia-thalamocortical circuits of modern brains, as well as in the parallel loops of the cerebellum. This evolutionary remnant further strengthens our argument about the involvement of the cerebellum in the formation of internal forward models. The drastic increase in cerebellar neurons of birds and possibly already non-avian paravian dinosaurs might be diagnostic of an evolutionary step towards higher predictive power within this lineage. More studies are needed to compare the evolution of predictive brains in mammals and birds to identify evolutionary trends and their remains in modern brains. Higher predictive power could be one of the reasons why dinosaurs were successful for such a long time and why some of their living descendants are among the cleverest animals on this planet.

In the light of principles of cognitive evolution, an evolutionary trend towards increased predictive power and error reduction appears to be a more sensible driver for cognitive evolution than social group living as proposed by the social intelligence hypothesis. Animals undoubtedly face complex challenges when living in social groups. However, these challenges can be, like other uncertainties in the environment, be solved through constantly striving for a minimization of prediction error. The findings of this thesis support predictive processing as a possible underlying principle of cognitive evolution, as it explains various factors investigated in this work, such as social information gathering and play.

7 Concluding remarks

This thesis represents some of the first attempts at studying dinosaur cognition. When drawing inferences about non-fossilizing traits of extinct species, one must be cautious. In this thesis, we phylogenetically bracketed dinosaurian cognition as closely as possible by studying aspects of the social cognition of extant archosaurs.

Even though the species chosen for this thesis are the best neurocognitive models of non-avian paravian dinosaurs that we have, they are still only that: a model - although a true and living one. Future studies will need to compare a wider range of palaeognath and crocodylian species to establish whether the skills and behaviours described in this thesis are shared among members of their respective clade.

Simultaneously, we drew many parallels to mammals and their evolutionary trajectories. It is thus just as important to study these topics more deeply in mammals. This would aid in manifesting the notion that primates are distinct from other species in their cognitive skillset. Secondly, the study of neurocognitive models of ancestral species, such as marsupials and monotremes, would serve a similar purpose as studying palaeognath birds and crocodylians – to obtain an understanding of ancestral cognitive capacities within a group. In fact, they would even yield stronger results compared to our studies, as we used crocodylians as a model for the earliest ancestors of dinosaurs, though they are members of a sister-taxon. Marsupials and monotremes are both mammalian taxa and are thus even better neurocognitive models for ancestral mammals.

Finally, I would like to propose that more studies focus on connecting their findings to neurocognitive measures, such as neuronal numbers. By using this method, it is possible to uncover evolutionary steps enabling cognitive capacities and draw parallels to other lineages.

We are only at the beginning of the quest of shedding light on the evolution of cognition. By joining forces with neuroscientists, palaeontologists, and developmental psychologists, we have a good chance at solving the puzzle of cognitive evolution.

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This thesis concerns the evolution of social cognition in Archosauria, an animal group that - besides the extant crocodylians and birds - includes the extinct non-avian dinosaurs. Through studying aspects of the social cognition of extant archosaurs, it is possible to draw inferences on the socio-cognitive capacities of extinct dinosaurs. This thesis investigates gaze following and play in five avian and one crocodylian species. The findings are subsequently used to hypothesize about the origins of these skills in non-avian dinosaurs as well as principles of cognitive evolution.

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