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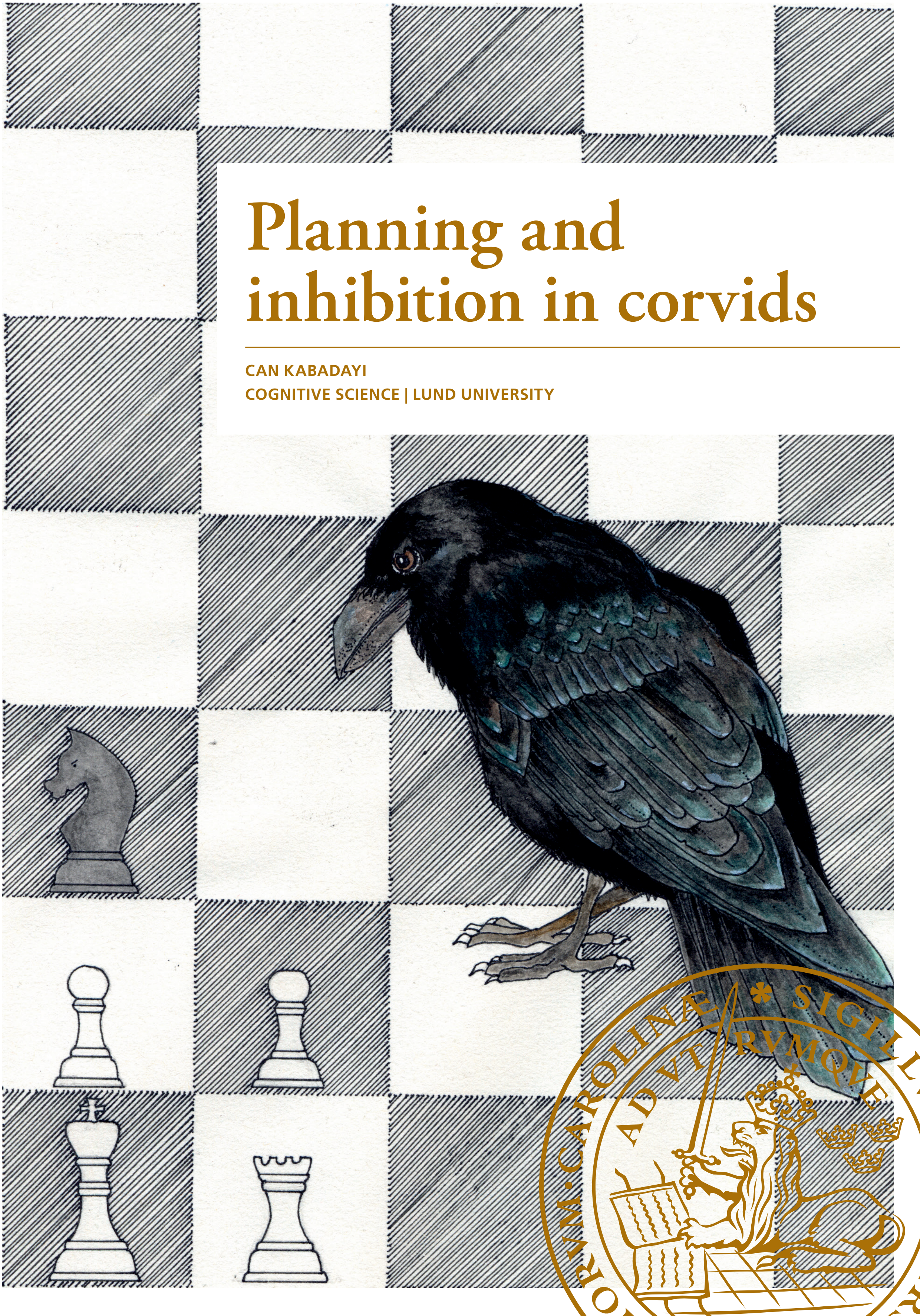

Planning and inhibition in corvids

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Abstract

Executive functions (EF) denote the host of top-down mental processes that mediate self-regulation to achieve a goal. Among other things, EF support cognitive flexibility by allowing inhibition of automatic responses in favour of obtaining future goals. Corvids, the bird group that is comprised of ravens, crows and jays, are distinguished by their cognitive flexibility. This thesis investigates two components of EF – planning and inhibition – in corvids, in an attempt to understand the evolution of complex cognitive abilities.

Planning is a cognitive ability that is at the core of human society. Human planning is flexible and domain-general: we can plan across different contexts, for example when planning to go to the moon or when planning to organize a party. It was long considered that flexible planning skills were restricted to the great ape lineage. Previous studies documented corvids can plan their food caching behaviour, but since corvids are habitual food-cachers, some argued their planning skill is restricted to the caching domain and thus may not be domain-general. We tested whether corvid planning is domain-general, by testing ravens on ecologically-invalid planning tasks that did not involve caching (tool-use task and bartering task; Paper I). This study mainly replicated but also extended the previous studies on great apes. The results suggest ravens perform remarkably well – often on a par with great apes - in such planning tasks. Thus, the study suggests that corvid planning abilities are domain-general, and that flexible planning skills evolved independently in corvids and great apes, warranting future investigations on possible similarities at the level of underlying mechanisms.

Inhibitory control is a core EF component and it allows inhibiting prepotent responses in favour of more appropriate behaviour. Motor self-regulation is a basic inhibitory mechanism that allows stopping a prepotent motor response. Given it's a fundamental cognitive mechanism that is necessary for higher-order skills, investigating motor self-regulation comparatively can inform on broader aspects on cognitive evolution. We tested motor self-regulation in three species of corvids – ravens, New Caledonian crows and jackdaws –using a detour task that involved inhibiting a dominant motor tendency of directly reaching for a visible reward behind a transparent barrier (Paper II). This study replicated a previous large-scale study that tested 36 species on the same task. This large-scale study found absolute brain size was the best predictor of task performance, with great apes being the best performers. We found that corvids perform excellently on this task, on a par with great apes, despite their vastly smaller absolute brain sizes. This finding provided counter evidence for the importance of absolute brain volume in predicting the cognitive performance. Instead, given the large neural density of the corvids, it was suggested that total number of pallial neurons might be a better predictor.

We thus investigated parrots, another bird group that has a large number of pallial neurons, on the same task (Paper IV). However, parrots performed significantly worse than corvids and great apes on this task. Further analyses revealed some of their failures were caused not by inhibitory incompetency but by bodily exploration of the barrier. Such methodological issues are discussed further in Paper V, which provides a review of the detour paradigm, a widely used task in animal cognition. In this paper we review the cognitive skills measured by the detour paradigm and suggest methodological improvements to make the task meaningfully applicable to wide range of species. In Paper III, we compare motor self-regulation developmentally: we attempt to answer whether the similarity between ravens and great apes in cognitive performance by mature individuals entails similarity on their development. The results suggest raven chicks undergo a similar pattern of development when succeeding on the detour tasks to those of human and rhesus monkey infants, but at a remarkably faster rate. These findings have implications for the mechanism behind the independent evolution of complex cognition; that is, whether complex cognitive skills can be attained independently using completely different pathways. Cognitive zoology is still a relatively young field, and future studies testing more species will give a clearer picture on the proximate and ultimate factors behind the evolution of complex cognitive skills.

Key words: executive functions, corvids, evolution of cognition, planning, inhibitory control, homoplasy

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To the great raven characters that made this thesis possible

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Content

List of original papers

PAPER IA

Kabadayi, C. & Osvath, M. (2017). Ravens parallel great apes in flexible planning for tool-use and bartering. *Science*, 357, 202-204. doi: 10.1126/science.aam8138.
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http://science.sciencemag.org/content/357/6347/202

PAPER IB

Kabadayi, C. & Osvath, M. (2017). Supplementary Material: Ravens parallel great apes in flexible planning for tool-use and bartering.
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http://science.sciencemag.org/content/suppl/2017/07/12/357.6347.202.DC1

PAPER II

Kabadayi, C., Taylor, L.A., von Bayern, A.M., Osvath, M. (2016). Ravens, New Caledonian crows and jackdaws parallel great apes in motor self-regulation despite smaller brains. *Royal Society Open Science 3*:160104. doi: 10.1098/rsos.160104
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http://rsos-royalsocietypublishing.org/content/3/4/160104

PAPER III

Kabadayi, C., Jacobs, I.F., Osvath, M. (in review). The development of motor self-regulation in ravens.

PAPER IV

Kabadayi, C., Krashheninnikova, A., O'Neill, L., van de Weijer, J., Osvath, M., von Bayern, A.M.P. (in review). Are parrots poor at motor self-regulation or is the cylinder task poor at measuring it?

PAPER V

Kabadayi, C., Bobrowicz, K., Osvath, M. (in review). The detour paradigm in animal cognition.

Other papers by the author not included in the thesis

Osvath, M., Kabadayi, C., & Jacobs, I.F. (2014). Independent evolution of similar complex cognitive skills: The importance of embodied degrees of freedom. *Animal Behavior and Cognition, 1*, 249-264. doi: 10.12966/abc.08.03.2014

1. Introduction

We are creatures of habit. Often times we follow old routines, repeat learned behavioural patterns, and choose immediate gratification over delayed rewards. Changing our habits and leaving the ‘autopilot mode’ takes effort and cognitive control. Executive functions (EF) refer to the cluster of top-down processes that mediate diverse functions ranging from overriding impulses to working memory and cognitive flexibility (Diamond, 2013). EF are required when one needs to pay attention and deliberate over choices, e.g. when you drive to your workplace for the first time, when you take a step back from your immediate situation and play out the consequences of your actions in your head before you make a move. EF therefore support complex cognitive skills like planning, reasoning and problem-solving (Collins and Koechlin, 2012). Given the fundamental role of the executive system in supporting behavioural flexibility, investigating whether and how it functions in different species can provide insights into the evolution of complex cognition.

The corvid family (*Corvidae*) represents an ideal candidate to investigate EF given its renowned behavioural flexibility. Consisting of more than 120 species, the corvid family includes ravens, crows, jackdaws, magpies, treepies, jays, nutcrackers and coughs. Corvids are widely dispersed across the globe, and live in vastly different environments, ranging from warm tropics and deserts to cold tundras and mountain tops, as well as cities. Their cognitive flexibility is the most likely causal factor behind this high level of environmental adaptability (Osvath et al. 2014).

This thesis investigates two EF components – planning and inhibition – in corvids, and in some extent parrots, in order to understand the evolution of complex cognitive skills. Previous studies that have measured these skills mostly focused on primates (Mulcahy and Call, 2006; Osvath and Osvath, 2008; Stevens, 2014). The study of corvid cognition is informative in many respects. Corvids display complex cognitive abilities in various domains such as causal reasoning, memory and social cognition, and corvid cognition is often compared to those of great apes in complexity (Emery and Clayton, 2004). Thus, expanding the comparisons between these groups can inform whether this similarity also holds in other domains. Moreover, given the vast phylogenetic separation between corvids and great apes, comparing the cognitive skills of these groups might elucidate some of the mechanisms behind independently evolved complex cognition (Osvath et al. 2014).

1.1 Structure of the thesis

This thesis is structured around two components of executive functions – planning and inhibitory control. The main body of this thesis consists of five papers, comprising four empirical studies and one review paper. In order to provide a background for those papers, three chapters precede them (Chapter 2, 3 and 4).

Chapter 2 focuses on planning and sketches a brief history of its investigation in animals, preparing the reader for the empirical study on planning skills of ravens (PAPER I). Chapter 3 focuses on motor self-regulation (motor inhibition), which is an underlying cognitive mechanism supporting more complex forms of self-control as well as planning. This chapter gives a background and the motivation for the study of motor self-regulation, which is the subject of three empirical papers in this thesis: motor self-regulation in corvids is investigated comparatively (PAPER II) and developmentally (PAPER III). In PAPER IV we studied motor self-regulation in another bird group: parrots. PAPER V is a review paper that focuses on the detour paradigm, which is a widely used test in animal cognition research for measuring motor self-regulation among other skills. Chapter 4 gives an overall account for the main findings of the papers in this thesis – that corvids perform on par with great apes in complex planning as well as in basic motor inhibition. The findings are discussed from the perspective of independent evolution of complex cognition. Special attention is given to the avian brain and the possible selective pressures behind the planning and inhibitory skills of corvids. Finally, some attention is given to the question of how cognitive skills that allow certain detachment, like planning, may be grounded in anticipatory sensorimotor processes.

1.2 On terms and concepts

Planning and inhibition are broad terms that historically referred to various different processes, thus here I will specify in which context these terms are used in this thesis.

1.2.1 Planning

Planning is an everyday term that can be broadly defined as "predetermination of a course of action aimed at achieving some goal" (Hayes-Roth and Hayes-Roth, 1979, p. 275). This broad definition involves various processes like sequential planning, for example when solving the problem of tower of Hanoi, as well as route planning (McCormack and Atance, 2011). However, in this thesis, 'planning' refers to the decision making that affect future outcomes at a different location from where the decision was made (the decision is measured through actions). Chapter 2 will introduce the history of the field that gave rise to this particular definition of planning, and its significance for research on animals.

1.2.2 Inhibitory control

Inhibitory control is a core component of executive functions and refers to wide range of processes that involve overriding and inhibiting prepotent responses, internal predispositions or external enticement in order to generate an appropriate response. Potent inhibitory control allows one to not become a slave to one's impulses as it allows one to set aside automatic responses and instead consider alternative options, thus generating behavioural flexibility (Diamond, 2013; Mischel, 2014). As inhibitory control is studied in all empirical papers in this thesis (PAPER I, II, III, IV), I will briefly explain how it is measured behaviourally.

Inhibitory control is measured behaviourally using diverse tasks ranging from delay-of-gratification, which involves inhibiting taking a smaller reward in favour of obtaining a future larger reward, to motor inhibition tasks which involve hindering a motor response (Cohen et al. 2013; Bari and Robbins, 2013). There is still an ongoing debate whether delay-of-gratification and motor inhibition tasks are neurologically dissociable (Duckworth and Kern, 2011; Muraven and Baumeister, 2000). Some have suggested that inhibitory control is a non-unitary phenomenon not subserved by a single neural network (Jahanshahi et al. 2015). Thus, caution is still needed when classifying inhibitory skills in a single category, such as self-control and motor inhibition (Friedman and Miyake, 2004).

Beran (2015) suggested using the term 'self-control' for tasks where there is a decision between two options which are separated in time: an immediate but a smaller reward and a larger but later reward. Thus, delay-of-gratification tasks are self-control tasks. He suggests using the term 'motoric self-regulation' for those behavioural inhibition tasks that involve inhibiting a prepotent motor response without incurring a major cost (Bari and Robbins, 2013). The papers in this thesis follow Beran's distinction. This distinction is consistent with previous research, where the term self-control has primarily been used for delay-of-gratification contexts (Ainslie, 1974; Mazur and Logue, 1978; Vanderveldt, 2016). Thus, in PAPER I in this thesis, self-control is studied as it involves delay-of-gratification experiments, while motor self-regulation is investigated in PAPER II, PAPER III and PAPER IV.

1.3 Independent evolution of complex cognition

In the biological world, we see that many similar traits have evolved multiple times independently in different lineages, such as the camera eye, echolocation, warm bloodedness, flight, myelin and perhaps even neurons (Conway Morris, 2003; Moroz, 2015). What about intelligence? Can it too evolve multiple times? This question was answered negatively by Stephen Jay Gould (1990), who famously claimed that a replay of life on earth would lead to completely different outcomes than we see today – due to various contingent historical events – with no guarantee of intelligence evolving again. It is worth noting that around the time Gould articulated this idea, which is also called 'the radical contingency hypothesis' (Powell and Mariscal, 2015), humans were considered to be the only intelligent species on earth (at least by palaeontologists) – perhaps leading Gould to perceive intelligence as an extremely rare natural phenomenon, almost as an evolutionary accident (Conway Morris and Gould, 1998).

Radically opposed to Gould's view, Conway Morris (2003) claims that convergence is ubiquitous in evolution and that there are many different paths that all might lead to a few similar end points. This suggests a certain degree of independence from the initial conditions: regardless of the starting position, evolution will eventually reach similar adaptive peaks. According to this view, the power of natural selection in finding good tricks, such as complex cognition, is so powerful that, given enough time, human-like intelligence is highly likely to evolve no matter what the initial conditions are.

These diverging views on independent evolution have implications for how to understand the place of the human mind. One way to test these views is through careful investigation of cognitive similarities in distantly related taxa. This thesis provides some approaches to these questions, as we found that corvids display remarkable behavioural similarities to great apes in tasks that require skills of flexible planning and motor self-regulation (PAPER I and PAPER II). Given that the lineages leading to corvids and great apes separated around 320 million years ago, these similarities likely are not inherited from the common ancestor in their current forms (homology), but rather a result of independent evolution (homoplasy). Understanding the principles of independently evolved cognitive abilities can shed light on underlying principles of complex cognition. Chapter 4 examines these issues in greater detail. Special attention is given to the possible selective pressures behind complex cognition, as well as to the neuroanatomical parallels between birds and mammals.

2. Planning

We humans represent events that will take place at a different place and time, and we make decisions about future situations. We can use this skill-set across domains: planning for a dinner party or a future career. What is the evolutionary history of such flexible planning skills? Can other animals plan flexibly? These questions are among the most disputed questions in the field of animal behaviour.

Many animals exhibit future-oriented behaviour such as migration, nest building and food caching. But such behaviours rarely qualify as genuine examples of cognitive foresight. A future-oriented behaviour does not necessarily entail a planning agent. Hard-wired adaptations for nest building and migrating allow animals to achieve future benefits without planning (Raby and Clayton, 2009). Where should we look then in order to find out whether animals can make intentional decisions for delayed outcomes? As animals lack language to communicate about their future intentions, one needs behavioural tests to answer this question.

2.1 Köhler’s proposal

The base of the behavioural criterion of planning used in this thesis, dates back to the proposal of Wolfgang Köhler (1922), who studied problem-solving in chimpanzees. When facing a banana hanging from the ceiling, Köhler’s chimpanzees stacked boxes on top of each other to reach it. But the means (boxes) to secure the solution and the goal were always simultaneously perceptually available to the chimpanzees. Köhler concluded that chimpanzees can plan for such immediate situations, but that it remained to be tested whether they could plan for a goal which is outside their sensory scope. He formulated a planning experiment that he never conducted. First leave a hungry ape in a room full of boxes, with no access to food. Later, give the same hungry animal access to another room which contains food hanging from the ceiling, however without access to the first room that contained boxes. This procedure should be repeated few times. Köhler was interested in whether the ape would eventually make the connection, and secure the means ahead of facing the problem, and bring boxes to the banana room. According to Köhler, this experimental design would detect planning abilities. He also argued that it would be an even higher achievement if the animal could override smaller immediate reward in order to secure the means for a future larger reward, thus hinting at the role of executive functions in planning. More than 80 years after Köhler's initial proposal, the first experimental planning studies were conducted. I will briefly recapitulate the theoretical framework of these studies.

2.2 Memory research

The theoretical roots of the experimental studies on animal planning are found in memory research. Tulving (1972) made a distinction between two types of memory systems that together comprise declarative memory: episodic and semantic memory. While semantic memories can be defined as general 'knowledge about the world', episodic memories refer to recollections of specific episodes in one's personal past. Broadly, the semantic and episodic distinction can be thought of as a knowing/remembering distinction. According to Tulving (1972, p. 385), "… episodic memory receives and stores information about temporally dated episodes or events, and temporal-spatial relations among these events". This definition of episodic memory focuses on its information content (what happened, where did it happen, when did it happen?). Later definitions included a phenomenological distinction between episodic and semantic memory. Tulving (1983) claimed that these memory systems were accompanied with different forms of consciousness: episodic memory is associated with autonoetic (self-knowing) consciousness, i.e. the experienced first-person perspective of the recalled event. This consciousness creates the feeling of that the event belongs to one's own past and it enables re-experiencing and pre-experiencing episodes. Suddendorf and Corballis (1997) introduced the term 'mental time travel' to describe this ability to travel to one's personal past or future and re- or pre-experience events. Semantic memories, on the other hand, come with noetic (knowing) consciousness that refers to the feeling of familiarity without any personal reference.

Memories are essential for planning. Since the future does not yet exist, it cannot have a causal influence on current actions; instead, past causes leave various traces in cognition, such as memories that may lead to actions which influence future outcomes (Osvath and Martin-Ordas, 2014). This close relationship between memory and foresight has been identified before (e.g. Ingvar, 1979, 1985). Many have argued that the functional and evolutionary benefit of memories is that they allow preparation for the future (Klein, 2013; Michaelian, 2016; Suddendorf and Corballis, 2007; Tulving, 2005). One can either be guided by a particular memory of a situation, which get cued in certain settings, or one can simulate new events by combining elements of different memories. In fact, episodic memories are never carbon copies of what happened in the past, but labile and constructive, which provides adaptive benefits as the gist information and the recombination of those memories enable novel future simulations (Schacter and Addis, 2007).

The link between memory and foresight has also been documented in patients suffering from amnesia. Tulving worked with a patient called K.C. who suffered a severe form of retro- and anterograde amnesia (due to a brain trauma), with a degenerated the episodic system but an intact semantic system. K.C. could not recall a single episode of his life, and he was also unable to imagine a personal future scenario. He described the subjective state as 'blank' when attempting to remember or imagine personal situations. The failures of the episodic memories where strongly correlated with failures in episodic foresight. Consistently, later studies in humans have found a large overlap between the brain regions supporting episodic memory and future-thinking (Addis et al. 2007; Buckner, 2010; Hassabis and Maguire, 2007; Schacter et al. 2012; Szpunar et al. 2014). Developmental studies in humans have also found that episodic memory and episodic foresight abilities develop around the same age (Atance and Meltzoff, 2005; Atance and O'Neill, 2001; Atance and Sommerville, 2014; Busby and Suddendorf, 2005; Payne et al. 2015; Scarf et al. 2013).

Tulving (1983, 2002) claimed that semantic memories exist in non-human animals, but that episodic memories do not. Since true mental time travel is considered episodic in nature, and as animals were considered to lack episodic memories, it was concluded that animals can not engage in mental time travel, including flexible planning (Suddendorf and Corballis, 1997). These views gained support from the then-dominant view that animals are highly impulsive and hence stuck in time (Roberts, 2002). However, such conclusions were made before any actual experiments targeting animal planning had been conducted. The lack of evidence, mostly based on anectodes and field reports, was posited to be the evidence for absence (Suddendorf, 1994).

Early research on mental time travel in animals focused on episodic memories. These studies formulated behavioural criteria for episodic memories which, following Tulving's first definition (1972), stressed the flexible integration of *what-where-when* components of an event in a memory (Clayton and Dickinson, 1998). Tulving's later definition of episodic memories (1983), which involved autonoetic consciousness, was not used because it is empirically difficult, if not impossible, to determine whether animals have autonoetic consciousness. Hence, defining episodic memory with autonoesis made it problematic to conclude whether animals have episodic memories (Clayton et al. 2001; 2003). Instead, the term was replaced by 'episodic-like memory', which fulfilled the *what-where-when* criterion but bypassed addressing autonoetic consciousness (Clayton and Dickinson, 1998).

However, some claimed that a demonstration of what-where-when memory is not sufficient to demonstrate episodic (-like) memory because semantic memory can also store what, where and when information of a past event (Suddendorf and Busby, 2003). For example, I can semantically know the place and time of my own birth, without episodically remembering it. Suddendorf and Busby (2003) thus suggested replacing the term 'episodic- like memory' with 'www-memory' (what-where-when memory). WWW-memories have been demonstrated in many species, ranging from birds, rodents and primates to cephalopods and insects (Babb and Crystal, 2006; Dere et al. 2006; Eacott and Easton, 2010; Eichenbaum et al. 2005; Feeney et al. 2009; Hampton et al. 2005; Jozet-Alves et al. 2013; Martin-Ordas et al. 2010; Meyers- Manor et al. 2014; Menzel, 2005; Pahl et al. 2007; Schwartz et al. 2005; Zentall et al. 2001; Zinkivskay et al. 2009).

The demonstrations of www- memories in animals were not viewed as decisive evidence of animals engaging in mental time travel, because they failed to show autonoetic consciousness, and, as mentioned above, they do not behaviourally distinguish between episodic and semantic memory (Suddendorf and Busby, 2003; Tulving, 2002). Tulving (2005) suggested that this problem becomes tractable through planning tests, if one accepts that autonoetic consciousness and mental time travel involve not only the past but also the future.

2.3 Episodic foresight and the 'spoon test'

The human uniqueness hypothesis initially focused on our ability to prepare for future motivational states, independent from our current motivational states. In a nutshell, the argument can be exemplified as this: while a recently fed non-human predator pose no danger to its prey, a recently fed human might, because only humans can foresee that they will be hungry tomorrow and thus they can act now to satisfy those future needs (Suddendorf, 1994). Suddendorf and Corballis (1997) formulated this idea in so-called the Bischof-Köhler hypothesis, which states only humans can flexibly anticipate their future states of need and act now to secure them. Ever since it's formulation, the Bischof-Köhler hypothesis (henceforth the BK-hypothesis) has led to various controversies such as whether it has been falsified in certain animal studies, whether humans can make decisions truly unaffected by their current needs, or whether the hypothesis rather tap into the semantic instead of the episodic system (Naqshbandi and Roberts, 2006; Osvath and Martin-Ordas, 2014; Raby et al. 2007). The hypothesis is notoriously difficult to interpret in precise motivational and cognitive mechanisms (Osvath, 2016).

Devising non-linguistic planning tests thus became critical for testing the BK-hypothesis. Suddendorf (1994) offered one such test, which share similarities with

Köhler's original proposal as it involves two rooms; however, the critical issue was the satisfaction of a future motivational states instead of the current ones. Again, inspired by the BK-hypothesis, and again similar to Köhler's ideas, Tulving (2005) devised the 'spoon test', which was meant to measure episodic foresight and autonoetic consciousness, and to be administered non-linguistically. Tulving explains the spoon test with an Estonian child tale, in which a girl dreams of attending a party where chocolate pudding is served. Unfortunately, she cannot eat any because the pudding is served only to those who brought their own spoon. The next night the girl brings a spoon to her bed, anticipating the upcoming party that will occur in her ensuing dream. Tulving (2005) set out three requirements for the spoon test: 1) the behaviour must not be instigated by a current physiological or psychological need 2) the cues from the learning situation should be absent at the time of planning (in order to exclude non-autonoetic associative learning mechanisms) 3) the behaviour must satisfy a future motivational state.

Suddendorf and Corballis (2010) made the spoon test requirements more precise. Their new criteria involve: 1) use of single trials (to ensure the planning action is based on a memory of a specific event), 2) use of novel problems (to avoid innate response tendencies and related learning histories) 3) use of spatiotemporal separation between the planning action and its consequence (to show long-term memory) and 4) use of problems from range of domains (to avoid predispositions and to show domain flexibility).

Others have developed additional behavioural criteria, by including a self-control component to planning experiments (Osvath and Osvath, 2008). The self-control aspect approaches planning from the angle of executive functions. Solving the spoon test while also executing pronounced self-control provides a good test of deliberate future orientation. First, self-control experiments induce a competition between two qualitatively different motivations (between an immediate small reward and a later but a larger reward), and this addresses the BK-hypothesis' requirement of considering future motivational states. Second, self-control is intimately related to future orientation: it becomes hard to explain self-control without attributing the agent some sort of representation of the future, as otherwise it would always choose an immediate gratification that is perceptually present. A self-control setting also reveals whether the animal expects to get immediately rewarded by the means themselves that lead to the future reward, and thereby whether it is planning or not (it should always select the means if they are intrinsically rewarding and hence have a higher value in themselves than the small reward). As mentioned, this approach was first articulated by Köhler (1922), however it has only been used in two planning studies (Osvath and Osvath, 2008; PAPER I). As part of the planning study, these studies gave the animals a choice between an immediate food reward and an item that could be used in the future to get a larger reward. Such intertemporal choice tasks involving selections between token versus immediate food reward are highly taxing for most animals as well as for human children (Beran and Evans, 2012; Hackenberg, 2009; Judge and Essler, 2013; Lemmon and Moore, 2007; Mischel and Metzner, 1962; Thompson et al. 1997).

Ever since its formulation, the spoon test (and its variations) has become a benchmark test to measure animal planning skills. The essential idea relies on selecting and saving the 'spoon' that will only be useful in the future, in the absence of any perceptual cues emanating from the goal situation, except obviously from the spoon itself. Thus far, experimental studies on planning skills have only targeted two distinct animal groups: primates and corvids (for detailed reviews see: Osvath and Martin-Ordas, 2014; Raby and Clayton, 2009; Scarf et al. 2014; Thom and Clayton, 2016).

2.3.1 Studies on primates

Before reviewing the experimental studies, it is worth mentioning some observations from the wild and from zoo settings, that indicate planning in great apes. Field observations have suggested that wild chimpanzees flexibly plan the next morning's breakfast (Janmaat et al. 2014), and that they transport tools to be used for out of sight food resources (Boesch and Boesch, 1984; Goodall, 1964; Sanz and Morgan, 2009). Wild orangutans appear to communicate the next day's travel directions to conspecifics by long calls (van Schaik et al. 2013). A male chimpanzee in a zoo in Sweden was observed piling stones near the visitors area – hours before the arrival of the visitors – and later throwing the stones at the visitors when they appear, which indicated a dissociation between (expressed) emotional states (Osvath, 2009). Later, more controlled observations suggested that this chimpanzee also planned for deception. The chimpanzee hid projectiles out of sight from the visitors, by placing them under self-manufactured concealments, thus catching the visitors unprepared (Osvath and Karvonen, 2012).

Experimental studies on primates have used tasks from two different domains: tool-use and bartering with humans. While the studies slightly differed in methodology, they all tested whether animals can secure the means ahead of time to solve a future problem at a different location (See PAPER IB for comparisons and results). In the tool-use tasks, great apes were generally successful (Dufour and Sterck, 2008; Mulcahy and Call, 2006; Osvath and Osvath, 2008); however long-tailed macaques failed (Dekleva et al. 2012). In the bartering tasks, there was large a variation in the performances of the great apes, and chimpanzees performed the poorest (Bourjade et al. 2014; Dufour and Sterck, 2008; but see Osvath and Persson, 2013). In fact, the poor performance of the chimpanzees seen in the first bartering study (Dufour and Sterck, 2008) led to the idea that their planning skills are domain-specific

(Suddendorf and Corballis, 2010). However, a later study showed that chimpanzees can successfully plan for a bartering event (Osvath and Persson, 2013), while a more recent study again found chimpanzees performed markedly poorly in bartering tasks compared to other great apes (Bourjade et al. 2014). Tonkean macaques and brown capuchins also mostly failed in the bartering tasks (Bourjade et al. 2012).

It is worth noting that the long-tailed macaques who failed in these planning tasks readily solve the problem when the means and the goal are within their sensory scope (Dekleva et al. 2012). However, inducing a spatiotemporal separation between the means and the problem creates difficulties. Solving such tasks requires a host of skills that must be coordinated, such as mental representation of a spatiotemporally detached events, inhibition, and some sort of means-end-reasoning, to mention a few. Children pass similar tests, although not including self-control settings, only around the age of four, coinciding with certain maturation of the episodic memory system and inhibitory skills (Atance and Sommerville, 2014; Redshaw and Suddendorf, 2013; Russell et al. 2010; Suddendorf et al. 2011).

2.3.2 Studies on corvids

There are few studies to date (before PAPER I) on corvid planning skills (Cheke and Clayton, 2012; Correia et al. 2007; Raby et al. 2007). All studies aimed to test the BK-hypothesis by investigating whether the birds could act in the present to satisfy future motivational states. The experiments made use of the food-caching behaviour typical to most corvid species. One study suggested that scrub-jays (*Aphelocoma californica*) planned for the next morning's breakfast when caching the previous evening: the birds cached significantly more food in a room where they received no breakfast for six consecutive mornings compared to another room where they received breakfast (Raby et al. 2007). The behaviour of the birds was also sensitive to what type of food that would be lacking at a specific place the next morning. Later studies extended these findings and suggested that scrub-jays and Eurasian jays (*Garrulus glandarius*) can dissociate their current motivational state from future motivational states, i.e. they arrange their caching behaviour to satisfy their future needs independently from their current needs (Cheke and Clayton, 2012; Correia et al. 2007).

Although these studies seemed to falsify the BK-hypothesis, they were criticized on other grounds. One recurrent objection questioned the domain generality of the corvid planning ability (Premack, 2007; Shettleworth, 2010; Suddendorf and Corballis, 2008, 2010). Planning skills of humans are domain-general. We can plan for various contexts, such as when shopping for the weekend's party or when preparing to go to the moon. The corvid studies all tested the birds within the caching domain. Since these corvids are habitual food cachers, their planning abilities might be limited to caching contexts and might thus reflect species-specific predispositions. Suddendorf and Corballis (2008) argued that jays might have evolved ways to bridge the long-term effects of their caches – akin to the taste aversion phenomenon in rats (Garcia et al. 1966). However, they argued this ability might manifest only within the restricted domain of caching and may not apply across contexts. Suddendorf (1994) called such domain-specific cognitive feats 'laser-beam cognition', a term first used by Cheney and Seyfarth (1990). Thus, there was a need for investigating whether corvid planning also apply to non-caching domains, and this question was addressed in PAPER I.

2.4 Domain-general planning in ravens

We investigated whether the planning skills of some corvids are domain-general, by testing ravens (*Corvus corax*) in non-caching domains in series of four experiments, using two conditions in each that were selected for their ecological invalidity: a tool-use task and a bartering task (PAPER I). Since ravens do not use tools in the wild or engage in bartering with humans, successful performance cannot be explained by species-specific predispositions. And importantly, using these tasks also allowed us to compare the performances of the ravens with those of primates, who, as mentioned above, have been tested in tool-use and bartering tasks. Our study mainly replicated, but also extended, the studies on primates. We met all criteria by Suddendorf and Corballis (2010): we investigated the first trial performances separately, we used novel problems, we inserted spatiotemporal separation between the means and the problem, and we used two tasks from different domains. In addition, one experiment (Experiment 2) extended the waiting duration from 15 minutes to 17 hours, replicating a previous study on great apes (Mulcahy and Call, 2006). A self-control experiment was conducted (Experiment 3) by offering the ravens a selection between an immediate reward and the tool/bartering token that could be used to obtain a larger reward in the future. Experiment 4 extended beyond the primate studies. It was again a self-control experiment, but this time the future problem was much closer in time and space compared to Experiment 3. It tested whether ravens would take into account this temporal and spatial distance when making their decisions, i.e. whether the value of the tool in relation to the immediate food item would differ with this distance. Such temporal sensitivity indicate that the decisions are made for non-arbitrary futures, and that the functional item is not carrying an intrinsic value only.

In the tool-use condition, the ravens matched the great apes' performance (Dufour and Sterck, 2008; Mulcahy and Call, 2006; Osvath and Osvath, 2008) despite lacking predispositions for tool use. In the bartering condition, the ravens performed better than the great apes (Bourjade et al. 2014; Dufour and Sterck, 2008; Osvath and Persson, 2013; PAPER 1B). The ravens also displayed pronounced self-control abilities by significantly often resisting an immediate reward to obtain a larger reward in the future, again matching performances of great apes in a previous study (Osvath and Osvath, 2008). We also found that ravens ascribed a higher value to the functional item, in relation to the immediate food reward, when the future problem was closer in time. This shows a temporal sensitivity behind their decisions, and suggest that the functional tool was not selected 'blindly', i.e. through implicit associative learning processes (Jenkins and Moore, 1973; Shanks, 2010). Thus, when considering all four experiments together, we concluded that the corvids possess flexible planning skills that are not restricted to the caching domain, and which have so far only been documented in few great ape species (Bourjade et al. 2014; Dufour and Sterck, 2008; Mulcahy and Call, 2006; Osvath and Osvath, 2008; Osvath and Persson, 2013).

It's worth mentioning that our study documented the similarity between raven and great ape planning on a behavioural/functional level, and that more studies are needed to tease apart whether the cognitive mechanisms are equally similar as well. The episodic system seems to be required to solve similar planning tasks in humans, and when chimpanzees and orangutans were successful in such an experiment (Osvath and Osvath, 2008), it was parsimonious to suggest that they also use an episodic system, given their close phylogenetic proximity to humans. When it comes to ravens, we cannot yet assume that they use memory systems identical to great apes, given the vast phylogenetic separation between these lineages. However, we can probably conclude that ravens rely on long-term declarative memories to solve such tasks.

2.5 Future directions

The intense emphasis on human uniqueness and autonoetic consciousness might steer the research away from investigating the evolutionary conserved cognitive mechanisms supporting prospection (Osvath, 2016; Osvath and Martin-Ordas, 2014; Raby and Clayton, 2009). Attempting to find what makes us humans cognitively unique is of course interesting, however it risks unwarranted dichotomies that ignore biological continuity. Instead, we should focus on the cognitive mechanisms underlying prospection from a broader biological perspective (Osvath, 2016).

Similarly, we should question the criteria that were set to reflect human uniqueness. Take the '*future need'* requirement – the backbone of the BK-hypothesis. It's not at all clear what is meant with terms such as 'current motivational states' and 'future needs' (Osvath, 2016; Thom and Clayton, 2016). There are good grounds to suggest that many future decisions are based on current motivational states, or current motivational states that arise from “memories” of the future (Boyer, 2008; Gilbert and Wilson, 2007). This relates to the issue of complete contextual detachment – the assertion that human mental time travel can go above and beyond the cues in the environment (Suddendorf and Corballis, 2007). One should also question whether such detachment is possible, given the importance of the environmental cues in evoking episodic memories (Matute et al. 2011; Nairne, 2002; Osvath, 2016).

Consequently, studying the cuing mechanisms behind memory retrieval and subsequent planning action is a promising avenue for understanding the mechanisms behind animal prospection (Osvath and Martin-Ordas, 2014). For example, chimpanzees and orangutans seem to remember specific events that took place three years ago given specific cues in the environment, and use those memories in a simple planning task involving tool-use (Martin-Ordas et al. 2013). The results strongly suggest that the memory is cued by a certain setup, which leads to an intentional action ‘towards’ the memory (Klein, 2013; Underwood et al. 2015). In our raven experiment (PAPER I), a similar cuing mechanism might have been in play, for example the presentation of the items on selection board might have constituted a cue that evoked a memory about a specific task. One can also argue that the cuing evoked memories not only about the specific task but also the whole situation, including the waiting interval between the selection and the future event. This could partly explain the temporal sensitivity behind the ravens’ decisions. Currently these are so far qualified speculations that need controlled experiments for verification. However, they are empirically testable and this gives better prospects for the prospection research on animals compared to the requirement for autonoesis (Osvath, 2016).

Similarly, one should also avoid a strict dichotomy between episodic and semantic memory and pay attention to the intimate link between these memory systems in supporting planning (Irish, 2012; Irish and Piguet, 2013; Kwan et al. 2012; Schacter et al. 2012). Recently, Szpunar and colleagues offered a working taxonomy for the broad concept of prospection, with a focus on four modes of future thinking (simulation, prediction, intention and planning) ranging through the episodic-semantic memory continuum (Szpunar et al. 2014). Although this taxonomy mainly focuses on humans, where strict non-linguistic behavioural criteria is not needed, it appears as the ravens’ performances in our study fit at least with ‘episodic intention’, which Szpunar et al. (2014) define as “setting a goal in relation to a specific autobiographical future event”. The ravens’ behaviours do not fit very well with the semantic end of this spectrum as the animals must form a specific link between the tool/token and the future task in order to be successful. Nonetheless, the proposal of such an organizational framework on mental time travel is promising in distinguishing between different forms of future thinking and inspiring a dialogue between different disciplines studying prospection (Szpunar et al. 2014).

3. Motor self-regulation

Investigating the evolution of cognition is challenging (MacLean et al. 2012). Ever since Tinbergen's formulation of the four questions (1963), comparative psychologists acknowledge that a trait can be analysed on four different levels: ontogeny (how it develops), causal mechanisms (e.g. how it is instantiated in the brain), function/adaptation (how it impacts reproduction/survival) and phylogeny (its evolutionary history). In order to gain a full understanding of the evolution of any trait, all these four questions must be answered (Shettleworth, 2010). When it comes to the evolution of cognition, the last two questions (function and phylogeny) are the most challenging to address because they require large-scale comparative research (MacLean et al. 2012). Importantly, what is often lacking is a robust quantification of the targeted cognitive skill together with valid and reliable tests that can be applied to wide range of species (MacLean et al. 2012). Instead, previous research on cognitive evolution has largely relied on proxies for cognition such as various brain size measures (Deaner et al. 2007; Dunbar, 1998).

Inhibitory control is a fundamental cognitive mechanism that is necessary for many higher cognitive skills such as planning. Thus, its comparative investigation can shed light on aspects of cognitive evolution, such as whether well-developed inhibition correlates with complex cognitive skills as well as with neural and ecological factors (MacLean et al. 2014). It is only recently that comparative studies have begun to address the evolution of inhibitory control (Amici et al. 2008; MacLean et al. 2014; Vlamings et al. 2010). Since cognition cannot be directly observed but only inferred from behaviour, comparative zoologists must find robust ways to quantify the cognitive skill in question, and use cognitive tests that can be applied to a wide range of species (MacLean et al. 2012). When it comes to inhibitory control, it's precisely the absence of a certain (impulsive) behaviour that implies potent inhibition.

Large-scale comparisons mostly adopted inhibition tasks that required overriding a strong motor tendency to select a more appropriate response (motor self-regulation). Detour tasks around transparent barriers have become benchmark tasks to yield large comparative data on motor self-regulation (MacLean et al. 2014; Vlamings et al. 2010).

3.1 Detour tasks and motor self-regulation

When an animal faces a reward, a direct reach for it is often a natural motor response. What happens when you introduce a transparent barrier between the animal and the reward? Then the animal has to inhibit the prepotent motor response of directly reaching for the reward and instead take a detour around the barrier. The visible reward exerts a strong perceptual pull for a direct reach, and inhibiting this pull and taking a detour is often difficult for animals, including human children (Diamond, 1990; Köhler, 1927; Vallortigara and Regolin, 2002). This need of inhibiting strong motor impulses makes detour tasks promising candidates to study motor self-regulation (PAPER V).

Over the years, detour tasks have taken many shapes and forms, and recently they were simplified in order to be aptly administered to many different species in comparative research (MacLean et al. 2014). One detour task – the cylinder task – appeared to be simple and suitable for such studies (Bray et al. 2014). The cylinder task involves a transparent cylinder that has openings on its ends. The reward is placed at the centre of the cylinder and the animal has to inhibit the prepotent tendency of directly reaching for the reward, thus bumping into the barrier, and instead reach for the reward through the open end of the cylinder. Before being tested on the cylinder task, subjects are trained on an opaque cylinder, where they learn to retrieve the reward from inside the cylinder by a detour. Failures in the transparent cylinder task may thus not be explained by lack of task knowledge, but of inhibition.

Recently, the cylinder task was one of the tests used in a large-scale comparative study that investigated the evolution of motor self-regulation (MacLean et al. 2014). This study comprised 36 different species (29 mammal and seven bird species) on two motor self-regulation tasks. The results were correlated with various neurological (e.g. absolute and relative brain size) and ecological (e.g. social group size and dietary breadth) factors in order to find possible proximate and ultimate mechanisms behind inhibitory control. The study found that in the cylinder task, the great apes were the most successful of all tested animals, and that absolute brain size was the best predictor of the task performance. The authors then suggested that bigger brains offer a cognitive advantage, potentially because they allow a greater number of neurons.

The effort of MacLean and colleagues should be applauded as they managed to obtain an unprecedented amount of comparative data from 567 animals and 36 species, which is a good approach for looking at the arguably two most difficult aspects of Tinbergen's level of analysis: phylogeny and function. However, the tested species in this study were mostly mammals, and in particular primates, whereas avian species were underrepresented. Out of seven bird species tested in

MacLean et al. (2014), two belonged to corvid family (Eurasian jays and scrub-jays), however, there were no species from the *Corvus* genus. *Corvus* species are known for their complex cognitive abilities (Bird and Emery, 2009; Güntürkün and Bugnyar, 2016). When it comes to self-control, they also demonstrate well-developed delay-of-gratification skills (Dufour et al. 2012; Hillemann et al. 2014). We thus tested three *Corvus* species (ravens, New Caledonian crows and jackdaws) in the cylinder task, and found that all three species performed similar to the great apes in the replicated study (PAPER II, MacLean et al. 2014). These results suggested that the absolute brain size may not be a good predictor for motor self-regulation when comparing different taxa such as birds and mammals (Chapell, 2016; PAPER IV).

3.2 Development of motor self-regulation

Comparative developmental studies seek to understand how various cognitive mechanisms come together in different lineages to build adaptive systems (Gomez, 2005; Rosati et al. 2014). Since cognition is not created *de novo* but develops through the combination of cognitive mechanisms, understanding how and when these are combined in different species can shed light on cognitive evolution. Findings from evolutionary developmental biology suggest that many differences in mature traits between species can be traced to the changes in the pace and pattern of the developmental pathways (Gould, 2002; West-Eberhard, 2003). For example, comparative developmental studies have revealed various differences in developmental pattern and timing (heterochrony) between great apes and humans in social and physical cognition (Herrmann et al. 2010; Wobber et al. 2010), which partly explain their cognitive differences in later life (Rosati et al. 2007, 2014).

Comparative developmental studies can also be informative when it comes to the understanding of independent evolution of complex cognition: they can answer whether cognitive skills shared in distantly related species, such as corvids and primates, also show similarity in their developmental pattern (homologous developmental pathways) (Bertossa, 2011). Is the cognitive similarity between corvids and great apes in motor self-regulation (PAPER II) paralleled in the developmental pattern? We attempted to answer this question by examining the development of motor self-regulation in ravens using three detour tasks (PAPER III). The results suggest ravens follow a developmental pattern similar to that of primates, albeit at a considerably faster rate (See Chapter 4 for an interpretation of these results from the perspective of independent evolution of complex cognition). Similar investigations on heterochrony are missing in other bird species when it comes to the motor self-regulation tasks involving detours, but I hope PAPER III will set the stage for more developmental studies on birds.

Besides the comparisons with other species, studying the development of inhibitory control is valuable in its own right as inhibitory processes are acknowledged to play a key role during cognitive development (van den Wildenberg and Crone, 2005). Immature cognition is prone to attentional and behavioural interference, and a gradual overriding of this interference is due to the development of inhibition skills (Dempster, 1992; van der Molen, 2000). Consistently, children experience big difficulties with inhibition, and they only gradually get better throughout development on various inhibitory control tasks (Davidson et al. 2006; Diamond, 1990). There is evidence that this improvement correlates with the maturation of the prefrontal cortex (Durston et al. 2002). Do birds also experience similar inhibitory problems during the juvenile period? Can parts of avian cognitive development also be linked to the maturation of inhibitory competency? These are some of the questions that can be approached by more developmental research on birds.

3.3 Parrots, inhibition and neuronal numbers

In PAPER II, we concluded that the absolute brain size cannot be a reliable predictor of the cylinder task score across birds and mammals as *Corvus* corvids had excellent scores despite having vastly smaller brains compared to great apes. Can there be a more meaningful brain measure in predicting the cognitive performance across taxa? Recently, it was shown that brains of songbirds and parrots have much higher neural densities than mammalian brains (Olkowicz et al. 2016). Same study found corvids and parrots have higher percentage of neurons located in the pallium compared to mammals and other birds. For example, ravens have a similar number of pallial neurons to capuchin monkeys, despite having a much smaller absolute brain size.

Recently, it was suggested that the number of neurons in the pallium is a better predictor of the cylinder task performance across birds and mammals than the absolute brain size (Herculano-Houzel, 2017). In this paper, the cylinder task scores of the *Corvus* species tested in our study (PAPER II) was plotted together with the other species' scores tested in the multi-species study (MacLean et al. 2014), and the pallial neural numbers roughly predicted the task performance. This hypothesis led to a prediction: other bird species that also have a large number of pallial neurons – such as parrots – should also reach high scores on the cylinder task. We thus tested four parrot species (African grey parrots, blue-headed macaws, blue-throated macaws and great green macaws) on the cylinder task (PAPER IV). However, somewhat surprisingly, parrots performed remarkably worse than *Corvus* species and great apes. We offered different explanations for this poor performance, ranging from possible differences in brain architecture to the involvement of other cognitive and non-cognitive contextual factors affecting task performances (PAPER IV).

3.4 The cylinder task: some methodological concerns

In PAPER IV, we also found that parrots displayed strong learning effects in the cylinder task as there was a significant increase in successful performance over trials. This marks a discrepancy between the cylinder task and other motor self-regulation tasks, where such rapid learning effects are largely missing (Berkman et al. 2014; Gerstadt et al. 1994; Piaget, 1954; Zelazo et al. 1996). Inhibitory problems present a knowing/acting mismatch: knowing the rules often does not lead to perfect performance as one can still act inappropriately due to an inhibitory deficit (Diamond, 2013).

Take the Piagetian test of conservation of liquid volume (Piaget, 1954). In this task, an equal volume of water is distributed into two containers respectively. One is tall and thin and the other is short and thick. The subject is then asked which container has more water. Despite *knowing* that the same amount of water is present in both containers, even 4 to 5-year old children sometimes indicate that more water is found in the tall container because the higher water level creates a perceptual pull (Diamond, 2013). The action is not consistent with the knowledge; one also needs inhibition. Other motor self-regulation tasks use a task-switching component to create a knowing/acting mismatch: on certain trials, subjects must switch their previously reinforced behaviour in response to a different stimulus (e.g. stop-signal task, go/no go task). Subjects know the rule that they need to change their response when a new stimulus arrives, however they have problems inhibiting the previously repeated action.

Potentially as a result of such dissociation between rule knowledge and action, it is rare to observe a strong learning effect in motor self-regulation tasks, thus inhibitory control is often considered as ‘hard to train’ (Killcross and Coutureau 2003). How can then the observed rapid learning curves in the cylinder task reconcile with the inhibitory requirements of this task? Can the knowing/acting mismatch weaken after repeated trials on the cylinder task? How about the species like ravens and chimpanzees that do not show any learning curves and perform well already on the first trials? These questions are discussed in PAPER V.

PAPER V is a review paper on the detour paradigm in animal cognition. It identifies some of the cognitive mechanisms involved in solving the detour problem, and critically investigates the inhibitory requirement of the detour tasks in relation to learning effects. A main conclusion from these considerations is that some species differences in the cylinder task might not only reflect differences in motor self-regulation but often also in functional generalization from the opaque cylinder to the transparent cylinder as well as the learning speed in solving the transparent cylinder task. Thus, acknowledging the potential involvement of these other cognitive mechanisms might provide a more balanced approach to comparative studies, instead of merely looking at the terminal scores over ten trials as a measure of a species inhibitory competence. Besides, these other cognitive mechanisms are meriting to study on their own behalf. For example, it was recently proposed that neuronal numbers might be a better predictor of the flexible application of rules to new situations as well as of the speed of learning, rather than the absolute cognitive skill (Güntürkün et al. 2017). With careful modifications to, and controls of, the setup (as discussed in PAPER V), the cylinder task can be a versatile tool for testing such skills along with inhibition.

One of the major challenges in phylogenetic comparative studies is to develop robust tests that reliably quantify the cognitive skill in question across a wide range of species. Thus, critical analyses of the methodology and cognitive requirements of the cylinder task may make this task more robust. For example, the current criterion of the cylinder task counts *all* touches to the barrier as an inhibition failure, even if the touch was not directed towards the reward behind the barrier. This might create a bias against those species – especially exploratory and tactile ones – that touch the barrier for other purposes than attempting to reach the reward (Noland and Rodrigues, 2012). PAPER IV analysed such error patterns in four parrot species, and found two species made many touches of the barrier that were not ‘food-directed’, suggesting that those behaviours were not inhibition failures. This relates to a general challenge in the field of comparative psychology: tasks should be adapted to the sensorimotor apparatus and the ecology of the tested species. This is a way to avoid the mistake of measuring athletic skills by testing fish, monkeys, birds and humans on climbing a tree (Macphail, 1987; de Waal, 2016).

4. Homoplasy and complex cognition

Two papers in this thesis found that corvids perform on a par with great apes: in planning (PAPER I) and motor self-regulation (PAPER II). These papers thus extend the list of cognitive skills that corvids show similarities to great apes (Emery and Clayton, 2004; Güntürkün and Bugnyar, 2016). What is the evolutionary mechanism that produces this similarity in these distantly related groups? Is this similarity due to homology (due to common ancestry), or homoplasy (due to independent evolution)? The homology explanation is not sufficient in explaining this similarity because the common ancestor of the groups – a stem amniote – likely did not have such complex cognitive skills. Therefore, we have to posit a homoplastic explanation: corvids and great apes evolved similar levels of complex cognitive abilities independent of each other. This leads to a conclusion that there might be different ways to build complex cognitive skills. Understanding the underlying principles behind such independent cognitive similarity can help us understand the building blocks of complex cognition – and its repeatability (Gould, 2002; Osvath et al. 2014). Despite the surge of comparative studies on cognitive abilities, the mechanisms behind such independently evolved complex cognition have received relatively little theoretical interest (Papini, 2002; Seed et al. 2009; Osvath et al. 2014).

In order to better understand the mechanism behind the independent evolution of complex cognitive skills, it is useful to distinguish between two major homoplastic mechanisms: convergence and parallelism. Convergence describes a trait similarity in two different lineages, independently arising from different developmental mechanisms or underlying substrates. A text-book example of convergence is insect wings and bird wings. While bird wings are constructed using forelimbs, insect wings are built using body scales. Parallelism, on the other hand, refers to a similarity arising independently from the same developmental mechanisms or underlying substrates. An example of parallelism is the bird wings and bat wings, as both lineages used the same underlying structure (forelimb) when building the wings independently from each other (their last common ancestor did not have wings, but had forelimbs). Both mechanisms give central importance to selective pressures as a major evolutionary force. However, parallelism also stresses the importance of the previously evolved characters that limit the future trajectory of evolution: the evolution of wings in birds and bats depended on their common ancestor evolving forelimbs. Such constraints indicate that the possible evolutionary trajectories are restricted, due to past contingencies, and the degrees of freedom in building intelligence are perhaps more limited (Gould, 2002; Osvath et al. 2014).

There is an ongoing debate in biology on the precise characterization of homology and homoplasy, given the presence of genetic deep homologies of independently built traits; as well as the presence of non-homologous developmental pathways behind homologous traits in different lineages (Arendt and Reznick, 2004; Beatty, 2006; Hall, 2013; Pearce, 2011; Powell and Shea, 2014; Scotland, 2011; Shubin et al. 2009; Wray, 2002). Similarly, there is no single, undisputed definition of the term parallelism and many different classifications have been offered. The term has been restricted to genotypic homoplasy (Gould, 2002; Hall, 2007; Pearce, 2011; Scotland, 2011), homologous developmental pathways generating the homoplastic trait (Powell, 2007) and whether the taxa that independently evolved a particular trait are closely related (Arendt and Reznick, 2008) or share a comparable ancestral starting point (Güntürkün and Bugnyar, 2016; Rehkämper and Zilles, 1991).

The issue becomes even more complex when it comes to cognition, as it comprises multiple interacting levels such as the body, the brain, neuro-regulatory genes etc. (Bertossa, 2011; Güntürkün and Bugnyar, 2016). Since all animals share a common ancestor, they inevitably share deep homologies on some level of analysis (Bogonovich, 2011; Wagner, 2007). For example, the same gene family (Pax) is involved in eye development in vastly diverged taxa such as arthropods and vertebrates (Shubin et al. 2009). This suggests that the homology/homoplasy as well as the parallelism/convergence distinction might be level dependent: it depends on what level of biological organization is selected when making the distinction (Ereshefsky, 2007; Griffiths, 2007; Hall, 2003). We thus need to focus on multiple levels when investigating the independent evolution of complex cognition between different groups. Brains constitute one level, but perhaps equally important is the pattern of cognitive development (Osvath et al. 2014).

4.1 Developmental parallels

In PAPER III we investigated the development of motor self-regulation in ravens using three detour tasks, and found similarities to primates, including humans, in the pattern of development: the sequence in which these detour tasks were solved throughout infancy were similar in raven chicks to those of rhesus macaque and human infants (Diamond, 1990). This finding provides some support for parallelism as it hints at the shared developmental mechanisms used by taxa as distant as corvids and primates. However, there might also be convergent elements on other levels of development. For example, one future way to address this issue might be to investigate whether these groups require fully developed motor self-regulation skills before developing self-control competency to pass delay of gratification tasks used in PAPER I.

When it comes to planning skills, developmental studies in corvids are lacking, as opposed to such studies on children (Hudson et al. 2010). Children generally succeed in the planning tasks studied in PAPER I around the same time they develop episodic memory skills (Busby and Suddendorf, 2005). Future studies should investigate the developmental trajectory of episodic memory and planning abilities in ravens and other corvids, to figure out the potential developmental parallels to those of children.

4.2 Homoplastic brains

Does cognitive similarity between corvids and great apes entail similarity in their neural architecture? This is one of the cardinal questions in the field of comparative neuropsychology (Güntürkün and Bugnyar, 2016). Before looking at this question, a brief summary of avian brains is necessary, together with the identification of the components within the avian brain that likely support inhibition and planning skills.

On the surface, the avian and mammalian brain are strikingly different. While the mammalian forebrain comprises most of the neocortex that has a laminar and columnar architecture, a similar structure is missing in the bird brain, which instead contains multiple large aggregations (nuclear architecture) without an apparent laminar or layered structure. This apparent lack of neocortex in the bird brain together with the old and erroneous assumption that bird brains cannot support complex cognitive skills led to the incorrect conclusion that the it was mostly the subpallial regions that birds and mammal brains shared (Edinger, 1899).

However, this picture gradually changed, thanks to studies that found similarity in the neural connectivity and neural architecture between avian and mammalian brains (Karten, 1969). The discoveries of homologous neural types and circuits as well as other functional similarities between avian and mammalian brains through genetic, physiological and anatomical studies led to a redefinition of the nomenclature of the bird brain, where it was declared that the large parts of the bird cerebrum are pallial instead of striatal (Jarvis et al. 2005; Güntürkün and Bugnyar, 2016; Karten, 2013). Later studies found other striking similarities such as the presence of laminar and columnar wiring in bird brains (Wang et al. 2010; Jarvis et al. 2013). More recently, it was found that parrot and songbird brains have markedly high neural densities than mammalian ones (Olkowicz et al. 2016).

The prefrontal cortex is thought of as the seat of executive functions in mammalian brains (Güntürkün, 2005). Birds have an associative brain structure called nidopallium caudolaterale (henceforth NCL), and it is considered to be an analogue of the prefrontal cortex, given its role in executive functions (Güntürkün, 2005; Helduser and Güntürkün, 2012; Mehlhorn et al. 2010; Mogensen and Divac, 1982; Rose and Colombo, 2005; Veit and Nieder, 2013). NCL shows remarkable similarity to the prefrontal cortex in neurochemistry and connectivity pattern (Güntürkün, 2005; Shanahan et al. 2013). However, despite sharing many homologous elements, NCL and prefrontal cortex also diverge in some characteristics such as certain gene expression patterns and their relative position in the cerebrum, which indicates they represent a case of homoplasy (Güntürkün and Bugnyar, 2016).

Can complex executive skills of corvids (e.g. planning and inhibition) be explained by their brain architecture? On a gross scale, corvids have a large brain-to-body-ratio (Cnotka et al. 2008; Olkowicz et al. 2016), as well as some of the largest brains of all birds (Lefebvre et al. 2004). However, from a mosaic evolution perspective, it might be more meaningful to focus on the specific regions involved in executive functions, such as NCL. When it comes to inhibitory control, NCL supports motor self-regulation (Güntürkün, 1997; Hartmann and Güntürkün, 1998; Kalt et al. 1999) and delay-of-gratification (Kalenscher et al. 2006). NCL is also considered to play an important role in supporting episodic memory and planning skills in birds (Allen and Fortin, 2013). The associative brain regions (nidopallium – thus NCL – and mesopallium) are relatively enlarged in corvids compared to other bird species, with the exception of parrots (Mehlhorn et al. 2010; Sayol et al. 2016). Interestingly, a similar enlargement occurred independently in primates as they possess relatively larger associative brain regions compared to other mammals (Rehkämper et al. 1991).

Humans need an intact episodic system to solve the planning tasks the ravens were tested on in PAPER I (Schacter et al. 2012). Do ravens use similar neurocognitive structures when planning? In humans, the brain network supporting episodic memory largely overlaps with the network supporting future planning (Addis et al. 2007). The core network involves the prefrontal cortex, parahippocampal regions and the hippocampus. Birds have analogous regions to the prefrontal cortex (NCL) and the parahippocampal region (parahippocampalis). The bird hippocampus is largely homologous and functionally similar to the mammalian one, although the finer details of this homology is yet to be established (Rattenborg and Martinez-Gonzalez, 2011; Striedter, 2016). Allen and Fortin (2013) investigated the evolutionary roots of the episodic memory network, and concluded that the fundamental circuitry is present in birds, and possibly even in reptiles. Episodic memories critically depend on the binding and integration of the contextual details of a single event such as where-what-when information; and this binding is mediated by the hippocampus (Buckner, 2010; Buzsaki and Moser, 2013; Hassabis et al. 2017). In all vertebrates, the main function of the hippocampus appears to be spatial navigation (‘where’ information), and it has been postulated that the episodic memory evolved when the hippocampus gained this new function of contextual binding, once it started receiving highly processed contextual input from associative brain regions (Allen and Fortin, 2013; Buzsaki and Moser, 2013). Some suggested that the episodic memory evolved and become more complex independently in birds and mammals, due to the relative enlargement of the hippocampus as well as the higher processing of the contextual information in the association brain areas in both groups (Striedter, 2016). Unfortunately, at this stage these hypotheses remain rather speculative as we do not know the finer neurological details of the episodic system in birds, and whether corvid planning skills are mediated by the episodic system as in mammals. However, future studies can shed light on the precise involvement of different neural components (such as NCL), e.g. by intervention studies on avian species that has demonstrated both episodic memory as well as planning skills, such as scrub-jays (Clayton and Dickinson, 1998; Clayton and Emery, 2015; Raby et al. 2007).

Corvids have a long developmental period compared to other birds, just as many primates have a longer developmental period compared to other mammals. Corvids are altricial birds, which means that hatchlings are incapable of locomotion. This is in contrast to precocial birds, like chickens, where hatchlings are mobile. Whereas brain growth is to a great extent finished before hatching for precocial birds (Bennett and Harvey, 1985), it continues during the post-hatching period for altricial birds (Starck and Ricklefs, 1998). The majority of post-hatching brain expansion in altricial birds occurs in the telencephalon (Charvet and Striedter, 2011), which contains structures such as NCL that support executive functions (Güntürkün, 2012). Such post-hatching telencephalic enlargement might be especially pronounced in corvids that go through slower developmental period with extended parental care and delayed brain maturation compared to other bird species (Striedter and Charvet, 2008).

Given these considerations, the executive feats of ravens (PAPER I and PAPER II) can partly be explained by enlargement of associative brain regions – especially the NCL. However, rather than the size alone, the level of analyses should also include the number of neurons within the associative regions (Herculano-Houzel, 2017). In primates, including humans, it was recently found that the prefrontal cortex holds around 8% of all cortical neurons (Gabi et al. 2016). We are so far lacking information about the corresponding numbers in birds, and future studies might reveal whether corvids differ from other birds as well as from primates in the proportion of neurons located in NCL. A potential difference in such numbers between corvids and parrots might also provide an explanation for why parrots performed poorly in the cylinder task compared to corvids (PAPER IV).

Bird brains can no longer be considered as just birdbrains, given their large neural densities and the presence of brain structures supporting complex cognition, as well as their complex cognitive skills in various domains (PAPER I, II). In fact, bird brains might arguably be more efficient than the mammalian brains with the same neural numbers, because the low inter-neuronal distances – due to high neural density – allow a faster processing speed, thus increasing the information processing capacity (Dicke and Roth, 2016; Olkowicz et al. 2016). This might partly explain why ravens outperform capuchin monkeys, which have a very similar number of pallial neurons, on planning tasks (PAPER I), as well as on the cylinder task (PAPER II). The number of neurons seems to provide a better measure for the information processing capacity of brains than the previously used gross measures, such as absolute or relative brain volume, however, future studies might shed light on the involvement of other neural factors such as myelinization, number of synapses and the speed of synaptic transmission (Dicke and Roth, 2016).

4.3 Selective pressures for complex cognition

The evolution of cognition is generally considered to reflect adaptations to environmental complexity (Powell et al. 2017). What are the selective pressures behind the evolution of cognitive skills such as inhibition and planning in corvids? I will discuss a few candidates, but we are still far from a well-founded hypothesis.

According to the social intelligence hypothesis, navigating complex social environments is the key evolutionary factor behind complex cognition (Dunbar, 1998; Humphrey, 1976). Most corvids live in complex social environments where individuals are attuned to social dynamics such as kin relationships, affiliations and hierarchical group structures (Boeckle and Bugnyar, 2012; Bugnyar, 2013; Massen et al. 2014a, 2014b). However, in contrast to primates, in birds it is not the size of the social group but rather long-lasting partnerships that correlates with brain size (Dunbar and Shultz, 2007; Shultz and Dunbar, 2007). Both long-term memories and inhibition could be particularly useful in such complex social settings: episodic memory would allow remembering specific social events (e.g. who was aggressive or cooperative?), and this information can be used in forming alliances and engaging in reciprocal social exchanges (Allen and Fortin, 2013; Loretto et al. 2017; Müller et al. 2017). Episodic memories would also be useful when protecting food caches from potential pilferers (Bugnyar, 2013). Indeed, many corvid species such as scrub-jays, ravens and Clark's nutcrackers seem to remember which individual was watching a particular food caching event and they protect their caches accordingly (Bugnyar et al. 2016; Bugnyar and Heinrich, 2005; Bugnyar and Kotrschal, 2002; Clary and Kelly, 2011 Dally et al. 2006; Emery and Clayton, 2001; Heinrich, 1999).

Perhaps more related to prospection skills, a more complex social environment can also lead to an "arms race of prediction" (Osvath, 2016). Being predictable is not an evolutionarily stable strategy (Brembs, 2011), as it can lead to unfavourable outcomes such as falling prey to predators or being outcompeted by conspecifics for limited resources. It's been suggested that predicting the behaviour of conspecifics may be particularly beneficial for species such as corvids and great apes, which live in complex social environments, and this in turn may have led to the evolution of more complex planning abilities (Osvath, 2016).

Similarly, inhibitory control would be useful in a social setting, e.g. when inhibiting feeding in the presence of a dominant individual (Amici et al. 2008; Stevens, 2010, 2014). Indeed, increased capacity of inhibition was posited to be one of the driving forces behind high levels of cooperation in our species, by enabling high levels of social tolerance (MacLean, 2016). In primates, species having high levels of fission-fusion dynamics – that is characterized by a high degree of variation in group composition across time – have higher levels of inhibitory control compared to species with more cohesive group structure (Amici et al. 2008; Aureli et al. 2008). While a similar investigation is yet to be conducted on birds, it's worth noting that raven non-breeders also display high levels of fission-fusion dynamics where the individuals disperse over large areas and they form temporary groups near food sources and for night roosts, and they engage in repeated interactions with each other in different locations (Loretto et al. 2017).

According to the cognitive buffer hypothesis, the need for solving novel problems in a dynamic environment is the central driving force behind complex cognition rather than navigating complex social life *per se* (Deaner et al. 2003; Rosati, 2017; Sol, 2009). Corvids first arose and diversified in the beginning of the Miocene epoch, about 20 million years ago (Jønsson et al. 2012). This period is characterized by large climatic changes, marked by middle Miocene extinction that wiped out large number of terrestrial and aquatic species due to cooling. Could corvid cognitive skills be better explained by an adaptation to the harsh environmental conditions in Miocene, which necessitated unique problem-solving skills (Bogonovich, 2011; Osvath, 2013)? Especially relevant for the evolution of planning skills might be the need to forage for food that is displaced in time and space, which might have been required in harsh Miocene conditions (Clayton and Emery, 2008). Representing the out-of-sight food requires certain detachment from 'here and now'- hence a form of displacement. Interestingly, such out-of-sight events has been suggested as a key environmental pressure for the evolution of symbolic communication in humans (Bickerton, 2014; Gärdenfors and Osvath, 2010; Osvath and Gärdenfors, 2005) and some have suggested that ravens display certain form of displacement when recruiting conspecifics to out-of-sight food resources (Fitch et al. 2010).

It's worth noting that these hypotheses are not mutually exclusive as social and environmental factors interact in shaping the evolution of cognitive skills. We need large-scale comparisons involving many species in order to get a clearer picture of the selective pressures driving cognitive evolution.

4.4 Embodied cognition

Around 30 years ago, humans were considered as a singleton in evolution with their complex cognitive abilities. This picture gradually changed with the demonstration of complex cognitive abilities in e.g. great apes, dolphins, parrots and corvids. As the scope of comparative cognitive research grows, we realize that behaviours requiring some form of cognitive sophistication may not be limited to vertebrates but may also be present in molluscs such as octopuses and in arthropods such as jumping spiders and honeybees (Cheng et al. 2002; Cross and Jackson, 2016; Finn et al. 2009). However, as the range of tested species increases, we might need to re-examine our view of cognition and make it less human-centred in order to reach a better understanding of the evolution of mind in its broadest biological context (Keijzer, 2017).

Keijzer claims it is inadequate to take human intelligence as the reference for assessing complex cognition in different species, and it is also not sufficient to define cognition fundamentally as information processing (Shettleworth, 2010). He proposes that 'biologically embodied cognition' might provide a broader view, as it assigns cognition to wide range of systems which do not display mind in any ordinary way, and yet they allow smooth bodily coping with the environment for self-preservation. This is a similar idea that has been postulated by the well-established field of embodied cognition and the Bayesian approach to mind (Osvath, 2016). In short, the idea is that cognition exists not in order to understand the world but to guide action to keep the agent in equilibrium with its environment (homeostasis) (Clark, 2013; Friston, 2010; James, 1890; Pezzulo and Cisek, 2016). All life is embodied and homeostasis is a universal property of living systems: all life engages in active regulation to maintain the system within certain boundary conditions (goal state) for its preservation and reproduction. This view suggests life and mind are connected, and cognition should be understood similarly (e.g. Deacon, 2011; Pezzulo, 2008).

Anticipation and prediction are essential components for sensorimotor control, as can be exemplified by the funny observation that you cannot tickle yourself: your brain predicts and expects the effect of your action, thus killing the surprise. According to the 'predictive brain hypothesis', brains constantly attempt to predict what is to come in order to cope with the ever-changing environment (Bar, 2009;

Clark, 2013). These predictions are formed through extracting environmental regularities, and they get updated when the sensory inputs do not confer with those predictions (Friston, 2010). The hypothesis is that higher-order detached skills such as planning and imagination are grounded in this fundamental mechanism of predictive sensorimotor processing; and some cognitive models do not even distinguish between perception, action, and planning (Toussaint, 2009). Thus, higher and detached faculties like planning and mental time travel are grounded in sensorimotor mechanisms that are anticipatory in nature (Pezzulo, 2008). Consistently, it has been suggested that neural mechanisms supporting mental time travel originally evolved to support spatial navigation (Buzsaki and Moser, 2013; Hills, 2006).

This idea also forms the basis of the ideomotor/feeback control theory. Anticipation arises from the very principles of feedback control: actions are selected based on the anticipation and the evaluation of their sensory consequences (James, 1890; Pezzulo, 2008). Thus, animals are not mere stimulus-response machines but they constantly engage in prospection and prediction – a process also called active inference (Friston, 2010; Pezzulo and Castelfranchi, 2009; Seligman et al. 2013). There is thus a continuity between simpler and more complex forms of prospection.

Since bodies are fundamentally and causally part of cognition (Chemero, 2011), and since corvids and great apes vastly differ in their embodiment, can we really conclude they are cognitively similar? Are we not neglecting this bodily aspect of cognition when naming corvids as ‘feathered apes’ (Barrett, 2011; Emery, 2004; Osvath et al. 2014)? Corvids are adapted to flight, which requires fast decisions making on the wing. Thus, calling corvids feathered apes might neglect this fundamental embodied aspect of corvid cognition which is different than the apes (Emery, 2016). But there are attempts to bring to attention this bodily contribution to cognition, by the idea of bodily developmental constraints (Barton, 2012; Holekamp et al. 2013). The idea is that the variation in body plans between species, due to phylogeny and past adaptations, can partly explain the variation in their cognitive flexibility. Thus, comparative studies should pay attention to this bodily aspect of cognition instead of only focusing on the selective pressures.

5. Concluding remarks

Cognitive zoology is a relatively new research area that aims to understand the evolution of cognition. As the comparative scope of tested species grows, we have a better understanding of why and how cognition evolves. This thesis contributes to this endeavour by studying the components of executive functions in corvids, and (to some extent) parrots. The studies in this thesis found behavioural (functional) parallels between corvids and great apes, leading to questions such as whether the parallels also exist on the mechanistic level (e.g. on the neural and developmental mechanisms). The picture of cognitive evolution will not be sufficiently clear until comparisons expand to multiple levels of biological organization. It is remarkable that birds and mammals show similar complex cognitive skills despite being separated from each other for around 300 million years. Future studies should expand the horizon of phylogeny by testing basal mammals and basal birds, in order to understand what is novel and what is conserved in evolutionary history.

It is exciting to see many labs around the world cooperate to understand the evolution of the mind. While the number of species tested is growing, there is a need of finding valid and reliable cognitive tests to yield robust comparisons of the targeted cognitive skill in wide array of species. This thesis highlights some of the challenges of such large-scale species comparisons and offers some ways to tackle them.

Studying the evolution of cognition brings its unique challenges compared to studying other biological phenomena. First, cognition cannot be observed but only inferred from behaviour (in case of animal cognition: non-linguistic behaviour). Thus, creative test designs are necessary to eliminate alternative explanations for the observed behaviour (Shettleworth, 2010). Second, cognition is not static, like a bone in a body, but an active embodied process that emerges though the interactions with various components that are in constant flux (e.g. attention, motivation, memory, bodily orientation, the environment itself etc.). Thus, cognitive tasks should take into account these factors as well as the ecology of different species to make the comparisons meaningful (Bitterman, 1975). Third, the same concept can mean different things to different researchers within the field of cognitive science, creating a problem of incommensurability (Kuhn, 1982). For example, terms like ‘planning’ and ‘self-control’ can evoke different representations in different people, thus it is essential to be clear about in which contexts these terms are used and measured in cognitive studies on animals. Paying attention to such factors will be fruitful in understanding the place of the mind in the universe.

References

Addis DR, Wong AT, Schacter DL (2007) Remembering the past and imagining the future: common and distinct neural substrates during event construction and elaboration. Neuropsychologia 45:1363-1377

Ainslie GW (1974) Impulse control in pigeons. J Exp Anal Behav 21:485-489

Allen TA, Fortin NJ (2013) The evolution of episodic memory. Proc Nat Acad Sci 110:10379-10386

Amici F, Aureli F, Call J (2008) Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. Curr Biol 18:1415-1419

Arendt J, Reznick D (2008) Convergence and parallelism reconsidered: what have we learned about the genetics of adaptation? Trends Ecol Evol 23:26-32

Atance CM, Meltzoff AN (2005) My future self: Young children's ability to anticipate and explain future states. Cognit Dev 20:341-361

Atance CM, O'Neill DK (2001) Episodic future thinking. Trends Cognit Sci 5:533-539

Atance CM, Sommerville JA (2014) Assessing the role of memory in preschoolers' performance on episodic foresight tasks. Mem 22:118-128

Aureli F et al. (2008) Fission-fusion dynamics: new research frameworks. Curr Anthropol 49:627-654

Babb SJ, Crystal JD (2006) Episodic-like memory in the rat. Curr Biol 16:1317-1321

Bar M (2009) The proactive brain: memory for predictions. Phil Trans R Soc B 364:1235-1243

Bari A, Robbins TW (2013) Inhibition and impulsivity: behavioral and neural basis of response control. Prog Neurobiol 108:44-79

Barrett L (2011) Beyond the brain: How body and environment shape animal and human minds. Princeton University Press, NJ.

Barton RA (2012) Embodied cognitive evolution and the cerebellum. Phil Trans R Soc B 367:2097-2107

Beatty J (2006) Replaying life's tape. J Philos 103:336-362

Bennett PM, Harvey PH (1985) Brain size, development and metabolism in birds and mammals. J Zool 207:491-509

Beran MJ (2015) The comparative science of “self-control”: what are we talking about? Front Psychol 6 doi:10.3389/fpsyg.2015.00051

Beran MJ, Evans TA (2012) Language-trained chimpanzees (Pan troglodytes) delay gratification by choosing token exchange over immediate reward consumption. Am J Primatol 74:864-870

Berkman ET, Kahn LE, Merchant JS (2014) Training-induced changes in inhibitory control network activity. J Neurosci 34:149-157

Bertossa RC (2011) Morphology and behaviour: functional links in development and evolution. R Soc B 366: 2056-2068

Bickerton D (2014) More than nature needs: Language, mind, and evolution. Harvard University Press, Cambridge

Bird CD, Emery NJ (2009) Insightful problem solving and creative tool modification by captive non tool-using rooks. Proc Nat Acad Sci 106:10370-10375

Bitterman M (1975) The comparative analysis of learning. Sci 188:699-709

Boeckle M, Bugnyar T (2012) Long-term memory for affiliates in ravens. Curr Biol 22:801-806

Boesch C, Boesch H (1984) Mental map in wild chimpanzees: an analysis of hammer transports for nut cracking. Prim 25:160-170

Bogonovich M (2011) Intelligence's likelihood and evolutionary time frame. Int J Astrobiol 10:113-122

Bourjade M, Call J, Pelé M, Maumy M, Dufour V (2014) Bonobos and orangutans, but not chimpanzees, flexibly plan for the future in a token-exchange task. Anim Cogn 17:1329-1340

Bourjade M, Thierry B, Call J, Dufour V (2012) Are monkeys able to plan for future exchange? Anim Cogn 15:783-795

Boyer P (2008) Evolutionary economics of mental time travel? Trends Cogn Sci 12:219-224

Bray EE, MacLean EL, Hare BA (2014) Context specificity of inhibitory control in dogs. Anim Cogn 17:15-31

Brembs B (2011) Towards a scientific concept of free will as a biological trait: spontaneous actions and decision-making in invertebrates. Proc Royal Soc B 278:930-939

Buckner RL (2010) The role of the hippocampus in prediction and imagination. Annu Rev Psychol 61:27-48

Bugnyar T (2013) Social cognition in ravens. Comp Cogn Behav Rev 8:1-12

Bugnyar T, Heinrich B (2005) Ravens, Corvus corax, differentiate between knowledgeable and ignorant competitors. Proc Royal Soc B 272:1641-1646

Bugnyar T, Kotrschal K (2002) Observational learning and the raiding of food caches in ravens, Corvus corax: is it ‘tactical’deception? Anim Behav 64:185-195

Bugnyar T, Reber SA, Buckner C (2016) Ravens attribute visual access to unseen competitors. Nat Commun 7 doi:10.1038/ncomms10506

Busby J, Suddendorf T (2005) Recalling yesterday and predicting tomorrow. Cogn Dev 20:362-372

Buzsaki G, Moser EI (2013) Memory, navigation and theta rhythm in the hippocampal-entorhinal system. Nat Neurosci 16:130-138

Chappell J (2016) Bird brains: Does absolute size matter? Learn Behav 45:1-2

Charvet CJ, Striedter GF (2011) Developmental modes and developmental mechanisms can channel brain evolution. Front Neuroanat 5 doi:10.3389/fnana.2011.00004

Cheke LG, Clayton NS (2012) Eurasian jays (Garrulus glandarius) overcome their current desires to anticipate two distinct future needs and plan for them appropriately. Biol Lett 8:171-175

Chemero A (2011) Radical embodied cognitive science. MIT press, Cambridge

Cheney DL, Seyfarth RM (1990) How monkeys see the world: Inside the mind of another species. Chicago University Press, Chicago, IL

Cheng K, Peña J, Porter MA, Irwin JD (2002) Self-control in honeybees. Psychon Bull Rev 9:259-263

Clark A (2013) Whatever next? Predictive brains, situated agents, and the future of cognitive science. Behav Brain Sci 36:181-204

Clary D, Kelly DM (2011) Cache protection strategies of a non-social food-caching corvid, Clark’s nutcracker (Nucifraga columbiana). Anim Cogn 14:735-744

Clayton NS, Bussey TJ, Dickinson A (2003) Can animals recall the past and plan for the future? Nat Rev Neurosci 4:685-691

Clayton NS, Dickinson A (1998) Episodic-like memory during cache recovery by scrub jays. Nat 395:272-274

Clayton NS, Emery NJ (2008) Canny corvids and political primates: A case for convergent evolution in intelligence. In: Conway Morris S (ed) The deep structure of biology: Is convergence sufficiently ubiquitous to give a directional signal? Templeton Foundation Press, West Conshohocken, PA, pp 128-142

Clayton NS, Emery NJ (2015) Avian models for human cognitive neuroscience: a proposal. Neuron 86:1330-1342

Clayton NS, Griffiths D, Emery N, Dickinson A (2001) Elements of episodic–like memory in animals. Phil Trans R Soc B 356:1483-1491

Cnotka J, Güntürkün O, Rehkämper G, Gray RD, Hunt GR (2008) Extraordinary large brains in tool-using New Caledonian crows (Corvus moneduloides). Neurosci Lett 433:241-245

Cohen JR, Berkman ET, Lieberman MD (2013) Intentional and incidental self-control in ventrolateral PFC. In: Stuss DT & Knight RT (eds) Principles of frontal lobe function. Oxford University Press, Oxford, pp 417-440

Collins A, Koechlin E (2012) Reasoning, learning, and creativity: frontal lobe function and human decision-making. PLoS Biol 10:e1001293

Conway-Morris S (2003) Life's solution: inevitable humans in a lonely universe. Cambridge University Press, Cambridge

Conway-Morris S, Gould SJ (1998) Showdown on the Burgess shale. Nat Hist 107:48-55

Correia SP, Dickinson A, Clayton NS (2007) Western scrub-jays anticipate future needs independently of their current motivational state. Curr Biol 17:856-861

Cross FR, Jackson RR (2016) The execution of planned detours by spider-eating predators. J Exp Anal Behav 105:194-210

Dally JM, Emery NJ, Clayton NS (2006) Food-caching western scrub-jays keep track of who was watching when Sci 312:1662-1665

Davidson MC, Amso D, Anderson LC, Diamond A (2006) Development of cognitive control and executive functions from 4 to 13 years: Evidence from manipulations of memory, inhibition, and task switching. Neuropsychologia 44:2037-2078

de Waal F (2016) Are we smart enough to know how smart animals are? WW Norton & Company, New York

Deacon TW (2011) Incomplete nature: How mind emerged from matter. WW Norton & Company, New York

Deaner RO, Barton RA, van Schaik CP (2003) Primate brains and life histories: renewing the connection. In: Kappeler PM & Pereira ME (eds) Primate life histories and socioecology. University of Chicago Press Chicago, pp 233-265

Deaner RO, Isler K, Burkart J, Van Schaik C (2007) Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. Brain Behav Evol 70:115-124

Dekleva M, van den Berg L, Spruijt BM, Sterck EH (2012) Take it or leave it: transport of tools for future use by long-tailed macaques (Macaca fascicularis). Behav Proc 90:392-401

Dempster FN (1992) The rise and fall of the inhibitory mechanism: Toward a unified theory of cognitive development and aging. Dev Rev 12:45-75

Dere E, Kart-Teke E, Huston J, Silva MDS (2006) The case for episodic memory in animals. Neurosci Biobehav Rev 30:1206-1224

Diamond A (1990) Developmental Time Course in Human Infants and Infant Monkeys, and the Neural Bases of Inhibitory Control in Reaching. Ann New York Acad Sci 608:637-676

Diamond A (2013) Executive functions. Ann Rev Psychol 64:135-168

Dicke U, Roth G (2016) Neuronal factors determining high intelligence. Phil Trans R Soc B 371:20150180

Duckworth AL, Kern ML (2011) A meta-analysis of the convergent validity of self-control measures. J Res Personal 45:259-268

Dufour V, Sterck E (2008) Chimpanzees fail to plan in an exchange task but succeed in a tool-using procedure Behav Proc 79:19-27

Dufour V, Wascher CA, Braun A, Miller R, Bugnyar T (2012) Corvids can decide if a future exchange is worth waiting for. Biol Lett 8: 201-204

Dunbar RI (1998) The social brain hypothesis. Brain 9:178-190

Dunbar RI, Shultz S (2007) Evolution in the social brain. Sci 317:1344-1347

Durston S, Thomas KM, Yang Y, Uluğ AM, Zimmerman RD, Casey B (2002) A neural basis for the development of inhibitory control. Dev Sci 5:9-16

Eacott MJ, Easton A (2010) Episodic memory in animals: remembering which occasion. Neuropsychologia 48:2273-2280

Edinger L (1899) The anatomy of the central nervous system of man and of vertebrates in general. The FA Davis company, Philadelphia

Eichenbaum H, Fortin NJ, Ergorul C, Wright SP, Agster KL (2005) Episodic recollection in animals: “If it walks like a duck and quacks like a duck…” Learn Motiv 36:190-207

Emery NJ (2004) Are corvids ‘feathered apes’? Cognitive evolution in crows, jays, rooks and jackdaws. In: Watanabe S (ed) Comparative analysis of minds. Keio University Press, Tokyo, pp 181-213

Emery NJ (2016) Bird Brain: An exploration of avian intelligence. Princeton University Press, New Jersey

Emery NJ, Clayton NS (2001) Effects of experience and social context on prospective caching strategies by scrub jays. Nat 414:443-446

Emery NJ, Clayton NS (2004) The mentality of crows: convergent evolution of intelligence in corvids and apes. Sci 306:1903-1907

Ereshefsky M (2007) Psychological categories as homologies: lessons from ethology. Biol Phil 22:659-674

Feeney MC, Roberts WA, Sherry DF (2009) Memory for what, where, and when in the black-capped chickadee (Poecile atricapillus). Anim Cogn 12:767-777

Finn JK, Tregenza T, Norman MD (2009) Defensive tool use in a coconut-carrying octopus. Curr Biol 19:R1069-R1070

Fitch WT, Huber L, Bugnyar T (2010) Social cognition and the evolution of language: constructing cognitive phylogenies. Neuron 65:795-814

Friedman NP, Miyake A (2004) The relations among inhibition and interference control functions: a latent-variable analysis. J Exp Psychol Gen 133:101-135

Friston K (2010) The free-energy principle: a unified brain theory? Nat Rev Neurosci 11:127-138

Gabi M et al. (2016) No relative expansion of the number of prefrontal neurons in primate and human evolution. Proc Nat Acad Sci:201610178

Garcia J, Ervin FR, Koelling RA (1966) Learning with prolonged delay of reinforcement. Psychon Sci 5:121-122

Gärdenfors P Osvath M (2010) Prospection as a cognitive precursor to symbolic communication. In: Larson RK, Deprez V, Yamakido H (eds) The evolution of human language. Cambridge University Press, Cambridge, pp 103–114

Gerstadt CL, Hong YJ, Diamond A (1994) The relationship between cognition and action: performance of children 3.5–7 years old on a stroop-like day-night test. Cogn 53:129-153

Gilbert DT, Wilson TD (2007) Prospection: Experiencing the future. Sci 317:1351-1354

Gomez JC (2005) Species comparative studies and cognitive development. Trends Cogn Sci 9:118-125

Goodall J (1964) Tool-using and aimed throwing in a community of free-living chimpanzees. Nat 201:1264-1266

Gould SJ (1990) Wonderful life: the Burgess Shale and the nature of history. WW Norton & Company, New York

Gould SJ (2002) The structure of evolutionary theory. Harvard University Press, Cambridge

Griffiths PE (2007) The phenomena of homology. Biol Phil 22:643-658

Güntürkün O (1997) Cognitive impairments after lesions of the neostriatum caudolaterale and its thalamic afferent in pigeons: functional similarities to the mammalian prefrontal system? J Hirnforschung 38:133-143

Güntürkün O (2005) The avian 'prefrontal cortex' and cognition. Curr Opin Neurobiol 15:686-693

Güntürkün O (2012) The convergent evolution of neural substrates for cognition. Psychol Res 76:212-219

Güntürkün O, Bugnyar T (2016) Cognition without cortex. Trends Cogn Sci 20:291-303

Güntürkün O, Ströckens F, Scarf D, Colombo M (2017) Apes, feathered apes, and pigeons: differences and similarities. Curr Opin Behav Sci 16:35-40

Hackenberg TD (2009) Token reinforcement: A review and analysis. J Exp Anal Behav 91:257-286

Hall BK (2003) Descent with modification: the unity underlying homology and homoplasy as seen through an analysis of development and evolution. Biol Rev 78:409-433

Hall BK (2007) Homoplasy and homology: Dichotomy or continuum? J Hum Evol 52:473-479

Hall BK (2013) Homology, homoplasy, novelty, and behavior. Dev Psychobiol 55:4-12

Hampton RR, Hampstead BM, Murray EA (2005) Rhesus monkeys (Macaca mulatta) demonstrate robust memory for what and where, but not when, in an open-field test of memory. Learn Motiv 36:245-259

Hartmann B, Güntürkün O (1998) Selective deficits in reversal learning after neostriatum caudolaterale lesions in pigeons: possible behavioral equivalencies to the mammalian prefrontal system. Behav Brain Res 96:125-133

Hassabis D, Kumaran D, Summerfield C, Botvinick M (2017) Neuroscience-inspired artificial intelligence. Neuron 95:245-258

Hassabis D, Maguire EA (2007) Deconstructing episodic memory with construction. Trends Cogn Sci 11:299-306

Hayes-Roth B, Hayes-Roth F (1979) A cognitive model of planning. Cogn Sci 3:275-310

Heinrich B (1999) Mind of the raven: Investigations and adventures with wolf-birds. Harper Collins, New York

Helduser S, Güntürkün O (2012) Neural substrates for serial reaction time tasks in pigeons. Behav Brain Res 230:132-143

Herculano-Houzel S (2017) Numbers of neurons as biological correlates of cognitive capability. Curr Opin Behav Sci 16:1-7

Herrmann E, Hare B, Call J, Tomasello M (2010) Differences in the cognitive skills of bonobos and chimpanzees. PloS one 5:e12438

Hillemann F, Bugnyar T, Kotrschal K, Wascher CA (2014) Waiting for better, not for more: corvids respond to quality in two delay maintenance tasks. Anim Behav 90:1-10

Hills TT (2006) Animal foraging and the evolution of goal-directed cognition. Cogn Sci 30:3-41

Holekamp KE, Swanson EM, Van Meter PE (2013) Developmental constraints on behavioural flexibility. Phil Trans R Soc B 368:20120350

Hudson JA, Mayhew E, Prabhakar J (2010) The development of episodic foresight: emerging concepts and methods. Adv Child Dev Behav 40:95-137

Humphrey NK (1976) The social function of intellect. In: Bateson PPG & Hilde RA (eds) Growing points in ethology. Cambridge University Press, Cambridge, pp 303-317

Ingvar DH (1979) “Hyperfrontal” distribution of the cerebral grey matter flow in resting wakefulness; on the functional anatomy of the conscious state. Acta Neurol Scan 60:12-25

Ingvar DH (1985) “Memory of the future”: an essay on the temporal organization of conscious awareness. Hum Neurobiol 4:127-136

Irish M, Addis DR, Hodges JR, Piguet O (2012) Considering the role of semantic memory in episodic future thinking: evidence from semantic dementia. Brain 135:2178-2191

Irish M, Piguet O (2013) The pivotal role of semantic memory in remembering the past and imagining the future. Front Behav Neurosci 7 doi:10.3389/fnbeh.2013.00027

Jahanshahi M, Obeso I, Rothwell JC, Obeso JA (2015) A fronto-striato-subthalamic-pallidal network for goal-directed and habitual inhibition. Nat Rev Neurosci 16:719-732

James W (1890) The principles of psychology. Henry Rolt and Company, New York

Janmaat KR, Polansky L, Ban SD, Boesch C (2014) Wild chimpanzees plan their breakfast time, type, and location. Proc Nat Acad Sci 111:16343-16348

Jarvis ED et al. (2005) Avian brains and a new understanding of vertebrate brain evolution. Nat Rev Neurosci 6:151-159

Jarvis ED et al. (2013) Global view of the functional molecular organization of the avian cerebrum: mirror images and functional columns. J Comp Neurol 521:3614-3665

Jenkins H, Moore BR (1973) The form of the auto-shaped response with food or water reinforcers. J Exp Anal Behav 20:163-181

Jønsson KA, Fabre P-H, Irestedt M (2012) Brains, tools, innovation and biogeography in crows and ravens. BMC Evol Biol 12:72

Judge PG, Essler JL (2013) Capuchin monkeys exercise self-control by choosing token exchange over an immediate reward. Int J Comp Psychol 26:256-266

Kabadayi C, Osvath M (2017) Ravens parallel great apes in flexible planning for tool-use and bartering. Sci 357:202-204

Kabadayi C, Taylor LA, von Bayern AM, Osvath M (2016) Ravens, New Caledonian crows and jackdaws parallel great apes in motor self-regulation despite smaller brains. R Soc Open Sci 3:160104 doi:10.1098/rsos.160104

Kalenscher T, Ohmann T, Güntürkün O (2006) The neuroscience of impulsive and self-controlled decisions. Int J Psychophysiol 62:203-211

Kalt T, Diekamp B, Güntürkün O (1999) Single unit activity during a Go/NoGo task in the “prefrontal cortex” of pigeons. Brain Res 839:263-278

Karten HJ (1969) The organization of the avian telencephalon and some speculations on the phylogeny of the amniote telencephalon. Ann NY Acad Sci 167:164-179

Karten HJ (2013) Neocortical evolution: neuronal circuits arise independently of lamination. Curr Biol 23:R12-R15

Keijzer F (2017) Evolutionary convergence and biologically embodied cognition. Interface Focus 7 doi: 10.1098/rsfs.2016.0123

Killcross S, Coutureau E (2003) Coordination of actions and habits in the medial prefrontal cortex of rats. Cereb Cortex 13:400-408

Klein SB (2013) The complex act of projecting oneself into the future. Wiley Interdiscip Rev: Cogn Sci 4:63-79

Köhler W (1922) Zur psychologie des schimpansen. Psychologische Forschung 1:2-46

Köhler W (1927) The Mentality of Apes. Routledge & Kegan Paul, London

Kuhn TS (1982) Commensurability, comparability, communicability. Proc Bienn Meet Phil Sci Assoc 1982: 669-688

Kwan D, Craver CF, Green L, Myerson J, Boyer P, Rosenbaum RS (2012) Future decision-making without episodic mental time travel. Hippocampus 22:1215-1219

Lefebvre L, Reader SM, Sol D (2004) Brains, innovations and evolution in birds and primates. Brain Behav Evol 63:233-246

Lemmon K, Moore C (2007) The development of prudence in the face of varying future rewards. Dev Sci 10:502-511

Loretto MC, Schuster R, Itty C, Marchand P, Genero F, Bugnyar T (2017) Fission-fusion dynamics over large distances in raven non-breeders. Nat Sci Rep 7 doi:10.1038/s41598-017-00404-4

MacLean EL (2016) Unraveling the evolution of uniquely human cognition. Proc Nat Acad Sci 113:6348-6354

MacLean EL et al. (2012) How does cognition evolve? Phylogenetic comparative psychology. Anim Cogn 15:223-238

MacLean EL et al. (2014) The evolution of self-control. Proc Nat Acad Sci 111:2140-2148

Macphail EM (1987) The comparative psychology of intelligence. Behav Brain Sci 10:645-656

Martin-Ordas G, Berntsen D, Call J (2013) Memory for distant past events in chimpanzees and orangutans Curr Biol 23:1438-1441

Martin-Ordas G, Haun D, Colmenares F, Call J (2010) Keeping track of time: evidence for episodic-like memory in great apes. Anim Cogn 13:331-340

Massen JJ, Pašukonis A, Schmidt J, Bugnyar T (2014a) Ravens notice dominance reversals among conspecifics within and outside their social group. Nat Commun 5:3679 doi:10.1038/ncomms4679

Massen JJ, Szipl G, Spreafico M, Bugnyar T (2014b) Ravens intervene in others' bonding attempts. Curr Biol 24:2733-2736

Matute H, Lipp OV, Vadillo MA, Humphreys MS (2011) Temporal contexts: filling the gap between episodic memory and associative learning. J Exp Psychol 140:660-673

Mazur JE, Logue A (1978) Choice in a "self-control" paradigm: effects of a fading procedure. J Exp Anal Behav 30:11-17

McCormack T, Atance CM (2011) Planning in young children: A review and synthesis. Dev Rev 31:1-31

Mehlhorn J, Hunt GR, Gray RD, Rehkämper G, Güntürkün O (2010) Tool-making New Caledonian crows have large associative brain areas. Brain Behav Evol 75:63-70

Menzel C (2005) Progress in the study of chimpanzee recall and episodic memory. In: Terrace H and Metcalfe J (eds) The missing link in cognition: origins of self-reflective consciousness, Oxford University Press, Oxford, pp 188-224

Meyers-Manor JE, Overmier JB, Hatfield DW, Croswell J (2014) Not so bird-brained: Pigeons show what-where-when memory both as time of day and how long ago. J Exp Psychol 40:225-240

Michaelian K (2016) Against discontinuism: Mental time tracel and our knowledge of past and future events. In: Michaelian K, Klein S, Szpunar K (eds) Seeing the future: Theoretical perspectives on future-oriented mental time travel. Oxford University Press, New York, pp 62-92

Mischel W (2014) The marshmallow test: understanding self-control and how to master it. Penguin Random House, New York

Mischel W, Metzner R (1962) Preference for delayed reward as a function of age, intelligence, and length of delay interval. J Abnorm and Soc Psychol 64:425-431

Mogensen J, Divac I (1982) The prefrontal 'cortex' in the pigeon. Brain Behav Evol 21:60-66

Moroz LL (2015) The genealogy of genealogy of neurons. Commun Integ Biol 7:e993269

Mulcahy NJ, Call J (2006) Apes save tools for future use. Sci 312:1038-1040

Müller J, Massen JJ, Bugnyar T, Osvath M (2017) Ravens remember the nature of a single reciprocal interaction sequence over 2 days and even after a month. Anim Behav 128:69-78

Muraven M, Baumeister RF (2000) Self-regulation and depletion of limited resources: Does self-control resemble a muscle? Psychol Bull 126:247-259

Nairne JS (2002) The myth of the encoding-retrieval match. Mem 10:389-395

Naqshbandi M, Roberts WA (2006) Anticipation of future events in squirrel monkeys (Saimiri sciureus) and rats (Rattus norvegicus): tests of the Bischof-Köhler hypothesis. J Comp Psychol 120:345-357

Noland JS, Rodrigues NP (2012) Direct touches to clear barriers: Developmental sensitivity of a new measure of the production of ineffective responses in infancy. Child Neuropsychol 18:506-511

Olkowicz S, Kocourek M, Lučan RK, Porteš M, Fitch WT, Herculano-Houzel S, Němec P (2016) Birds have primate-like numbers of neurons in the forebrain. Proc Nat Acad Sci:201517131

Osvath M (2009) Spontaneous planning for future stone throwing by a male chimpanzee. Curr Biol 19:R190-R191

Osvath M (2013) A cognitive zoology approach to potential universal principles of intelligence . In: Duner D, Parhemore J, Persson E, Holmberg G (eds) The History and Philosophy of Astrobiology: Perspectives on Extraterrestrial Life and the Human Mind. Cambridge Scholars Publishing, pp 128-142

Osvath M (2016) Putting flexible animal prospection into context: escaping the theoretical box. Wiley Interdiscip Rev: Cogni Sci 7:5-18

Osvath M, Gärdenfors P (2005) Oldowan culture and the evolution of anticipatory cognition. Lund Univ Cogn Stud 122:1-16

Osvath M, Kabadayi C, Jacobs I (2014) Independent evolution of similar complex cognitive skills: the importance of embodied degrees of freedom. Anim Behav Cogn 1:249-264

Osvath M, Karvonen E (2012) Spontaneous innovation for future deception in a male chimpanzee. PloS one 7:e36782

Osvath M, Martin-Ordas G (2014) The future of future-oriented cognition in non-humans: theory and the empirical case of the great apes. Phil Trans R Soc B 369:20130486

Osvath M, Osvath H (2008) Chimpanzee (Pan troglodytes) and orangutan (Pongo abelii) forethought: self-control and pre-experience in the face of future tool use. Anim Cogn 11:661-674

Osvath M, Persson T (2013) Great apes can defer exchange: A replication with different results suggesting future oriented behavior. Front Psychol 4:698-705

Pahl M, Zhu H, Pix W, Tautz J, Zhang S (2007) Circadian timed episodic-like memory–a bee knows what to do when, and also where. J Exp Biol 210:3559-3567

Papini MR (2002) Pattern and process in the evolution of learning. Psychol Rev 109:186-201

Payne G, Taylor R, Hayne H, Scarf D (2015) Mental time travel for self and other in three- and four-year-old children. Mem 23:675-682

Pearce T (2011) Convergence and parallelism in evolution: a neo-Gouldian account. Brit J Phil Sci 63:429-448

Pezzulo G (2008) Coordinating with the future: the anticipatory nature of representation. Mind Mach 18:179-225

Pezzulo G, Castelfranchi C (2009) Thinking as the control of imagination: a conceptual framework for goal-directed systems. Psychol Res 73:559-577

Pezzulo G, Cisek P (2016) Navigating the affordance landscape: feedback control as a process model of behavior and cognition. Trends Cogn Sci 20:414-424

Piaget J (1954) The construction of reality in the child. Basic Books, New York

Powell R (2007) Is convergence more than an analogy? Homoplasy and its implications for macroevolutionary predictability. Biol Phil 22:565-578

Powell R, Mariscal C (2015) Convergent evolution as natural experiment: the tape of life reconsidered. Interface Focus 5 doi: 10.1098/rsfs.2015.0040

Powell R, Mikhalevich I, Logan C, Clayton NS (2017) Convergent minds: the evolution of cognitive complexity in nature. Interface Focus 7 doi: 10.1098/rsfs.2017.0029

Powell R, Shea N (2014) Homology across inheritance systems. Biol Phil 29:781-806

Premack D (2007) Human and animal cognition: Continuity and discontinuity. Proc Nat Acad Sci 104:13861-13867

Raby C, Clayton N (2009) Prospective cognition in animals. Behav Proc 80:314-324

Raby CR, Alexis DM, Dickinson A, Clayton NS (2007) Planning for the future by western scrub-jays. Nat 445:919-921

Rattenborg N, Martinez-Gonzalez D (2011) A bird-brain view of episodic memory Behav Brain Res 222:236-245

Redshaw J, Suddendorf T (2013) Foresight beyond the very next event: four-year-olds can link past and deferred future episodes. Front Psychol 4 doi:10.3389/fpsyg.2013.00404

Rehkämper G, Frahm HD, Zilles K (1991) Quantitative Development of Brain and Brain Structures in Birds (Galliformes and Passeriformes) compared to that in mammals (Insectivores and Primates) Brain Behav Evol 37:125-134

Rehkämper G, Zilles K (1991) Parallel evolution in mammalian and avian brains: comparative cytoarchitectonic and cytochemical analysis. Cell Tis Res 263:3-28

Roberts WA (2002) Are animals stuck in time? Psychol Bull 128:473-489

Rosati AG (2017) Foraging Cognition: Reviving the ecological intelligence hypothesis. Trends Cogn Sci doi:10.1016/j.tics.2017.05.011

Rosati AG, Stevens JR, Hare B, Hauser MD (2007) The evolutionary origins of human patience: temporal preferences in chimpanzees, bonobos, and human adults. Curr Biol 17:1663-1668

Rosati AG, Wobber V, Hughes K, Santos LR (2014) Comparative developmental psychology: how is human cognitive development unique? Evol Psychol 12:448-473

Rose J, Colombo M (2005) Neural correlates of executive control in the avian brain PLoS Biol 3:e190

Russell J, Alexis D, Clayton N (2010) Episodic future thinking in 3-to 5-year-old children: The ability to think of what will be needed from a different point of view. Cogn 114:56-71

Sanz CM, Morgan DB (2009) Flexible and persistent tool-using strategies in honey-gathering by wild chimpanzees. Int J Primatol 30:411-427

Sayol F, Lefebvre L, Sol D (2016) Relative brain size and its relation with the associative pallium in birds. Brain Behav Evol 87:69-77

Scarf D, Gross J, Colombo M, Hayne H (2013) To have and to hold: Episodic memory in 3- and 4-year-old children. Dev Psychobiol 55:125-132

Scarf D, Smith C, Stuart M (2014) A spoon full of studies helps the comparison go down: a comparative analysis of Tulving's spoon test. Front Psychol 5 doi:10.3389/fpsyg.2014.00893

Schacter DL, Addis DR (2007) The cognitive neuroscience of constructive memory: remembering the past and imagining the future. Phil Trans Royal Soc B 362:773-786

Schacter DL, Addis DR, Hassabis D, Martin VC, Spreng RN, Szpunar KK (2012) The future of memory: remembering, imagining, and the brain. Neuron 76:677-694

Schwartz BL, Hoffman ML, Evans S (2005) Episodic-like memory in a gorilla: a review and new findings. Learn Motiv 36:226-244

Scotland RW (2011) What is parallelism? Evol Dev 13:214-227

Seed A, Emery N, Clayton N (2009) Intelligence in corvids and apes: a case of convergent evolution? Ethol 115:401-420

Seligman ME, Railton P, Baumeister RF, Sripada C (2013) Navigating into the future or driven by the past. Perspect Psychol Sci 8:119-141

Shanahan M, Bingman VP, Shimizu T, Wild M, Güntürkün O (2013) Large-scale network organization in the avian forebrain: a connectivity matrix and theoretical analysis. Front Comp Neurosci 7 doi: 10.3389/fncom.2013.00089

Shanks DR (2010) Learning: From association to cognition. Ann Rev Psychol 61:273-301

Shettleworth SJ (2010) Cognition, evolution, and behavior. Oxford University Press, Oxford

Shubin N, Tabin C, Carroll S (2009) Deep homology and the origins of evolutionary novelty. Nat 457:818-823

Shultz S, Dunbar RI (2007) The evolution of the social brain: anthropoid primates contrast with other vertebrates. Proc Royal Soc B 274:2429-2436

Sol D (2009) Revisiting the cognitive buffer hypothesis for the evolution of large brains Biol Lett 5:130-133

Starck JM, Ricklefs RE (1998) Avian growth and development: evolution within the altricial-precocial spectrum. Oxford University Press, Oxford

Stevens JR (2010) Intertemporal choice. In: Breed M & Moore J (eds) Encyclopedia of Animal Behavior, Elsevier, Amsterdam, pp 203-208

Stevens JR (2014) Evolutionary pressures on primate intertemporal choice. Proc R Soc London B 281:20140499

Striedter GF (2016) Evolution of the hippocampus in reptiles and birds. J Com Neurol 524:496-517

Striedter GF, Charvet CJ (2008) Developmental origins of species differences in telencephalon and tectum size: morphometric comparisons between a parakeet (Melopsittacus undulatus) and a quail (Colinus virgianus) J Comp Neurol 507:1663-1675

Suddendorf T (1994) Discovery of the fourth dimension: Mental time travel and human evolution. University of Waikato, Hamilton

Suddendorf T, Busby J (2003) Mental time travel in animals? Trends Cogn Sci 7:391-396

Suddendorf T, Corballis MC (1997) Mental time travel and the evolution of the human mind. Genet Soc Gen Psychol Monogr 123:133-167

Suddendorf T, Corballis MC (2007) The evolution of foresight: What is mental time travel, and is it unique to humans? Behav Brain Sci 30:299-313

Suddendorf T, Corballis MC (2008) New evidence for animal foresight? Anim Behav 75:1-3

Suddendorf T, Corballis MC (2010) Behavioural evidence for mental time travel in nonhuman animals. Behav Brain Res 215:292-298

Suddendorf T, Nielsen M, Von Gehlen R (2011) Children's capacity to remember a novel problem and to secure its future solution. Dev Sci 14:26-33

Szpunar KK, Spreng RN, Schacter DL (2014) A taxonomy of prospection: Introducing an organizational framework for future-oriented cognition. Proc Nat Acad Sci 111:18414-18421

Thom J, Clayton NS (2016) Evolutionary perspectives on prospective cognition. In: Michaelian K, Klein S, Szpunar K (eds) Seeing the future: Theoretical perspectives on future-oriented mental time travel. Oxford University Press, New York, pp 287-305

Thompson C, Barresi J, Moore C (1997) The development of future-oriented prudence and altruism in preschoolers. Cogn Dev 12:199-212

Tinbergen N (1963) On aims and methods of ethology. Ethol 20:410-433

Toussaint M (2009) Probabilistic inference as a model of planned behavior. KI 23:23-29

Tulving E (1972) Episodic and semantic memory. In: Tulving E & Donaldson W (eds) Organization of memory. Academic Press, New York, pp 381-403

Tulving E (1983) Elements of episodic memory. Oxford University Press, Oxford

Tulving E (2002) Episodic memory: from mind to brain. Ann Rev Psychol 53:1-25

Tulving E (2005) Episodic memory and autonoesis: Uniquely human? In: Terrace HS & Metcalfe J (eds) The missing link in cognition. Oxford University Press, Oxford, pp 3-56

Underwood AG, Guynn MJ, Cohen AL (2015) The future orientation of past memory: The role of BA 10 in prospective and retrospective retrieval modes. Front Hum Neurosci 9 doi:10.3389/fnhum.2015.00668

Vallortigara G, Regolin L (2002) Facing an obstacle: lateralization of object and spatial cognition. In: Rogers L & Andrew R (eds) Comparative vertebrate lateralization. Cambridge University Press, Cambridge, pp 383-444

van den Wildenberg WP, Crone EA (2005) Development of response inhibition and decision-making across childhood: A cognitive neuroscience perspective. In: Marrow JR (ed) Focus on Child Psychology Research. Nova Science Publishers, New York, pp 23-42

van der Molen MW (2000) Developmental changes in inhibitory processing: Evidence from psychophysiological measures. Biol Psychol 54:207-239

van Schaik CP, Damerius L, Isler K (2013) Wild orangutan males plan and communicate their travel direction one day in advance. PloS one 8:e74896

Vanderveldt A, Oliveira L, Green L (2016) Delay discounting: Pigeon, rat, human—does it matter? J Exp Psychol: Anim Learn Cogn 42:141-162

Veit L, Nieder A (2013) Abstract rule neurons in the endbrain support intelligent behaviour in corvid songbirds Nat Comm 4 doi:10.1038/ncomms3878

Vlamings PH, Hare B, Call J (2010) Reaching around barriers: the performance of the great apes and 3–5-year-old children. Anim Cogn 13:273-285

Wagner GP (2007) The developmental genetics of homology. Nat Rev Genet 8:473-479

Wang Y, Brzozowska-Prechtl A, Karten HJ (2010) Laminar and columnar auditory cortex in avian brain. Proc Nat Acad Sci 107:12676-12681

West-Eberhard MJ (2003) Developmental plasticity and evolution. Oxford University Press, Oxford

Wobber V, Wrangham R, Hare B (2010) Bonobos exhibit delayed development of social behavior and cognition relative to chimpanzees. Curr Biol 20:226-230

Wray GA (2002) Do convergent developmental mechanisms underlie convergent phenotypes? Brain Behav Evol 59:327-336

Zelazo PD, Frye D, Rapus T (1996) An age-related dissociation between knowing rules and using them. Cogn Dev 11:37-63

Zentall TR, Clement TS, Bhatt RS, Allen J (2001) Episodic-like memory in pigeons. Psychon Bull Rev 8:685-690

Zinkivskay A, Nazir F, Smulders TV (2009) What–where–when memory in magpies (Pica pica). Anim Cogn 12:119-125

Corvids, the bird family that includes ravens and crows, are renowned for their cognitive abilities. This thesis investigates two cognitive skill-sets in corvids – planning and inhibitory control – in order to gain insights on the evolution of complex cognition.

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