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On the origins of physical cognition in corvids

IVO JACOBS
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Corvids, the bird family that includes crows and ravens, have remarkable cognitive abilities. This thesis investigates what they understand about the physical world by asking how their physical cognition works, how it develops, what it is for, and how it evolved.

On the origins of physical cognition in corvids

Ivo Jacobs



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DOCTORAL DISSERTATION

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Title and subtitle: On the origins of physical cognition in corvids		
<p>Abstract</p> <p>Physical cognition involves a host of cognitive abilities that enable understanding and manipulation of the physical world. Corvids, the bird family that includes crows, ravens and jays, are renowned for their cognitive abilities, but still little is known about their <i>folk physics</i>. This thesis explores the origins of physical cognition in corvids by investigating its mechanisms, development, fitness value and phylogeny in a wide context that includes theoretical and empirical studies.</p> <p>String pulling is a valuable paradigm for addressing these questions. Many animals can pull a string with food attached to its end, but uncovering the cognitive abilities involved in this behaviour requires further testing. Paper I reviews the string-pulling paradigm, which is one of the oldest tests of animal cognition. It is a highly suitable test for species comparisons, socio-ecological correlations, and phylogenetic questions. Paper II tests several corvids, apes and peafowl on a string-pulling task where the first pulls do not result in the food moving closer. Despite the absence of such visual feedback, most subjects pulled strings in completely, although corvids appeared to choose randomly.</p> <p>Tool use is the archetypical example of physical cognition. Many corvids are remarkably adept at using tools in experimental settings. Paper III reviews animal tool use in general. It is now clear that customary tool-using species do not necessarily outperform their non-tool-using relatives on tests of physical cognition. For corvids that frequently use tools in the wild, such as New Caledonian crows and 'Alalā, tool use appears to have a significant fitness value and may have resulted in morphological adaptations. Paper IV describes a novel tool-use mode in New Caledonian crows. They inserted sticks into objects and then moved away, thereby transporting both. One crow could not grasp the target object, which suggests that such <i>insert-and-transport</i> tool use facilitates control over unwieldy objects. Paper V briefly argues that some corvids have shown the ability to make novel causal interventions, although this question should be addressed in a clearer theoretical framework that makes testable predictions.</p> <p>Sensorimotor cognition is a set of fundamental cognitive abilities that enables the integration of sensory and motor information into practical behaviour. It underlies much of corvid physical cognition. Paper VI investigates the development of sensorimotor cognition in ravens. Their skills developed rapidly and exceeded those of some mammals. They reached the same final sensorimotor stage as great apes, albeit at a markedly accelerated rate. The propensity of corvids to cache objects was investigated in Paper VII. Ravens, which often cache food, frequently cached objects, but surprisingly at similar rates as non-food-caching jackdaws. New Caledonian crows mostly cached objects that resembled functional tools.</p> <p>Anthropomorphism is the attribution of human traits to animals. Fear of mistakenly anthropomorphising animals has resulted in biased principles and an uneven burden of proof, which may hinder scientific progress more than it is supposed to offer protection against making mistakes. Cognitive zoology should not be misguided by overcompensating for such potential pitfalls.</p>		
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*Two times to Charles D.
Ageless curiosity as key
For their discovery of wonderlands
Under ground and at sea*

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PAPER I

Jacobs, I. F., & Osvath, M. (2015). The string-pulling paradigm in comparative psychology. *Journal of Comparative Psychology, 129*, 89-120. doi: 10.1037/a0038746
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<http://psycnet.apa.org/journals/com/129/2/89/>

PAPER II

Jacobs, I. F., von Bayern, A., & Osvath, M. (in review). Apes and corvids do not require visual feedback for successful string pulling.

PAPER III

Jacobs, I. F., & Osvath, M. (in press). Non-human tool use. In T. K. Shackelford & V. A. Weekes-Shackelford (Eds.), *Encyclopedia of Evolutionary Psychological Science*. Springer.
The final publication is available at www.springerlink.com.

PAPER IV

Jacobs, I. F., von Bayern, A., & Osvath, M. (2016). A novel tool-use mode in animals: New Caledonian crows insert tools to transport objects. *Animal Cognition, 19*, 1249–1252. doi: 10.1007/s10071-016-1016-z
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PAPER V

Jacobs, I. F., von Bayern, A., Martin-Ordas, G., Rat-Fischer, L., & Osvath, M. (2015). Corvids create novel causal interventions after all. *Proceedings of the Royal Society B, 282*, 20142504. doi: 10.1098/rspb.2014.2504
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PAPER VI

Jacobs, I. F., Kabadayi, C., & Osvath, M. (in review). Development of executive functions in common ravens: Motor self-regulation and sensorimotor cognition.

PAPER VII

Jacobs, I. F., Osvath, M., Osvath, H., Mioduszevska, B., von Bayern, A. M., & Kacelnik, A. (2014). Object caching in corvids: incidence and significance. *Behavioural Processes*, *102*, 25-32. doi: 10.1016/j.beproc.2013.12.003

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<http://www.sciencedirect.com/science/journal/03766357>

Other papers by the author not included in the thesis

Jacobs, I. F., & Gärdenfors, P. (in press). The false dichotomy of domain-specific versus domain-general cognition. *Behavioral and Brain Sciences*.

Jacobs, I. F., & Osvath, M. (in press-a). Innate and learned tool use. In T. K. Shackelford & V. A. Weekes-Shackelford (Eds.), *Encyclopedia of Evolutionary Psychological Science*. Springer.

Jacobs, I. F., & Osvath, M. (in press-b). Meta-tool. In T. K. Shackelford & V. A. Weekes-Shackelford (Eds.), *Encyclopedia of Evolutionary Psychological Science*. Springer.

Jacobs, I. F., & Osvath, M. (in press-c). Proto-tool. In T. K. Shackelford & V. A. Weekes-Shackelford (Eds.), *Encyclopedia of Evolutionary Psychological Science*. Springer.

Jacobs, I. F., & Osvath, M. (in press-d). Social tool. In T. K. Shackelford & V. A. Weekes-Shackelford (Eds.), *Encyclopedia of Evolutionary Psychological Science*. Springer.

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

Embla the dinosaur approaches a bright-yellow, worm-shaped, googly-eyed, plastic toy. She is only seven weeks old and has just learned to walk. Her feet clumsy without practice and mouth inept without teeth, the toy's destruction will take some time. She tosses it off the table, but it never reaches the floor. Tied to a string, the limp worm now dangles from the table's edge—close to her bright-blue eye but far from her four-toed grasp. She pulls the string in frustration, which happens to bring the toy closer. With the rest of the unkindness observing, her walnut-sized brain finds a solution as she presses her scaly black foot on a loop of the string. She yanks the toy off of the string after it comes within reach, and proceeds with the inevitable demise of her artificial foe. Meanwhile, a bipedal ape, with whom she shares an ancestor that lived millions of years ago, scribbles in his notebook and wonders how creatures so different can be so similar.

Embla and her raven kin belong to the corvid family (*Corvidae*), which includes crows, jackdaws, rooks, magpies, jays, treepies, choughs, and nutcrackers. More than 120 corvid species are scattered around the globe, living in blistering deserts, dense forests, high mountains, tropical islands, freezing tundras, monotonous farmlands, and crowded cities. Many of them survive in rapidly changing environments where other birds cannot. Such behavioural flexibility demonstrates the cognitive abilities of corvids that this thesis is about. It is no coincidence that Odin's ravens, Huginn and Muninn, are named after mind and memory.

Physical cognition is an umbrella term that includes but is not limited to: instrumental learning, spatial knowledge and navigation, means-end understanding, tool use and manufacture, object representation, memory, causal understanding, analogical reasoning, sensorimotor cognition, categorisation, insight, innovative capacities, numerical competence, functional generalisation, concept formation, affordance learning, and technical reasoning (Emery & Clayton, 2009; Hood & Santos, 2009; Parker & McKinney, 1999; Povinelli, 2000; Reznikova, 2007; Shettleworth, 2010b; Tomasello & Call, 1997; Wynne & Udell, 2013). In short, the kind of *folk physics* we also use in our daily lives: how we understand and interact with the physical world around us.

Despite many ancient and cross-cultural portrayals of the wit of corvids (Marzluff & Angell, 2005), research on corvid cognition was scarce until a few decades ago. It is now clear that some of these stories are more than just folktales. One notable example is Aesop's fable of the crow and the pitcher: a thirsty crow comes across a

pitcher filled with water but cannot reach it because the water level is too low, so the crow drops stones into it to make the water level rise. Several corvid species have shown this ability in controlled experiments (Jelbert et al., 2015), and although it remains disputed what corvids really understand about water displacement, it shows that even millennia-old fables can be a valuable starting point for research.

There is an older and still larger research programme on primates, which often forms the basis for research on corvids. Species comparisons are a great tool in the study of animal cognition—its evolution in particular. For lineages that diverged over 300 million years ago (see Figure 1), the cognitive abilities of corvids and great apes are remarkably similar (Güntürkün & Bugnyar, 2016; Plotnik & Clayton, 2015; Seed et al., 2009; Taylor, 2014; van Horik et al., 2012). This includes many aspects of physical cognition as mentioned above. However, the evolutionary processes that gave rise to these cognitive similarities are poorly understood (Osvath et al., 2014a).

While putting together the puzzle of physical cognition in corvids, it becomes clear that many pieces are missing and that the puzzle might be larger than anticipated. This thesis attempts to find some of these missing pieces and put them in correct locations relative to the others, which may involve rearrangement of previously placed sections. Pieces are added to these pre-existing parts, which has the consequence that this thesis partially follows an established uneven distribution. Nonetheless, by identifying open areas we can work towards creating an eventually clearer picture.

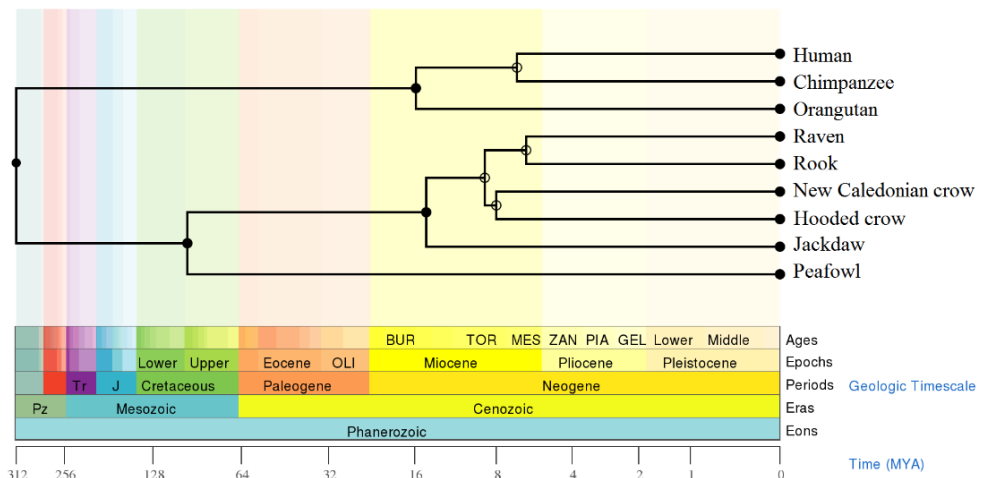


Figure 1. Phylogenetic tree of species tested in the empirical papers of this thesis
 The eight non-human species tested in the empirical papers (PAPERS II, IV, VI AND VII). Many other species are compared through literature studies. Created with timetree.org.

1.1 Structure of the thesis

This thesis is organised around three paradigms and cognitive abilities, which I discuss in separate chapters. Ideally for a thesis on cognition, all chapters should centre on cognitive abilities, but extensive research has shown that the paradigms of the next two chapters cannot be summarised as such, although they have historically often been described as a single cognitive ability. I chose these particular paradigms and physical cognitive abilities because they involve a host of cognitive building blocks that, aside from being interesting in themselves, can be studied developmentally, comparatively, and evolutionarily. Chapter 2 focuses on the string-pulling paradigm, wherein many animals have shown the ability to pull a string to obtain food attached to its end. PAPER I reviews this paradigm and PAPER II is an empirical study on many species. Tool use is the topic of Chapter 3. It is the archetypical example of physical cognition in animals, but this view is now poorly supported, as we discuss in PAPER III, which is a general review of tool use in animals. We describe a novel form of tool use in New Caledonian crows in PAPER IV. Causal cognition is included in this chapter, which is not exclusive to tool use or physical cognition overall but underlies much of it. PAPER V discusses the conceptual confusion around this cognitive ability and its presence in corvids. Chapter 4 is about sensorimotor cognition, which is fundamental to several other cognitive abilities. We investigate its development in ravens in PAPER VI, and empirically compare object-directed behaviour of several corvids in PAPER VII. In Chapter 5 I review misguided views on anthropomorphism (ascribing human traits to animals) and related issues that hinder research on animal minds, including physical cognition in corvids.

“Origins” in the title of this thesis should be conceived of in the widest possible manner. *Cognitive zoology*, a term originating in our research group, emphasises that cognition is an integral part of all facets of animal life. It is an interdisciplinary field, and for a good reason. Considering this kind of research is only around a century and a half old, it has had a surprisingly large number of names (and associations with other disciplines), such as: animal behaviour, animal cognition, animal intelligence, animal psychology, behaviourism, cognitive biology, cognitive ecology, cognitive ethology, comparative psychology, ethology, evolutionary anthropology, evolutionary cognition, evolutionary psychology, neuroecology, phylogenetic comparative psychology, and sociobiology. Traditionally, these disciplines either had theoretical standpoints that turned out to be incorrect, or they were limited in their scope. Cognitive zoology aims to avoid these pitfalls by placing cognition into a larger zoological context that may overlap with some of these disciplines. A useful method towards achieving this goal may be the framework provided by Tinbergen’s questions.

1. 2 Tinbergen's questions

More than half a century ago, Tinbergen (1963) defined ethology as the biological study of behaviour. Psychology, he claimed, was developed too hastily in hopes of becoming a natural science, and thereby skipped the important observational and descriptive stages essential to the study of all natural phenomena. He argued that the aims and methods of ethology had been unclear: “we are still very far from being a unified science, from having a clear conception of the aims of study, of the methods employed and of the relevance of the methods to the aims” (p. 410). He emphasised the value of observation and description in natural settings as a starting point for this young science. His conviction was that in order to reach an integrated, comprehensive understanding of behaviour in all its biological aspects, we must ask and explicitly address the following four questions:¹

- Mechanism (causation or control): how does it work?
- Development (ontogeny): how does it develop?
- Fitness value (function or survival value): what did it evolve for?
- Phylogeny (evolution): how did it evolve?

In this thesis, I investigate physical cognition in corvids, and specifically string pulling, tool use, causal cognition and sensorimotor cognition, in the context of these questions. However, Tinbergen (1951, 1963) might not have approved of the content of this thesis because he regarded many cognitive concepts – even learning and play – to have subjectivist and anthropomorphic undertones that are not appropriate in the objective study of behaviour. I discuss this issue in Chapter 5. The mere idea of animals being cognitive was unacceptable to many scientists at that time, when it was mostly a question of subjective experience, which should be a fifth question according to Burghardt (1997). Since attributing cognition to animals is now widely accepted, especially when disregarding the question of subjective experience for the moment, I see no major problem in asking Tinbergen's questions about animal cognition. That is not to say that this approach is perfect, but I am convinced that it is better than the conflicting sub-sciences and isolated “-ism's” that he aimed to avoid. Cognitive abilities then fall under the question of mechanism, as they may be the immediate causes (or cues) of behaviour or control it (Burghardt, 1997; Hogan, 2005; MacLean et al., 2012; Shettleworth, 2010, 2012). I will now briefly introduce the four questions when applied to physical cognition.

¹ Tinbergen's original terms (here in parentheses) are replaced with clearer, more appropriate and modern terminology (e.g., Bateson & Laland, 2013; Burkhardt, 2005, 2014; Dewsbury, 1992). The questions of mechanism and development are often viewed as proximate (“how”) questions, and fitness value and phylogeny as ultimate (“why”) questions. I do not use this distinction here because it is problematic for several reasons, such as its oversimplification of causality and its incompatibility with contemporary concepts such as evo-devo, epigenetic inheritance, niche construction, and cultural evolution (Dewsbury, 1992; Laland et al., 2011, 2013, 2015).

Mechanism. How does physical cognition work in corvids? The question of mechanism focuses on what cognitive abilities corvids have and how they use them, and is undoubtedly the most investigated. Mechanistic questions are often addressed within the context of tool use (e.g., whether individuals select appropriate tools based on some understanding of their functional properties), or through other problem-solving tasks investigating means-end understanding (e.g., string pulling) or causal cognition.

Development. How does physical cognition develop in corvids? Within ethology, the question of development has historically focussed on innateness and instinct, which are presumably independent of learning. This dichotomy no longer holds and is replaced by views that integrate rather than separate them (Bateson & Curley, 2013; Burkhardt, 2005; Jacobs & Gärdenfors, in press). Behavioural mechanisms are always investigated at a certain developmental time, so these questions are only pragmatically distinct (Bateson & Laland, 2013). Investigating the development of physical cognition in corvids reveals much about how their abilities are formed and what their building blocks are.

Fitness value. What are the physical cognitive abilities of corvids for? This question was, and sometimes still is, asked in terms of function, survival value, adaptive significance, or design. These are problematic because: function has several different meanings, which may be accompanied by accusations of teleological reasoning; survival value leaves out inclusive fitness; adaptive significance carries adaptationist assumptions and does not distinguish between current and past utility; and design has creationist connotations (Bateson & Laland, 2013). When adding cognition to this question it becomes increasingly tricky, as the value of much cognition appears to be its flexibility; i.e., it can be used extensively for behaviours that were not originally selected for (Osvath et al., 2014a). Concerning physical cognition, this question asks why corvids have evolved particular cognitive abilities and whether these help them survive and reproduce.

Phylogeny. How did physical cognition evolve in corvids or in their ancestors? In Tinbergen's time, the question of phylogeny was difficult to answer. It still is, but progress in phylogenomics, epigenetics, cladistics and statistics bring plausible answers within reach (Bateson & Laland, 2013; MacLean et al., 2012). It begins with describing which species has the trait in question and, if possible, to what extent. This is why, seemingly paradoxically, this thesis includes non-corvids when investigating corvid cognition.

2. String pulling

One of the oldest tests of animal cognition is pulling a string to bring food attached to it within reach. More than 200 studies have tested over 170 species on this string-pulling paradigm, as we describe in our review (PAPER I). The last few years have seen an explosive interest in this paradigm, especially for testing birds; however, divergent methods, descriptions, and interpretations have often resulted in unnecessary conceptual confusion. One of our main points is that any given configuration of string patterns is by itself not sufficient for testing a species' physical cognitive abilities. Many explanations have been given for string pulling, ranging from instinct to insight. For this reason, it is imperative that researchers test animals on several configurations and keep track of their relevant experience and other factors that may affect performance.

2.1 Mechanism

In one influential account, pulling a single string shows means-end understanding because it involves the deliberate execution of a sequence of actions to overcome the distance to an out-of-reach reward (Piaget, 1951, 1952, 1954). It is now clear that string pulling may have several underlying cognitive mechanisms, not all this sophisticated. In PAPER I we discuss the wide variety of cognitive abilities ascribed to animals based on their string-pulling performance. Depending on time, place and the observer's beliefs, the same behaviour of an animal pulling a string could be described as an interesting trick, insight, innate action patterns, or animal cruelty. Divergent explanations for a single phenomenon are often proposed, which can be a significant limitation to progress in this research (see Chapter 5). By controlling for several factors that may affect string-pulling performance, or at least becoming aware of them, researchers can design experiments around these limitations, which provides them with better explanations.

Perceptual feedback is one such factor that may explain string pulling to a large extent but has not been investigated often enough. Food moves closer with every pull in most configurations, which could be incentive enough for the animal to continue pulling until it is within reach. Explanations involving cognitive abilities such as means-end understanding, insight and an understanding of connections are

then superfluous. This issue extends beyond the string-pulling paradigm as many tests of physical cognition involve an out-of-reach reward moving closer as the result of an animal's actions (e.g., Cole et al., 2012; Jelbert et al., 2015; Völter & Call, 2012).

Some animals do not require visual feedback for successful string pulling. For instance, Swedish ice fishers have often reported that crows and ravens have stolen their fish by successfully pulling the lines up (Holmberg, 1957; Larsson, 1958). The length of the lines and darkness of the water in winter makes it difficult if not impossible for the birds to see the fish. However, the experience of these corvids is not known, so it is possible that it took them many trials before succeeding or that they can discriminate empty and baited fishing lines by weight, which is a different kind of perceptual feedback.

Fortunately, some experimental studies have directly addressed these possibilities. Several neotropical parrots pulled a vertical string connected to a reward more often than a similar broken string. Both strings were coiled on a table underneath the parrots, so that pulling did not immediately result in either visual or proprioceptive feedback (Schuck-Paim et al., 2009). This study has never been replicated with corvids, but Taylor and colleagues (2012b) tested New Caledonian crows (hereafter "NC crows") on a similar horizontal set-up. Most crows stopped participating after some trials, and none of them chose the correct string above chance level. The authors therefore concluded that string pulling in NC crows is governed by perceptual feedback.

We conducted a study to explore alternative explanations of string-pulling behaviour in NC crows, common ravens, jackdaws, a rook, a hooded crow, peafowl, chimpanzees and Sumatran orangutans (PAPER II). Corvids and apes are among the best performers on string-pulling tests, but this is the first-ever empirical study to directly compare string pulling in mammals and birds, and also the first to test peafowl. The first condition was similar to the coiled test of Taylor and colleagues (2012b). The second condition involved straight strings, with one being broken to test the effects of the gap. The third condition was identical except that a piece of paper was covering the part of the correct string where the gap would be, which introduces a perceptual but not a structural discontinuity. We used these conditions and five variables to test five hypotheses that make different predictions based on visual feedback, operant conditioning, visual continuity, means-end understanding, and means-end understanding *after* random choice.

Results showed that three apes and two NC crows did not rely on visual feedback because they chose the correct coiled string significantly above chance. The hooded crow approached significance. Two orangutans performed above chance on all three conditions. In contrast, most corvids performed at chance levels on all conditions, did not improve, and had side biases. However, reliance on visual feedback does not explain these results, even for subjects performing poorly, because they stopped pulling more often when they chose the incorrect than the correct string. It appears

they experienced difficulties choosing between strings, but after they did they could anticipate whether pulling would result in a food reward.

Several string-pulling studies have been published after our review was completed, and I will briefly discuss those involving species tested for the first time. Great-tailed grackles, a behaviourally flexible invasive species, failed to pull vertical and horizontal strings (Logan, 2016), while two out of 31 closely-related Carib grackles did succeed on the vertical test. Barbados bullfinches were more successful (18/42 passed), but their performance was not related to neophobia, shyness, problem solving, discrimination, or reversal learning (Audet et al., 2016). This suggests that string-pulling tests capture a unique set of physical-cognitive abilities, at least for this species.

The majority of wild kaka, a parrot species closely related to the highly successful string-pulling kea (Werdenich & Huber, 2006), were able to completely pull in vertical strings. Successful individuals spent more time interacting with the string, showed more exploratory behaviours, and occasionally learned from observing others pull strings (Loepelt et al., 2016). Red-shouldered macaws and black-headed caiques were tested on a horizontal string-pulling task. In one condition, the tray containing food was of the same size for both strings, but had to pass through a gap in a barrier, with only one gap being wide enough. In another condition, both gaps were of equal width but the trays were of different sizes. After passing one condition, most subjects did not perform above chance when tested on the other condition, with the exception of one caique that appears to have attended to the size of both the tray and the gap simultaneously (van Horik & Emery, 2016). The number of elements in a task that subjects should monitor in order to perform well is a useful method of quantifying the task's complexity (Fragaszy and Cummins-Sebree, 2005; Laumer et al., 2016).

Some zebra finches and diamond firetails can solve a horizontal string-pulling task, but Bengalese finches could not, possibly because they were not very explorative or active (Schmelz et al., 2015). Most juvenile Hamadryas baboons, like their close relatives, can successfully pull in horizontal strings (Anikaev et al., 2015). For the first time, an animal that is not a bird or mammal has solved a string-pulling test. Bumblebees were trained to pull a string connected to an artificial flower, but they failed when the strings were coiled and visual feedback was not immediate. Two out of 135 bumblebees spontaneously pulled a straight string within 10 minutes. Social learning allowed the behaviour to spread through the colony (Alem et al., 2016).

Two corvid species can be added to the list of successful string-pullers. Several wild Steller's jays solved a vertical string-pulling task. Successful birds were more persistent, explorative, bolder, and in some cases first observed others pull strings (Harvey, 2015). Western-scrub jays were tested on several horizontal patterns. They showed goal-directedness by performing above chance on the parallel condition, but overall they appeared to rely on proximity because they failed the slanted and

crossed tests, and preferred to pull the string near the side where the reward was closest (Hofmann et al., 2016).

The variety in experiments conducted, species tested, and explanations offered attests to the broad utility of the string-pulling paradigm. It is a valuable tool in the study of physical cognition in corvids, but it should be wielded with care. Due to the many different cognitive mechanisms that may underlie string pulling, strong conclusions should not be made without exploring possible confounding factors and administering several conditions.

2.2 Development

The development of string pulling has mostly been investigated as part of the Piagetian sensorimotor series (see Chapter 4). In humans, string pulling is considered to be one of the first means-end actions performed by infants when they are approaching their first birthday. Embla, the avian dinosaur from the introduction, successfully pulled up a vertical string in her seventh week. We describe the ravens' development of sensorimotor cognition, which includes string pulling, in PAPER VI. Their failures can be very informative. For example, they often failed to step on a loop of string to anchor it, or pulled up an empty string after having just removed the reward attached to it. This goes against explanations that involve sudden “aha!” moments, although it does not exclude the possibility of this happening in adult ravens. Some fledglings had a side bias from the beginning, which suggests side biases do not solely arise from repeated testing, as also concluded in PAPER II. Several observations of juvenile ravens and NC crows trying to fly off with a stopwatch hanging on a string around my neck supports the explanation that successful string pulling is, in itself, not a good indicator of understanding physical connection (PAPER I). Heinrich (1995a) describes a 1.5-year-old raven that never successfully pulled vertical strings. She once stole the food, still attached to the string, pulled up by a conspecific. After getting yanked back, she never tried to do so again. It took two American crows several additional trials to learn to drop the food attached to a string when flying off with it.

Heinrich's (1995a) seminal study on string pulling in ravens also featured some observations on juveniles that were 3–4 months old.² In contrast to our ravens, they only pecked and yanked at the vertical strings, never succeeding in pulling it up. He

² In his book *Mind of the Raven*, Heinrich (1999) writes that this idea came to him when reading an article about it in *Ranger Rick* magazine, which was a present for his son. Like Aesop's fable, this is another example of how solid research can be based on any source, no matter how anthropomorphic, anecdotal or unscientific it may seem (see Chapter 5). Unfortunately, such unconventional studies may be met with unnecessarily harsh criticism; his paper was rejected five times (Heinrich, 1999).

retested them two years later, during which they had not been exposed to food on strings, and most of them pulled it up immediately. This suggests that their general development in the intermediate years enabled them to successfully solve a virtually novel problem without having learned the appropriate action sequence in this specific context.

Another group of ravens was tested at the ages of nine and ten months. They had been habituated to strings but were never given the opportunity of pulling up one and stepping on it. After spending some minutes pecking, yanking and twisting the string, five out of six birds succeeded in pulling it up (Heinrich, 1999; Heinrich & Bugnyar, 2005). Their explorative and experimental tendencies were intermediate between younger and older ones. Together with our study (PAPER VI), this shows that the propensity to explore strings decreases with age, and that general development without specific experience with strings may be sufficient to immediately pull up vertical strings.

Similarly, wild Steller's jays appear to be better string-pullers as adults than juveniles (Harvey, 2015). Ravens and Steller's jays are the only corvids that have been studied in the development of string-pulling abilities. They follow a general pattern found across many mammal and bird species (PAPERS I AND VI). Juveniles are often more explorative and playful, and therefore more likely to attempt string-pulling tasks. If adults try to pull strings they are typically more successful than juveniles because they have better motor control, attention and are more cognitively developed. Studies on string pulling should monitor such behavioural differences because they can greatly influence performance. A disinterested animal that does not attempt to pull strings should not be said to lack this ability.

2.3 Fitness value

String pulling has sometimes been regarded as a meaningless test of animal cognition due to its ecological parallels (e.g., Altevogt, 1954; Newton, 1967; Thienemann, 1933). These critics claim that if pulling and stepping is a natural behavioural repertoire, string pulling cannot be clearly used as a valid test. Many birds use their feet to hold food, and some even pull caterpillars by their threads, or pull and step on twigs to get at berries and insects (PAPER I). The aforementioned crows and ravens pulling fishing lines show that this behaviour can also be beneficial for animals living in closer proximity to humans.

The importance of these foraging behaviours for survival has not been quantified for corvids, but orangutans obtain 61% of their plant diet by pulling branches to reach leaves (Chevalier-Skolnikoff et al., 1983). Anchoring food by stepping on it is of general utility, which only occasionally may be used for behaviours resembling string pulling. Bird that use their feet in feeding typically perform better on string-

pulling tasks than those that do not (PAPER I). Comparative studies should take this factor into consideration when choosing species to be tested or conclusions to be drawn. If dissimilar bird species are tested, configurations with horizontal strings may offer a fairer comparison.

Although there are no studies on the fitness value of the cognitive abilities underlying string pulling in corvids, which have been studied in a broader socio-ecological context (e.g., Jolles et al., 2013; Pfuhl et al., 2014), they have been done on other birds. In a large study on great tits, 25% obtained food from a vertical string within an hour. Successful individuals also succeeded when retested one or two years later, and they were more likely to solve an operant lever-pulling task. Their performance was not predicted by exploration tendency, feeding motivation, activity level, neophobia, sex, body condition, or motivation to feed after human disturbance, which shows their cognitive abilities to be individually consistent and relatively independent from ecological factors (Cole et al., 2011). Problem-solving³ females had larger clutch sizes, without a reduction in fledgling condition or adult viability, and were more efficient at exploiting their environment. However, this potential fitness effect of cognitive abilities was offset by problem solvers being more likely to abandon their nests, which indicates sensitivity to disturbance and predation pressure, leading to little or no overall selection (Cole et al., 2012). This is the first study to provide empirical evidence for a positive link between problem-solving ability and reproductive success, which had frequently been predicted to exist (Healy, 2012).

2.4 Phylogeny

Around 170 species have been tested on the string-pulling paradigm, which therefore offers an exceptional sample size for evolutionary studies (PAPER I). A phylogenetic tree of species that have succeeded on single string-pulling tasks is shown in Figure 2. Although this may not involve means-end understanding, single-string pulling may be seen as an essential precursor to it. It also shows that these species are capable of executing the necessary actions and have sufficient sensorimotor cognition (see Chapter 4), making them suitable targets for deeper research.

³ Although this study measured problem-solving ability as success rate on the lever-pulling task, these results can probably be extended to (single straight) string pulling because both involve operant conditioning mediated by a perceptual-motor feedback loop (Cole et al., 2012) and performance between them is strongly correlated (Cole et al., 2011). Studies on the fitness value of specific cognitive abilities, rather than broad problem-solving abilities such as lever- or string-pulling, are an important avenue for future research.

Primates constitute the vast majority of mammals tested. Many carnivores succeed as well. Cetaceans would be a valuable taxon for testing, considering their complex cognitive abilities with an anatomy significantly different from other mammals. Quokkas and an unknown kangaroo species are the only marsupials that have been tested, and monotremes are absent. Many parrots and passerines can pull single strings, but not many other birds have been tested. Our empirical study showed that peafowl, the first fowl (*Galloanserae*) ever tested, were remarkably goal-directed in their string pulling (PAPER II). Paleognaths would be an especially important addition because they are a major bird clade that is distantly related to other birds tested so far. Investigating string pulling in non-avian reptiles is key for formulating evolutionary scenarios in amniotes. Bumblebees, the only invertebrate species ever tested, showed a surprising capacity for learning this behaviour, which encourages further research on invertebrates.

This large sample of species succeeding on a cognitive task has not yet been used in major phylogenetic analyses. Deaner and colleagues (2006) ran a meta-analysis of string pulling and several others tests in primates. They only used studies that compare species directly, which, unfortunately, often feature poorly described results and lack details on task performance (e.g., Guillaume & Meyerson, 1931; Herrmann et al., 2007; Millikan & Bowman, 1967). They found that apes generally outperform monkeys, but there was insufficient data for fine-grained analysis. Nonetheless, the string-pulling performance of primates appears to correspond well with the overall ranking of their physical cognition (Deaner et al., 2006; Reader et al., 2011).

MacLean and colleagues (2012) argued that not enough phylogenetic research is done in animal cognition. By testing a wide variety of species on a certain cognitive ability or task and comparing their phylogenies, four major questions can be addressed: (1) the degree to which phylogeny predicts performance; (2) whether cognitive abilities are correlated with species-specific factors such as anatomy and socio-ecology (this question concerns fitness value); (3) reconstructing the ancestral state for this cognitive ability and (4) phylogenetic targeting, which involves finding the most suitable species that provides the strongest test of an evolutionary hypothesis. This requires large datasets on many species, tests that are similarly applicable to these species, collaboration across research groups, established phylogenetic trees, and sufficient knowledge and control over contextual variables such as motivation, perception, attention, rearing conditions, motor skills, and experience. There are clearly many pitfalls in research on the phylogeny of cognition, but as long as they are reasonably understood and controlled, progress can be made. Phylogeny is arguably the most difficult of Tinbergen's questions to address, so it will take time to develop suitable methods and large databases on many species.

The string-pulling paradigm is highly suitable for these phylogenetic comparative methods. MacLean et al. (2012, p. 233) describe the first broad comparative studies

to be successful if they “(1) minimize or eliminate the need for training, (2) require few trials/sessions per subject, and (3) are easily implemented with few methodological modifications across species.” We discuss these merits of the string-pulling paradigm in our review (PAPER I): (1) many species pull strings immediately, or will do so after habituation or brief training; (2) performance can therefore be measured from a study’s start and varied along many dimensions thereafter; (3) the material requirements are minimal, and it is possible to adjust methods to each species, for example by basing string position and length on the species’ physical size. Analysing string-pulling performance with phylogenetic comparative methods is therefore an obvious aim of future research.

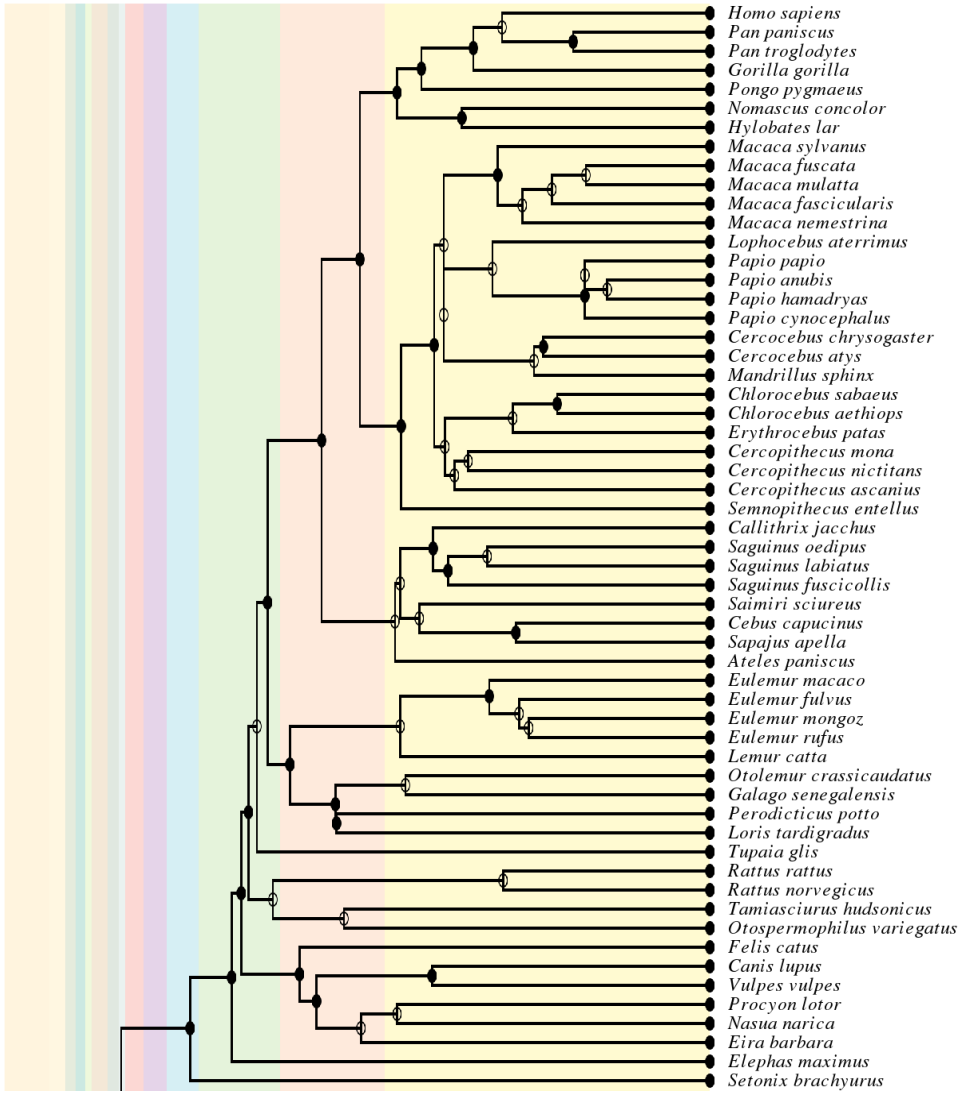


Figure 2. All species that have shown the ability to pull single strings (continued on next page)

Species are taken from PAPER I and supplemented with those reported since (Section 2.1). Species with ambiguous status or that are unrecognized by the timetree database are not included, with the exception of bumblebees (*Bombus* sp.), where the string-pulling species was not found in the database so another was chosen (which does not affect the structure of this phylogenetic tree). Mammals are shown on this page, birds and bumblebees on the next. The corvid family is marked by a bracket and includes ten species, of which six from the *Corvus* genus, that have been tested thusfar. Created with timetree.org.



3. Tool use

The ability to use and manufacture tools has long been regarded as uniquely human. Oakley (1956, 1972), for example, spoke of “Man the tool-maker”. This position can no longer be maintained; entire books have been written about tool use in animals, revealing a large number of species using tools in both captivity and in the wild, and using countless different actions for numerous different functions that reflect a range of underlying cognitive capacities (Baber, 2003; Berthelet & Chavaillon, 1993; Sanz et al., 2013; Shumaker et al., 2011). We review non-human tool use in PAPER III. Research has historically mostly focused on the underlying cognitive abilities of tool use, but with increasing attention for questions on development, ecology and evolution, it can fittingly be placed in Tinbergen’s framework.

3.1 Mechanism

Any discussion on tool use inevitably runs into the difficulty of defining it, or worse, does not define it at all. Clarity in definitions goes a long way, as otherwise there is a large chance of misunderstanding and disagreement arising where none may actually exist. In this thesis, I use the definition by Shumaker and colleagues (2011, p. 5) of tool use as: “The external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool.”

Their definition is not flawless, but any definition will be imperfect given the heterogeneous nature of tool use and the difficulty of finding the right balance between specificity and generality. Unlike some other authors (e.g., Bentley-Condit & Smith, 2010), Shumaker and colleagues define tool use in terms of motor actions (*modes*), not possible functions. Modes are descriptive categories that may have various functions, both within and across species, which have to be interpreted from context. However, they still require tool use to have some purpose, because otherwise all object manipulation could be considered as tool use, and then the term would become meaningless. Tool-use modes and functions can be wide-ranging,

such as throwing a rat on a string towards food to pull it back after it grabs the food, placing a stone underneath an anvil stone to stabilise it, hitting a conspecific with a dead monkey, hiding from predators in a coconut shell, or blocking a drain pipe to create a bathing place (PAPERS I AND III; Bentley-Condit & Smith, 2010; Jacobs & Osvath, in press-b, in press-d; Shumaker et al., 2011; St Amant & Horton, 2008)

It is now clear that sophisticated cognitive abilities do not necessarily accompany tool use. Many species (especially invertebrates) are stereotypical tool users in that tool use is widespread and shows little variation within the species, develops without social contact, and does not require much working memory (Hunt et al., 2013). Moreover, tool-using species often do not outperform their non-tool-using relatives on physical cognition tests, even if they involve tool use (Emery, 2013; Shumaker et al., 2011; Tebbich & Teschke, 2013).

An example of a species that is not known to use tools in the wild but has shown remarkable skills in tool-using tasks is the Goffin's cockatoo. After one captive male spontaneously manufactured and used stick tools to rake in out-of-reach food (Auersperg et al., 2012), several observing cockatoos learned to do so too, while those that observed only the movements of tool and food caused by hidden magnets did not (Auersperg et al., 2014). Some of these successful birds also made functional tools from different materials, such as twigs and cardboard (Auersperg et al., 2016). In another task, Goffin's cockatoos were able to simultaneously consider the functionality of a tool for obtaining out-of-reach food and the quality of this food type compared to another food type that was directly available. They made optimal decisions based on this information, although the number of task elements they could simultaneously process appears to be limited to six (Laumer et al., 2016).

Similarly, rooks are a normally non-tool-using species, but in a series of tests have shown outstanding tool-using abilities. These corvids selected tools based on their affordances or properties, such as size and shape; used task-appropriate techniques, such as dropping, pulling or pushing; used a tool to acquire another tool; and modified tools to make them functional (Bird & Emery, 2009a; Emery, 2013). Similar results have been found in other birds and apes, which suggests they possess the necessary cognitive machinery to use tools but do not use tools under natural conditions for other reasons (PAPER I) – probably because it is not substantially beneficial for them (see section 3.3).

New Caledonian crows are the best-known tool-using corvid, starting with Hunt's (1996) report that wild crows use and manufacture two distinct tool types.⁴ Novel tool-use modes and functions are frequently discovered (Shumaker et al., 2011). In

⁴ It should be noted that tool use in NC crows had been described earlier, which Hunt was aware of, but that such anecdotal observations are often lost or forgotten. Similarly, it is a common misconception that Goodall was the first to describe tool use in wild chimpanzees. Extensive reviews (e.g. PAPER I; Shumaker et al., 2011) should make it easier to find such forgotten reports, which often contain valuable information that can guide future research and prevent similar mistakes from being made again.

PAPER IV we describe a novel tool-use mode in NC crows: *insert-and-transport*. On several occasions, two crows inserted a stick into the hole of an object and moved away, thereby transporting both. No conclusive function can be ascribed based on this exploratory study, but so far the best explanation appears to be play or exploration. A single observation suggests another function: transport of unwieldy objects. This NC crow repeatedly tried to grasp a large wooden ball but failed. He then left the experimental area, returned with a thin stick, inserted it into the ball and flew off with both. This may indicate behavioural flexibility or innovation, but further research needs to be done before conclusions can be drawn.

Some aspects of tool behaviour are sometimes regarded as unique not only in humans, but other species as well. The relatively recent discovery of tool use in NC crows and many additional observations have sparked debates about the uniqueness of their tool use and manufacture. For instance, Hunt and Gray (2006) considered the tool manufacture of NC crows to be more humanlike than that found in other species, even chimpanzees. They identified ten specialised features of tool manufacture in NC crows: distinct types of tools, species-wide manufacture, diversification, hook tools, targeting of raw materials, different tools for different tasks, making tools to rule systems, lateralization, sculpted tools, and cumulative evolution in tool design.

These claims have been heavily contested (e.g., McGrew, 2013; Shumaker et al., 2011). Most of these features can also be found in chimpanzees and orangutans, with the most notable exception being the manufacture of hook tools by NC crows. However, the fact that NC crows may be unique in some aspect of their tool behaviour does not mean they alone are unique, as many other species are unique in other respects. McGrew (2013) compared tool behaviour in chimpanzees and NC crows by summing up several measures of type and frequency of tool use and manufacture. He concluded that chimpanzees score higher on all these measures, and are the most similar to hominins.

McGrew (2013) and Shumaker and colleagues (2011) provide a catalogue of the tool use modes of NC crows, and caution that it is not final because novel modes are continuously found, and their discovery strongly depends on research effort, sampling bias, and novelty. Comparing such numbers between species is not very meaningful because it oversimplifies many factors such as anatomy, ecology, cognition, attention, motivation, neophilia, and dexterity, and reduces them to a single number. For instance, it may rarely be beneficial, except under the most elaborate experimental circumstances, for a NC crow to use a tool for cutting, bridging or climbing, which are some of the modes that add to the long list found in chimpanzees. That being said, I take this opportunity to update the catalogue of tool use modes in NC crows with novel and overlooked observations. Despite my criticism on using the number of tool-use modes for species comparisons, catalogues are still useful because describing behaviour is the first step to understanding it, and defining and categorising it the second and third.

Shumaker and colleagues (2011) reported that NC crows use tools in two modes: *dig*, to search the forest floor for invertebrates; and *insert-and-probe*, to extract prey from crevices. McGrew (2013) called bending a wire into a hook by using a fulcrum *applying leverage*, but as he also admits, this is tool manufacture, not use. Furthermore, he considers the dropping of nuts onto hard surfaces as *drop* tool use, but this is proto-tool use, which some other corvids do too (Jacobs & Osvath, in press-c; Shumaker et al., 2011). Nonetheless, experiments have shown that NC crows will *drop* stones to trigger a collapsible platform (von Bayern et al., 2009) or raise the water level in a tube (Jelbert et al., 2014). They *jab* with sticks at inaccessible prey to extract them (Trosciano et al., 2008) and use tools to *reach* inaccessible food (Taylor et al., 2012a). In the context of our study on *insert-and-transport* tool use (PAPER IV), one NC crow inserted a stick into a wooden ball and then picked up the ball, which is *contain* tool use (unpublished observation). Moreover, I have observed NC crows placing objects over caches to conceal them, which Shumaker et al. (2011) consider to be *drape* tool use. This shows that not only are new modes often discovered in a given species, but also that known behaviour (such as covering caches) can sometimes be regarded as tool use when applying definitions consistently. The larger difference between humans and corvids compared to humans and apes may also contribute to a bias in more quickly classifying behaviour of apes as tool use (see Chapter 5).

3.1.1 Causal cognition

Hume (1740) believed causal thought to be so integral to the operations of the mind that he called it “the cement of the universe”. What causality is and how we may represent it are continuously debated questions, but it is clear that humans heavily rely on causal thought (Beebe, 2009; Blaisdell & Waldmann, 2012; Carey, 2009; Danks, 2009; McCormack et al., 2011; Mumford & Anjum, 2011; Penn & Povinelli, 2007; Young, 2012). Dissecting a phenomenon into causes and effects is typically an essential step towards understanding it; most “Why?” and “How?” questions are concerned with causality (Blaisdell & Waldmann, 2012).

Causality is often conceived of as a physical phenomenon, but it is much broader than that. Describing the causes of World War I, for example, would be bizarre in terms of physical principles. Nonetheless, here I include causal cognition under the header of physical cognition and tool use because many tests of causal understanding are formulated as tests of folk physics, often requiring subjects to use tools. As will hopefully become clear in this section, I am convinced that disagreement about what kind of causal cognitive capacities corvids might have is more of a theoretical-conceptual issue than an empirical-methodological one.

Three recent empirical studies illustrate this debate. Bird and Emery (2009a) tested rooks on a stone dropping task. In the training phase, rooks learned to nudge

stones down a tube, which triggered a platform to release the food reward. They then learned to pick up stones and drop them down the tube directly, which is tool use in the mode *drop*. One rook dropped stones down the tube after seeing her mate do so. The same apparatus was used by von Bayern and colleagues (2009) to test NC crows, which were split into two groups. One group learned to nudge stones like the rooks, while the other group first learned to peck the platform directly through a shortened tube (see Figure 3). Platform-pushers also succeeded on triggering the platform by dropping stones down the tube, which suggests that they learned the task affordances (platform collapsibility) and innovated a novel solution when necessary, despite having no previous experience with the required objects and actions (stone dropping).⁵

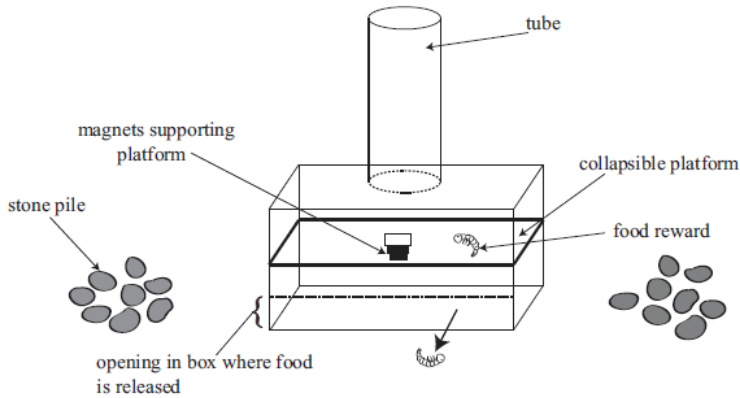
Taylor and colleagues (2014) tested NC crows on a transparent apparatus that contained a rotating cylinder, which would release food when a certain block fell on it. In observation trials, food was placed in an opening of the apparatus and attached to the block. When the food was taken, the block would drop and release the other food piece from the cylinder. In experimental trials, there was no food in the opening and the block was placed next to the apparatus. Crows had to pick up the block and insert it into the opening to get the food contained in the apparatus. All five crows always got both food pieces in observation trials, but never succeeded over the course of one hundred experimental trials. Taylor and colleagues therefore concluded that there was no evidence of NC crows creating causal interventions in their test.

We consider this study to be problematic for several methodological and conceptual reasons (PAPER V). Crucially, Taylor and colleagues (2014, 2015) argue that an unambiguous demonstration of understanding causal interventions can only result from subjects observing, rather than participating in, causal interactions. They

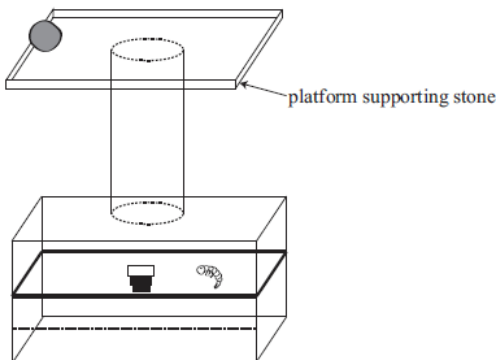
⁵ Several unpublished results support this finding. As part of an unrelated experiment, we trained NC crows on a similar apparatus (Jacobs, Osvath & von Bayern, unpublished data). There were four inverse L-shaped tubes on top, each of which led to a collapsible platform supporting a piece of food. When a small ball was inserted into a tube, the platform was triggered, causing the food to fall down. Birds could therefore optimise their food intake by inserting each of four balls into a different tube. At first, a ball was placed in the opening of each tube, with a piece of food in front of it, so that when a crow would take it, the ball would fall down and the food on the platform would become available. Four out of five crows learned to do this in up to 35 trials. We then placed the balls on the ground in front of the apparatus, and the four successful crows inserted at least one ball into a tube, with one bird already doing so in the first trial (the last initial success was in the seventh trial). A rook and hooded crow performed in a similar manner. Kabadayi and Osvath (in prep.) tested ravens on the tube platform task. They found that a platform-pushing raven dropped a stone down the tube on the first trial. (The picture on the back cover of this thesis also shows her in the process of using a stick tool to push food out of a horizontal tube.) Her mate failed to drop stones down the tube until he observed her do so, after which he immediately succeeded. Similarly, a rook (Bird & Emery, 2009a) and a NC crow (Mioduszevska et al., 2015), but not Eurasian jays (Miller et al., 2016b), succeeded after observing a demonstrator. Thus, there is strong evidence that rooks, NC crows and ravens can quickly succeed on the tube platform task when provided with different kinds of experience.

A

Experimental apparatus and setup



B *“Stone-nudging”*



C *“Platform-pushing”*

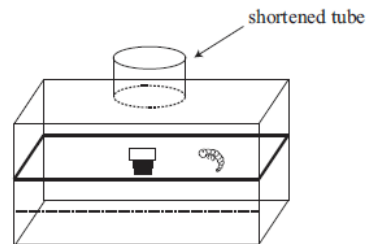


Figure 3. The tube platform task

This apparatus was first developed by Bird and Emery (2009a) to test the tool-using abilities of rooks. (A) shows the test phase, which requires the subject to pick up a stone and drop it into the tube to trigger the platform, thereby releasing the food reward. (B) shows the training phase, which requires the subject to nudge the stone into the tube. (C) shows the platform-pushing training, which requires the subject to push the platform with the beak to trigger it. Rooks were only tested with stone-nudging; NC crows were tested on both. Reprinted from *Current Biology*, 19, Auguste M.P. von Bayern, Robert J.P. Heathcote, Christian Rutz, and Alex Kacelnik, *The Role of Experience in Problem Solving and Innovative Tool Use in Crows*, 1965-1968, Copyright (2009), with permission from Elsevier. <http://www.sciencedirect.com/science/journal/09609822>

claim that von Bayern et al.'s (2009) platform-pushers can use causal information produced via their own direct actions but that this is not a true causal intervention because the interaction was not between two external objects. However, it is unclear why proprioceptive feedback would carry different significance from visual feedback. Both can be associative learning, as instrumental and classical conditioning, respectively. They argue that in studies of causal interventions, there should be no reinforcement history tied to the specific objects and apparatus used. Yet the observation trials, where the same individuals always obtained food, used the identical apparatus and object, which then likely became reinforced. Moreover, the crows instigated a causal chain through their own actions, just like in the criticised studies, so none of them involved observation alone. Furthermore, such criteria are not equally applied to human subjects, even pre-verbal infants, which illustrates the skewed burden of proof that is further discussed in Chapter 5.

Given these studies, do corvids have causal cognition? This question is overly broad so we should limit it to one species. NC crows are suitable here because their causal cognition has often been investigated. Causal understanding has been defined in many ways and consists of several proposed cognitive mechanisms, such as the ability to make causal interventions (Woodward, 2011). Egocentric causal interventions involve an agent manipulating a cause to produce (or inhibit) its effect; e.g., shaking a branch to make fruit fall. This is still too broad, as such behaviour can also be the result of instrumental conditioning. Woodward (2011) therefore looks at the explicitness of representation. Barring verbal reports, explicit causal representations in the wide sense are characterised by: little informational encapsulation, availability to other cognitive systems, integration with other knowledge, insight, rapid learning, behavioural flexibility, and means/ends decoupling. Woodward acknowledges that explicitness of representation has not yet been clearly defined or formalised, but that these characteristics are common features.

Means/ends decoupling is arguably the most important and operationalised. It requires the subject to represent means and ends as separate factors instead of a single connection. Knowledge that the manipulation by oneself, a conspecific and the wind independently result in falling fruit is a fused action/outcome representation. In contrast, knowing that means and ends are decoupled allows for inference of an intermediate variable, such as branch movement, which can guide novel interventions by the subject. An animal that has shaken a branch to get fruit and knows that the movement of the branch is the intermediate variable that causes it to fall, should predict similar actions on the branch (from others or the wind) to likewise cause fruit to fall (see Figure 4). An animal with only fused action/outcome representations does not consider this intermediate variable, and its knowledge that self-manipulation causes fruit to fall does not entail expecting the same result under other circumstances.

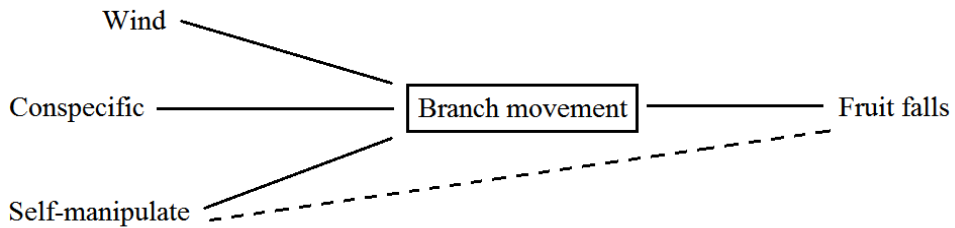


Figure 4. Causes, effect, and a possible intermediate variable

Knowledge that means and ends are decoupled indicates that the actions of the wind, conspecifics, and self-manipulation are seen as causing fruit to fall through the intermediate variable of branch movement. In contrast, an animal with fused action/outcome representations does not infer an intermediate variable, as shown here by the dashed line. Modelled after Woodward (2011).

Animals with means-end understanding can also disregard superfluous elements (i.e., those that do not make a difference), and recognize when the original means are no longer appropriate under changed circumstances (i.e., they express behavioural flexibility in response to novelty). This is the only kind of means/ends decoupling that is egocentric; the examples from the previous paragraph are not because they involve another conspecific (agent causal learning) or non-agent entities such as the wind (observation/action causal learning) (Woodward, 2011). Means-end understanding is often investigated in the string-pulling paradigm (PAPER I) by changing irrelevant properties of strings (e.g., colour and material) or the optimal response (e.g., not attempting to pull a string if it has a reward that is too heavy or is so long that the reward can be taken from the ground).

Based on this classification, my question here is whether NC crows can make novel egocentric means/ends-decoupled causal interventions (NEMEDCI). One likely reason for why opinions differ on whether NC crows have causal cognition is the vagueness of definitions and the broadness of hypotheses. Specific hypotheses are the most tractable, and are concrete enough to make testable predictions (Sober, 2015). Taylor et al.’s (2014) study can be seen as the latest to (tacitly) test this hypothesis.

Despite our debate, I fully agree with Taylor and colleagues (2014) when they say that “causal understanding is not based on a single, monolithic, domain-general cognitive mechanism” (p. 5). Woodward (2011) shows how multi-faceted causal cognition may be, and of course there are many other theorists that propose different models. Our disagreement largely appears to arise from our differing conceptions of what causal interventions are. Their experiment is in principle suitable for testing the ability to make NEMEDCI, but their NC crows likely failed for other reasons (PAPER V). Crucially, both the platform pushing and stone dropping of NC crows in von Bayern et al.’s (2009) study is strong evidence for this ability. The explicitness of the crows’ causal representations, here regarded as

means/ends decoupling, is shown by their successful transfer from one condition to the other. The collapsibility of the platform is central, possibly as an intermediate variable, and it can be achieved through either beak pressing or stone dropping.

Taylor and colleagues disagree because the responses by the subjects might be instrumental conditioning. Although I believe this interpretation is only consistent with their overall ideas if the kind of observational learning they discuss would be viewed as classical conditioning, their conception of causal cognition in general is different from ours (PAPER V). It appears they would not consider what I call NEMEDCI to be a causal intervention, no matter the empirical evidence: “egocentric causal interventions appear so closely tied to operant conditioning that work focused on this type of causal intervention is likely to generate a great deal of debate but little progress, owing to the many alternative ways of interpreting such results” (Taylor et al., 2015, p. 2). What is needed is a way of differentiating between operant conditioning and such causal interventions. I believe that the concept of NEMEDCI offers this possibility, or at least a step towards it.

Taylor and colleagues might instead be looking for what can be called NAMEDCI: novel agent means/ends-decoupled causal interventions (i.e., it only differs from NEMEDCI in that it involves another agent rather than being purely egocentric). Except for single observations on a rook (Bird & Emery, 2009a), a NC crow and a raven (see Footnote 5), there is indeed little evidence for the ability to make NAMEDCI in corvids. It seems we agree that progress heavily depends on conceptual clarity, and that is what I have aimed to provide here. The studies reviewed above (Bird & Emery, 2009a; von Bayern et al., 2009; see also Footnote 5) are strong evidence that NC crows, and likely other corvids such as rooks and ravens, have the ability to make NEMEDCI. Whether they can also make NAMEDCI, or other forms of novel causal interventions, is an open empirical question that remains to be explicitly formulated and tested.

3.2 Development

Not much is known about the development of tool use in corvids. One obvious limiting factor is that there are not many corvids that spontaneously use tools (see Section 3.4), but as we have seen, some species can learn to use tools as adults, which raises the possibility of studying this capacity developmentally. This section is limited to species-wide tool-users: NC crows and ‘Alalā (Hawaiian crow).

Hand-raised juvenile NC crows start using and manufacturing tools without having observed other crows or humans use tools. Successful stick tool use was first observed in four crows between the ages of 63 and 79 days, and half of which were untutored and the other half of which had been tutored (i.e., given demonstrations by a human foster parent). One juvenile also made a tool out of screw pine

(*Pandanus*) leaves, which wild NC crows regularly use in the wild (Kenward et al., 2005). Crows that had seen their human foster parents use stick tools had higher rates, compared to untutored birds, of handling and inserting sticks and preferred to manipulate the same objects as their tutors. The qualitative development of distinct behaviours was similar for both groups: frequent touching of objects before active locomotion, then repeated rubbing (see Figure 5) and poking objects against substrate, followed by caching food and immediately retrieving it, and finally inserting twigs into crevices, which resembles the tool use of adults (Kenward et al., 2006, 2011).



Figure 5. String tool use?

A NC crow holding a string and making repeated back-and-forth motions that resemble their typical tool use. This still-frame sequence (approx. 5 seconds) shows Aigaios choosing the wrong string in the sixth trial of the straight condition (PAPER II). The correct string is not displayed in these images. Aigaios and several other NC crows sometimes used strings as if they were stick tools, but they did not succeed because the strings were too short and flexible. Studies on tool length selectivity in NC crows have mixed results (Bluff et al., 2010; Chappell & Kacelnik, 2002; Hunt et al., 2006; Knaebe et al., in press; Taylor et al., 2012a; Wimpenny et al., 2011). Selection of rigid over floppy tools has been extensively investigated in chimpanzees (e.g., Povinelli, 2000, 2012), but not as much in NC crows, which seemed to preferentially use rigid sticks over flexible strings as tools to retrieve out-of-reach food (Taylor et al., 2011; cf. Kacelnik et al., 2006).

The development of tool behaviour has also been investigated in wild NC crows. In contrast to hand-raised juveniles, it takes wild juveniles a much longer time to learn to make *Pandanus* tools, reaching adult-like proficiency at around 12 months of age. This ability develops in four stages. Juveniles first manipulate and rip *Pandanus* leaves without much coordination, but they spend much time observing their parents using and manufacturing tools, and sometimes using their discarded tools successfully. Their coordination then improves, but their action sequence often fails to produce a functional tool. In the third stage, at around 12 months of age, they are able to manufacture functional *Pandanus* tools like their parents, but they do not reach adult speed until the final phase in their second year (Holzhaider et al., 2010a, 2010b). The effects of age on other kinds of tool use, manufacture and safekeeping are more mixed (Bluff et al., 2010; Klump et al., 2015a, 2015b).

Another corvid has recently been found to have a species-wide tool-using capacity: the ‘Alalā. They are extinct in the wild (Hawaii), and their numbers in captivity barely exceed one hundred, so learning more about them is an urgent matter, especially if their tool use is important for survival (see Section 3.3). Seven naïve juveniles kept in two social groups frequently attempted and sometimes succeeded in using sticks as reaching tools. This ability developed without training or social input from tool-using crows or humans. Their object manipulation increased over several months, but never reached the levels of juvenile NC crows, and excluded many precursors to functional tool use exhibited by NC crows, such as rubbing and poking (Rutz et al., 2016).

The ability to use tools develops without social input in both NC crows and ‘Alalā, but under normal conditions they benefit from observing conspecifics (or human foster parents). Moreover, this developmental pattern does not exclude other types of learning; their tool-using proficiency is never as good at their first attempt compared to having had more experience as adults. Developmental studies may deconstruct functional tool-use abilities into cognitive components, and reveal how they are inter-dependent and affected differently by various kinds of experience (Holzhaider et al., 2010b; Kenward et al., 2011; Meulman et al., 2013). This is an important step in eliminating outdated dichotomies, such as instinct versus learning and domain-specific versus domain-general, that oversimplify the interactions between genes, individual, development, and evolution (Bateson & Curley, 2013; Jacobs & Gärdenford, in press; Jacobs & Osvath, in press-a; Laland et al., 2011, 2013)

3.3 Fitness value

Although tool use is often considered to be interesting from a cognitive standpoint, some researchers believe it has little to no ecological or evolutionary significance in

wild animals (e.g., Alcock, 1981; Hansell & Ruxton, 2008). While this may apply to some species that have been observed to only infrequently use tools in the wild or show remarkable tool-using abilities in captivity but not in the wild, this sweeping generalisation does not hold water (PAPER III).

NC crows are the most prominent study subjects of issues surrounding tool use in corvids. In a study that will be discussed in the next chapter, many NC crows tried to move a big wooden ball but failed to do so (PAPER VII). After one such attempt, one crow inserted a stick in it and flew off. This *insert-and-transport* tool use (PAPER IV) may also be beneficial in the wild. One possible function may be for transporting snails, which constitute approximately 10% of their daily protein intake (Rutz et al., 2010). Crows sometimes drop snails on stones, as they may be very large (up to 25% of adult NC crow weight). Crows may have to transport them for substantial distances because rocky substrate is quite rare in their habitat (Tanaka et al., 2013). Inserting a tool into the shell may facilitate transport. They use these rocky sites mostly for dropping candlenuts, which are of approximately the same size as the large wooden ball from PAPER IV, but they are solid and therefore unsuitable for this kind of tool use. Transporting food items that do not require cracking, such as half-opened seashells, may still be beneficial under some circumstances, for example when predators or competitors are nearby. Finally, *insert-and-transport* tool use may aid in caching food or objects. We observed a NC crow using a stick to cache an object, a behaviour which should be investigated further to determine whether it is widespread.

We describe four dominant hypotheses on the fitness value of tool use in PAPER III. The *necessity hypothesis* proposes that tool use is beneficial when resources are scarce. The *opportunity hypothesis* suggests that animals use tools when the opportunity arises. The *relative profitability hypothesis* proposes that tool use arises when it is energetically more profitable than alternative foraging techniques. The *limited invention hypothesis* suggests that tool use may be common, even when innovations are rare, through social learning. These hypotheses make divergent predictions about the fitness value of tool use, which may also vary across populations, species, tool use modes, and functions. Investigating these elements is then vital in determining the fitness benefits of tool use.

Tool use appears to have high fitness value in NC crows. Three average-sized longhorn beetle larvae provide sufficient daily energy intake for an adult NC crow. Since they are normally buried deep into dead wood, they cannot be removed except through tool use by crows (Rutz et al., 2010). Tool use in NC crows seems to be an evolved adaptation because of its species-wide occurrence and development without training or social input, as we have seen in the previous section. Moreover, they have several morphological features that are beneficial for using tools. NC crows have large, forward-facing eyes that result in a wide binocular overlap, eye laterality, and a strong straight beak that projects the working end of the tool into their line of sight (Martinho et al., 2014; Matsui et al., 2016; Troscianko et al., 2012).

Similarly, nearly all ‘Alalā use tools, an ability they also develop in the absence⁶ of social input or training. They appear to have some morphological features that facilitate tool use, albeit less so than NC crows (Rutz et al., 2016). Another intriguing resemblance between these two corvids is that they inhabit remote tropical islands with few extractive foragers, which may have provided them with a favourable niche that they could exploit through tool use. The same may be said about the woodpecker finch of the Galápagos Islands (Rutz & St Clair, 2012; Rutz et al., 2016; Tebbich & Teschke, 2013).

3.4 Phylogeny

The phylogeny of tool use is, like string pulling, difficult to establish because it is a heterogeneous ability that spans many distinct capacities and cognitive abilities. The ability to use tools after extensive training is not very interesting from a phylogenetic perspective for the same reason that applies to pigeons playing ping-pong: animals can be trained to perform all sorts of behaviour. Of course, trainability itself can be investigated phylogenetically, but this is not very informative for the possible evolutionary scenarios of tool use (or ping-pong, for that matter).

Thus, when asking how tool use in corvids might have evolved, the first step is to look for species in which tool use appears to be an evolved adaptation. As discussed in the previous section, there is strong evidence for this in NC crows and ‘Alalā. Species-wide tool use is rare in the animal kingdom, and in a seemingly irregular distribution (PAPER III; Hunt et al., 2013; Jacobs & Osvath, in press-a; Rutz et al., 2016; Shumaker et al., 2011). The limited occurrence of such customary tool use makes it difficult to apply the phylogenetic comparative methods discussed in Section 2.4 (MacLean et al., 2012). This is especially problematic concerning phylogenetic signal and ancestral state estimations if closely related species do not show varying degrees of a trait, which is why continuous variables are more useful. Comparing species-specific factors with tool-using abilities is possible between distantly related species, as exemplified by the similar beak morphology of NC crows and ‘Alalā. Phylogenetic targeting of a rare ability such as customary tool use may lead to the initial recommendation of investigating the closest relatives of customary tool users.

Tool use spans many forms and functions (see Section 3.1; Shumaker et al., 2011), so rather than looking at the phylogeny of tool use in general it may be more meaningful to look at specific tool use modes. However, in doing so we again run

⁶ By excluding certain possibilities, we can increase our understanding of a phenomenon. As demonstrated by Goldschmidt (2016, p. 85), absence can have substantial causal power: “

into the problem of a limited phylogenetic distribution. The best candidates for this analysis may be stereotypical tool users such as certain insects (Hunt et al., 2013). In contrast, flexible tool use appears more sporadically and under variable circumstances. It explains why many species that do not normally use tools in the wild can learn to use tools in experiments, sometimes even performing at similar levels as customary tool users. Tool use in these species is expected to have virtually no fitness value, but the cognitive flexibility enabling it under artificial circumstances is likely adaptive. In that case, investigating spontaneous tool use in non-tool-using species such as rooks and ravens (see Section 3.1) is very informative in exploring phylogenetic questions of tool use.

4. Sensorimotor cognition

As the name implies, sensorimotor cognition involves the integration of an agent's sensory and motor systems, and allows for the adaptation to and manipulation of its environment (Müller, 2009; Parker & McKinney, 1999; Vilarroya, 2012). It has its roots in the work of Piaget (1951, 1952, 1954), who formulated a theory on the origins of knowledge by investigating the cognitive development of his own three children (discussed in more detail in Section 4.2). He believed that infants construct intelligence in their sensorimotor interactions with the world, which form a foundation for later-developing and more complex cognitive abilities. Although this strictly Piagetian notion has fallen out of favour, the fundamental importance of sensorimotor cognition remains established and plays a key role in theories of embodied and situated cognition (Wilson, 2002).

4.1 Mechanism

Sensorimotor cognition is a broad category so I will focus on what has been investigated in corvids (for general comparative reviews see PAPER VI; Antinucci, 1989; Doré & Dumas, 1987; Gómez, 2004; Parker & McKinney, 1999; Pepperberg, 2002; Tomasello & Call, 1997; Vauclair, 2012). As these reviews show, undoubtedly the most studied traditional sensorimotor ability in animals is the object concept, or object permanence as it is often called (although this is technically only the last stage of the object concept series). Fully fledged object permanence entails the ability to represent objects that are out of view. It develops through several stages, which start with visually tracking moving objects, followed by the ability to obtain first partially and then completely hidden objects, and finally, searching for visually and invisibly displaced objects. This separation into stages is not only useful from a developmental perspective but also suitable for species comparison because not all species reach the final stages, so their adult sensorimotor cognition can be compared through these stages.

The majority of corvids that have been tested have passed most tasks of the final stage and can therefore be said to represent object permanence. Corvid species that have been tested are: common ravens (Bugnyar et al., 2007b), carrion crows (Hoffmann et al., 2011), jackdaws (Ujfalussy et al., 2013), black-billed magpies

(Pollok et al., 2000), Eurasian jays (Zucca et al., 2007), and western scrub-jays (Salwiczek et al., 2009). Object permanence has an obvious connection to caching; placing food out of view and retrieving it later may be impossible without the ability to represent it. Indeed, the development of object permanence in corvids is often simultaneously investigated with the development of their caching abilities (Bugnyar et al., 2007b; Pollok et al., 2000; Salwiczek et al., 2009).

Caching is also hypothesised to have substantially shaped other cognitive abilities in corvids. For instance, corvids that rely strongly on caches for survival require better memory capacities for sufficiently reliable retrieval (Gibson & Kamil, 2009; Vander Wall, 1990). Socio-cognitive abilities allow corvids to reduce the chances of cache theft, while increasing their own pilfering skills (Bugnyar et al., 2007a, 2016). Caching requires holding off on immediately consuming a food item, which is thereby closely related to delay of gratification (Dufour et al., 2012).

Some corvids also cache objects, which is frequently considered to be a peculiar side-effect of a strong food-caching motivation. In that case, object caching would have no fitness value. We investigated object caching in NC crows, ravens and jackdaws in an exploratory study (PAPER VII). Ravens cached objects the most frequently, but NC crows and jackdaws cached to similar extents, which is surprising because jackdaws virtually never cache food and do not spontaneously use tools, whereas NC crows do. Ravens and jackdaws mostly cached spherical objects, but NC crows preferentially cached stick-like objects, which might be explained by their tool use. I further explore evolutionary explanations of this study in Section 4.3.

Executive functions, which sometimes overlap with sensorimotor cognition, form a broad set of cognitive abilities, such as inhibition, attention, and working memory (Carey et al. 2015; Diamond, 2013; Zelazo et al., 2003). Motor-self regulation involves stopping a prepotent and counter-productive action. It can be tested with the *cylinder task*: a reward is placed in the middle of a transparent cylinder, and in order to retrieve it, the subject has to reach through one of the cylinder's ends instead of reaching for the reward directly. Many corvids perform as well as great apes on this task (Kabadayi et al., 2016; MacLean et al., 2014).

Executive functions can drastically influence performance, and hence age of acquisition, in various tasks. This is reflected in tests of physical knowledge, which human infants pass at considerably younger ages when a violation-of-expectancy (VOE) paradigm is used. An infant is said to represent physical principles when looking significantly longer at unlikely or impossible events, such as an object seemingly passing through a wall. Infants appear to develop these cognitive abilities at a younger age when the necessity of reaching is removed, and instead their expectations are measured by their visual behaviour (Carey, 2009; Carey et al., 2015; Hood & Santos, 2009; Spelke, 1991). The VOE paradigm removes many requirements of executive function, and thus can increase infants' performance on various tasks. Failure on sensorimotor tasks can therefore often be attributed to the

requirement for bodily action—with associated problems in executive function—and not a lack of representational or conceptual understanding (Carey et al., 2015; Zelazo et al., 2003). However, Piaget’s sensorimotor stage theory is mostly descriptive and operational, involving spontaneous and functional behaviours (Lourenço, 2016; Lourenço & Machado, 1996). The VOE paradigm is useful because it enables testing cognitive abilities in a passive sense, but it does not completely replace the Piagetian framework, or alternative sensorimotor accounts, that involves goal-directed action. Animals have also been tested on VOE tasks, but some results are difficult to interpret due to methodological limitations (Winters et al., 2015).

There appears to be only one study using VOE methods on corvids. Bird and Emery (2010) tested what rooks might expect of physical support relations. They showed rooks pictures with different events, varying in the presence, type and amount of contact between object and support (e.g., an object floating over, sticking against the side of, and leaning over the edge of the supporting structure, respectively). Rooks looked longer at impossible than possible events in all conditions. This suggests that they have expectations about physical support events, similar to and possibly exceeding the capacity of 6-month-old infants. This type of research would be difficult if not impossible on non-verbal subjects without using the VOE method. Its strength is that, across species, the ability to observe is not as limited or varied as that of manipulation. However, this does not decrease the value of manipulation-based studies; the way animals interact with their surroundings forms an integral part of their sensorimotor cognition.

4.2 Development

We investigated the development of sensorimotor cognition in common ravens in PAPER VI. Their development has previously been described in several other domains. They start playing while still in the nest, and do so equally or more often than they perform flight training or maintenance behaviour (Osvath et al., 2014b). Their play behaviour diversifies and increases after fledging (around 40 days of age), and forms the basis for functional caching behaviour later in life. At first they repeatedly place objects against substrate, and with increasing age they start inserting objects into cavities and covering them with substrate or other objects, thereby forming completed caches (Bugnyar et al., 2007b; Kenward et al., 2011). The development of caching parallels that of object permanence (Bugnyar et al., 2007b). Ravens approach novel objects and interact with them more when they are juveniles, after which their neophobia increases (Heinrich, 1995b; Miller et al., 2015; Stöwe et al., 2006). Juveniles quickly approach a string with food attached to

its end, but most adults are so neophobic that they ignore it, and only a few engage in string pulling after several days of habituation (Heinrich, 1995a).

Ravens have prominent social skills (Bugnyar, 2013; Bugnyar et al., 2016; Heinrich, 2011), which have also been studied developmentally. By caching non-food objects, they learn to identify potential pilferers and how to prevent theft of food caches by caching farther away from competitors, caching behind visual barriers, aggressively defending caches and retrieving caches when observed (Bugnyar et al., 2007a, 2007b, 2016). During their first year, the number of social behaviours also increases, a linear dominance hierarchy is formed, and overall aggression decreases around 4-5 months. Tolerance, socio-positive behaviour and conflict support is mostly directed towards kin at this age (Loretto et al., 2012). Ravens start to follow the gaze of conspecifics and humans shortly after fledging, and are able to follow human gaze around a barrier at 8 months (Schloegl et al., 2007). In the end of their first year they are clearly subject to emotional contagion (Osvath & Sima, 2014), but might be so even as nestlings (Osvath et al., 2014b). Although individual ravens respond inconsistently to food and small objects throughout development, their behaviour is similar to that of their subgroup, which indicates their high social adaptability (Miller et al., 2016a).

We modified the Piagetian framework designed for testing human infants (Piaget, 1951, 1952, 1954) to study the sensorimotor development of ravens. It consists of six stages, which show an increasing amount of complexity, coordination, intentionality, functionality, voluntary control and variability in motor patterns (Doré & Dumas, 1987; Lourenço, 2016; Parker & McKinney, 1999). Piaget used the biological concepts of *assimilation*, *accommodation* and *equilibration* to describe development within and between stages. An example is the sucking reflex, which is present at birth. As the infant grows older, she finds novel targets for this behaviour. Thumb sucking involves assimilating a novel target—her thumb—into a pre-existing structure—sucking. This organisational structure in turn has to accommodate because the novel target is different from the innate reflexive sucking behaviour. Equilibration shows their eventual integration and results in a progressive, dynamic balance between oneself and the environment. Individual behavioural elements remain present throughout life, despite also forming more complex cognitive structures. This illustrates Piaget's idea of a stepwise consecutive order in cognitive development, leading to increased behavioural complexity (Lourenço & Machado, 1996; Müller, 2009; Parker & McKinney, 1999).

The age at which infants progress through each stage has been subject to much discussion. It has become clear that many stages are acquired at an earlier age than formulated by Piaget (Carey, 1991; Lourenço, 2016; Spelke, 1991; Uzgiris & Hunt, 1975). This is especially the case when the tasks are simplified by eliminating certain factors—such as motor self-regulation and working memory—that are perhaps not necessary for the ability being tested (Diamond, 1990; Spelke, 1991). VOE methods are one way of reducing these factors. However, Piaget maintained

that these performance factors are essential parts of these cognitive abilities, and cannot be separated from them. Furthermore, he regarded age of acquisition as an indicator—not criterion—of developmental stages, and instead focussed on their order and structure to identify universal aspects (Lourenço & Machado, 1996; Müller, 2009).

The ravens in our study reached the final stage but at a much accelerated rate compared to great apes (PAPER VI). Together with a study on yellow-crowned parakeets (Funk, 2002), this shows that birds can successfully be tested on Piagetian sensorimotor tasks. These results complement other developmental studies of sensorimotor cognition in ravens; they develop quickly and in close association with object permanence abilities (Bugnyar et al., 2007b; Kenward et al., 2011). The Piagetian framework can probably be adapted to a wide variety of species, which makes it suitable for phylogenetic comparisons (see Section 4.4).

4.3 Fitness value

Most corvids are moderate food cachers, and some are specialists. Only two species studied almost never cache: jackdaws and white-throated magpie jays. Ancestral state reconstruction suggests that the common ancestor of corvids was a food cacher, meaning these two species lost this ability or motivation (de Kort & Clayton, 2006). Since jackdaws perform at similar levels on object permanence tasks as food-caching corvids (Ujfalussy et al., 2013), caching propensity is not a strong predictor of this ability. The development of tool use in NC crows and ‘Alalā resembles the development of food caching in ravens, which raises the possibility that they evolved from a shared basis (Kenward et al., 2011; Rutz et al., 2016). There are many advantages of the ability to represent out-of-view entities, such as conspecifics, predators, and food items. Outside of the corvid family, many birds and mammals have fully-developed object permanence abilities, possibly resulting from a combination of these benefits (Antinucci, 1989; Doré & Dumas, 1987; Gómez, 2004, 2005; Parker & McKinney, 1999; Tomasello & Call, 1997).

In PAPER VII we review the limited literature on object caching, and summarize that explanations that involve questions of mechanism and development for object caching in birds are: (1) a form of *object play*; (2) a *side-effect* of food-caching motivation directed towards food-like objects when cacheable food is unavailable; and (3) a motivation present only as a passing *developmental stage*. Explanations that involve fitness value are: (1) *acquiring proficiency* in food caching, tool-use, or social interactions; (2) *storing materials* for nest building; (3) *courtship*; and (4) aiding in *territory defence*.

We presented 16 initially novel objects to ravens, jackdaws and NC crows. Ravens touched, moved and cached objects significantly more than the other

species, which did so at comparable rates between them. Their strong interest in objects is also reflected in the fact that in most trials they interacted with an object before taking freely available food. NC crows mostly cached stick-like objects, whereas ravens and jackdaws preferred to cache spherical objects. All species kept interacting with the same objects over trials, although the jackdaws and ravens gradually lost interest overall.

These results do not point to a unidirectional fitness value of object caching in corvids. They were tested individually outside of the breeding season, so explanations involving nesting material, courtship and territory defence are weak. They were adults and food was present, so explanations in terms of development or food caching are also unsupported. Although tool use may explain the kind of objects NC crows cached, ravens and jackdaws do not use tools but still cached objects. Furthermore, unlike the other species, jackdaws do not normally cache food. We considered the most likely explanation to be that object caching in our study is a form of play or exploration. This might have the fitness value of conferring behavioural flexibility and innovative capacities, which allow these corvids to adjust to changing circumstances. There is broad support for this hypothesis (discussed in PAPER VII), but there are not enough studies on object caching to explicitly apply this explanation to this behaviour.

We propose two hypotheses on how object caching might have evolved in non-food caching corvids. The *by-product hypothesis* suggests that object caching is a by-product of food caching, and that non-food cachers retained motivation for object caching but not for food caching. In this scenario, object caching has no fitness value and is only found in species that have a food-caching ancestor. The *precursor hypothesis* proposes that general object manipulation, exploration and play sometimes results in objects getting cached, and that this is a precursor to food caching. In this case, object caching has fitness value as a form of exploratory proclivity that may be adaptive, and can be found in non-food-caching species without food-caching ancestors. There is insufficient evidence to support one hypothesis over the other, but they offer testable predictions that require investigating the food- and object-caching propensities of ideally all corvids.

4.4 Phylogeny

The development of Piagetian sensorimotor cognition has been studied in thirteen species, as we review in PAPER VI. They are too few and too distantly related to conduct phylogenetic analyses, but the significance of this approach should be apparent through speculation too. All species started at the first stage, and subsequent stages were reached in an ordinal sequence. Final stage reached and the age of acquisition are similar for closely related species. Higher phylogenetic levels

showed more variation. The rate of development in capuchin monkeys resembles that of great apes, and the only clades that reach the final stage are ravens and great apes. We further hypothesize that because these thirteen species reach stage 4, their last common ancestor—a stem amniote—also did. Investigating the development of other cognitive abilities is likewise valuable. For example, object permanence and motor self-regulation can be assessed developmentally on a graded scale and across different taxa. However, they have not been compared and analysed extensively, which is a clear goal for future comparative phylogenetic research.

Six corvid species have passed most tasks on the object permanence series (see Section 4.1). This is only a small percentage, but it has been investigated in many species outside of the corvid family too. While reviewing the phylogenetic distribution of object permanence is beyond the scope of this thesis, I would like to point out its suitability for phylogenetic comparisons. It can be analysed in terms of overall performance or final developmental stage achieved, which is more useful than a dichotomous categorisation of absent versus present. MacLean and colleagues (2012) also view it as a highly suitable candidate for the phylogenetic comparative approach, which can address when object permanence likely first evolved, where in phylogeny it first appeared, what the likelihood is of an extinct taxon having possessed it, which species would be most informative to be tested next, and what socio-ecological variables predict this ability. An analysis of this popular cognitive test would be very informative, and is thus a key avenue for future research.

Developmental studies are important for distinguishing convergence from parallelism, which is a major question in evolutionary biology. Convergence involves a similar result reached through different underlying substrates or developmental mechanisms, such as insect and bird wings developing from different body parts. Parallelism comprises similarity reached through similar underlying substrates or developmental mechanisms, such as both bird and bat wings developing from forelimbs. This issue was expressed by Gould (1990) when he wondered what would happen if life's tape would be rewound and played anew. If it would eventually resemble life as it is now, then convergence is the dominant evolutionary process, which entails high predictability. In contrast, parallelism is evident if the end result would be very different. Cognitive similarities between apes, dolphins, parrots and corvids are often regarded as convergent, though this conclusion is premature (Osvath et al., 2014a).

This issue is one reason why developmental studies are important for phylogenetic reconstructions. Our relatively small (in the spectrum of theoretical biology) study that compares sensorimotor development across thirteen species provides stronger support for parallelism because the cognitive capacities develop in the same sequence, with variation only lying in rate and offset. However, many more levels and traits are involved. For instance, it cannot simply be said that the brains of birds and mammals are either parallel or convergent—a combination is

more likely. Cognition makes the question of independent evolution even more convoluted because of the behavioural flexibility and niche construction it enables (Güntürkün & Bugnyar, 2016; Laland et al., 2011, 2015; Osvath et al., 2014a). In short, we are a long way from understanding the evolution of cognition, especially when it is independent.

In the following chapter, I will discuss an issue that has always affected research on animal cognition. Anthropomorphism has frequently been recognised as a problem, but has also often gone unnoticed, with significant effects on what is believed to be a scientific approach to animal minds. Research on physical cognition, even in distantly related species such as corvids, is not immune to this perceived danger. As a consequence, the burden of proof may have reached hypochondriac proportions, which is inexcusable if the supposed decrease of anthropomorphism is not fully curable, and the proposed remedy may do more harm than good through its side effects.

5. Anthropomorphism

There's an elephant in the room of cognitive zoology. Her name is Anthropomorphism, or Anthrie for short. She has frequent violent outbursts, which most residents either deal with by looking away or caging attempts. Both groups clutter the room with a host of principles, parsimonies, rules, arguments, views, effects, biases, fallacies, and weapons. Many of these are unnecessary, so it is time to tidy up the room, and acknowledge the elephant in it without overreacting.

Anthropomorphism is the ascription of human traits to non-human animals. Arguably the most famous example was not an elephant but a horse called Clever Hans. He could tap his foot exactly as many times as the answer to any arithmetical question written on a board by his owner, Mr. von Osten. He could even answer non-mathematical questions by using a conversion table that translated number of taps into letters and other symbols. While this may seem as just another anthropomorphic story as often told by the general public, a commission of experts agreed that Hans really understood arithmetic and did not receive help from bystanders.

However, a more detailed investigation revealed that Hans responded to subtle, involuntary cues. He could only answer questions that the person asking already knew the answer to. It turns out that people made minute movements when Hans reached the correct number of taps, and that he would continue tapping without this signal (Heinzen et al., 2015; Pfungst, 1911). Hans was thus clever in his behaviour-reading skills, not arithmetic, and has since become a textbook example of how experimenters should be wary of any cues they might inadvertently be giving to their subjects (Andrews, 2015; Shettleworth, 2010b; Wynne & Udell, 2013). The story is a cautionary lesson in mistaken anthropomorphism: “all higher psychic processes which find expression in the horse's behaviour, are those of the questioner” (Pfungst, 1911, p. 241). It also reveals prejudices such as confirmation bias: even after the conclusive report, von Osten continued to showcase Hans as a mathematical genius, while not allowing for any further experimentation (Heinzen et al., 2015).

The study of physical cognition in corvids is anthropomorphic in the strict sense because humans have it. Do ravens have a sudden “aha!” experience when they suddenly pull a baited strings after a long impasse? Do New Caledonian crows reason about their tool use, and understand its causal structure in a similar manner to humans? Do Eurasian jays have an internal representation of an acorn when they

retrieve one from a hidden cache? In this chapter, I will argue that there is nothing unscientific about asking such questions in the first place. While attributing certain cognitive abilities to animals has historically often resulted from erroneous anthropomorphism, making mistakes are essential in the maturation of any science, so an overemphasis on avoiding such mistakes is a mistake itself.

5.1 A brief history

Humans have likely been projecting their own characteristics on other entities for a long time. Some 40,000 year old art forms depict animals with human features, and many contemporary hunter-gatherers impose human attributes on animals to aid in hunting (Mithen, 1996). The term anthropomorphism first appeared in the sixth century BC in the context of ascribing human qualities to Gods, which is indeed a common theme in many religions (Epley et al., 2007; Fisher, 1991; Guthrie, 1997). The extent to which it is regarded as acceptable or appropriate varies strongly between times and cultures (Asquith, 1997; Fisher, 1991; Root-Bernstein et al., 2013; Russell, 1927). Anthropomorphism is often defined as “the overestimation of the similarity of humans and nonhumans and hence by definition could not yield accurate accounts. But this is humpty-dumptyism” (Mitchell, 2005, p. 103); we should not decide what a word means *ad hoc* (see Figure 6). How do we know if anthropomorphism is incorrect if we do not know which qualities we share with animals and which ones we don't? We clearly share at least some traits with other animals so anthropomorphism *per se* cannot be a mistake (Fitzpatrick, 2008); if human psychology were completely unique, it would be the biological equivalent of the immaculate conception (Jamieson, 1998).

Descartes, the 17th century polymath and philosopher, was one of the strongest advocates for a categorical animal-human division. He wrote that animals are complex automata (*mechanomorphism*); just like a clock, a dog produces sounds when struck. Nonetheless, he treated his own dog with great kindness, which shows the incompatibility between his philosophy and desire for animal companionship (Jamieson, 1998). The 18th century philosopher Hume, who for the most part was very sceptical, held the opposite view. He argued that animals, like children and adults, learn from experience that the same events will follow from the same causes. He called this a kind of analogical reasoning, which varies strongly within mankind and between humans and animals. He believed the arguments for animal reasoning to be so obvious that they never escape even “the most stupid and ignorant” (Clatterbuck, 2016; Jamieson, 1998). Darwin, who read Hume's writing on animals a century later, expressed similar ideas in the oft-quoted passage that “the difference in mind between man and the higher animals, great as it is, is certainly one of degree and not of kind” (Darwin, 1871, p. 105).

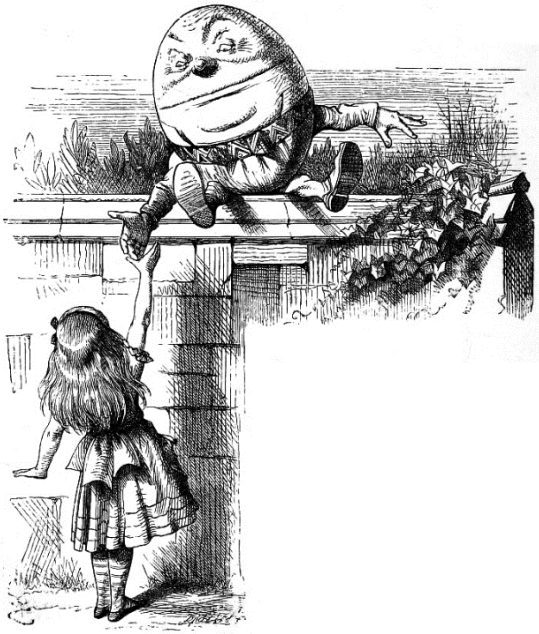


Figure 6. Humpty Dumpty, the anthropomorphic egg

In *Through the Looking-Glass, and What Alice Found There*, one of the most anthropomorphic books ever written, Lewis Carroll depicts a talking egg named Humpty Dumpty, who has a peculiar view on semantics: "When *I* use a word," Humpty Dumpty said, in rather a scornful tone, "it means just what I choose it to mean—neither more nor less." Although this may sound absurd, it is not uncommon in reduced forms. It applies to anthropomorphism when it is defined as the overestimation of animal-human similarities, which is why Mitchell (2005) calls it humpty-dumptyism. Illustration by John Tenniel in Carroll (1871), public domain.

Darwin and his protégé Romanes wrote extensively on animal minds. Their study method consisted of anecdotes, which were often relayed to them by others. They discussed religious devotion in dogs, magpie marriages, aesthetic appreciation in hummingbirds, alligator-cat friendships, and crows on trial for stealing nesting material (Darwin, 1871; Romanes, 1882). Not surprisingly, many of their contemporaries were not satisfied with this method, and called for more objective approaches. Morgan formulated his famous Canon with this aim (see Section 5.3), which is perhaps the most quoted statement in the history of comparative psychology (Dewsbury, 1984). Many contemporary textbooks still praise it as a valuable principle (e.g., Shettleworth, 2010b; Wynne & Udell, 2013). Morgan was the first to introduce experiments to this budding science. For instance, he investigated Romanes' claim that stressed scorpions would commit suicide by stinging themselves (Fitzpatrick & Goodrich, in press). His views inspired the onset of the anti-anthropomorphic behaviourists (Dewsbury, 1984).

Views on anthropomorphism have not only varied through time but also between disciplines. Biologists often echo Darwin's famous words of mental continuity, whereas many psychologists and anthropologists claim that the difference between humans and animals is in kind, not mere degree. The theories formulated, questions asked, species studied, and tests administered differ markedly between disciplines, which seriously hinders scientific progress (Andrews & Huss, 2014; Bekoff, 2000; Lockwood, 1985; Shettleworth, 2010b, 2012; Vonk & Shackelford, 2012; Wynne & Udell, 2013). For example, tool use has frequently been redefined, which appears to partially arise from efforts of maintaining it as a trait that makes humans unique (PAPER III; Shumaker et al., 2011).

Wide disagreement on how to conduct studies in cognitive zoology clearly exists both historically and across disciplines. Bekoff and Allen (1997, p. 317) complain that many critics "write as if the only alternatives are an unconstrained, fuzzy-minded use of anthropomorphism on the one hand, and the total elimination of anthropomorphism on the other." The latter position of denying or rejecting the possibility of similarities between humans and animals is called *anthropodenial* (de Waal, 1999) or *anthropectomy* (Andrews & Huss, 2014). Moreover, just because anthropomorphism used to have certain connotations that were regarded wrong, it does not follow that it can never be correct in current use: this is the *genetic fallacy* (Goodrich & Allen, 2007). Many of these disagreements come from a confusion of what kind of question is actually asked and whether certain explanations are mutually exclusive or not. This is one reason why Tinbergen's (1951, 1963) categorisation is so useful. We can only come to a full understanding of behaviour if we ask about its mechanisms, development, fitness value and phylogeny. Explanations from psychology, being mostly about (cognitive) mechanisms and development, are therefore not competing with typical explanations from behavioural ecology on fitness value and phylogeny.

5.2 Folk psychology

Clever Hans illustrates the perils of anthropomorphism. Humans are quick to jump to conclusions about animal minds, especially when it concerns valued abilities in their own species, such as mathematical reasoning (Karin-D'Arcy, 2005; Kennedy, 1992; Povinelli, 2012). This is reflected in what Povinelli (2012, p. 343) calls the hammer-wielding ape effect: "Placing a human artefact in an ape's hand will immediately increase its perceived IQ (unless he or she is holding it upside-down)." Ask anyone about their pets and you're bound to hear many examples of their deep emotional and cognitive lives, which is why Davis (1997) called anthropomorphism Disneyesque intellectual laziness that does more harm than good. Worse yet, people

even ascribe intentionality to an animated sequence of geometric figures (Heberlein & Adolphs, 2004; Heider & Simmel, 1944).

The kind of anthropomorphic attributions made depends on several factors. Species that are closely related to humans are more often referred to with gender pronouns, and are generally considered to be more loved, intelligent, sentient, empathetic, and communicative. Dogs and cats scored especially high on these factors, which suggests that personal contact and familiarity with animals plays an even bigger role than phylogeny or physical similarity (Eddy et al., 1993; Harrison & Hall, 2010; Hebb, 1946; Herzog & Galvin, 1997; Sealey & Oakley, 2013). However, physical similarity, familiarity or phylogenetic closeness did not affect psychological attributions to mammals when they were described in rich narratives with details about their behaviour and context (Mitchell & Hamm, 1997). The propensity to anthropomorphise also depends on personal factors. People who accept evolutionary theory are more likely to believe in emotional and cognitive continuity between humans and animals (Burghardt, 1985). Lonely people are more likely to anthropomorphise pets, and people who have a stable need for control are more likely to anthropomorphise unpredictable animals (Epley et al., 2008).

In some views, anthropomorphism is the overestimation of the cognitive abilities of animals when they are considered to be fundamentally different from humans. Some call anthropomorphism a disease that can only be cured through objective descriptions and neutral language (e.g., Kennedy, 1992). However, this kind of *amorphism* does not exist, whether it concerns animals or not (Crist, 1999; Karlsson, 2012; Sealey & Oakley, 2013; Spada, 1997). Even a supposedly neutral verb such as “walking” likely first elicits an image of a person rather than an animal walking. “Behaviour” is now widely accepted as an objective, neutral term, but in the 19th century it referred to how people conducted themselves in society. Talking about animal behaviour was erroneous anthropomorphism, and this use was introduced by none other than Morgan, whose Canon supposedly guards against it (Costall, 1998). Labelling cognitive abilities differently when found in animals, such as *episodic-like* memory (Clayton & Dickinson, 1998), is not a compelling solution because it requires redefining our entire vocabulary. It is unproblematic to talk about kidneys in different taxa despite considerable morphological and phylogenetic variation, and it does not require species-specific names, nor does it cause concern for *anthroporenalism* (Cartmill, 2000). Similarly, Tinbergen (1963) used the example of lens and compound eyes; physiologists do not make the mistake of assuming that their mechanisms are identical just because the same label is applied to both.

Most sceptics arbitrarily draw the line between harmlessly and erroneously humanizing animals. They devise rules to prevent anthropomorphism, even at the cost of introducing other biases, while ignoring or forgetting about other aspects of their folk psychology (see Section 5.3). Science is a human activity and so comes with human subjectivity no matter how supposedly neutral its language is. Anthropomorphism is more accepted in other sciences; nobody believes elements

truly like each other when we say they attract each other (de Waal, 1999). While all contemporary sceptics rightfully talk of animal *behaviour*, they start drawing the line at other concepts, claiming that their line marks the threshold with anthropomorphism. The problem with such sceptics is not only that their arguments against attributing certain qualities to animals are weak or trivial, but also that they rarely defend those qualities they do ascribe to animals, even when they might succumb to their very own reasoning (Allen, 2002; Andrews & Huss, 2014). Would they really consider it wrong to find a kitten cuddly if this feeling arises from its similarities to human babies (Fisher, 1991; Gould, 1980)?

Some points made by Döring and Chittka (2011) exemplify the arbitrary borders between supposedly right and wrong. They argue that using terminology such as a bee's "dance language" is unproblematic because of its clear double meaning and its large semantic distance to human language, but they do not clearly delineate when it becomes problematic. They condemn talk of insect "personality" because it implies that insects have person-like qualities, but is the same risk not tied to language? Their solution is the disambiguation of colloquial and technical language and the avoidance of anthropomorphism if it is not clearly purely metaphorical. However, this might apply to both language and personality. As we have seen, opinions differ on what colloquial language is, when it is metaphorical, and what anthropomorphism is, depending on historical, cultural, disciplinary, and personal grounds.

Human participants from Western, Educated, Industrial, Rich, and Democratic (WEIRD) societies frequently form outliers compared to people from other cultures, yet they are seen as representing the whole species in psychological studies (Henrich et al., 2010). Animal subjects are often equally unrepresentative and tested under conditions that differ significantly from those of their human counterparts (Boesch, 2007, 2010). For instance, chimpanzees are typically tested by themselves whereas children sit on the lap of a parent, which provides ample opportunities for the Clever Hans effect. Similarly, in studies on theory of mind, chimpanzees may be tested with human models as stimuli and human experimenters, which can thus better be said to be a test of *panmorphism*, or the attribution of chimpanzee qualities to other species, in this case humans (Povinelli, 1997). In a test of inhibitory control, NC crows performed better when trained on following rewards moved by the experimenter than when trained on another inhibitory control task (Jelbert et al., 2016). Many other factors may influence performance on any cognitive test, which is a pitfall we should be wary of, especially when making species comparisons.

The language used in the scientific study of infant and toddler cognition is generally accepted but would be considered anthropomorphic by most when applied to animals. Some justify this *adultomorphism* with the mere fact that infants will develop into linguistic adults of which we know their cognitive abilities, so we can infer them to already be present in pre-verbal form (e.g., Davidson, 1982). The scientific standard then seems to be different across disciplines, apparently allowing

for more assumptions when it comes to our own species (Andrews, 2015; Fisher, 1991; Goodrich & Allen, 2007; Singer, 2009). Such *anthropofabulation* (Buckner, 2013) includes adult humans too, no matter how WEIRD they are. For example, in the trap-tube task, animals use tools to extract food from a transparent horizontal tube while attempting not to let it fall into a hole in the middle. When the tube is inverted so that the hole is at the top, and cannot trap the food, many animals continue to avoid it. This was seen as a typical error suggestive of poor causal understanding in animals, until adult humans were tested, who also often avoided the inverted hole (Silva et al., 2005). Similar results of children and adults not performing as well as anticipated and making similar mistakes as animals have been found for other physical cognitive tests, such as string pulling (Mayer et al., 2014; Silva et al., 2008), tool use (Horner & Whiten, 2007; Remigereau et al., 2016; Silva & Silva, 2006, 2010, 2012), and tool manufacture (Beck et al., 2014; Chappell et al., 2013; Cutting et al., 2014; Sheridan et al., 2016; Silva et al., 2015).

Our anthropomorphic predispositions may not only overestimate the cognitive abilities of animals, but also underestimate them. For instance, pigeons are faster than humans in mental rotation tasks (Delius & Delius, 2012), so the speed of their performance cannot be described as anthropomorphic. Döring and Chittka (2011) argue that definitions are too often constructed from expected outcomes, leading to circular reasoning. They give the example of a textbook discarding learning speed as a suitable measure for intelligence because bees perform better than rabbits or children on a colour learning task. Hebb (1946) points out that there are no names for emotions humans do not possess, so ascribing emotions to animals is always anthropomorphic. Discovery of previously undescribed emotions in animals is therefore limited by such *anthropocentrism*, which is also a problem in other research. For instance, humans appear to find it difficult to conceive of the importance of different modalities in other animals. Rats and mice show a larger stress response when exposed to the smell of male than female experimenters (Sorge et al., 2014). This was discovered only recently, despite rats and mice having been animal models for a long time. One possible explanation for this late discovery is our anthropomorphism and anthropocentrism; rodents rely on olfaction much more than we do, so we are more likely to test for visual rather than olfactory factors that might make them stressed.

This is an example of *anthropomorphism by omission*, which is “the failure to consider that other animals have a different world than ours” (Rivas & Burghardt, 2002). This issue has been recognised for a long time, especially since von Uexküll’s (1909, 1957) formulation of *Umwelt* as the unique perceptual life-world of an animal in which it exists and acts. The “inner lives” of animals had been an important research topic (e.g., Bierens de Haan, 1946; Romanes, 1882), but Tinbergen (1951, 1963) viewed it as an unscientific endeavour due to its non-objectivity. Burghardt (1997) considered this to be such a major deficiency in Tinbergen’s classification that he called private experience the fifth question.

Although we may never know what it is like to be a bat (Nagel, 1974), we should at least recognise that the bat's world is different from ours. And as the example above illustrates, the *Umwelten* of rodents and humans are different, which is why they respond differently to the smell of male humans. Similarly, the same stick is not the same for a tool-using compared to non-tool-using species, as shown by the strong motivation of NC crows to cache sticks while ravens and jackdaws mostly cache spherical objects (PAPER VII).

5.3 Morgan's Canon, parsimony, and explanations

Many researchers and philosophers have argued that we need some rule to stop us from applying our default anthropomorphic tendencies to the scientific study of cognitive zoology. *Morgan's Canon* is often perceived to be a powerful weapon in the combat against this prejudice: "in no case is an animal activity to be interpreted in terms of higher psychological processes, if it can be fairly interpreted in terms of processes which stand lower in the scale of psychological evolution and development" (this is the final version of the Canon from Morgan, 1903, p. 292). From low to high, the psychological scale consists of instinct, intelligence, and reason. Most contemporary views hold that "higher" means being more cognitively sophisticated in general, such as abstract reasoning over associative learning or second-order over first-order intentionality or representation. According to this reading, the "lower" cognitive ability should be preferred when it has the same explanatory power as the "higher" ability. Morgan also applied this to humans, in what Andrews (2015) calls *Morgan's challenge*: "to interpret animal behaviour one must learn also to see one's own mentality at levels of development much lower than one's top-level of reflective self-consciousness. It is not easy, and savours somewhat of paradox" (Morgan, 1903, p. 250).

The Canon is so widely misunderstood and misused that Thomas (1998) calls it the most misrepresented statement in the history of comparative psychology, and Costall (1993) considers it to have backfired, becoming a scientific myth that directly opposes Morgan's intentions. It can be said to offer one kind of parsimony: preferring simpler psychological processes. This is not the kind of parsimony often associated with the Canon: preferring the explanation with the fewest parameters. The Canon is about the psychological level, not the number of entities as dictated by Ockham's razor (Dewsbury, 1984; Newbury, 1954; Sober, 2015; Starzak, in press). Morgan (1903) indeed believed that the simplest explanation of an animal behaving like a human is that it does in fact have the same cognitive abilities. In other words, he considered anthropomorphism to be the most parsimonious explanation (Sober, 2005, 2015).

Using the Canon to prevent the supposed bias of anthropomorphism, which eventually might be justified after further research, means introducing another bias of an *a priori* preference for lower over higher psychological explanations (Fitzpatrick, 2008; Starzak, in press). To illustrate this issue, Fodor (1999) proposes *Fodor's Pop Gun*, which prohibits interpretations of lower over higher psychological processes when they have equal explanatory power. However, whether a canon or a gun, such misguided pre-empirical prejudices are ill-suited for empirical science. Preventing bias with bias is like fighting fire with fire. The current burden of proof seems to be on “anyone wishing to explain behaviour in terms of processes other than associative learning and/or species-typical perceptual and response biases” (Shettleworth, 2010b, p. 18). Instead, if there is insufficient evidence for a hypothesis, no matter how anthropomorphic it may be, we simply have to reserve judgment until new evidence or other relevant considerations come to light (Andrews & Huss, 2014; Fitzpatrick, 2008; Mills, 1898).

Many other kinds of parsimony are applicable here, which aim at simplicity in terms of ontology, iteration, memory, evolutionary change, behavioural expression, representational resources, evidence, theory, pragmatism, causal connections, communicative economy, innateness, emotion, input data, and more (Dacey, 2016; de Waal, 1999; Fitzpatrick, 2008; Heyes, 2012; Karin-D'Arcy, 2005; Meketa, 2014; Montminy, 2005; Newbury, 1954; Sober, 2015; Starzak, in press; Thomas, 1998; Wright, 2006). The sheer number of parsimony types alone obviously leads to clashes. For instance, biological considerations such as the fitness costs of large brains can be said to favour “lower” over “higher” explanations, but the opposite can also be the case; larger brains may allow for fewer memory requirements, and the fact that they have evolved repeatedly suggests their adaptive significance under some circumstances (Fitzpatrick, 2008; Heyes, 2012).

The most discussed conflict is between cognitive and evolutionary parsimony. Chimpanzees are closely related to humans, so when they behave similarly, it appears to be reasonable to ascribe to them the same underlying cognitive ability. This phylogenetic approach is uncritically applied to non-cognitive traits, so why not treat cognition in the same manner? Cognitive parsimony, derived from Morgan's Canon, prefers explanations of less sophisticated cognitive abilities in chimpanzees, which clearly clashes with evolutionary parsimony (Dacey, 2016; de Waal, 1999; Fitzpatrick, 2008; Keeley, 2004).

How do we decide between types of parsimony? Rather than following Morgan's Canon, we should follow his claim that “surely the simplicity of an explanation is no criterion of its truth” (Morgan, 1903, p. 54). The best way of avoiding *any kind* of bias is simple: acknowledging the bias, followed by *evidentialism* (Dacey, 2016; Fitzpatrick, 2008; Sober, 2005), with agnosticism being the default approach in the face of insufficient evidence (Andrews & Huss, 2014; Mills, 1898; Starzak, in press). Evidence from all available sources should be used, which can then be assessed in terms of the accuracy of predictions, their scope, and their power

(Andrews, 2015; Buckner, 2013; Burghardt, 1985; Fodor, 1999; Heyes, 2012; Lockwood, 1985; Meketa, 2014; Mikhalevich, 2015; Shettleworth, 2010a, 2010b; Starzak, in press; Vonk & Shackelford, 2012).

Even with the disposal of unnecessary and conflicting principles of parsimony, many theoretical and empirical issues remain. The methods at the onset of comparative psychology were anecdotalism and introspection. Darwin (1871), Romanes (1882), and even Morgan (1903) typically gathered anecdotes from what they believed were respected observers – upper-class white men – and inferred the animal’s mental capacities through analogical reasoning with their own. Introspection is no longer believed to be a suitable method, even when it comes to human psychology, due to extensive differences between subjective individuals, the presence of biases, and overall poor reliability of folk psychology leading to naïve anthropomorphism and plain misjudgement (Andrews, 2015; Burghardt, 1985; Hull, 1943; Povinelli, 2012; Thompson, 1994).

A related approach is the argument by analogy for the existence of other minds. If a kind of behaviour is caused by a certain mental state in humans, then we can infer by analogy that a similar kind of behaviour is caused by a similar mental state in animals. This argument is why Hume and the first comparative psychologists were convinced of the mental continuity between humans and animals. Povinelli (2000) points out that it has the same weaknesses as introspection, and that since many attributions of cognitive abilities to animals rely on the anthropocentric argument by analogy, there is no strong evidence that animals actually possess them (see also Karin-D’Arcy, 2005). Davis (1997) protests the logical error of *affirming the consequent*: the common assumption that a complex behaviour can be caused by a corresponding mental state, which may often occur, but failing to consider this is not necessarily the *sole* cause.

This issue can be illustrated by purported insight in animals trying to reach suspended food, such as chimpanzees stacking boxes (Köhler, 1927) or ravens pulling strings (PAPER I; Heinrich, 1995a). These tests were often thought to reveal some of the most advanced cognition in animals, but later experiments have shown that it can also arise through simpler mechanisms. For example, pigeons can chain individually learned sequences into stacking boxes (Epstein et al., 1984), and bumblebees can learn to pull strings through trial-and-error or observation (Alem et al., 2016). Such studies are often seen as “killjoy” or “spoilsport” because they appear to deny mental continuity between humans and animals (Dennett, 1983; Döring & Chittka, 2011; Shettleworth, 2010a). They should not be turned on their head; just because a behaviour can be explained by a specified cognitive mechanism in some cases, regardless of how sophisticated it is, does not mean that the same mechanism is necessarily present in similar cases. In other words, just because pigeons and bumblebees were not insightful does not mean chimpanzees and ravens aren’t either, although it certainly warrants further investigation.

Many sceptics share the positions of Povinelli and Davis, although they often defend the argument by analogy in various ways when it comes to children by citing some kind of critical level of similarity (such as neurophysiology or behaviour; e.g., Mitchell, 2005) or a presumed defining human quality (such as language or rationality). For instance, Davidson (1982) argues that there is a fundamental difference between animals and human infants because the latter grows up and belongs to a species that is rational and linguistic, even though the infant cannot express either at the time. Lehman (1997) notes that there is always some similarity to be found between entities we consider to be very dissimilar. For example, both an elephant and a sneeze exist spatiotemporally, can cause fear in other creatures, can be the subject of poems, spread germs, are beneficial to mankind, etc. In his view, assigning the same mental states to them would clearly be ridiculous for this reason.

The main problem again comes down to the special position granted to humans, even by critics of anthropomorphism, despite their arguments often applying equally to animals and humans (Andrews, 2015; Buckner, 2013). Povinelli uses the weakness of the argument by analogy when claiming that chimpanzees do not have certain higher-order mental states. However, he does allow for other kinds of mental states, which he infers to be present in wild chimpanzees based on his experiments with captive ones that are equally fallible under this reasoning (Allen, 2002). By analogy, why do we even treat pets with psychoactive drugs, or infer they will work similarly for humans after animal testing (Bekoff, 2005; Guthrie, 1997; Lockwood, 1985)?

The argument by analogy and evolutionary parsimony predict that sophisticated cognitive abilities are more likely to be found in species closely related to humans. In that case, if we have good reason to believe that chimpanzees do not have these abilities, it seems to be safe to assume that other species do not have them either (Mitchell, 2005; Povinelli, 2000). On the other hand, creatures very different from us can of course have minds, something we can only find out by increasing our knowledge about them rather than *a priori* assumptions (Andrews, 2015; Mitchell, 1997). The risk of uncritical anthropomorphism is also lower for such species on account of them being more different from us (Burghardt, 1991; de Waal, 1999; Herzog & Galvin, 1997). The assumption that cognitive abilities are proportional to relatedness to humans does not hold; distantly related species outperform our closer relatives in some tests. For instance, songbirds and parrots are better vocal learners than primates (see Figure 7). It is therefore important to avoid the mistake of assuming that phylogeny always can explain how minds work – a distinction made explicit when applying Tinbergen's questions (Bolhuis, 2015; Bolhuis & Wynne, 2009).

Numerous other methods can be used in the attempt to explain how minds work. The type of introspection done by 19th century comparative psychologists is no longer accepted, but anecdotes are still frequently used, even though critics often

quip that “the plural of anecdote is not data”. How anecdotes are reported and used has changed, so they can now be better regarded as single observations. They are no longer the casual observations of untrained observers, transforming as they get passed down from person to person, each with their own added interpretation. Instead, they are often gathered and systematically categorised by trained observers that know their species well. These collections can then be used in various investigations on behavioural innovation, deception, and play (Bates & Byrne, 2007; Byrne, 1997; de Waal, 1991). The asymmetrical burden of proof when it comes to cognitive zoology is rather dramatically illustrated by Mitchell (1997): “If we can send people to death or life imprisonment based upon anthropomorphic analysis of anecdotes, surely we can use the same method to understand animals” (p. 162). This method can be wrong in both cases, but the possibility of being wrong does not stop us from scientific and philosophical endeavours in other fields (Jamieson, 1998; Keeley, 2004). There’s no reason for applying overly restrictive criteria to cognitive zoology alone.

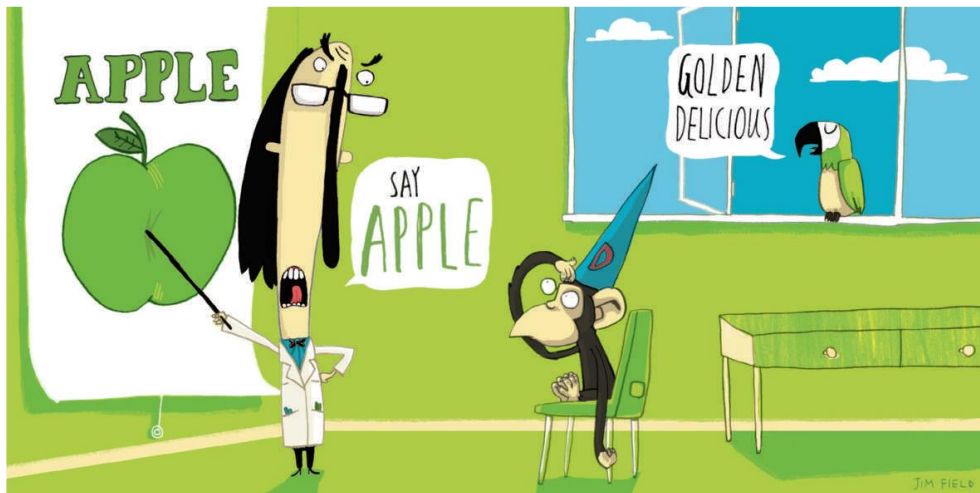


Figure 7. Our closest relatives are not necessarily the best in solving the tasks we give them

We should look for cognitive abilities in a wide array of taxa, and not just our closest relatives, because cognition does not necessarily correspond with phylogeny. As discussed in previous chapters, phylogeny plays an important role in cognitive zoology, but it does not substitute investigations of *how* animals solve tasks. Adapted by permission from Macmillan Publishers Ltd: *Nature* (Bolhuis, J. J., & Wynne, C. D. Can evolution explain how minds work? *Nature*, 458, 832-833. doi: 10.1038/458832a), copyright (2009). www.nature.com/nature

Many contemporary studies use experiments, which have a high degree of control, but also have the drawback of human involvement and modification of the animal’s environment (de Waal, 1991). Unfortunately, this is not always possible, so a decision has to be made whether to focus on external validity through studying

wild animals with little interference, internal validity by studying captive animals in controlled experiments, or a combination of these approaches (Vonk & Shackelford, 2012). Replacing the top-down with a bottom-up perspective is also likely to be fruitful (de Waal & Ferrari, 2010, p. 201): “instead of asking which species can do X, the question would become how does X actually work? What are the necessary ingredients of X and how did these evolve?” By dissecting X into defined and testable cognitive processes, we can still ask “to what extent does this species have X?” without reverting to naïve anthropomorphism and false dichotomies. This bottom-up perspective builds on the assumption that there may be shared and unique processes in humans, leading to a more comprehensive study of cognitive zoology that is less focussed on positive results and “Holy Grail” quests (de Waal & Ferrari, 2010; Döring & Chittka, 2011; Rollin, 2000; Shettleworth, 2010a, 2012; Vonk & Shackelford, 2012). Developmental approaches, such as Piagetian sensorimotor cognition (PAPER VI), are bottom-up because they investigate the underlying mechanisms of the cognitive ability in question. Bottom-up perspectives are also increasingly common in other physical-cognitive research areas, such as string pulling (PAPERS I AND II) and tool use (PAPER III).

How research questions are formulated can affect their outcome, and the importance of exploratory research should not be overlooked (Döring & Chittka, 2011). With the exception of the most sceptical critics (e.g., Blumberg, 2007; Wynne, 2007a, 2007b), there is wide agreement that the origin of a hypothesis is irrelevant, that what matters is its testability and theoretical support, and that anthropomorphism can therefore be useful for hypothesis formulation (Bekoff & Allen, 1997; Buckner, 2013; Burghardt, 1985, 1997; Davis, 1997; Dennett, 1983; Kennedy, 1992; Parker & McKinney, 1999; Rollin, 2000; Spada, 1997; Vidal et al., 1996). A very poignant example comes from Aesop, who long ago wrote a fable about a thirsty crow dropping stones into a pitcher to raise the water level so it could drink. Wynne (2007a) cites Aesop’s fable as a typical anthropomorphic example that is not reflective of reality or conducive to scientific progress. Ironically, the fable of the crow and the pitcher inspired researchers to test it with a modified apparatus, and they found that many corvids will in fact drop stones into a water-filled tube (Bird & Emery, 2009b; Jelbert et al., 2015).

In conclusion, fear of mistaken anthropomorphism has introduced many limitations, such as a bias towards one kind of parsimony and a skewed burden of proof. The room of cognitive zoology needs to be tidied up. First, let’s safely dispose of Morgan’s Canon before it backfires any further, or at least reduce its power to that of Fodor’s Pop Gun so that it does minimal damage. Anthrie the elephant should have nothing to fear, and we should not fear to consider the possibility of her having this very emotion. Questions, after all, cannot be erroneously anthropomorphic. Next, we should throw out whatever biases we can, and put a spotlight on the indisposable ones to never keep them out of sight, while still being able to properly assess evidence, which we neatly organise by Tinbergen’s questions. Through the

use of all available evidence types, we can move away from the anthropocentric viewpoint that has also proved to be an immense obstacle.

Consider the hypothetical case of Clever Shmans (Fisher, 1991, 1996), a horse that – as far as we know – can do arithmetic without any cuing or other “tricks”. Attributing mathematical abilities to him is not naively anthropomorphic; he fits the criteria of understanding arithmetic to the utmost extent. Of course, it is possible that we find other, previously unknown explanations for his performance, as was the case for Hans at the time, but this has nothing to do with the validity of anthropomorphism. Biased, unwarranted, outdated and asymmetric fear of making mistakes is ironically often considered as a scientific approach to animal minds. Mistakes are made in all sciences; without the risk of making mistakes, there would be no progress. Finally, the room is calm and tidy, its acknowledged elephant no longer standing in the way of our scientific efforts.

6. Concluding remarks

Cognitive zoology is a young science, and physical cognition in corvids but one of many pieces of a mostly unexplored puzzle. The broad scope of this thesis aimed not only to add some new pieces, but also to map the general layout of the field. Tinbergen's questions can be used as a guide, especially where parts of the field may overlap. The origins of physical cognition in corvids can only become clear by investigating its mechanisms, development, fitness value, and phylogeny.

String pulling, tool use, and sensorimotor cognition are some of the many aspects of physical cognition or behaviours that may reflect it. Methods used to investigate string pulling in animals are often unsuitable to distinguish between cognitive abilities. String-pulling studies should therefore test animals on multiple configurations, rather than aiming to show whether the species in question can pull strings or not. The large number of string-pulling species would be immensely more valuable if studies addressed more explicitly the cognitive abilities under investigation. The ability to use tools or pull strings should not be tied to a certain cognitive ability since many different ones may underlie them. Tool use appears to be adaptive for some corvids, but non-tool users may perform at remarkably similar levels, which shows how questions of mechanism and fitness value can have different answers. Sensorimotor cognition is important because it is a foundation on which many other cognitive abilities rest. These building blocks are revealed by investigating development, which in turn is highly informative for phylogenetic studies. Future directions are clear from the blank spaces on the map, but we should be wary of mistaken anthropomorphism, which leads us down a circular path and prohibits exploration of some of the most exciting locations.

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