



Independent Evolution of Similar Complex Cognitive Skills: The Importance of Embodied Degrees of Freedom

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Abstract - Recent years have seen acknowledgment from a number of researchers that similarities appear to exist in complex cognitive skills of distantly related species – most notably in corvids, parrots, delphinids, and great apes. Discoveries on complex cognitive skills in common hold the promise of interesting and fruitful new perspectives on cognition. That said, some theoretical approaches seem largely to be lacking. We draw attention to the importance of pre-existing constraints on and freedoms of the evolving animal, which might prove as important as external selective pressures in understanding the evolution of cognition. To elucidate our point, we briefly describe one contemporary cognitive-science approach to cognition. Accounts on cognitive evolution both in behavioral ecology and animal cognition are often hampered by simplistic input-output-based views on cognition. Cognition – in particular complex cognition – may influence animal behaviors in ways that cannot be captured by a purely selectionist account. We discuss the evolutionary processes underlying independently evolved yet similar characters. We highlight the importance of the difference between parallel and convergent evolution in understanding whether complex cognition arises repeatedly only through similar selective pressures; or whether underlying, previously evolved structures are crucial for the occurrence of cognitive similarities. In conclusion we suggest that the developmental sequences leading to apparently similar cognitive skills require further investigation to reveal the evolutionary processes behind them. Our aim is not one of providing ultimate answers to the questions we raise; instead, we draw attention to their existence, the better that they may be addressed.

Keywords – Convergent evolution, Embodied cognition, Animal cognition, Complex cognition.

Through first half of the 20th Century, the same learning processes were believed to apply to all vertebrates; studying a range of species was unnecessary. Humans were thought to be the only creatures possessing complex cognition. With developments in animal cognition, the picture gradually changed. The field has been growing, as has the number of species studied (Shettleworth, 2009). The realization came that, although many species share many basic cognitive skills, several cognitive expressions diverge. The idea that humans have a cognitive complexity well beyond the rest of the animal kingdom has been called into question. This began with great apes, whose cognitive capacities impressed, largely because of the similarity to our own capacities. Soon other taxa – e.g., corvids, parrots, and delphinids – were shown capable of comparable feats.

From a phylogenetic perspective, it was not surprising that our closest living relatives should share many cognitive skills with us. Emphasis has instead been placed on detailing the divergences between humans and other great apes, the better to understand what makes us unique. Far less attention has been paid to the theoretical implications of findings suggesting that some *distantly related* taxa are similar in their complex cognition, relative to both social and physical domains, memory and communication. Such

attention could prove fruitful toward understanding the nature of cognitive evolution in general and complex cognition in particular.

To date, only a few accounts exist of the apparent similarities in complex cognition between (phylogenetically distant) corvids, parrots, great apes, and dolphins (e.g., Marino, 2002; Seed, Emery, & Clayton, 2009; van Horik, Clayton, & Emery, 2012). For present purposes, we will present these accounts only briefly and not try to define complex cognition. Our focus instead is on discussing relevant conceptual analyses for these comparisons. We believe that comparisons of similar cognitive skills, independently evolved, could aid theoretical development in the field. Much of what we consider applies not only to such comparisons but to views on animal cognition more generally.

Most accounts of apparently similar cognition in distantly related taxa – indeed, most accounts on evolution of cognition – focus on selective pressures determining various cognitive skills (e.g., Humphrey, 1976; Jolly, 1966; Seed et al., 2009; Sol, 2009). Such approaches are, without doubt, fruitful and, indeed, indispensable. Nevertheless, they lack perspective for arriving at a fuller picture of why cognition in nature evolves as it does. Our aim in this paper is to broaden the view beyond selective pressures, by discussing the evolutionary processes that may result in similar outcomes in distantly related species. We draw attention to bodily and developmental degrees of freedom that may be as important as selective pressures for identifying the evolutionary mechanisms behind cognitive skills: i.e., the sensorimotor setup the animal already carries with it – when subjected to new selective pressures – must not be neglected.

We begin with a brief description of so-called embodied cognition. We show how the flexible nature of cognition – in particular involving cognitively complex creatures – clashes with an overly simplistic selectionist approach toward natural environments. We explicate the difference between parallel and convergent evolution, so as to describe the quite different implications these processes have for understanding independently evolved but similar cognition. We end with a discussion of the potential importance of comparing behavioral development related to cognitive skills as one of the approaches to investigating independently evolved yet similar complex cognition.

The aim of this paper is not to answer several of the questions raised, but rather to draw the attention towards them. We believe that far too little reflection has been invested in these issues in the disciplines of animal cognition and behavioral ecology.

Many of the issues relating to evolutionary and cognitive processes are laden with both philosophical controversy and subtlety. We aim to steer clear of or simplify many issues whose details, at this stage, have no bearing on how theoretically to approach independently evolved yet similar cognitive skills.

A point implicit throughout this paper is that one must be aware of the level – or the part of the causal chain – on which one performs the analysis. Debates may – indeed, do – arise easily on these issues.

Cognitive Cousins and Feathered Apes

Humans, along with the other great apes, have traditionally represented – and still represent – the pinnacle of cognitive complexity in nature. Findings of similar skills outside our taxon have typically been compared to us: e.g., dolphins have been called our “cognitive cousins” (Herman, 1980), and corvids have been adopted to our hominidae family in the guise of “feathered apes” (Emery, 2004).

Some accounts exist of apparent similarities in complex cognition between corvids, parrots, great apes, and delphinids (e.g., Marino, 2002; Seed et al., 2009; van Horik et al., 2012). It is noteworthy that these animal group are separated by vast evolutionary time spans: the last common ancestor of birds and mammals lived 296 million years ago, the last common ancestor of corvids and parrots 96 million years ago: close to the 94 million years separating dolphins from apes (see Figure 1). Obviously, these animals also differ strikingly in body forms and locomotion. The interesting question is: what it is that has struck these authors as being similar? We will not provide a full account here – that is best taken from the original writings – but we will identify the essential points.

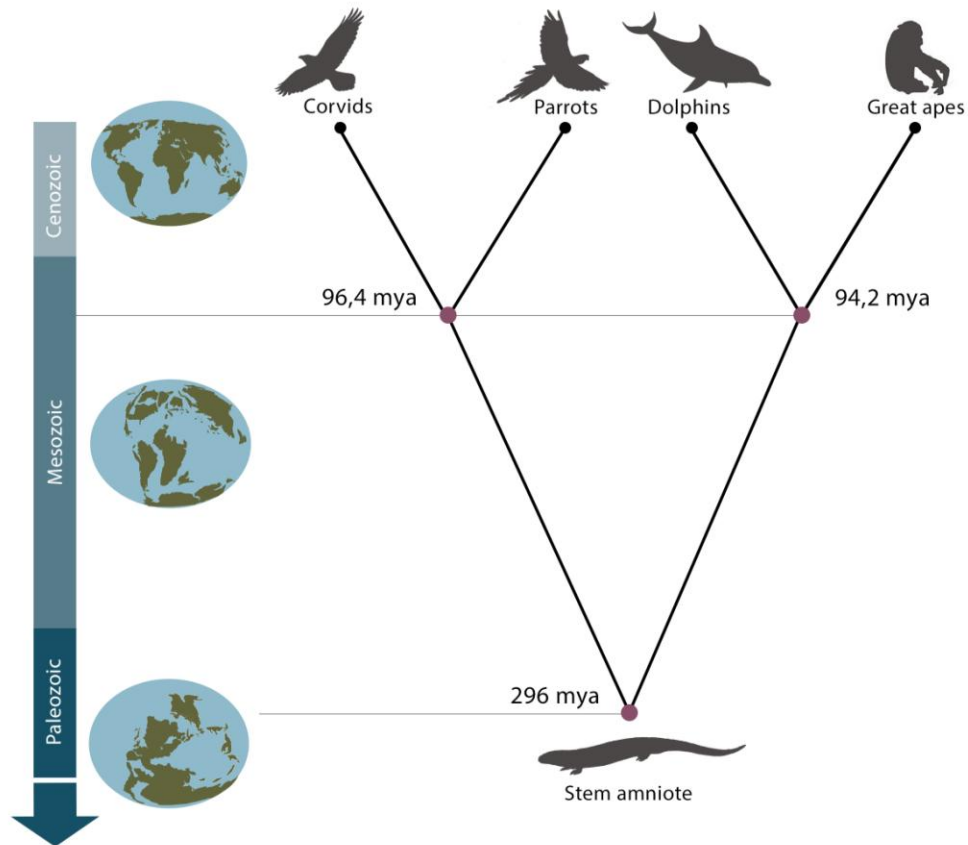


Figure 1. Evolutionary tree describing the phylogenetic distance between corvids, parrots, delphinids, and great apes. The numbers signify the distance in time of the last common ancestor of the diverging groups, as determined by the mean of the available studies as of 28 January 2014 using the web-based software Time Tree. The illustrations to left depict continental drift over the considerable geological time scale involved.

Most of the authors note that the brains of these animals are markedly larger than would be expected from body size. This is often also true in the “higher” brain regions, meaning that parts of the neurocognitive architecture are similar. The social skills are described as unusually complex: advanced behavior reading (perhaps even theories of mental states in others), use of deception, high levels of social learning, and rudiments of culture. Skills in the physical domain are likewise noteworthy, including innovations and some sort of physical reasoning. Their memory systems are described as unusually developed, similar to the episodic system in humans. They have been noted for other things, such as advanced communication skills. In short, these animals are united by a great behavioral flexibility, including high ontogenetic adaptability.

Many – though not all – of these noted similarities derive from studies using a variety of methodologies and approaches with partly different focuses. Some skills are better documented in some species than in others. Though one could question how warranted many of these comparisons are, we will not do so here. We view these accounts as initial discoveries that may lead to better understanding through more rigorous theoretical and empirical work. For now, we simply assume that these animals are similar as a working hypothesis and focus instead on conceptual analyses that might be needed for future investigations.

The Elusiveness of Similarity

The concept of similarity is a central theme in these discussions. Both cognition and evolution are complex processes, making it all the more useful to have some basic grasp of similarity’s difficulties.

Similarity and analogy – and identity – run deep through our conceptualization of the world and have a profound importance for science as well, especially where it relies on inductive reasoning. Reasoning on similarity quickly becomes circular: e.g., something is more similar to something else the more similarities they share. Indeed, a frequent complaint (e.g., Prinz, 2004) is that any two things in the universe resemble one another if one selects the right properties: which is to say that, as Aisbett and Gibbon (2001) note, similarity judgments are critically dependent on context.

Instead of delving into the philosophical issues, we prefer to highlight briefly those cognitive aspects involved in making similarity judgments: a process sometimes referred to as analogical reasoning, which has been the subject of research in animal cognition and may be an important skill in the flexible acquisition of affordances from the environment. Several accounts have been offered of how humans identify and categorize similarity (e.g., Gärdenfors, 2000). The take-home lesson is that such categorization may relate more to our species-specific cognition, given our environment, than to any objective (mind-independent) relationships in the world: i.e., looking for similar cognitive skills in other species might ultimately be an anthropocentric endeavor. The question is, would any of the animals that we think of as cognitively similar think the same of one another?

The Questions of Cognition: Information Processing or Embodiment?

Lately, many have asked for a firmer evolutionary approach to animal cognition (e.g., MacLean et al., 2012; Shettleworth, 2010). Despite this well-motivated enthusiasm, within the fields of animal cognition and behavioral ecology surprisingly few intellectual resources have been devoted to the question: what actually evolves when cognition evolves?

The question of what cognition and the mind really are has occupied philosophers for millennia. Over the past sixty years though, cognitive science has developed theoretical frameworks that have been able to be tested empirically. During the infancy of cognitive science in the 1950s, views on cognition were heavily influenced by the computer metaphor. Cognition was viewed as more or less equivalent to computation; the workings of mental representations could be described algorithmically or otherwise formally. Cognition meant the information processing happening between inputs and outputs whereby the organism receives the “outside” information more or less passively. To caricature this approach, known as *cognitivism*, one may say (nevertheless with some accuracy) that it puts the brain in a vat. Cognitivism was a response to the then prevailing behaviorism, which did not care much what happens between input and output. Even if cognitivism still has its merits, one finds a broad and strong movement in contemporary cognitive science towards releasing cognition from the vat to include the brain’s surroundings. The resulting framework, commonly known as *embodied cognition*, is not easy to capture in any precise theoretical account, as it comprises a range of approaches from different sub-fields. The core idea is that cognition results from bodily interactions with the environment. Any agent’s sensorimotor setup is intrinsic to its cognition, while bodily context gives cognition its degrees of freedom both for action and development.

The concept of *umwelt* – a term coined by von Uexküll (1957) – might be familiar to the ethology-oriented reader. *Umwelt* represents one of the early precursors to the idea of embodied cognition. It denotes the specific world of a specific organism on the understanding that categorization and perception of the world differs among organisms. The same mouse is perceived as one thing for a cat and as something else for a human; the same twig is seen as one thing a nest-building bird and as another for a sheep. Each organism’s *umwelt* is created through its bodily structure and way of life.

A later, related precursor to embodied cognition is the concept of *affordances*, found in the framework of ecological psychology (Gibson, 1979). Affordances are possibilities for action in the environment that a given organism may or may not be able to identify. Affordances are about perceiving the environment *as* something. So a stone of a certain size and composition affords the cracking of nuts for a chimpanzee but not for a raven, who might not even be able to carry it. Meanwhile, a particular tree branch affords a perch for the raven but not for the heavier chimpanzee. The difference between *umwelt* and affordance is roughly that affordance also involves the potential action, *umwelt* does not.

A large body of empirical evidence supports the view that cognition is embodied. The school of ecological psychology derived their hypotheses mainly from work on vision. Other evidence comes from studies on metaphors, some of the earliest and most famous being that presented by Lakoff and Johnson (1980). On their account, language, which partly mirrors the mind, is so dense with bodily-perspective metaphors that, without them, we would have few ways to express ourselves. Such abstract concepts as “power” and “love” and such central concepts to our everyday lives as “space” and “time” are inherently bodily metaphorical, with important consequences for how we cognize them. For example, we look forward in time for the sweet and warm love.

Work within cognitive robotics has likewise helped reveal just how much cognition is embodied. In early robotics, heavily pre-programmed robots could not do much with their environment. Change came with a shift to a bottom-up perspective, whereby robots now had to interact dynamically with their environment, taking advantage of their distinctive bodies and sensors, to gain knowledge and develop their behavioral repertoire. Andy Clark (1997) is among those who have argued most convincingly for an embodied perspective in robotics, writing that the mind is first for acting, not for thinking.

Developmental psychology offers another important perspective, where Thelen and Smith (1994) did the seminal work. Viewing a young child, early in its development, as a dynamic system rather than a genetically hard-wired creature provides richer ways of understanding the phenomena of development. Development essentially is not (merely) a series of pre-programmed steps but unfolds in interaction with the world. Children develop different motor patterns – e.g., reaching for cups – in subtly different ways (Thelen, Schoner, Scheier, & Smith, 2001).

Obviously, there is far more to the embodied perspective on cognition than what we have said here. Discussions run rampant on the details; researchers adhering broadly to the idea that cognition cannot be separated from body and environment may – and often do – stand apart from one another, but they agree that cognition is not, or not merely, an input/output process.

Surprisingly many textbooks in behavioral ecology and animal behavior do not even mention cognition. If it is mentioned, the account is usually rather oversimplified, either more or less equating it to learning or viewing it simply as information processing of perceptual inputs (e.g., Danchin, Giraldeau, & Cézilly, 2008; Davies, Krebs, & West, 2012; Kappeler, 2010). Even within cognitive ecology – the welcome initiative bringing cognition and behavioral ecology closer together – cognition is viewed as input-output-based information processing (e.g., Dukas & Ratcliffe, 2009). Cognition seems often to be viewed as a discrete part of only *some* behaviors: e.g., those where memory or attention is obviously needed. This stands in stark contrast to cognitive science, which hardly attempts to provide any explanations of behavior without cognition. Of course, this divergence is the result of different focus and different traditions.

Within animal cognition, one would expect to find more and better grounded accounts of cognition. Shettleworth’s (2010) influential, and impressingly complete, book on animal cognition studies offers a more nuanced picture. There, cognition is broadly defined as the mechanisms by which animals acquire, process, store, and act on information from the environment. In theory, such a definition could encompass both body and environment; in practice, it appears to promote a view of cognition as information processing. That said, the lack of transparency, as in most accounts on cognition within the discipline, makes it hard to identify any clear views.

It might be that mainstream animal cognition has not yet caught up with the theoretical concerns of cognitive science in its debates over and views on cognition, while behavioral ecology has a long way to go in incorporating cognition into its theories. This is somewhat surprising: embodied cognition should sit comfortably with explanations of cognitive evolution and lend itself well to species comparisons. Too, it can be an effective tool for understanding individual variation in cognitive skills within species. All of this is not to say that animal cognition lacks any movement towards an embodied perspective on cognition. Indeed, one finds several insightful studies and theoretical accounts based on embodied cognition (e.g., Barrett, 2011; Barton, 2012; Holekamp, Swanson, & Van Meter, 2013).

“Natural” Environments and Flexible, Embodied Cognition

In standard behavioral ecology, the role of the natural environment is pivotal for understanding behavioral adaptation. This is based on sound biological reasoning. When observing an animal’s interaction with its environment, one attempts to identify the purpose for which behaviors evolved. However, such a simplistic selectionist approach might occasionally prove inadequate.

Identifying the natural environment of an animal can be problematic; animals are not always found in the habitats where their species originated. Circular reasoning looms: finding an animal in an environment where it performs seemingly rational, functional behaviors leads to the conclusion that these functions are the purpose for which the behaviors are adapted.

Even if this state of affairs is often overlooked, it should not offer new insight; in discourse on behavioral evolution, behavioral or phenotypic plasticity does receive attention. That said, the most cognitively flexible creatures pose unusual challenges. Consider two extreme examples, in humans and ravens, of cognition-based behavioral flexibility. We need not expound on human flexibility; it is well known that humans occupy most habitats and can, for brief periods, survive on the deepest ocean floor and on the moon. Ravens are somewhat less adaptable but nonetheless inhabit the driest and hottest places on Earth as well as some of the coldest ones. They are sighted far up into the Himalayas and in large cities. Depending on their surroundings, they may nest on mountain cliffs or trees, on buildings, or even on the ground. Just like humans, they *prima facie* lack a natural habitat of their own. Similarly high flexibility is found in many of the other animals regarded as cognitively complex: great apes and parrots are geographically somewhat more confined but nonetheless inhabit a variety of habitats. The ranges for dolphins – even within the same species – are tremendously vast. (see Figure 2 for the ranges of humans, common ravens and bottlenose dolphins).

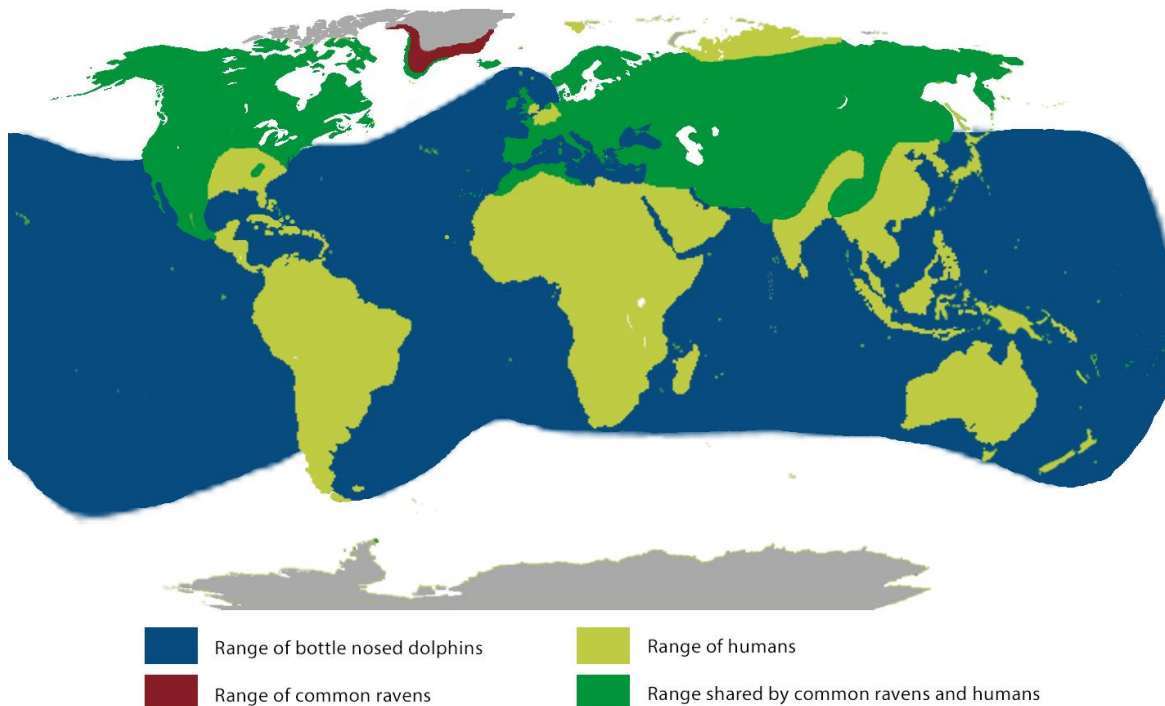


Figure 2. The ranges inhabited by humans, bottlenose dolphins and common ravens. Humans do not have as close of relatives as the common raven or the bottle-nosed dolphin; among the corvids and delphinids, many species have only minor morphological differences. Therefore, taken as a whole, the ranges of corvids and delphinids exceed those shown in the map.

The upshot is that some animals, through their cognitive capacities, in a sense adapt their environments to fit them, instead of having to adapt to the environments through natural selection. Through their cognitive capacities, they also “adapt ontogenetically” to their environment. One might say that the animal’s cognition integrates well with its environment – likely to a degree that, were one to place the animal in its “natural” environment – where its species originated – it would have difficulty coping without extensive re-learning. Suppose one were placed on the African savanna, where *Homo sapiens* originated – equipped only with Stone Age tools. Most would probably feel unfit to the environment. If one were then observed by a behavioral ecologist, she would likely conclude that one’s behaviors appear maladapted. Presumably, this applies to any cognitively complex animal: placed in an unfamiliar habitat where other conspecifics thrive, it would be maladapted.

Major body adaptations are insufficient to explain these species’ ability to cope with a range of habitats. Indeed, the apparent lack of any such adaptations is regarded as a strong sign of a species having high levels of so-called *niche construction* (Laland, Odling-Smee, & Feldman, 2000). This does not negate the possibility of minor phenotypic adaptations to varying environments within a species: e.g., skin color or body proportion. At the same time, such adaptations can be seen as ultimately resulting from cognition; the cognition that provided the opportunity for the same-species-ancestor to inhabit various environments. In similar vein, it is likely that cognition could itself provide selective pressures for cognitive development.

This is not a novel take on behavioral evolution, having pre-Darwinian roots in Lamarck (for an in-depth review see Corning, 2013). The idea that behavior brings about evolution is close to a truism in behaviorally oriented biology, but what is usually not appreciated is that the origin of most flexible behavior in animals lies with cognition. We have said that cognition is best understood as embodied: an interactive partner with its environment and not a passive receiver of environmental inputs. The insight that cognition is interactive and not merely receptive has major consequences.

Corning (2013) makes a strong case that the “purposiveness” of organisms is a major causal factor in evolution, based on nearly two centuries of theoretical development in biology and related sciences. He claims that even those biologists who are proponents of phenotypic plasticity usually view animals as reactors rather than autonomous actors. Switching perspective from reactor to actor makes the animal an active part of the selective process – either by buffering out potential pressures or creating new ones through behavioral innovation. For example, New Caledonian crows have not adapted their beaks for pecking wood substrate to access grubs; instead they use tools – a behavioral innovation that has led to the evolution of extreme binocular vision and a straight bill (Troscianko, von Bayern, Chappell, Rutz, & Martin, 2012). One could expect that the behavioral flexibility in apes, corvids, parrots, and delphinids provides an effective buffer to environmental circumstances that otherwise might constitute selective pressures – something that, if true, might obscure how they evolved their ontogenetic adaptability in the first place. As we will argue, one must study how these animals develop their cognitive skills individually over time if one is to understand whether this development across individuals reveals important similarities. First, however, we must address the question of independently evolved cognitive similarities.

Independent Evolution of Similar Characteristics: Selectionism and Internalism

Recently, theoretical efforts in animal cognition have worked to incorporate evolutionary reasoning into the discipline (e.g., MacLean et al., 2012; Shettleworth, 2010). Most of the work has focused on how to perform phylogenetical reconstructions of cognitive skills, such as identifying homologies and divergences between species. Far less has energy has gone into theoretical considerations over independently evolved but similar cognitive skills.

The few existing accounts of cognitive similarities between corvids, parrots, apes, and dolphins invariably use the concept of *convergent evolution* to describe the process underlying these similarities (e.g., Marino, 2002; Seed et al., 2009; van Horik et al., 2012). Though not necessarily wrong, this might be a too hasty choice of terminology that could unfairly influence views on independently evolved cognitive skills.

Key concepts describing different possible evolutionary outcomes already existed before Darwin came out with his theory of biological evolution. The renowned comparative anatomist Richard Owen is usually credited with introducing the concepts of *homology* and *analogy* into modern biological science in 1843. Homology can be described as similarities between two species resulting from common descent: e.g., the similarities in human and chimpanzee hands are homologies, as they were present in our common ancestor; the differences are divergences. Analogy is similarity that has arisen through independent evolution. The fingerprints of a human or chimpanzee are similar to those of a koala bear, but this is an analogous relationship, because fingerprints were not present in the common ancestor of apes and koalas.

Analogous structures can be arrived at in different ways. The overarching cladistic notion for independently evolved similarity is *homoplasy*. Homoplasy comprises three sub-classes: *convergence*, *parallelism*, and *reversal*. Convergence can be described as arrival at similar structure through different underlying substrates or developmental mechanisms: e.g., the wings of insects versus birds, where the insect appendages come from body-segment structures, while birds use their forelimbs. Parallelism is similarity arising from the same underlying structure or developmental mechanism: e.g., both birds and bats use their forelimbs as wings. Note the difference from homology: the common ancestor of birds and bats did not have wings derived from forelimbs – indeed it had no wings at all – but it did have forelimbs, meaning that the forelimbs in birds and bats are homologous. Reversal is when a feature that existed in an ancestor and then disappeared appears again: e.g., the loss of wings in fleas, whose immediate winged ancestor evolved from a non-winged insect – a state to which the flea has returned.

The above account may appear well-defined but only because of its textbook-style simplification. In practice, these processes can be looked at in various ways, with implications for how one interprets biological phenomena. The most difficult distinctions lie between convergent and parallel evolution. Views on these concepts profoundly impact how we understand the principles of biological evolution and the life forms we see today. A key example is the debate over whether biological macroevolution is grossly predictable given similar environmental circumstances: i.e., similar selective pressures. Stephen Jay Gould (1989) was perhaps the first strong voice against such a view. He believed instead that pre-existing “internal” factors, such as developmental mechanisms, in the organism are equally crucial to evolutionary outcome. The debate is vigorous and ongoing with various arguments put forward (e.g., Arendt & Reznick, 2008; Beatty, 2006; Conway Morris, 2003; Gould, 2002; McGhee, 2011; Pearce, 2012; Powell, 2009; 2012). It boils down to how one distinguishes between convergent and parallel evolution. Nature is abundant with examples of homoplasmically evolved characteristics and traits. If most are the result of convergent processes, this would indicate that evolution – in the face of similar selective pressures – settles on the same solutions over and over again, regardless of preceding developmental (or other) mechanisms. This suggests that evolution is predictable, and that a reboot of life on Earth would, after 3.7 billion years or so, end up looking pretty much as it does today. If, on the other hand, most homoplasy results from parallel evolution, then the underlying pre-existing mechanisms are pivotal. Historical events could have a major impact on future evolution across a broad range of organisms, and biological evolution would be much less predictable from a general perspective. The wings of bats, birds, and pteranodons could all depend on an event whereby forelimbs evolved, in turn depending on an event introducing a mirroring left-right body plan – and so on, in a long, intricate chain. Many of these events that later support independently evolved similarities might be extremely unusual and arise only once in life’s history, as so-called *hard steps*.

Much of the controversy arises from what part of the causal chain or what “level” one focuses on. Basing one’s analysis on the genes involved in enabling various characters biases one towards the conclusion that analogous characters are parallel, given the deep homologies often found in genomes (e.g., Christin, Salamin, Savolainen, Duvall, & Besnard, 2007; Colosimo et al., 2005; Liu et al., 2010; Shubin, Tabin, & Carroll, 2009; Sucena, Delon, Jones, Payre, & Stern, 2003). Genes were not discovered yet during Owen’s and Darwin’s time, so their evolutionary concepts focused more on morphological features: an approach that in many ways continues today; but even seemingly clear cases of morphology can easily lead to disputes. We stated earlier that the wings of bats and birds are the result of parallel evolution, because both used their forelimbs to create wings. Studying their wings more closely, however,

one sees that the bones in the wings are used differently: something that could be thought of as convergent evolution. Defining a process like flight is even more difficult. Is flight a result of convergence or parallelism?

Cognition is an active process, a causal chain in the body and brain in relation to their environment. It is never static. More static though are its potentiators such as brain structures and sensorimotor morphologies. One might think that cognition would always be reflected in behavior; however, such behaviors as inhibition of action, or thinking that is not immediately (or perhaps ever) acted upon, are not easily observable. This unavoidable character of processes adds to the difficulties of defining the evolutionary mechanisms behind cognitive skills.

The discussions are far more complex and multifaceted than we have described. Nevertheless, these basics are important for evolutionary oriented cognitive scientists and cognitively oriented behavioral ecologists to understand. When considering the selective pressures that might have led to certain behaviors and related cognition, one must pay equal attention to pre-existing structures in the evolving animal (Ereshefsky, 2007; 2012). Not only the external but also the internal environment provides the necessary degrees of freedom for the evolution and expression of cognitive skills. One must attend to both these aspects if one is to understand the principles behind the evolution of the complex cognitive skills one finds in nature today. Can complex cognition arise over and over again, regardless of any “hard steps” that were taken only once? Another, much important lesson is that whether one regards a certain apparently analogous expression of cognition as the result of convergence or parallelism depends on what part of the causal chain leading to the expression one observes.

Parallel or Convergent Brains?

No matter how one views cognition, brains are essential: a necessary and complex part of the causal chain of cognitive processes. The brains of the animals in the four groups we are concerned with appear radically different: avian brains differ markedly from mammalian brains, while the brains of great apes and dolphins also have notable differences. These differences are the main reason for regarding independently evolved complex cognitive skills as the result of convergence (e.g., Marino, 2002; Seed et al., 2009; van Horik et al., 2012). That said, a closer look at the organization and evolution of the brains of these animals suggests some reconsideration.

A detailed understanding of how a brain is involved in the production of complex cognition is lacking. The traditional approach has been to make gross comparisons of overall brain volume relative to body size, usually factoring in that smaller animals have a larger surface area compared to their volume, resulting in proportionally larger brains (e.g., Jerison, 1973). The resulting *encephalization quotient* comes in several versions; regardless, animals thought of as cognitively complex – including the four groups we are discussing – always have brains larger than expected from their body size (e.g., Cnotka, Güntürkün, Rehkämper, Gray, & Hunt, 2008; Iwaniuk & Hurd, 2005; Marino, 2002; Roth & Dicke, 2005). Brain-to-body-size measures have been used to find many correlations with varying types of behavioral flexibility (e.g., Reader & Laland, 2002; Sol, 2009). In short, large brains generally correlate with higher behavioral complexity. That said, such overall measures have been called too crude, leading to more detailed analysis on correlations between behavioral complexity and the proportional size of *specific* brain regions. Once again, the four groups we are discussing show enlargement in areas usually associated with behavioral flexibility (e.g., Iwaniuk & Hurd, 2005; Mehlhorn, Hunt, Gray, Rehkämper, & Güntürkün, 2010; Reader & Laland, 2002; Rehkämper, Frahm, & Zilles, 1991).

However suggestive these correlational studies may be, they fail to address whether the neural structures of distantly related but cognitively complex animals result from convergent or parallel evolution. *Prima facie*, avian and mammalian brains are exceedingly different. The mammalian brain has a layered outer cortical structure, while the avian brain has a nuclear organization in the cerebrum. Traditionally, the neocortex has been associated with “higher” intelligence. Lacking such structure, with brains seen to consist largely of basal ganglia – mainly associated with instinctive behaviors – birds have not been considered viable candidates for cognitive complexity. In the late 1960’s came the discovery that

a structure once believed to be part of the basal ganglia – the DVR – receives visual, auditory, and somatosensory input from the thalamus – just as the mammalian neocortex does (Karten, 1969). Other areas of the avian brain were found to have downstream projections to the brain stem and spinal cord – again similar to output circuits in the mammalian brain (Nauta & Karten, 1970). These and other findings have resulted in a major re-writing of the avian brain nomenclature (Jarvis et al., 2005), with the realization that the pallial proportion of the avian brain is similar to that of mammals.

The so-called *nuclear-to-layer hypothesis* provides an evolutionary account of the relationship between the avian DVR and the mammalian cortex (Karten, 1991). The cell types and neural circuits in the DVR appear to be homologues to those found in different layers of the cortex, implying that they existed in rudimentary form in the common ancestor of birds and mammals. In the one case, they were incorporated into a nuclear brain, in the other into a layered brain (Karten, 1969; Nauta & Karten, 1970; Reiner, 2000). This conclusion is supported by recent results from gene-expression studies (Jarvis et al., 2013; Karten, 2013; Suzuki, Kawasaki, Gojobori, & Hirata, 2012; Wang, Brzozowska-Precht, & Karten, 2010).

Separately evolved brain structures aside, many vertebrate brains contain important conserved structures such as the hippocampus, basal ganglia, and cerebellum. The hippocampus – which, among other things, is crucial to episodic memory and foresight and to spatial orientation – is found even in teleost fish (Allen & Fortin, 2013). The basal ganglia – universal in vertebrates and also found in lampreys – performs important motor-control functions and has also been associated with procedural memory, language, and planning (Anderson, Albert, & Fincham, 2005; Packard & Knowlton, 2002; Prat, Keller, & Just, 2007). The equally conserved cerebellum is well known for its central role in sensorimotor control and has recently been identified as playing a role as well in working memory, language function, and decision making (Barton, 2012; Bellebaum & Daum, 2011; Leiner, 2010; Strick, Dum, & Fiez, 2009).

Taken together, the evidence strongly suggests that the operations of mammalian and avian brains are largely the result of parallel evolution: i.e., common underlying structures are re-used to arrive at similar solutions. The same reasoning likely holds for the brain adaptations found in corvids, parrots, great apes, and dolphins. They have evolved analogous enlargements and other brain dispositions to support their complex cognition: an evolutionary process probably based on common underlying structures. Lori Marino (2002) has argued that the complex cognition of dolphins should be considered the result of convergent evolution, because their brain organization is significantly different from that of primates. Cetacean and primate brains are dissimilar both at the gross morphological level and the cortical circuitry level. Nevertheless, their brains underwent similar changes, leading to high encephalization and a higher neocortex ratio. Marino's argument appears to be based on the levels "above" that of the conserved features. We believe that these conserved features could be understood as the common underlying structures and that most likely several features of the dolphin brain are the result of parallel evolution.

It may well be that there has been too much focus, in comparative studies of complex cognition, on those parts of the brain traditionally associated with "higher" functions" at the expense of more conserved structures. Arguing from an embodied perspective, Barton (2012) makes a strong case for the cerebellum's importance to vast numbers of cognitive abilities through its substantial interconnections with the cortex. Primates have a larger neocortex compared to other mammals – but they also have a larger cerebellum, suggesting that the cortico-cerebellar circuits in primates are more elaborated. This might be the underlying reason for their fine motor-control skills both in technical domains such as tool use and social domains such as production and comprehension of speech. This suggests that sensorimotor function and complex cognition are highly connected: in particular, that complex cognition emerges from the elaboration of basic sensorimotor structures.

Development and its Role in Behavioral Comparisons

Accounts of cognitively similar but distantly related animals usually try to identify analogous socio-ecological factors in their search for comparable selective pressures (e.g., Seed et al., 2009; van Horik et al., 2012). Classifying such potential selective pressures is an important endeavor in need of more in-depth work. However, it is, as we have suggested, equally important for understanding evolutionary processes to compare underlying developmental mechanisms. Given the embodied nature of cognition, we believe that such investigations are essential.

If two species display a similar cognitive skill, the underlying evolutionary process(es) could partly be recognizable from the path of its development in each species. If development of the skill differs markedly, it is likely the result of convergent evolution. If the developmental sequences overlap, it might be the result of parallel evolution.

Genotypic and environmental factors determine the development of phenotypic traits (Lickliter & Honeycutt, 2003); cognition cannot be reduced to a certain gene-based or otherwise pre-programmed unfolding of brain structure, and the role of development might be even more important to study for understanding cognition than for understanding morphological traits. Cognition is investigated primarily through behaviors, which are, as well, a source for studying cognition's development. Piaget (1954) suggested a developmental bridge connecting infant sensorimotor activities to complex adult cognition. His now widely influential idea of searching for the roots of complex cognition in infant sensorimotor development is of particular importance from an embodied cognition perspective: it offers a bottom-up approach whereby complex cognition is built on and elaborated from sensorimotor interaction with the environment. Such a perspective establishes a biological continuity: brains are evolved to control action in the dynamic and ever-changing environment in which animals live (Koziol, Budding, & Chidekel, 2012). Continuous sensorimotor interaction with the environment throughout development is a prerequisite to building flexible cognition that deals with environmental contingencies.

Piaget's framework for modeling infant sensorimotor development has been used for comparing cognitive development between species since the 1970s, given its firm biological grounding and focus on nonverbal behavior. Within that framework, a child proceeds through six stages from birth to the age of two years: starting from simple reflexes and ending with mental representation. Mammals and birds that have been tested typically go through the same sequence, though they may not reach the later stages and the timings can be highly variable (Doré & Dumas, 1987; Vauclair, 2012). Initially, gorillas develop faster than humans; but it takes them longer to succeed on difficult tasks such as tool use (Redshaw, 1978).

However, Piaget's theory lacks detail in the finer points of sensorimotor interaction (e.g., Pepperberg, 2002). Thelen and colleagues (2001) showed the embodied nature of cognitive development as revealed by Piaget's so-called *A-not-B error*, whereby infants choose Location A, from which a desired object has previously been retrieved, even if they have observed the object subsequently being placed at Location B instead. In reviewing studies of the *A-not-B error*, it became obvious to Thelen and colleagues that the infants' performance does not result from rigid, predetermined factors associated with specific brain regions; instead, it depends on subtle changes of experimental cues and sensorimotor feedback from the environment.

As the previous section implies, several neurocognitive accounts strongly emphasize the role of the prefrontal cortex in development of cognitive skills such as self-control, planning, and memory (e.g., Diamond, Prevor, Callender, & Druin, 1997). The prefrontal cortex is indeed central to such skills; however, viewing it as a kind of top-down-controlling "chief executive" neglects the pivotal developmental contribution of sub-cortical structures associated with sensorimotorics and sensorimotor integration – especially the cerebellum. The cerebellum appears to "train" the frontal lobes to predict motor outcomes through sensorimotor feedback (Koziol et al., 2012). It is telling that not only the prefrontal cortex but also the cerebellum matures slowly (Casey, Giedd, & Thomas, 2000; Rakic & Sidman, 1970). That the mind is first for acting not for thinking appears well supported from an integrated neuro-developmental perspective.

Developmental constraints limit the possible expression of biological characters and so reveal the possible dimensions for such expression, regardless of whether or not expressions currently exist (McGhee, 2011). From an embodied perspective, developmental constraints are central: every species inherits a unique “body plan” through historical contingencies; bodies differ in terms of both “external” affordances and sensorimotor interactions with the world. Holekamp and colleagues (2013) found that carnivores’ tactile interaction with the environment is more limited than that of primates, implying a more restrained developmental space for cognition, as reflected in levels of complex cognition.

Understanding constraints on interaction and degrees of freedom for cognitive development might well be key to making productive comparisons between species. We submit that, by making fine-grained comparisons of the development of various cognitive skills, one can identify whether a given skill is the result of parallel or convergent evolution – based on the view that cognition is an embodied *process*, one that is often revealed through behavior. The behavior is not only an expression of cognition; it is part of cognition. Cognition is more than brain states; it is the integration of them in action – or in active, intentional non-action. Unlike physical traits, cognition cannot lie dormant; only its potentiators such as sensorimotor systems or other brain structures can. Cognition *is* the causal process in the agent’s interactive flow with its environment. The development of that process reveals some of the essential sub-parts of the causal chain. Similarities in these sub-parts would indicate a parallel process. Obviously, one can challenge what amounts to a stipulation that the developmental sequence is the most vital aspect of the causal chain of cognition; but any other choices will likewise be stipulations. The advantage of our approach is that it appears empirically tractable for behavioral research. Current understanding of the brain processes underlying complex skills seems too shallow for detailed analysis; the brain, with its various structures, only lends itself to coarser – albeit informative – correlations with complex behaviors. Systematic comparison of developmental sequences as they unfold through behavior is an informative – even key – addition to understanding the evolution of cognition.

Needless to say, this approach entails several methodological and theoretical difficulties, such as how to demarcate cognitive skills or do fine-grained systematic and comparative measurement of developmental sequences. Individual developmental sequences seem to differ slightly within species; therefore, between-species comparisons require consideration of within-species variation. An obvious problem is that birds, marine mammals, and primates differ extensively in their embodiment and overall speed of physical maturation. From a radical – possibly, but not necessarily, false – embodied view, one might argue that animals with such vast bodily variation cannot have similar cognition. Once again, one must agree on, or otherwise argue endlessly over, what similarity is for us as researchers. Such difficulties – and more – must be part of the design and development of empirical work. That in no way diminishes the importance of such comparisons toward revealing the evolutionary processes at work in cognition.

Conclusion

We hope to have explicated several of the intricacies involved in making comparisons between species with independently evolved complex cognition. We hope as well to have shown the value, regarding several issues in the evolution of cognition, in taking a more carefully elaborated perspective on cognition than that which posits a simple input/output-based process. By highlighting the distinctions between the evolutionary processes behind similar but separately evolved characters, one realizes their importance for addressing the larger questions of how – and how often – complex cognition has evolved on Earth. Is independently evolved complex cognition a sign of the inevitableness of such cognition, given external selective pressures; or are the chances narrower, ultimately governed by rare events that create the necessary underlying structures? Drawing distinctions helps one appreciate the importance not only of focusing on selective pressures in evolutionary investigations, but also of addressing developmental constraints in the species under investigation. Based on a brief review of the neurobiology literature, we suggest that, as essential parts of the cognitive process, the brains of distantly related species may share many relevant underlying structures, leading to similar solutions over and over again. Meanwhile, we stress that one of the most fruitful ways to investigate whether apparently similar

cognition is the result of parallel or convergent evolution is to look at whether the species in question share similar developmental sequences in arriving at their complex cognitive skills.

We have not discussed theories on the selective pressures for evolving cognitive skills, although several such accounts exist: e.g., the *social intelligence hypothesis* (Humphrey, 1976; Jolly, 1966) and the *cognitive buffer hypothesis* (Sol, 2009). In failing to address such accounts, we do not intend in any way to diminish their importance. We are merely trying to add a few of the likely necessary components for understanding cognition's evolution. The idea that development is key to understanding evolution is far from new; it has been appreciated since the dawn of evolutionary reasoning. We only put a somewhat more cognitive angle on it, regarding the distinction between convergent and parallel evolution.

One final note: we hope to have added our own weight to those voices stressing the intrinsic role of the observer in any scientific account. The similarities one “finds” may ultimately be the product of one's perspective. The parts of the cognitive causal chain one focuses on – from genes to behaviors – are likewise unavoidably subjectively and intersubjectively biased, as is how one attempts to distinguish evolutionary processes.

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