

Brianna Wilson

## Evolution of Cognition

The evolution of cognition is a rather difficult subject to research. First, the concept of complex animal cognition does not extend roots as deeply as many of the concepts of evolution-natural selection, drift, and adaptations, to name a few. In fact, some of the earliest influential papers on the subject do not emerge until mid-1900's, and then are still based primarily around very few small, easy-to-study mammals like rats. Hobbs wrote about many important concepts related to animal emotion and emphasized that the use of anthropomorphic terminology for great apes was not counterintuitive, unwarranted, or incorrect in his landmark paper "Emotion in man and animal: an analysis in the intuitive processes of recognition" (1946). It had been-and still is mostly frowned upon to anthropomorphize the behavior of non-human animals. While it can be dangerous to assume the root of behavioral expressions that resemble those in humans, the evolution of these emotions and behaviors suggest that using this language is not as far-fetched as originally thought. Understanding the general human superiority thoughts of much of the European nations throughout history is important to comprehending the incredibly slow progress of researching evolutionary cognition. History is full of studies drenched in misunderstanding. One of my favorite books, The Truth About Animals by Lucy Cooke, explores early behavioral studies in which experimental designs were not created with species-specific tasks in mind. Many of these early studies expected animals to perform tasks that they either were physically incapable of completing or that were so irrelevant to their ecology, it would not make sense to expect them to be completed. Setbacks like this inhibited research into the evolution of cognition, but progress over recent years is much more promising.

The evolution of cognition is interesting in part because of the lack of permanence in any historical records. For instance, fossils can explain significant detail in the structure of extinct species, and DNA can further explain relatedness and other confounding physical characteristics. However, cognition is not something that can be explored in extinct species. Because of this, its general evolution involves a significant number of assumptions based around phylogenies of extant species. As such, it is well known that birds are direct descendants of dinosaurs. Scientists can use what is known about bird behavior and, using fossil record combined with known behaviors of their extant relatives to make educated assumptions as to the behavior of certain dinosaur species (Lockley et al., 2016). However, these discoveries are quite recent, and using these same measures to compare cognition have not been commonly established. As of this point, more energy has been placed into understanding extant animal cognition as opposed to extinct. The classic and well-cited 1993 paper "Comparative cognition: Beginning the second century of the study of animal intelligence" by E. A. Wasserman delves into the history of the study of cognition, and then into what were current research tactics at the time. Later, this paper will expand on the theories relating to evolution of cognition to a more current review paper discussing the best methods of establishing phylogenetic cognitive relationships, and finally will finish with a current research article regarding comparative cognition of ravens.

Wasserman opens his paper contemplating the significance of cognition without language and dangers of anthropocentrism that dominated early in the field. He discusses the origin of animal intelligence studies around 1894 but suggests more reliable methods were not established until the times of well-known researchers Thorndike and Pavlov. Further along the study of cognition, researchers recognized and commented on the perceived inability to study subjective emotions and experiences (pp. 212-213). This paper suggests the previously conceived possibility that "nonhuman animals are [not] even capable of conceptual behavior", meaning that

animals are not able to behave conceptually by processing objects and events into classes of stimuli (pp. 216-217). This claim is then refuted exclusively by studies regarding artificial (man-made objects) and natural conceptualization skills of pigeons. They showed an impressive memory and ability to categorize. Pigeons are a great study species, and this is primarily true because of their origin in domestication. Dr. Gregory Berns' lab has discovered that dogs show an ability to recognize facial features and expressions of humans, an ability originally thought to exist only with other closely related primates (Dilks et al., 2015). Because pigeons were artificially bred by humans and primarily exist in anthropogenic areas, it is not a reach to assume their cognitive recognition of human activities may be partially attributed to their side-by-side evolution with *Homo sapiens*. At this point in time, most cognition studies revolved around pigeons, rats, and primates. Therefore, the evolution of cognition could not be properly extended to wild animals or throughout other phylogenies.

Wasserman primarily focuses on comparative cognition through evolutionary theory. He asks multiple questions all relating to comparative cognition and its relationship to evolution and ethology. In regard to the feasibility of cognition being comparative, he discusses the importance of expanding research to cover underrepresented species in order to compare across species, clades, and classes. He also previews the difficulty in studying cognition without a lens on behavior. Gottlieb suggests that comparative psychology may be studied both through anagenesis and cladogenesis, which Wasserman interpreted as a potential that researchers may be able to track cognition through distant lineages by studying the progression of certain levels of cognition (Wasserman, 1993, p. 223). Additionally, these two lenses are encouraged to be studied as "parallel and complementary lines of evolutionary inquiry" (p. 223). Anagenesis is defined in this context by Gottlieb as "the progressive evolution of adaptive behavior, learning ability, or intelligence" (1984, pp. 448-449). The combination of these two approaches would directly connect and compare the genetic process of speciation with differences in cognitive mechanisms over time. While this is a positive step in understanding the evolution of cognition, dangers with this line of inquiry imply a consideration that each new act of cladogenesis is associated with an *improvement* instead of just a newfound difference in ecologically relevant traits. However, this combination of inquiries suggested a profound step in the right direction.

Research delving into phylogenetic relationships with behavior propelled the studies of cognition in the same direction. The problem was that relationships involving behavior could be established, but the mechanisms through which they existed could not. Thus, studies in controlled environments began to look at these mechanisms as thoroughly as they could without being able to know the internal motivations of the mind. To be fair, these are also rather unreliable when looking at humans, as the only way to study emotions and thought processes in humans is through personal reports of introspection. Although more progress has been made in human cognitive neuroscience, this is largely due to the fact that human brains may be examined while conscious. However, recent studies allow potential comparison of cognition and emotion through an understanding of neurobiological similarities in function. For instance, Dr. Gregory Berns has studied dog preference using fMRIs to evaluate brain activity in the caudate nucleus, the region of the brain known to be associated with positive emotion (Berns et al., 2015). This is perhaps the one of the first truly, consciously ethical studies quantifying emotion in combination with cognition and neuroscience.

The field of cognition has undergone multiple subject focus changes since its inception. In their review of the evolution of cognition, MacLean et al. (2012) looks to test correlations between life history and cognitive ability, measure predictable cognitive qualities based on

phylogenetic relatedness, and “estimate the ancestral state of a given cognitive trait” (p. 2). They first discuss four fundamental questions postulated from Tinbergen’s challenge: ontogeny mechanisms, causal mechanisms, phylogeny, and function of cognitive abilities. The first two are considered a simpler research path, whereas latter two are historically difficult to research (p. 4). Following the anagenesis and cladogenesis lenses, the first comparison these authors make is through the social intelligence hypothesis. This concept suggests that “changes in social complexity on different evolutionary lineages should be coupled with changes in the cognitive abilities required to live in increasingly complex social groups” (p. 4). Currently this theory is still difficult to generalize across species, and especially across different taxonomic groups-i.e., it is difficult to generalize between hyenas and orca whales. However, methods using correlated evolution (testing nonindependence between data points representing two traits-one behavioral and one cognitive), phylogenetic signals (“resemblance due to shared evolutionary history”), reconstructing ancestral states (nodal reconstructions of likely cognitive performance based under a Brownian evolution model to determine degrees of divergence), and phylogenetic targeting (comparative approach using closely related species with few confounding variables and adding few species that maximize variation) together allow a more thorough peak into the evolution of cognition (MacLean et al., 2012, pp. 6-11).

This review paper suggests that the combination of those different methods can help explain the phylogenetic and functional components of Tinbergen’s approaches. Using what is known about the causal and developmental mechanisms may also be of use when establishing phylogenetic connections. While this is not a theory on its own, it supports the idea that evolution of cognition may follow quantifiable traits as they exist in separate areas of a phylogeny. For instance, correlated evolution methods may lead to the creation of a more accurate phylogeny should they find certain behavioral and cognitive traits to be non-independent. Or, assuming these quantifiable traits also evolve in a predictable manner, they may be able to reconstruct ancestral states by degrees of divergence as they would with any other genetic change. Linking behavior and cognitive adaptations together may also help determine functionality of both. The methods above can be used to ask questions like: Would cognitive traits follow the same parsimonious evolutionary pattern as behavior? What components of ecology are most explanatory in the evolution of cognition throughout different taxonomic groups? Do behavior and cognition diverge at similar rates? Answering these last two approaches would contribute astronomically to our understanding of how cognition has evolved. Perhaps most popularly, it could also explain the relationship between human and non-human cognition. MacLean et al.’s paper also suggests the importance of working collaboratively and across fields.

Corvid advanced cognition and intelligence is well-documented and well-established. In a recent paper, Pika et al. (2020) addressed three questions related to raven cognition. These questions compared physical versus social cognition, addressed early cognitive development, and compared overall abilities to great apes (p. 3). MacLean et al.’s earlier paper mentioned the importance of incorporating multiple types of tests to find repeatability in cognitive abilities. Pika et al.’s paper (2020) is composed of physical domain and social domain subjects. For the physical cognitive domain, nine tasks were spread between three scales (causality, quantity, space). The social cognitive domain tests were also composed of three scales (communication, social learning, theory of mind) with six total tasks. The tasks were simple and well-thought-out methods of testing multiple forms of cognition.

Both domains were tested with the same experimental set up: a single crow was released in a room divided by wire mesh. A researcher sat on the other side of the mesh behind a board that extended like a table into the crow's side. Three upside-down cups were arranged in a line with food under only one of them. Using this simple set-up, researchers were able to test spatial memory, object permanence, problems solving through board rotation and cup transposition, relative numbers, recognition of food presence through sound and shape, and use of tools under the physical domain. Under the social domain, they used the same set-up to test comprehension and theory of mind. The theory of mind test looked to see if the ravens would direct researchers towards the baited cup even considering a change in observer or whether the orientation of the researcher allowed them to see the bird's cue or not. This was additionally tested through gaze following and decision making based on a researcher's cue.

Notably, they found that ravens had intraspecifically significantly higher scores on quantitative tests, and lower on spatial skills. They performed similarly to great apes in quantitative and theory of mind scores (not significantly different), slightly below great apes in causal and communicative skills (not significantly different), and lower performance in spatial skills (pp. 4-12). Overall, their results expressed stark similarities in the cognitive performance of ravens and great apes (significant).

This concept is interesting when applied to the evolution of cognition. In order to accurately compare across taxonomic groups, they created a multiple-task common raven test (CCTB) derived from the established common great ape test (PCTB). The purpose of their study was not to establish any evolutionary link between the two, but they found results that posed interesting questions regardless. Ravens belong to the corvid class association, and similar to great apes, multiple species in this class display advanced cognition and intelligence. However, corvids can be further grouped as songbirds. Songbirds as a whole do not perform similarly to their subgroup. Where in the phylogeny does cognitive ability diverge? Could the lack of similar performance in other songbirds be a result of secondarily lost characteristics? Is the social evolution hypothesis the primary explanation for the cognitive performance in corvids? While the paper largely supports the social evolution hypothesis, it also opens doors for further investigation into the phylogenetic connections of the evolution of cognition. For instance, ravens and great apes face similar social pressures based on both cooperative and competitive interactions with conspecifics. The authors emphasize that, although ravens and great apes have comparable abilities, it is important to remember that "similarity at the behavioral level does not need to reflect the same underlying cognitive mechanisms" (Pika et al., 2020, p. 16). This line of thinking supports the social cognition hypothesis and suggests that the trend evolved in two separate lineages (given how distant the common ancestor of birds and mammals is). In a way this poses even more questions.

Although there are steps in the right direction, there still seem to be a lack of papers focused on Tinbergen's phylogenetic approach in regard to cognition. Multiple papers have been published to establish the best-known mechanisms for tackling this tough subject, but even an experimental outline does not equate to an easy test. The field of evolutionary cognition is likely to continue to expand as technologies and proper cross-species testing techniques become more wide-spread. Researching the mechanisms of cognition may seem nearly impossible in the time being, but for now may be supplemented with techniques and lenses mentioned above.

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