Overview

Evolution of cognition

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Renewed interest in the field of comparative cognition over the past 30 years has led to a renaissance in our thinking of how cognition evolved. Here, we review historical and comparative approaches to the study of psychological evolution, focusing on cognitive differences based on evolutionary divergence, but also cognitive similarities based on evolutionary convergence. Both approaches have contributed to major theories of cognitive evolution in humans and non-human animals. As a result, not only have we furthered our understanding of the evolution of the human mind and its unique attributes, but we have also identified complex cognitive capacities in a few large-brained species, evolved from solving social and ecological challenges requiring a flexible mind. © 2011 John Wiley & Sons, Ltd. *WIREs Cogn Sci* 2011 DOI: 10.1002/wcs.144

INTRODUCTION

The way in which animals respond to changes in their environment varies considerably, yet functions to maximize their fitness. In many species, responses occur at fundamental levels, such as reflexes, orienting, taxis, and simple forms of learning, such as habituation and sensitization. However, some species respond using more sophisticated psychological processes, such as conditioning, memory, and reasoning, to predict and even manipulate environmental regularities. As such, *cognition* can be described as the ability to acquire, process, and retain information, which can then be used to influence decision making.[1] Such processes are commonly inferred when animals apply generalized principles obtained from learned experiences to solve novel problems. It is thus in the manipulation of 'knowing that' information (declarative; episodic and semantic), rather than 'knowing how' information (procedural), that animals may demonstrate reasoning about the underlying causality of problems they experience in their environment.[1]

Darwin[2] noted that certain behaviors found in non-humans, such as imitation, tool use, and the use of sounds in communication may provide insights into human intellect. Consequently, he concluded 'the difference in mind between man and the higher animals, great as it is, certainly is one of degree and not of kind' (Ref 2, p. 128). Although research in comparative psychology has progressed considerably since Darwin, similar key questions remain today as to whether animals, like humans, possess a number of cognitive abilities that collectively contribute to their intelligence.[3,4] Research on animal intelligence has traditionally focused on our closest living relatives, the great apes, based on the erroneous view of a 'ladder of life' or '*scala naturae*', which places humans at the top and apes, dolphins, birds, reptiles, fish, amphibians, and insects below in relative order.[5] As a result, the special status of apes, based on their evolutionary relationship to humans, has predisposed views that cognition in non-human animals is largely focused within the primate family. This elementary approach soon developed into a phylogenetic model based on the tree of life, maintaining similar assumptions that complex cognition (so-called intelligence) is coupled with recent evolutionary events.[6]

However, cognitive evolution does not conform to a simple linear scale aligned with phylogeny. Irrespective of phylogenetic relationships, species may share commonalities in the socio-ecological challenges they face in their environments.[1,7] Such problems might include learning about the nutritional values of certain foods, the location, and timing of ephemeral resources, or the recognition of a territory, nesting or dwelling site relative to local landmarks. Common ecological selection pressures, like those responsible for analogous (i.e., convergent) evolution of flight in bats and birds, might then converge on similar cognitive functions due to how an organism interacts with its habitat rather than its ancestry.[8] Thus, the comparison of cognitive processes among more

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DOI: 10.1002/wcs.144

distantly related species, such as birds and mammals and their particular environments, might also reveal clues to how cognition evolved.[9]

METHODS FOR RECONSTRUCTING THE EVOLUTION OF COGNITION

To describe how cognitive traits may have evolved, changes in the history of observed characteristics of living and extinct ancestral species that may be proxies for behavior and cognition need to be examined. Such tangible clues such as nest building, burrowing sites, or stone-tool artifacts may provide the best clues we have because behavior does not fossilize. Aspects of cognitive evolution may be inferred by describing changes in the length and shape of certain bones, cranial size, and patterns in brain endocasts or fossil materials found with other fossil remains, but what is more important are those actions in extant species with clues to cognitive functioning, such as patterns of locomotion, manual dexterity, food gathering, and communal activities.[10] Indeed, this is how biological anthropologists reconstruct views of what human ancestral life may have been like. For example, we can observe the adaptation of bipedal locomotion from skeletal remains, leading to speculation about whether the hands were freed to carry objects or make tools, freeing the mouth and facilitating vocal communication. Did an increase in cranial size support the enlargement of the frontal and temporal lobes furthering linguistic capabilities? What about evidence for the cognitive processes underlying the use of fire, hunting with tools, religion, or the production of art? Are these mere speculations ('Just So Stories') that fit our assumptions or viable, testable hypotheses?

Phylogenetic Analyses

If we revisit Darwin's statement—the distinction between human and non-human intelligence is one of degree, not of kind—we might expect there to be no qualitative differences in cognition between species.[11] That is, cognition is governed by *general processes* common to all animals. This claim has been supported by experimental psychologists who proclaim basic rules of association account for learning and memory throughout the animal kingdom.[11] The General Process view considers that the fundamentals of complex cognition result from the strengthening of positive, neutral, or negative responses that are paired with associative stimuli and applied across an extensive range of problems.[12] Simpler processes, such as habituation, are shared by all species, whereas conditioning, problem solving, and the formation of abstract concepts are restricted to more cognitive species. Of the greatest complexity—said to be unique to humans, but with precursors in other animals—is language.[13]

Our closest non-human relatives, chimpanzees, share about 98% of our genetic profile.[9] However, major cognitive changes have occurred during human evolution. Humans and chimpanzees might be very similar in their DNA, but are vastly different in the size and structure of their brains and their resulting cognitive faculties.[14] With this in mind, are the great apes the best model for inferring early human behavior and cognition? We will address this question later.

Ecological Correlates of Cognition

It is possible, with the use of large data sets, to demonstrate global trends across species and infer relationships between cognitive traits and socio-ecological variables.[15] However, caution is warranted as methodological inconsistencies may confound interpretations. For example, experimental designs need to incorporate ecologically valid approaches, as it may be illogical to rank complex cognition among different species with different life histories.[16,17] Thus, behavior may be influenced by a number of processes that are not specifically cognitive. For example, polygynous species may require a larger home range to successfully breed, whereas monogamous species, which have ready access to mates, may not. As a result, differences in species' ecologies may influence their spatial memory abilities. To control for such variation, alternative methods that incorporate more comparable cognitive correlates such as relative brain size may prove more productive.

Brain Size and Cognitive Ability

Larger organisms tend to possess larger brains than smaller organisms. However, overall brain size *per se* is not a particularly useful proxy for cognitive ability. This is because brains are composed of many components that are not directly associated with cognition, but serve to control sensory, visceral, and motor functions. For this reason, measures of cognitive capacity are often gauged by comparing those areas of the brain more closely associated with cognition, such as the neocortex in mammals and the nidopallium (cortex equivalent) in birds, with an organism's overall body mass. The resulting measure is referred to as *relative brain size*.

Hypotheses about the function of relatively large brains have generally focused on the relationship between relative brain size and correlates of cognition such as behavioral innovation, group size, social learning, and tool use.[18] This connection assumes

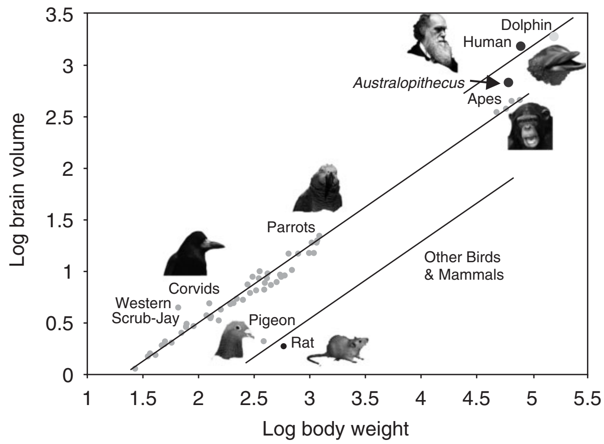

FIGURE 1 | Relative brain size across birds and mammals. Graph displaying the relationship between (log) body weight and (log) brain volume across various birds and mammals (e.g. corvids, parrots, apes, dolphins, *Australopithecus* and modern *Homo sapiens*, pigeons, and rats). Data taken from various sources.

that larger brains must be functionally adaptive considering the increased energetic costs associated with maintaining them.[19] Although studies on vertebrate species generally support this view, investigations into the cognitive mechanisms that underpin invertebrate behavior contest whether bigger brains are actually better.[16] In mammals, primates and dolphins have the largest brains for their body weight, with humans showing the largest overall relative brain size.[20] Trends also appear for larger brains during vertebrate evolution.[19] As a result, birds, although generally considered inferior in intellect to mammals, have larger, more cortically based brains and are thus considered more intelligent than their evolutionary predecessors, the reptiles. Surprisingly, however, some birds such as parrots and corvids (crows, rooks, jays, etc.) possess brains that are relatively comparable in size to those of chimpanzees[21] (Figure 1). Recent research also suggests that parrots and corvids share many of the features believed to be associated with advanced cognitive processing in primates such as high sociality, longevity, slow development, long parental investment, as well as a large forebrain size.[22]

A large forebrain in birds is thought to be associated with innovative behavior.[23] Adaptations of this kind allow species to behave flexibly, enhance their ability to learn quickly, and thus adapt to environmental irregularities. Species that respond rapidly to novel or ephemeral food sources, or develop innovative foraging techniques, such as using tools, might benefit from accessing additional resources. Cognitive adaptations may subsequently influence species fitness by reducing extinction risk or enhancing invasion success.[24] It thus appears that the benefits of behavioral plasticity support the view of cognition as a generalized process.

In fact, brain size appears to be correlated with a number of ecological factors and life history traits throughout different taxonomic groups.[19] Although forebrain size in birds is particularly associated with innovative behavior, brain size (neocortex) in primates and ungulates is more closely linked to social dynamics, such as group size and intragroup coordination.[25] Sociality has thus influenced complex social intelligence such as tactical deception and social learning.[26] However, bird sociality differs from primate sociality. Flock size in birds often varies seasonally and at times can comprise thousands if not millions of individuals. As such, sociality *per se* does not appear to correlate with brain size in birds; instead it may be the type and quality of bonded relationships that are more influential.[27]

Interpretations of correlations may therefore be confounded by differences in species' life histories. Frugivorous primates tend to have larger brains and larger home ranges than folivores. As such, a large home range size might be necessary to accommodate the spatial and temporal variations in fruit supply, whereas leaves that are abundant year-round permit smaller home ranges. Nonetheless, other species that share polygynous or promiscuous mating systems also exploit large home ranges.[28] Locating mates or tracking resources throughout large home ranges might require certain cognitive capacities that result in an advanced spatial memory or sophisticated mental maps. For example, spatial cognition of food-storing birds may appear to have driven an increase in brain size. However, evidence to support such claims remains controversial.[18] Such discrepancies provide clear examples that large home ranges are not necessarily good predictors of large brains. Furthermore, these studies emphasize the importance of focusing on specific brain components, such as the hippocampus (in the case of spatial memory and caching), rather than brain size *per se*.

Methodological Problems

Using large data sets to interpret correlations between brain size and behavioral traits has resulted in numerous hypotheses, but they should be treated with some caution.[18] In an attempt to increase sample sizes, researchers have integrated data from a variety of studies, some with different intentions that use different methods. Brain size, for example, has been calculated using postmortem and frozen tissue, structural neuroimaging data, and brain sections processed using outdated methods. Proxies of brain size have also been derived from cranial volume.[19] Few studies attempt to address individual-specific factors such as age, which is known to influence brain size. Different measurements for body weight have also been applied, including substituting body weight for brain stem volume.[19] Thus the application of such a variety of controversial measurements may, as a result, obscure comparisons and compromise the integrity of interpretations, particularly if they are not consistent within a study. Large bodied species also tend to have large brains and may thus require larger neurons and hence more brain mass to process equivalent cognitive information compared to small-bodied organisms such as invertebrates.[16]

The use of collated data sets detailing incidences of complex cognition as represented by behavioral flexibility and innovation, initiated by Lefebvre and colleagues,[23] has been integral to the analysis of species-wide comparisons in brain size. However, the frequency of reported instances of such behaviors may be subject to inadvertent observer bias. For example, large, diurnal species distributed within close proximity to human settlements may be more frequently observed than small, nocturnal species that reside in inaccessible habitats. Experimental versus observational accounts of behavior may also fall prone to reporter bias. Incidences of social learning, for example, may easily be inferred by field observations but more difficult to establish experimentally in the laboratory.

Caution is also required when defining analogous traits (i.e., those traits that arise independently among unrelated species through processes of convergent evolution), as ecological correlations between distantly related species are likely to be fundamentally different. Generalized definitions of social bonds or group structures, for example, between birds and mammals may not be directly comparable or representative of different species' life histories. As such, assumptions that social complexity, for example, has arisen from increased group size may be an overgeneralization of more complex behavior. Social organization in ungulates or flock size in birds, for example, is dynamic and varies throughout both time and space. Indeed, there appears to be no relationship between flock size and brain size in birds,[27] although birds that engage in complex forms of social cognition appear to have relatively large brains.[29]

When inferring cognitive abilities as the result of environmental selection pressures, it is also important to consider the phylogenetic relatedness of species. Species may exhibit similar characteristics not because they share similar environments, but because they are closely related. Any cognitive similarities may therefore have been inherited from a common ancestor rather than having been evolved independently under similar selection pressures. By considering species as independent data points, irrespective of their phylogenetic relationships, analyses may overestimate the importance of any relationships between variables,[15] which dramatically enhance the probability of obtaining positive associations. It is therefore important to correct for phylogeny by using approaches such as independent contrasts.[30] Independent traits that then occur repetitively across species can be more confidently identified as adaptive.

Comparative Analyses

An alternative approach to the generalized mechanisms thought responsible for enhanced cognition is that cognition is adaptive and domain specific.[31] Such adaptations may arise to solve specific problems associated with particular environments and then be generalized and applied to novel situations. This hypothesis emphasizes an ecological perspective, focusing on how an animal's environment shapes its cognitive abilities.[6,32] Natural selection shapes the morphology and behavior of organisms in terms of differential survival and reproduction. Consequently, distantly related species may converge on similar cognitive characteristics due to shared environmental selection pressures. Adaptive changes caused by natural selection may also lead species to converge on similarities such as omnivory, agility, or acute vision; characteristics required for success in certain habitats such as dense forest. Similarly, animals that occupy the vast open plains of Africa might share characteristics of an herbivorous lifestyle. To determine whether such selection pressures produce similar cognitive abilities across species, it is necessary to systematically compare differences and similarities in cognitive tasks between closely as well as distantly related species. As such, different species that inhabit similar environments may develop similar intellectual abilities, enabling them to better survive in specific habitats. Species may therefore differ not only in degree, but also in the nature of their intelligence.

Comparing Abilities

The comparison of closely related species with different ecologies is essential when investigating cognitive adaptations. Any divergence in cognitive ability may therefore be attributed to independent evolution under different selection pressures.[12] Many corvids and parids, for example, store food for retrieval in periods of food scarcity. Within these two families, some species store more food than others and depending on the species and their environment, recovery can occur from hours to months later. Such differences in caching propensity and latency of retrieval may then result in species-specific differences in spatial memory. Thus by comparing memory among closely related species within the same family, ecological influences on certain cognitive and neural processes may be revealed. Although research in this area has provided mixed results, it has been proposed that birds that store more food have a better spatial memory than those that do not. Support for this hypothesis is from a positive correlation between the relative size (and thus 'storage' capacity) of the hippocampus, the brain area involved with spatial memory processing, and the caching propensity of a given species.

Comparisons between distantly related species may also provide valuable insights into convergent evolution of cognition.[8] Although any comparisons between distantly related species must account for differences in perceptual and/or morphological characteristics, similarities in life history traits and environmental conditions might provide analogous cues to the development of cognition. For example, the convergent evolution of complex cognition in apes and corvids is thought attributable to shared environmental pressures.[7,8] Such comparisons are supported by the fact that both groups are omnivorous, visual animals that live in complex social groups and demonstrate sophisticated forms of object manipulation, manifest in extractive foraging, and tool use.

When evaluating species differences, it is important that any assessments are ecologically representative of the challenges that individual species could confront in their environment. In this regard, standardized tests may not necessarily account for differences in a species' physical ability. It is thus important to adopt paradigms that can be generalized and applied to numerous species irrespective of their physical capabilities. For example, a battery of tests that incorporates functional similarities, but varies in terms of its independent variables, such as retention intervals or levels of difficulty, can allow direct comparisons of cognitive processes between distantly related species such as apes, dolphins, and birds. However, such tasks should not be too difficult that most animals fail, or too easy that they all pass, resulting in 'floor' or 'ceiling' results that obscure group differences. Potentially unavoidable experimental circumstances may also confound interpretations. For example, when comparing human children with chimpanzees, it is the children who are tested by members of their own species, probably while their mothers are present, whereas apes are tested by another species (humans) on a task designed by humans.[33]

Why an Evolutionary Approach is Important

By comparing differences in cognitive abilities across species, inferences can not only be made about how animals perform certain tasks with respect to environmental selection pressures, but also when such capabilities evolved. Distantly related species may show similar cognitive abilities such as tool use or social cognition, for example, corvids and apes.[7,8] Although these characteristics appear to have functional similarities, they are likely to result from very different cognitive mechanisms.[7] Traits that are not shared by a common ancestor may have converged through independent evolutionary processes (Figure 2). Similarly, if the common ancestor showed the trait, then it is the absence of the trait in extant species that also signifies adaptation. For example, in the case of tool use, it was recently assumed that only New Caledonian crows (*Corvus moneduloides*) habitually used tools in the wild and therefore there was something 'special'

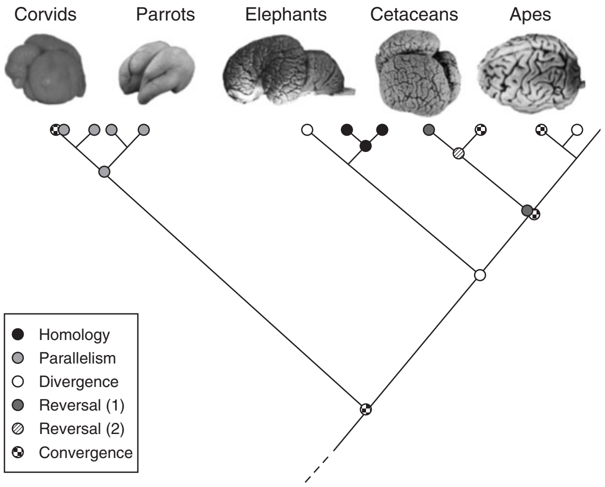

FIGURE 2 | Phylogenetic trees and evolutionary principles. Schematic representation of a phylogenetic tree with relatively large-brained vertebrates—corvids, parrots, elephants, cetaceans, and apes. The circles represent the types of evolutionary principle that may govern the evolution of cognition.[14] Homology (black circle) refers to evolution of similar traits in closely related species with a common ancestor (e.g., African elephant and Indian elephant). Parallelism (light gray circle) refers to the evolution of similar traits in relatively closely related species (e.g., corvids and parrots). Divergence (white circle) refers to the evolution of dissimilar traits by distantly related species (e.g., elephants and apes). Reversal (dark gray circle and hatched circle) refers to the evolution of a trait seen in a descendant that recovers features of the common ancestor (e.g., cetaceans). Convergence refers to the evolution of similar traits in distantly related species (e.g., apes and corvids). Chimpanzee, elephant, and dolphin brains from Comparative Mammalian Brain Collection (brainmuseum.org). Parrot brain provided by Andrew Iwaniuk (University of Lethbridge). Corvid brain from own collection.

about their cognitive adaptations for tool-related cognition.[34] However, recent studies on non-tool-using rooks (*Corvus frugilegus*) have found complex forms of innovation and flexibility in the use of objects as tools, similar to that demonstrated by New Caledonian crows.[35] Therefore, we may now assume that the common ancestor of corvids, or at least members of the *Corvus* genus, likely possessed the cognitive adaptations for object manipulation that developed into tool use—under the correct environmental conditions—for one species of crow. Reconstructing the evolutionary relatedness of species and the presence or absence of cognitive traits may therefore help clarify when cognitive adaptations arose. In this case, we need to determine whether other corvids both inside and outside the *Corvus* genus can use tools or manipulate a variety of objects in tool-related contexts in the same way as rooks, to determine when these particular adaptations may have arisen.

Another reason why a broad *evolutionary approach* to comparative cognition is important is because it removes anthropocentric bias. The historical focus of animal cognition has centered on a limited number of species,[36] specifically great apes, pigeons, and rats. However, the fundamental processes of learning and cognition are said to be the same for all animals.[37] By comparison, the *anthropocentric approach* has focused on whether supposedly unique human cognitive abilities, such as categorization, reasoning, theory of mind (ToM), mental time travel, and symbolic communication are also found, to some degree, in other animals. More recently, comparative studies have incorporated an increased variety of species into this project.[38]

MAJOR THEORIES OF COGNITIVE EVOLUTION

A number of theories have posited evidence that the evolution of cognition is linked to specific aspects of species' life histories, such as sociality, qualitative relationships, culture, extractive foraging, tool use, or behavioral flexibility, yet no one all-encompassing hypothesis fits a global model. As such, it is likely that there are a number of environmental selection pressures contributing to cognitive evolution, each depending on particular species and their socio-ecological circumstances.

Social Living

The Social Intelligence Hypothesis[39] proposed that the flexible intelligent mind of primates was attributable to challenges that species experience in their social environment. This hypothesis later transformed into the Machiavellian Intelligence Hypothesis emphasizing social manipulation as an attribute to the understanding that primates view conspecifics as intentional agents that can be deceived,[40] and then the Social Brain Hypothesis focusing on the relationships between social intelligence in primates and relative neocortex size.[25,41] Fundamental to all three hypotheses is an association between the complexities of primate social interactions and social cognition. As such, it is those animals that live in large social groups, where individuals have to keep track of the identities and interactions of numerous individuals, which have developed advanced cognitive processes. Although this view has largely been restricted to primates, other species such as cooperative breeding birds also show comparably complex social systems. As a result, positive correlations between relative brain size and aspects of sociality have more recently appeared in other species.[25,27]

Sex, Mating, and Relationships

The relationship between group size and brain size in birds is less clear. This is not surprising as birds do not reside in stable groups like primates, but form seasonal flocks, colonies, or roosts, sometimes comprising millions of individuals. Thus, brain size in birds, unlike primates, does not appear to increase linearly with social group size. Yet some birds, that live in pairs or small to medium flocks, such as corvids and parrots have relatively large brains.[27] This raises the question of whether sociality, in terms of group size, is directly comparable between such distantly related species. Although intelligence in primates and birds may have arisen through convergent processes, such selection pressures may be constrained by differences in life histories.[8] Primates, for example, tend to form stable polygynous groups, whereas birds are often monogamous, either forming transient pairs each breeding season or remaining in lifelong bonds with the same partner across years. The type and quality of relationships between individuals within each taxa may be equivalent, but the extent of social relationships in birds may be more relevant to a few individuals, such as in monogamously mated pairs. After all, monogamous relationships require cooperation when establishing and maintaining strong affiliative pair bonds, particularly when defending a nest site, and rearing offspring. As such, those birds with lifelong pair bonds or birds that cooperatively breed tend to have the largest brains.[27]

In some animals, certain ecological problems such as survival, foraging, or the rearing of offspring are more effectively solved socially than individually. Thus, it may be those mechanisms that enhance social cohesion that drive brain-size evolution rather than group size *per se*. However, individuals that develop stable social relationships must also face cognitive demands that solitary individuals do not.[25] But which aspects of sociality require such additional processing powers?

Cognition may play a role in maintaining long-term relationships, so-called relationship intelligence.[27] This is reflected in the social bonds that are established and maintained by active food giving, behavioral synchronization, allopreening, and post-conflict affiliation. Relationship intelligence, compared to general social intelligence, focuses on the role of cooperation and coordination in dyadic interaction, allowing individuals to better read the subtleties of their partner's behavior, thus providing a competitive edge.

Finding, Extracting, and Protecting Food

Social learning and the evolution of socio-cognitive skills also play important roles in efficient foraging strategies.[41] Social foraging may impose greater cognitive demands than individual foraging, as it may require the ability to store and manipulate information about social relationships.[25] An awareness of other group members also presents the opportunity to acquire specific foraging techniques through direct observation of more experienced group members. Individuals may thus benefit from social learning by enhancing their efficiency in manipulating or extracting foods that would have otherwise been more difficult or harmful to obtain through trial and error learning. As such, those species that use manipulative and explorative foraging techniques are less neophobic and more innovative than other species.[42] Similarly, those species that adopt a generalized diet, opposed to a specialized diet, possess greater behavioral flexibility and knowledge about food sources and foraging techniques.[41] Thus, both social and generalized foraging behaviors may contribute to the evolution of cognition.

Species that track ephemeral food sources or retrieve food items stored in numerous locations also confront additional cognitive challenges. To efficiently locate food, frugivorous primates and food-storing birds rely on spatial and temporal abilities for learning and remembering the locations and permanence of food items that are scattered.[43,44] Food-storing birds must be sensitive to their social context when caching, as their stores may be pilfered by nearby observers.[45] When storing food in the presence of potential thieves, corvids evaluate the quality of visual information available to observers and adopt strategies to reduce this information and thus minimize the risk of theft. Ravens and scrub-jays will wait until observers are distracted or cannot see them before storing food, store at further distances from observers, store behind objects, or in dark areas. Ravens and scrub-jays also use strategies that appear to tactfully deceive potential thieves such as leading them away from food stores, making false stores, or returning alone to restore food in new locations unbeknown to an observer.[45]

Technology, Tools, Innovation, and Culture

The application of flexible foraging and technical skills may be as important to the evolution of cognition as sociality.[46] Technical innovation and the acquisition of new food resources positively correlate with an increased brain size in both birds and primates.[23] Such flexibility may then be maintained or even improved through social learning and cultural transmission. Species that demonstrate proficient use and manufacture of tools show particularly complex cognitive capacities.[34,47] Some corvids have demonstrated the ability to manipulate nonfunctional novel objects into functional tools to retrieve food rewards.[35,48] Such innovative behaviors not only display an accomplished perception of the problems at hand, but also suggest an understanding of the inadequacies and physical properties of available nonfunctional tools.

Sociality may facilitate the transmission of innovative behavior through observation and social learning. As a result, population differences in the types of tools manufactured, like those observed in New Caledonian crows[49] and chimpanzees,[50] might culminate in cultural differences. The cumulative evolution of tool complexity or foraging techniques may also provide analogous clues to the technical innovations of humans.[49] Is the proficient use of tools then an expression of a pre-existing physical intelligence or the result of a technological ratchet; a mechanism that provides selective pressures for further cognitive adaptations?

ALTERNATIVE VIEWS

The above views focus on evolutionarily adaptive explanations for the current functions of cognitive traits. However, the adaptive aspects of evolutionary history, as a direct result of natural selection, may not necessarily account for the causal basis of enhanced cognition. There may be other potential reasons for the origin of such traits. Complex cognition (i.e., cognitive processes that are over and above the basic psychology required by most species in order to survive) may instead be the result of nonadaptive processes that arose as a necessary by-product of other adaptations. Similarly, it may also be that complexities of a structure and its development impose restrictions on adaptive cognitive change.[10,51] Certainly, the brain is an incredibly sophisticated structure that controls millions of different bodily processes, of which cognition is but one. However, the brain is too metabolically expensive to have resulted in a collection of traits that arose as an evolutionary accident.

New processes of evolution appear through previously existing organs or physiological activities.[9] Advanced cognitive capacities may therefore have evolved as secondary consequences, or 'correlations of growth',[52] that later became useful through exaptive processes.[10] It is therefore important, when searching for the evolution of cognition, not to separate current utility of adaptations from their historical origin. Making inferences about the ultimate reasons for the evolution of cognitive structures or behaviors with respect to a species' current fitness may only result in speculative 'Just So Stories'.[9]

IS THERE ANY EVIDENCE FOR DOMAIN-GENERAL INTELLIGENCE IN ANIMALS?

The ecological view proposes a modular approach to learning mechanisms. For example, learning about space, time, or number is attributed to specific contexts. Hence in this view, cognition is considered a collection of adaptive specializations that are domain specific.[1] However, it is the generalization of such adaptive processes and their application to novel tasks that construe behavioral flexibility. It is for this reason that evolutionary psychology promotes the metaphor of the mind as a Swiss Army knife; a general-purpose tool made up entirely of special-purpose devices. But the question remains whether there is a module for everything?

Cognitive adaptations may initially develop under certain selection pressures, but during the course of evolution become applicable to an expanding range of stimuli.[53] Can this process of generalization, from adaptations to exaptations, promote a domain-general intelligence? Examples might be found outside of adaptive specializations in species that may have secondarily lost adaptive traits characteristic of a common ancestor. For example, rooks and various species of monkeys do not use tools in the wild and yet demonstrate tool use and physical cognition in the laboratory.[35,54,55]

THE FUTURE OF COGNITIVE EVOLUTION

As cognitive adaptations do not fossilize, is trying to reconstruct an animal's (including human's) cognitive evolutionary history redundant? Testing evolutionary hypotheses about cognition can be difficult because cognitive processes affect fitness indirectly through behavior. Are then any hypotheses inferring adaptation no better than mere speculations?[9] It is difficult to infer the mechanisms that drove divergence in brain size and cognition between humans and nonhuman apes, as all intermediate species that could provide such clues are extinct. Evidence from fossil remains of early hominids may provide useful clues, as *Archaeopteryx* did for birds and reptiles, but more rigorous tests of the relationships between adaptive behavior and the environment are required.

Testing cognition relies on direct observation, model building, experiment, and the comparative method.[1] However, the evolutionary questions about cognition are both of the evolution of cognition and the effects of cognition on evolution. Therefore, traits must be considered as both objects and subjects of evolutionary processes—consequences of a process of change and also the cause of change.[9] Tests may claim that traits are adaptive by (1) modeling how well a character serves a hypothesized function, (2) comparing whether variations of a trait correspond to variations in ecology, or (3) directly by experiment. Comparisons can be made between contrasting groups of species; those with, those without, or those possessing traits at different degrees. Measurements of the reproductive effects of variation of the trait can then be made and any genetic differences that underlie different forms of the trait can be illuminated. However, it is important to remember that any interpretations of adaptations are limited to observations of their current effects on fitness. It might be interesting to know how cognition arose, spread, and changed, but our interpretations may always be reduced to elaborate speculations, and thus we may never know.

UNIQUELY HUMAN COGNITION

This review has discussed how different species may have evolved similar cognitive abilities in response to either shared learning mechanisms or analogous environmental selection pressures. Examples such as causal reasoning in tool use, episodic-like memory of the type, state and location of food caches, and the ability to predict the behavior of others during competition for food all suggest that a few species (e.g., apes, corvids, parrots, elephants and cetaceans) are endowed with more sophisticated cognitive capacities than other animals.[21] These examples appear to be related to socio-environmental traits such as complex social systems, unpredictable environments, altricial offspring, and an omnivorous diet, which are shared among these same large-brained, cognitively endowed species.[56] Importantly, these complexities may also have been present in early hominids and so potentially responsible for driving the evolution of flexible forms of innovative behavior in our ancestors. But do humans possess any unique cognitive abilities that do not show parallels in other animals?

Occasionally, observations of previously unexpected human-like abilities appear in non-human animals, including those that are distantly related to humans, such as teaching,[57] culture,[50] recursion,[58] episodic memory,[59] and planning.[60] However, it has been argued that these abilities differ between humans and animals because they are based on a profoundly different cognitive architecture.[61] For example, animals do not form symbolic representations that can be used during communication and cannot reason about unobservable states (e.g., feelings and forces) rather than behavior. An additional contrast is that these behaviors tend to be highly domain specific, relatively inflexible, and species typical. Yet it remains unclear why such abilities should be considered less sophisticated just because they are domain specific.

Although the search for human uniqueness has traditionally been sought from studies of apes,[62] more distantly related species also appear to share cognitive adaptations with humans for space, objects, tools, categorization, quantification, understanding social relationships, intentional communication, social learning, and social cognition.[1,8] But many aspects of human cognition appear to be totally unique: people communicate across continents, write poetry, perform calculus, and make wine. Therefore, the question posed is whether a small difference in our evolutionary (or cultural) history made a big difference to the human brain and cognition? In this final section, we will assess whether supposedly unique aspects of human cognition are shared with other animals.

Theory of Mind

Humans have developed unique sociocultural adaptations that enable them to pay attention to the behavior of other individuals in their social group. This ability is thought to have developed from an understanding of others as distinct mental entities that possess beliefs and desires of their own.[63] In short, these processes involve concepts of mental representation or a *ToM*. The possession of a ToM is derived from an understanding that the behavior of others is intentional, which can then be used to predict others' future behaviors and provide explanations for their actions.[64]

To determine whether animals possess concepts of a ToM, tests have focused on different categories of mental states, based on perceptual, informational, and motivational domains. For example, examining what animals know about what another can or cannot see tests their understanding that others have perceptual mental states, whereas examining what animals know about what another may know (for example, from what they may have seen in the past) tests their understanding that others have informational mental states. However, the benchmark for human ToM is testing whether animals form concepts of false beliefs that (1) may contradict reality and (2) may be different from what the observer knows to be true.[65] Some animals, such as chimpanzees, dogs, and corvids show advanced predispositions to respond to certain behavioral cues, but no non-human animal has demonstrated convincingly an understanding of false belief; therefore, the possession of a true ToM may still be considered unique to humans.[66] Only children around 4 years old have demonstrated the ability to separate their own representations of a situation from another's.

Tomasello and colleagues[66] suggest that this socio-cognitive skill promotes uniquely human joint attentional activities and shared intentionality that form the basis for culture. Shared intentionality requires the ability to view others as causal agents and make cognitive representations of others' minds, thus providing the motivation to collaborate in shared goals. Such collaboration may thus form the basis of cultural evolution, facilitating the creation and use of linguistic symbols, the construction of social norms and individual beliefs, and the establishment of social institutions.[66] The development of such traits further enhances their transmission across generations allowing for cumulative cultural learning and unique processes of cultural cognition and evolution.

Mental Time Travel

Mental time travel is the process of recollecting one's past information about what happened where and when (retrospection) and using this information to project one's self into the future to anticipate future needs (prospection).[67] Episodic memory, in contrast to semantic memory, is information about personally experienced events, rather than just knowledge of the event itself. An example may be the reconstruction of where and when, and the associated emotional responses elicited from learning that George W. Bush was re-elected, as opposed from merely knowing the fact that he won a second term. The ability to make retrospective and prospective decisions may have direct implications on survival in the future and thus be an important component of human cognitive evolution. In a fluctuating environment, species that distinguish certain regularities based on prior experiences and adapt this knowledge to future decisions have an advantage over those that do not. The question remains whether mental time travel is unique to humans because two critical components of human mental time travel involved phenomenological consciousness, namely autonoesis (awareness of authorship) and chronesthesia (awareness of the passage of time),[67–69] which are difficult to test without the faculty of language.

Recent research suggests that apes, corvids, parids, and rats demonstrate behaviors indicative of episodic-like memory and future planning.[44] For example, research on food-storing birds has utilized the natural caching behavior of these animals to develop paradigms for investigating what jays may know about what they cached, where and when, who was present when they cached, as well as decisions about what and where to cache for future needs.[44] However, it remains difficult to interpret non-verbal approaches to mental time travel and infer whether animals possess unconstrained capacities analogous to those of humans, rather than limitations imposed by instincts or conventional learning. Therefore, an approach based on behavioral rather than verbal criteria has to be adopted.[70]

Culture

Human culture has flourished as a result of identifying intentional behaviors in others. By distinguishing actions as a means to achieving underlying goals and recognizing shared intentions in terms of aligning ones own goals with those of conspecifics, individuals can learn and be taught through the medium of a social–collective culture. Many animals display traits that are suggestive of culture.[49,50] However, what may make human culture unique is the mechanism by which information passes within and between social groups.[71] Material or symbolic artifacts can also be culturally transmitted through succeeding generations. A cumulative process ('ratchet effect') of modifying, improving, or finding new ways to incorporate an artifact into social practices then results in cultural evolution; the new and improved version gets passed onto the next generation, and so on. Successful cultural transmission not only relies on imitation and teaching, but is also facilitated by collaboration and communication.[66] These pressures may then result in the evolution of symbolic forms of communication such as language.

Language

Some researchers claim that humans alone are capable of acquiring language and that it is this capacity that accounts for our unique intellectual abilities.[4] There is no doubt that language has played a central role in the evolution of human cognition. However, it is clear that language is not necessary for cognition to occur. Language is the result of adaptations derived from shared intentions and group-orientated coordination and collaboration.[66] It is those underlying cognitive and social skills that motivate people to share personal information, knowledge, and perspectives that are unique to humans. As a result, language and thought are likely to have coevolved, 'ratcheting' each other up as language created new cognitive niches.

CONCLUSION

Over the past 30 years, the resurgence in comparative cognition has dramatically extended our understanding of the human and non-human mind. Such renewed vitality has spawned many creative and imaginative studies, each furthering our insight into the evolution of cognition. Research comparing subtle differences in cognitive processes between humans and other closely related species highlights evolutionary divergences in cognitive trajectories, whereas cognitive similarities between humans, other apes, and more distantly related species, such as corvids, highlight evolutionary convergence. For example, contemporary approaches that focus on more distantly related species such as birds have revealed previously unsuspected human-like abilities, such as mental attribution, episodic memory, future planning, and self-awareness, further illuminating the convergent processes of cognitive evolution. We now know empirically, as Darwin once speculated, that humans and non-human animals share many fundamental cognitive abilities, yet the development of such abilities differs in degrees across species. These differences are likely to be based on different computational demands in those species' socio-ecological environments,[61] and especially that of the ancestral species. Although we will never fully realize what this environment and the associated selection pressures were like, many critics suggest that this makes the study of cognitive evolution a ‘scientific dead end’. We believe that comparative, phylogenetic, experimental, and theoretical tools are in place to allow us to try to reconstruct the evolution of specific cognitive traits and their neural correlates.

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