Intelligence, evolution of

To appear (2016) in the *International Encyclopedia of Anthropology* (ed. Callan, H). Blackwell: Oxford.

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Abstract

Although intelligence has been deemed a uniquely human trait, there is extensive evidence that intelligence has evolved and that evidence is not restricted to our close relatives, the great apes. Many birds, such as corvids and parrots, cetaceans and elephants display complex, flexible behaviors in the wild that can be employed when faced with unpredictable ecological challenges, or used in novel laboratory experiments. This section will discuss the following: a definition of intelligence accommodating our updated zoological knowledge; why intelligence is adaptive; ten approaches to studying the evolution of intelligence with their individual problems; the role of brains in intelligence, and the main theories for why intelligence evolved.

What is intelligence, and how can it evolve?

A definition of intelligence is almost impossible, because everyone knows what intelligence is and yet, everyone differs in what they think it means. For our purposes, intelligence is defined as the application of cognition to solve novel problems in a flexible manner. As such, intelligence is much more than just cognition. An animal may use cognitive processes in its behavior, but will not necessarily be intelligent. Indeed, recent studies in comparative cognition have revealed the somewhat surprising mental abilities of animals, such as numerosity, timing, spatial memory, tool use and social cognition (Shettleworth 2010), but these abilities will have evolved as adaptive specializations to solve specific ecological challenges. For example, Clark's nutcrackers living in the Rocky Mountains can store around 33,000 individual pine seeds in thousands of different locations and accurately recover them up to 9 months later. To human minds, this is impressive stuff. Surely this is intelligent, especially when many people have difficulties in finding their keys where they left them the night before. But we shouldn't be fooled. Clark's nutcrackers are adept at hiding and recovering large amounts of food over long time periods, but less adept at finding a variety of different foods over shorter time periods when they degrade at different rates or protecting their caches from thieving conspecifics. If pine seeds fail to be produced in abundance for one year, Clark's nutcrackers may have great difficulty adapting to caching alternative foods.

By contrast to nutcrackers, closely related Western scrub-jays cache a smaller number of pine seeds, but they also cache a variety of different foods as well, such as berries and invertebrates. Pine seeds can be stored for long periods without anything happening to them, and as Clark's nutcrackers are relatively territorial, there is little chance of them being stolen by an individual watching them cache, whereas scrub-jays are more social and they steal one another's caches. The caches are also frequently perishable foods that will degrade quickly, especially in the heat of the Californian Central Valley, so scrub-jays need to keep track of both the time since caching and whether another bird watched them cache. Therefore, they need to employ more flexible strategies to cope with a changing social and physical environment. The nutcrackers are perhaps employing a highly cognitive strategy, whereas the scrub-jays are employing an intelligent strategy. The difference is that nutcrackers have evolved a series of domain-specific modules that deal specifically with hiding and remembering lots of the same caches, but which only differ in where they have been hidden. By contrast, scrub-jays have evolved (probably on top of the modules evolved by the nutcrackers, as they share a common ancestor) domain-general intelligence that can be employed across different contexts, including those for which it did not originally evolve.

At first, this dichotomy may seem to be problematic. Evolutionary psychologists stress that human minds evolved as a series of dedicated, encapsulated modules, each dealing with a specific environmental challenge, such as perceiving faces or dealing with social threat, the so-called Swiss Army Knife model of the mind or massive modularity and based on a specific area of the brain (Geary and Huffman 2002). Most evolutionary psychologists suggest that only domain-specific modules can evolve, as domain-general intelligence is a "jack of all trades" with no specific focus. Evolution only works by tinkering with specifics, such as eyes evolving to process light energy and translate it into a form that can be perceived by the brain enabling seeing or wings evolving enabling an animal to fly. In these cases, the adapted trait made the species with the new trait more reproductively successful than the ancestral species without the trait, and so the ancestral species eventually dies out.

Analysis of a hypothetical scenario about the evolution of general intelligence may be illuminating. Mutations act on genes that code for proteins, some of which may be involved in building a brain. Such a mutation may cause part of the cortex to develop along a different neural pathway that makes the passage of information between two brain regions ultimately faster and more efficient, therefore influencing behavior in a positive manner. The individual that develops such a brain may be more successful in gaining food or attracting a mate and subsequently, more reproductively successful. The trait will be retained and passed onto subsequent generations who will quickly outcompete those without the trait, who will die off. This scenario does not suggest that the mutation intended to change the brain for good or bad, but enhanced cognitive abilities were the result and so were selected. It is therefore biologically plausible that intelligence itself may evolve as a domain-general module, and this may be the key to our superior intelligence (Kanazawa 2004). Such a scenario was found in generations of a family with a high incidence of mutations in the *FOXP2* gene encoding development of a neural pathway for speech. Family members had developmental verbal dyspraxia (problems in speech production) resulting from difficulties in moving their lips, tongue, jaw and palate. Therefore, a mutation of a single gene can affect a specific cognitive ability.

The cognitive module(s) underlying intelligence can be quite varied, and deployed depending on circumstances. They may have originally evolved to solve specific ecological problems, such as spatial memory for locating caches, but have been co-opted for a different problem, such as remembering the place of individuals in a social hierarchy. Based on similarities in the cognitive abilities of corvids and apes, Emery and Clayton (2004) suggested four cognitive tools or modules, including flexibility, causal reasoning, imagination and prospection, that were domain-general and could be applied whatever the stimulus input. Therefore, domain-general intelligence does not have to be restricted to hominoids.

Intelligence assumes a rank or scale, so that individuals X and Y can be compared. After a series of tests, X is found to be more intelligent than Y. In humans, intelligence is measured using a tests for different cognitive traits, such as mental rotation, language and numeracy that ultimately produces an Intelligence Quotient (IQ), but such tests are not without criticism. They tend to focus on educational intelligence in Westernized societies, foregoing tests of social or emotional intelligence. Individuals with a higher IQ are said to be more intelligent than those on a lower IQ (high and low are determined from a population average). For animals, the assumption is that species that resemble us, or are more closely related, such as chimpanzees, or for which we have extensive experience or to whom we have formed attachments, such as dogs, are more intelligent. The first problem with this assumption is that it views evolution as a progressive ladder with humans at the top as the most evolved creatures, and other animals on lower rungs; primates under us, then other mammals, birds under the mammals, reptiles under the birds and invertebrates and single-celled organisms at the bottom. However, since Darwin, evolution is perceived as tree-like, with all extant species at a similar evolutionary stage at the tips of the branches, with no species more or less evolved (or more or less superior) than another.

A second problem is that intelligence is viewed as uniquely human. Whether something is intelligent is based entirely on our anthropocentric criteria. For example, a being may only be intelligent if they possess language. This does not appreciate that what may be considered important for a species may be irrelevant to us. For example, if one male squid can lateralize their body patterns to fend off a rival whilst at the same time attract a female, that male could be said to be more intelligent than another male who can only produce one pattern at one time. Therefore, this form of squid intelligence may differ across individuals, but it is unimportant for the issue of human intelligence. This problem is (not surprisingly) rife in anthropology. Paleoanthropologists describe cognitive stages in human evolution, such as the development and use of tools without any recourse to those nonhuman animals that also possess the same skills (and for which there is often stronger evidence).

A third problem is that human intelligence is strongly influenced by our cultural evolution. Human knowledge accumulates over time and space, potentially shared by all members of our species. We therefore have access to more knowledge than our ancestors, but that does not mean that we are individually smarter, as we may fail to utilize that knowledge successfully or rely on others to do the tasks that our ancestors would have done for themselves. Our ancestors may have surpassed our natural and technical intelligence, but were probably less socially intelligent. Therefore, human intelligence has to be assessed in the context of when it evolved and how it has changed throughout the development of culture. Any comparison between humans and animals is not strictly fair because it is between two or more species that are the product of their time. Do any other species have cultural evolution? Is it fair to compare animals on intelligence or should we focus less on comparisons, rather than how an animal expresses its intelligence, what it is for and what advantages it provides? This is particularly important when we consider that the most successful species, such as cockroaches and locusts are not necessarily psychologically intelligent, but should be thought biologically intelligent.

Why being intelligent is adaptive?

Surviving and thriving in an unpredictable world

Many species are very successful without being intelligent. Behavioral programs intact at birth can be highly adaptive, requiring little energetically expensive neural tissue. They can be powerful when addressing specific problems, but are inflexible and cannot cope with unpredictability. This may not be an issue for animals that never encounter fluctuations in their environment. However, most animals do, and so a more flexible system, such as associative learning is more beneficial. However, having to learn associations between stimuli, or actions and their consequences, does not facilitate coping with rapid changes in climate, habitat, diet/food availability or sociality (fission-fusion). Only intelligence is capable of leading to greater reproductive success than a minimally flexible (e.g. learning) or an inflexible (e.g. innate) system.

For example, Western scrub-jays remember *what* they cached, *when* and *where* they cached it which can be life-saving when food has a limited shelf-life. This is an intelligent, flexible strategy that copes with changes in decay rate, such as when environmental conditions speed up (e.g. increase heat) or slow down (e.g. decrease heat) decay. Now imagine a creature that hides food that can also decay, but instead of evolving a what-where-when memory, they have evolved a physiological process – a natural preserver they produce – that can be injected into prey to slow down the decay process. They have evolved a perfectly feasible solution to the problem of storing and eating perishable food, but one that is independent of intelligence. Which process is better or more successful? The latter physiological adaptation is inflexible, as food decays at different rates in changing temperatures, so in this case the intelligent solution will always trump the physiological.

Specialization is the enemy of intelligence

When predicting which species are intelligent, we start from a simple fact. Species that are specialized, either in terms of their diet, sociality, habitat, etc. are not likely to be as intelligent as more generalized species. This idea comes directly from our definition of intelligence, as the problems faced by such creatures are likely to be predictable and unchanging. For example, territorial species are likely to be less intelligent than species with a multilevel or fission-fusion society because they interact with fewer individuals, so requiring less knowledge about their day-to-day lives, and relationships. Similarly, species that eat one food type in large amounts that is available all year round and distributed across their habitat, are predicted to be less intelligent than omnivorous species that opportunistically eat a wide variety of foods, some of which are available for short periods, such as ripening fruit, or which decay after capture, such as many invertebrates. Finally, species that evolve morphological traits enabling them to extract food, such as specialized beaks are likely to be less intelligent than species that have to create and use tools to fulfill the same behavioral need. This does not mean that specialized species are not cognitive; indeed, they will have evolved specializations that have become adapted to specific socioecological challenges, only they cannot be flexibly deployed to solve different problems, even within the same domain of knowledge.

Ten approaches to studying the evolution of intelligence

Ever since Thorndike (1911) developed an empirical method for comparing the intelligence of different species, using a puzzle box, the study of how intelligence may have evolved has proven of interest to a wide range of behavioral scientists, using a variety of different approaches. The following list does not assume that one method is better or worse than another, but does highlight specific problems with each approach (although some problems are more of an issue than others).

1. Natural behavior. This approach asks how well an animal adapts to its environment, and how well it copes with natural challenges. Researchers study their chosen species in their natural habitat. They either use the observational method to examine complex behavior assumed to be intelligent, such as the making and using of tools, or they present their subjects with experimental manipulations based on natural behavior in which they face challenges testing their use of their cognition. For example, Salwiczek and colleagues (2014) provided cleaner wrasse (fish) with artificial problems based on their propensity to remove ectoparasites from client fish, such as determining the optimal order of artificial clients to target in order to maximize their total reward intake. Fish that service clients that move around (ephemeral or time limited food source) before those tied to a particular area (permanent or time unlimited food source) will maximize their food intake over those that are non-selective. Problem: the animals' intelligence is being examined in the context in which it became adaptive, so the expectation of any result is that the animal will perform well on any tests. In many cases, there is little challenge and no novelty to the tests. Any attribution from observations is speculative on what "looks" to be intelligent behavior.

2. Laboratory tests. The traditional method for examining animal intelligence is to test how well an animal performs on a novel laboratory task. The number of trials taken to learn the task (assumed to be the result of trial-and-error and so not intelligent) is recorded. Animals that perform correctly on the first trial onwards are deemed to have understood the affordances of the task (i.e. how it works) and so reflect their intelligence. Laboratory tests are often designed to investigate intelligence as a unitary phenomenon (such as factor *g*) using the equivalent of IQ tests, or the correlated performance on a series of tasks or some measure of performance related to intelligence, such as the ability to learn and apply a rule (learning sets), speed of learning or number of errors against a criterion. For example, animals can be ranked on their performance on learning sets that seem to adhere to assumptions about their intelligence. Problem: this assumes that intelligence is a unitary phenomenon; that animals can be ranked on a *scala naturae*, and this can be used to predict an animal's performance; it is dependent on recording an appropriate measure of intelligence. It is important to consider the issue of contextual variables, such as different sensory biases and motor behavior influencing performance. Bitterman (1965) suggested that differences between species in their motivation, perception and motor capability have the capacity to significantly affect performance that will have little to do with differences in cognitive capacity.

3. Comparative analyses. These test how closely and distantly related species differ on tasks said to measure intelligence. The species may differ in ecology or sociality that correlates with performance. The specific task used may relate to these variables, for example, the serial reversal learning task is said to test for an animal's ability to flexibly switch from using one rule to another after the learning contingencies have changed. Therefore, we may predict that a species that lives in a complex social group with frequent changes in dominance status will also be proficient at reversal learning. If a large number of species can be compared, then various phylogenetic analysis methods can be employed to determine when the ability may have evolved (Maclean et al. 2012). Problem: this approach assumes that the tasks are comparable across species. This assumption becomes more apparent when comparing distantly related species, so it maybe fairer to compare species that share the behavioral trait under consideration, so ceiling or floor effects are not the likely outcome (i.e. a species either cannot perform the task at all, so displays no evidence of comprehension, or one species finds the task so simple that they easily achieve maximum performance). Comparisons using phylogenetic methods are dependent on an accurate evolutionary tree.

4. Socioecological and life history correlates. Brain size has been suggested to be a clear proxy for intelligence, but this claim is not without criticism. In many cases, brain size (or some other appropriate neural variable) is the only variable available for comparing large numbers of species and making predictions of their intelligence. Despite decades of study, it is not clear that possessing a larger brain means that an animal is more intelligent than one with a smaller brain. The size of the brain (or brain area) frequently correlates with certain socioecological (group size, mating system, diet, habitat, innovation rate, frequency of tool use, etc.) or life history (longevity, length of developmental period, etc.) variables that may or may not be dependent on some form of intelligence. Problem: this assumes that any brain measure used (e.g. absolute or relative brain size, cell number, Encephalization Quotient [EQ], etc.) is an adequate proxy for intelligence, and that the socioecological variables reflect a trait that is dependent on information processing. For example, group size may not properly represent the complexity of a social group, therefore social network size maybe a more appropriate measure. Group size can vary across seasons, as in birds, and so not represent the same computational challenges at different points in the year, especially in species with very large groups that have evolved to reduce predation risk.

5. Anthropocentrism. Whether an animal is intelligent often tends to refer to whether an animal is capable of doing what a human can do. If an animal passes a task associated with a uniquely human cognitive ability, such as theory of mind or analogical reasoning, this suggests they are intelligent. Problem: it is not often clear how an animal passes a task, as usually the animal is given a task to which they either pass or fail. If they fail, this may be because the task has no ecological validity or because they do not possess human-like intelligence. If tasks are based on natural behaviors, the tests may not examine the same attributes as the same tests designed for humans.

6. Artifacts. Artifacts such as tools, art, jewelry, dwellings or graves, may be used to make inferences about their creator's mind. Such objects are relatively rare in the animal kingdom, except for some tools (including stone tools created by chimpanzees or stick tools created by New Caledonian crows; see also the tool counterparts of *Pandanus* leaf tools), bowers and nests.

Problem: as these items are the output of behavior, a high level of extrapolation and speculation is required, based on extant behavior, to make assertions about the intelligence of the artisan. Despite this, this technique has proven essential for reconstructing the intelligence of our hominin ancestors.

7. Anatomical adaptations. Morphological traits, such as teeth, beaks, and bones may constrain behavior and subsequently, intelligence. For example, the opposable thumb has allowed our species to exploit niches unavailable to other species. The relationship between anatomy and intelligence is most profound for brain structure. Knowledge of the size of brain structures and neural responses to specific stimulus categories provides important information about a species' ability to solve problems. Such data can also provide useful information for closely related species. Endocasts made from inside the skull are the only method for measuring brain size in our early relatives, and sulcal patterns on the surface of the brain have been used to theorize about the presence or absence of certain traits, such as language. Problem: similar problems as seen for artifacts, as a high level of extrapolation is required, but for extinct species, it may be the only information available, as behavior does not fossilize.

8. Agent-based modeling. Agent-based models of natural behavior may be used to make predictions about how an animal responds to environmental challenges, but it is uncertain whether such simulations have the potential to model intelligent strategies. Problem: predictions are constrained by natural behavior (how animals have behaved in the past and which have been recorded), so may be limited in application to relatively uncommon behaviors. Computer simulations may also tend towards the simplest form of a programmed response, which is not necessarily how the animal thinks about the world. For example, models of scrub-jays caching behavior predicted a simpler solution to the question of what they should do with caches observed by a pilferer, than was actually applied by real scrub-jays.

9. Mechanistic. The mechanisms underlying behavior tend to be placed into one of two camps, either associative learning or cognition. Associative learning is suggested as simple, whereas cognition is complex, with intelligence at the higher end of cognitive complexity. In extreme cases, if a behavior is not learned, then it is intelligent, with no middle ground. Problem: not all cognition is intelligent, not all learning is simple, and intelligence requires some learning. Most animals, including the most successful species in terms of their numbers and reproductive success, could not be identified as intelligent, only employing learning as a strategy. However, sophisticated training procedures can be used to simulate intelligence. For example, Epstein (1981) developed a series of tests on pigeons in order to replicate studies on self-awareness, insight, symbolic communication, tool use and imitation in chimpanzees, after strict patterns of conditioning. The pigeons' resultant behavior looked intelligent, but was only the result of trial-and-error learning.

10. Philosophical. By observing an animal's behavior, we may make inferences about their minds and how they form representations of different stimuli. Philosophers frequently make assumptions about an animal's intelligence from reports of their behavior in the wild, especially for creatures where it is not practical to give them cognitive tests, such as ocean-living whales and even from experiments that were not designed to examine the problem at issue. This is particularly rife when discussing the evolution of consciousness. Problem: only an empirical approach can directly inform us about the intellectual capabilities of animals Whereas other approaches have some utility, especially when making predictions about the expected intelligence of a species, the philosophical approach often comes across largely as an intellectual exercise that does not keep up to date with experimental research.

Brains are the engines of intelligence

Cognition is not possible without a brain. A larger brain, especially the neocortex in mammals, and the pallium in birds, may endow an animal with greater intelligence. There is a clear allometric relationship between body and brain weight in mammals, so as the body gets bigger, so does the brain. Animals with larger brains should be more intelligent than animals with smaller brains, and at a basic level, this relationship holds. The largest extant species, whales and dolphins, elephants and apes, have the largest absolute brain size and these are the species we tend to think of as intelligent. However, there are exceptions. Dinosaurs, some that dwarfed all but the largest whales, tended to have tiny brains. The blue whale has the largest living brain, but on the ground of lack of challenges that it has to face in the wild, it is not considered particularly intelligent. Some bird groups, such as corvids and parrots, have small brains in absolute terms, but have displayed cognitive abilities on a par or exceeding the great apes and dolphins (Emery and Clayton 2004). Even some invertebrates with much smaller brains, such as bees and octopuses, have demonstrated sophisticated forms of cognition. Within our own species, individuals with larger brains do not appear to be more intelligent - measured using IQ and other psychometrics - and despite males having larger bodies, their brains do not tend to be larger than females.

Large parts of the brain are involved in the significant task of keeping the body running: directing the automatic nervous system to control heart rate, blood pressure, breathing and balance, coordinating muscle movements, sensation and perception, controlling the endocrine system and directing emotional responses. It is reasonable to suggest that the function of the rest of the brain is controlling behavior and cognitive processing. Some species have brains that are larger than predicted from their body size (compared to other members of their taxa). This extra bit represents relative brain size. Now, those animals with a small absolute brain size, such as crows, have a relative brain size that matches their intelligence, being as relatively large as chimpanzees (Emery and Clayton 2004).

As brains get bigger, they need more neurons. Smarter species tend to have more neurons (Roth, and Dicke, 2005). However, increasing the number of neurons and the distance between them reduces conduction velocity down a dendrite. In order to retain processing speed, dendrites that double in length would have to quadruple in diameter. For most species, there is a limit on how large brains can get. This is particularly true for birds, with an overall constraint on brain weight because of flying. The opposite is true for sea creatures, such as cetaceans, where the buoyancy of salt water helps maintain their larger brain size without the constraints on terrestrial species. One way around increasing overall brain size is to increase neuronal density. Indeed, crows appear to have twice as many neurons in the same brain space as pigeons, which are the same body size. This increase produces a decrease in proportional connectional density, as the absolute number of connections per neuron has to be maintained. To reduce wiring, either crows have evolved a class of different neurons with fewer dendrites or shorter connections develop between brain regions. Areas close together develop similar functions, and more distant regions become functionally independent or modular and more specialized. This ‘small world architecture’ may aid in the efficient passage of information through the brain, which itself may be related to intelligence.

The question remains as to what measure of brain is most appropriate when discussing intelligence (Healy and Rowe 2007). It is unlikely that absolute size alone is important, but relative size is also problematic if we think of brains as information processors. We expect a greater amount of information to require a larger processor. Bees, for example, only contain about a million neurons (Chittka and Niven 2005). It is uncertain if this number is sufficient to produce flexible solutions to unpredictable problems. One reason that animals do not evolve bigger brains, aside from the issue of body size, is that brains are energetically costly. In humans, brains require over 20% of the resting body’s energy intake. Therefore, animals that evolve a bigger brain must use them efficiently. Intelligence needs brains, brains are costly, and intelligence therefore has to be adaptive in order to afford these costs. How do brains become more efficient without increasing dramatically in absolute size? Delius and Delius (2012) suggested increasing nerve conductance speed, improving synaptic efficiency, augmenting neural connectivity, increasing the variety of synapses, developing novel types of neurons, miniaturizing neurons, packing more neurons into a smaller space, increasing the energy efficiency of neuron metabolism and increasing lateralization. Although we have little information on any of these traits across species, the collection of such data should be the focus of future research.

Why did intelligence evolve?

Broadly speaking, original hypotheses for the evolution of intelligence can be divided into those concerned with challenges of the physical environment, and those that focus on the social environment. Specifically, physical challenges focus on food. The spatial-temporal mapping hypothesis stressed that intelligence was used by monkeys to locate fruiting trees for which their fruit ripens for only short periods of time. The trees were distributed in both time and space and foragers needed to integrate this information in order to find the trees at the right time and so benefit from this resource. The extractive foraging hypothesis stressed that some foods are located inside a tough casing or shell or within plant material or substrate that has to be broken into or accessed in order to extract the contents. Some species have evolved a specialized morphology to allow them to accomplish this, whereas others use their intelligence, such as developing tools to break open nuts or probe into inaccessible trees or termite mounds. A specific tool-use hypothesis focused on those species that can employ tools in an intelligent manner, making so-called true tools (such as hammers and anvils, or probe tools), rather than proto-tools, such as thrushes hitting snails onto stone to break their shells or otters breaking shellfish on stones placed on their stomachs. In the social realm, interactions with conspecifics can either be positive (cooperation) or negative (competition). Intelligent strategies may underlie each type of interaction. Individuals with a strong, valuable relationship, such as a pair-bond, cooperate in their behaviour, such as helping raise and protect their offspring, and do so by coordinating their actions to maximum efficiency, enabling them to predict their partner's behaviour. This has been termed the relationship intelligence hypothesis. Similarly, the cultural intelligence hypothesis suggests that the prosociality at the core of cooperative breeding provided a scaffold for theory of mind, social learning and eventually culture that were driving forces for the evolution of human intelligence. By contrast, members of large social groups with dominance hierarchies, try to outcompete one another to gain resources, especially if those resources are outside their reach because of their low status. The Machiavellian intelligence hypothesis stresses that individuals will use their intelligence to deceive one another to distract others' attention, steal from them and form strategic relationships in order to get ahead.

Additional evidence from a wide number of species aside from the great apes can be adduced for these hypotheses (van Horik et al. 2012). One consideration to note is that these theories are somewhat concurrent or not mutually exclusive. For example, monkeys that eat fruits also tend to be social, as the ephemeral food source will attract lots of individuals, from either the same group, species or even heterospecifics. One key is that all these hypotheses actually depend on a degree of flexibility that is assumed with the definition of intelligence employed earlier. So, each theory may have its own merits, especially to those for which it is relevant, but the outcome is that intelligence evolved in order to cope with unpredictability, in whatever form.

SEE ALSO:

Brain Evolution and Energetics of Encephalization; Cognition, Evolution of Social; Comparative Cognition; Comparative Method, Phylogenetic; Culture in Nonhuman Animals; Evolutionary Psychology; Imagination; Modularity and Domain-specificity; Social Brain Hypothesis; Theory of Mind in Primate and Humans: Comparative Evolution; Tool-use in Non-human Primates

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