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## Evolution of Intelligence, The

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### Definition

Definitions of intelligence in the scientific literature center around the idea that intelligence refers to cognitive processes that allow humans and other animals to solve novel problems in their environments. Thus, Jerison (1973, pp. 16–17) notes that “Although experts differ with regard to the nature of human intelligence, a more or less common ground is that it is a dimension of cognitive behavior – the way one knows the world and the way one uses that knowledge when adapting to changing conditions.”

### Introduction

However, intelligence is not the only set of mechanisms designed to enable organisms to cope with environmental novelty. Intelligence is usually distinguished from learning which subsumes a variety of mechanisms that allow the organism to take

advantage of temporary regularities in its environment – paradigmatically classical and operant conditioning (MacDonald 2013). Social learning is also usually distinguished from intelligence. Unlike classical and operant conditioning, social learning is not dependent on environmental regularities but on being able to learn by observing how the behavior of others enables the achievement of goals (MacDonald 2013). Organisms capable of social learning are then able to use this information to achieve the same or similar goals.

Intelligence, on the other hand, assumes no environmental regularities (although see discussion of Barrett and Kurzban (2006) below) – even temporary ones – nor does it refer to learning how to achieve a goal by observing others who have already solved the problem. Rather, as stated in Jerison’s definition, there is the implication that the organism has a goal and is integrating its knowledge in order to solve problems.

For example, New Caledonian crows are able to quickly process causal information and use it to solve novel problems utilizing new tool types (dropping stones into water in order to gain access to buoyant food items) that are not utilized in their natural environments and have no relationship to their established behavioral repertoire (Taylor et al. 2011). These results do not appear explicable by the use of associative learning, nor is the causal rule linked to regularities utilized by the crows in their EEA. Nor is it the result of having observed other animals or humans successfully solve the

problem. Rather, the behavior indicates an ability to develop and utilize an abstract causal rule in order to solve an affective goal – assuaging hunger – by novel means.

## Review

### Evolution of Intelligence: Theories

There are several theories for why human intelligence evolved, including climate change, the challenges of foraging, and the need to compete with and cooperate with other humans.

### Climatic Selection

Vrba (1995) focuses on the finding that harsher ecological conditions (lower temperatures during the early Pleistocene period [2.5–2.8 million ybp]) resulted in higher encephalization quotient (the ratio between actual brain mass and predicted brain mass for an animal of a given size), theorized to be due to the benefits of increased cognitive ability for survival under harsher conditions. Encephalization quotient increased rapidly after this period as well, particularly in the last 500,000–1,000,000 years.

Lynn (2006) proposes that, based on contemporary worldwide IQ patterns, confronting colder, harsher climates resulted in selection for increased cognitive ability. Unlike equatorial Africa, in more northerly climates, humans had to provide means of warmth, and plant foods were only seasonally available, with the result that hunting animals and means of storing food were required. Lynn points to studies indicating an association between latitude and brain size; for example, mean winter temperatures at the present time and during the Würm glaciation are correlated with brain size (which is correlated approximately 0.24 with IQ, with northeast Asia having the lowest mean temperatures and the highest contemporary IQ).

### Variability Selection

Related to the climate hypothesis is the theory that humans and other mammals were forced to adapt to inconsistent selection pressures because of rapidly changing ecological conditions – what Potts

(1998) terms “variability selection.” Environmental fluctuations became increasingly extreme from the Miocene to the present. These shifts (e.g., between dense, moist forests, and cold, dry steppe) were unpredictable and nonrepetitive rather than cyclic and included decade-scale fluctuations between glacial and warm conditions and century-long shifts between cold steppe and warm forested conditions, interspersed with periods of climatic stability. Rapid local change also resulted from volcanoes, earthquakes, and tectonic activity.

These climatic shifts are associated with increased diversity of encephalization among mammalian lineages, with some lineages – prototypically the lineage leading to humans – evolving toward larger brains and increased behavioral flexibility. There was a broad trend during the Pleistocene toward the evolution of mammalian taxa that were more flexible in eating habits, patterns of social grouping, and group size in relation to resource availability. “Hominids became less inclined to track particular habitats as change occurred and more capable of adjusting to novel conditions and the increasing range of [climatic] oscillation” (Potts 1998, p. 93).

Across mammalian species, and particularly in the line leading to humans, there are associations among brain size, mental ability, learning ability, flexibility of response, and developmental plasticity. There are also associations among these variables and the elaboration of costly parenting practices, delayed sexual maturation, and a prolonged juvenile period in which social learning is of great importance (e.g., Jerison 1973).

Associations between brain size and innovation have been found among both mammals and birds. Reader and Laland (2002) found an association between executive brain ratio (neocortex and striatum volume over brainstem) and innovation, tool use, and social learning. Their results suggested that there was selection among primates for “adaptive complex variable strategies, such as inventing new behavior, social learning, or using tools” (p. 4440). Social learning frequency was independent of group size, providing support for ecological (foraging) hypotheses for brain evolution in primates.

Harsh and varied climates dovetail with ecological models of increased hominid cranial capacity, since ecological models posit increased ability to extract resources from the environment, posited by climate theorists to make greater demands in harsh and varied climates. Thus Kaplan et al. (2000) show that humans in traditional societies are adept at extracting resources. However, extracting resources would always be beneficial, independent of harshness of environment, so the ecological theory cannot explain the findings summarized above regarding the association between latitude and brain size and between brain size and highly variable environments.

### Ecological Dominance

Several theorists have pointed to social competition among humans as a factor (Alexander 1989; Geary 2015). The essential idea is that once humans established ecological dominance, perhaps as a result of being able to maximize resource extraction as proposed by ecological and climate theories, the main source of selection was competition with other humans.

[T]he ecological dominance of evolving humans diminished the effects of ‘extrinsic’ forces of natural selection such that within-species competition became the principle ‘hostile force of nature’ guiding the long-term evolution of behavioral capacities, traits, and tendencies. (Alexander 1989, p. 458)

As populations get larger due to increased ability to extract resources, there are boom and bust cycles, such as described originally by Malthus, and different human groups come into contact with other groups. These forces create competition among humans. As Geary (2015, p. 109) notes, “the inverse relation between social status, resource control, and mortality risk creates a never-ending cycle whereby Darwin’s and Wallace’s . . . conceptualization of natural selection as a ‘struggle for existence’ becomes in addition a *struggle with other human beings for control* of the resources that support life and allow one to reproduce.” These theorists point to associations among fertility, mortality, and resource control in traditional human societies.

Finally and as elaborated below, it should be noted that confronting novel problems and

opportunities is evolutionarily ancient and that animals have developed a variety of means of solving these challenges, prototypically learning mechanisms capable of taking advantage of ephemeral regularities. Theories of climate change, efficiency at resource extraction, and social competition should be seen as forces that likely selected for greater intelligence in particular species at particular times. However, being able to solve novel problems, being able to take advantage of novel opportunities, and being able to solve ancient evolutionary challenges in a more efficient manner would always be advantageous for any organism. Intelligence would thus be beneficial in any environment. As a result, the theories of the evolution of intelligence discussed above should be seen as proposals about the forces resulting in greater selection pressures for intelligence but that the evolution of intelligence per se need not depend on climate changes, resource extraction, or social competition. As indicated below, there is evidence for a general factor of intelligence in a wide range of mammals and birds, indicating that intelligence evolved many times in many different lineages.

### Slow Life History Selection

Another model of the evolution of intelligence posits that it is a consequence of selection favoring slow (high-K) life history strategies. Life history describes the ways in which species trade bioenergetic resources between different domains in order to optimize fitness given variable degrees of environmental harshness and predictability (Ellis et al. 2009). Fast or r-selected life histories are characterized by high investment into mating coupled with diminished investment into offspring care. r-selected species are typically short-lived and tend to be small in size (i.e., rabbits). Slow life history or K-selected life histories by contrast are characterized by high levels of parenting effort coupled with the production of relatively fewer offspring, which will typically attain larger body masses and will live longer (i.e., elephants). Brain mass is positively correlated with indicators of K-selection across mammalian taxa, suggesting that higher intelligence is part of a suite of high-somatic effort behavioral

adaptations in which insight, planning, and behavioral control would be favored, as in harsh, unpredictable environments, thus dovetailing with research on latitude and intelligence cited above (Rushton 2004). Within the lineage leading up to modern humans, dietary shifts, specifically increases in the efficiency with which homins were able to extract resources, may have been a major factor driving the slowing of hominin life history speed, as evidenced both by the increase in encephalization and also longevity characteristic of the more advanced hominins (Kaplan et al. 2000). Among populations of modern humans, it has been suggested that the patterns that exist among group-level variation in intelligence, brain size, longevity, fertility, impulsivity, and prosociality among other traits may have resulted from selection having favored those with slower life history traits (i.e., greater intelligence, brain size, and prosociality coupled with lower fertility and impulsivity), who were better able to anticipate and take advantage of seasonal variability (i.e., predictability) in resource availability, via stockpiling, etc. in more northerly and easterly regions of the globe (Rushton 2004).

### Modular Views of Intelligence

From its origins, evolutionary psychology has taken a strong stance on how the minds of animals and humans were constructed, proposing that the minds of animals and humans consist predominantly of highly specialized mechanisms designed to solve specific problems – the massive modularity hypothesis (Tooby and Cosmides 1992). The specific problems that the human mind is designed to solve are those that repeatedly confronted our ancestors over evolutionary time. When organisms are repeatedly confronted by challenges or opportunities, the optimum response is to develop specialized methods of dealing with them. The basic logic of evolutionary psychology is that when the environment presents long-standing problems and recurrent cues relevant to solving them, the best solution is to evolve domain-specific mechanisms, or *modules*, specialized to handle specific inputs and generate particular solutions (Geary 2005).

Applied to intelligence, several theorists have attempted to develop a modular theory of intelligence. A key issue for a modular view is to account for the available data indicating that humans and animals are able to solve novel problems. The difficulty is that modules must necessarily be activated by particular content domains for which they are specifically designed:

Advocates of evolutionary views do not deny that humans learn, reason, develop, or acquire a culture; however, they do argue that these functions are accomplished at least in part through the operation of cognitive mechanisms that are content-specialized – mechanisms that are activated by particular content domains and that are designed to process information from those domains. (Tooby and Cosmides 1992, p. 166)

Barrett and Kurzban (2006) attempt to retain a modular perspective on intelligence by interpreting domains as referring to the formatting requirements that are required by the brain in order to process the information: “Domains should be construed in terms of the formal properties of information that render it processable by some computational procedure. In this sense, even the rules of so-called content-independent logics – for example, *modus ponens* – are domain specific, in that *modus ponens* operates only on propositional representations of a particular form” (Barrett and Kurzban 2006, p. 634). Defining domains in terms of formatting requirements avoids proposing that mechanisms like working memory are restricted to particular content domains that would be used to solve specific adaptive problems, as proposed by Tooby and Cosmides (1992). Thus, for example, working memory, which is commonly viewed as a component of general intelligence, would be considered modular because the input to working memory must be encoded in a specialized manner, but there is no implication that the contents of working memory are specialized to solve particular problems encountered over evolutionary time.

Within this formulation, modules related to intelligence were thus not designed by natural selection to solve specific problems repeatedly encountered by the organism over evolutionary time. Mechanisms such as *modus ponens* and

working memory are not designed to solve any particular problem; rather, they may be used to solve a very wide and undefined range of problems – solving mathematical problems, making analogies, or figuring out the most efficient way to manufacture pianos. Such processes necessarily conform to a modular view because, while they do not require specific inputs to solve specific adaptive problems, they have specific formatting requirements for the information that they act upon.

The modular view of Barrett and Kurzban (2006) retains the concept that adaptations for intelligence must have evolved in response to environmental regularity. This reflects traditional definitions of adaptations in general. For example, Tooby and Cosmides (1992, 61–62) define adaptation as follows:

An adaptation is (1) a system of inherited and reliably developing properties that recurs among members of a species that (2) became incorporated into the species' standard design because during the period of their incorporation, (3) they were coordinated with a set of statistically recurrent structural properties outside the adaptation (within in the environment or in other parts of the organism), (4) in such a way that the causal interaction of the two (in the context of the rest of the properties of the organism) produced functional outcomes. . . . (Tooby and Cosmides 1992, pp. 61–62; emphasis added)

It is only those conditions that recur, statistically accumulating across many generations, that lead to the construction of complex adaptations . . . For this reason, a major part of adaptationist analysis involves sifting for these environmental or organismic regularities or invariances. (Tooby and Cosmides 1992, p. 69; emphasis added)

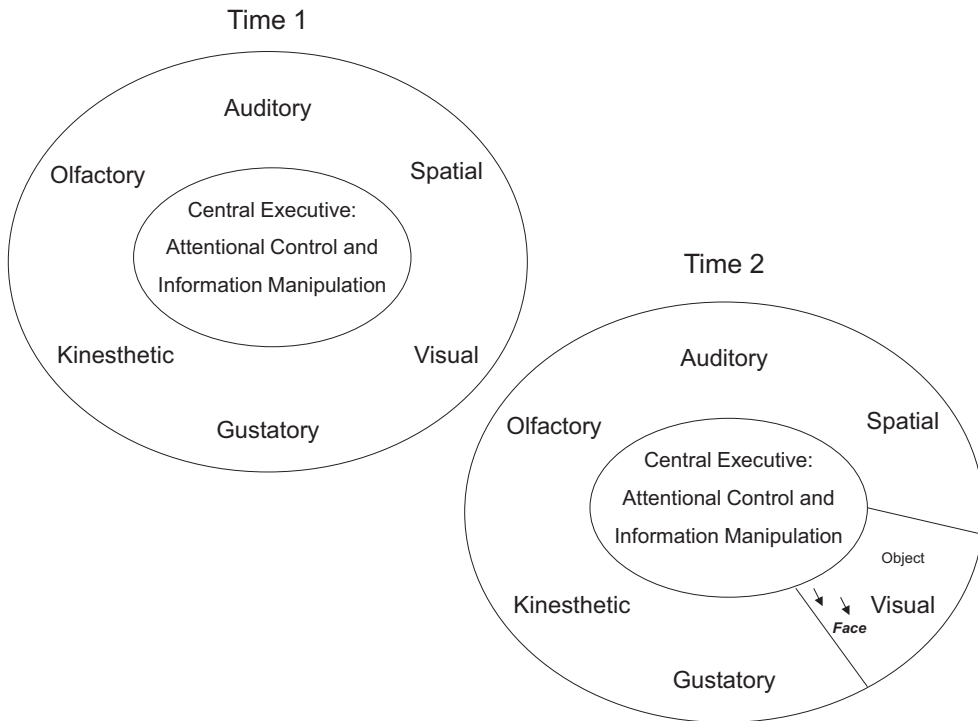
Recurrences are thus essential to the construction of adaptations, but this presents a problem for understanding how novel problems can be solved since, by definition, novel problems are not recurrent. Barrett and Kurzban (2012) attempt to analyze the adaptations underlying intelligence and ability to solve novel problems while retaining the idea that adaptations necessarily require recurrences:

Here, we think, there is a definitional issue: at a certain level, the terms “design” and “novelty” are incompatible with each other, because adaptation is impossible without *some* environmental signal, even if statistical and fuzzy, to adapt to. If “novel”

means “bears no resemblance to anything in the past,” then design to deal with novelty is a priori impossible. . . . To be clear, we don't think adaptations designed for novelty are impossible, but only if we redefine “novelty” so as to not make adaptation to it impossible. (Barrett and Kurzban 2012, p. 686; emphasis added)

Thus, according to Barrett and Kurzban (2012), adaptation to novelty would be impossible without recurrences to adapt to. They show that some adaptations may respond to novelty as a by-product of past selection. Novel tokens of types that recurred over evolutionary time are a paradigmatic example. For example, a novel food item (say genetically modified food or a novel creation of a chef) would be processed by the digestive system because it has enough similarity to the sorts of food for which the digestive system was designed. Similarly, a novel three-dimensional object will be processed in an appropriately functional manner by the visual system because the novel item does not depart substantially from the regularities that resulted in the evolution of the visual system.

There is wide agreement among both modular and domain-general theorists that there are specialized content spheres with specific formatting requirements that are component processes in intelligence. These mechanisms are conceptualized as responsive to particular types of recurrent information with specific formatting requirements. As noted, Barrett and Kurzban emphasize the formatting requirements of the inputs to working memory. The model of intelligence proposed by Case et al. (2001) includes specialized, domain-specific content areas (quantitative/relational, spatial/imaginal, verbal/propositional, qualitative/analytic, and causal/experimental) that feed into the executive processing that is central to working memory. An example would be the specialized language centers that process verbal input and produce output into conscious awareness and working memory; this output is thus accessible to executive processing. Geary (2005; see Fig. 1) proposes a variety of highly specialized, domain-specific mechanisms (spatial, verbal, visual object recognition, face recognition,



**Evolution of Intelligence, The, Fig. 1** An illustration of the proposed relationship between the central executive and a partial list of inputs: auditory, spatial, visual, gustatory, kinesthetic, and olfactory. The central executive directs attention to particular domains (e.g., spatial),

resulting in a conscious representation of the information from that domain. At Time 1 there is no specific focus of attention, but at Time 2, attention is focused on a face, resulting in conscious awareness of the face (From Fig. 7.1 of Geary 2005)

auditory, olfactory, kinesthetic, and gustatory) whose highly specialized, appropriately formatted outputs feed into and may be acted on by the executive processes of working memory.

Cosmides and Tooby (2000, 2002) proposed a quite different modular theory of novel problem solving, proposing to account for the ability of humans to solve novel problems by the evolution of metarepresentational abilities. For example, they propose a “scope syntax” (Cosmides and Tooby 2002, p. 182) that marks some information as only locally true or false. This syntax includes “a set of procedures, operators, relationships, and data-handling formats that regulate the migration of information among subcomponents of the human cognitive architecture” (Cosmides and Tooby 2002, p. 183). Of particular importance are metarepresentations that allow us to decouple representations of locally true information from

the rest of our knowledge base (e.g., John believes that X, where X may be true or false). This allows people to explore the properties of situations, in order to identify sequences of improvised behaviors that may lead to novel, successful outcomes.

This theory of Cosmides and Tooby implies that intelligence involves what one might term “hyper-contextualization” because it highlights local contingencies and an unspecified set of mechanisms that allow for solutions of localized problems in ways not coupled to the modular mechanisms designed to solve evolutionarily recurrent problems. As noted below, this emphasis on hyper-contextualization is quite different than data gathered by intelligence researchers showing that general intelligence facilitates solving novel problems not by emphasizing local contingency but by decontextualization and abstraction.

### A Motivational Theory for the Evolution of Domain-General Mechanisms

The first question that a domain-general theory of intelligence must confront is to conceptualize how domain-general mechanisms could evolve. As noted above, a standard account of evolutionary adaptations is that they must respond to environmental conditions that were recurrent over evolutionary time and that adaptations cannot evolve in the absence of such cues. Environmental regularities effectively frame a problem to be solved and enable the evolution of mechanisms able to respond to the regularity. Regularities provide a built-in sense of relevance – a built-in sense of what the problem is, thus solving what is often termed the “frame problem” in cognitive science. Input stemming from an environmental regularity is automatically framed by the relevant modules because they are designed to be attuned to a particular environmental regularity.

An important aspect of evolution has been to solve the frame problem in a manner that does not rely on environmental regularities for the evolution of psychological adaptations (MacDonald 2013; see also Chiappe and MacDonald 2005). Humans and other animals have evolved motivational systems that solve the frame problem with systems that provide signals when their evolved goals are being met. For example, temperature regulation systems provide signals to seek means of attaining warmer or cooler environments. How a person or animal solves this problem is unspecified and does not depend on environmental regularities over evolutionary time. However, the temperature-regulating mechanisms effectively frame the problem: They yield information regarding the nature of the problem (i.e., the feeling of being too cold or too warm), and they yield information when the problem has been solved (i.e., attaining a more comfortable temperature). This signal is not a response to an environmental regularity, but rather signals that an internal goal has or has not been met; further, achievement of this internal goal must have been linked to reproductive success in the EEA; but there is no need for reproductive success to be linked to any environmental regularity. As described in the following, such a system enables the evolution of

mechanisms able to take advantage of ephemeral environmental regularities (classical and operant conditioning) or imitate successful others (social learning). Ultimately, via the elaboration of the domain-general mechanisms of general intelligence, affectively grounded systems enable organisms to solve novel problems and (more commonly) to solve ancient evolutionary problems by novel means – means that are more efficient than any possible architecture that is linked to environmental regularities.

From this perspective, a watershed event in evolutionary history was the evolution of subjective psychological signals – positive or negative feelings – that inform the animal when its goals of survival and reproduction are being met or unmet. Imagine a primitive organism equipped only with “if  $p$ , then  $q$ ” devices, where  $p$  represents recurrent environmental events and  $q$  represents an evolved response to the event: If a certain environmental situation  $p$  occurs (e.g., presence of food), then respond with behavior  $q$  (eating). Such an organism would completely satisfy the requirements for a psychological adaptation as described above. The mind is constructed with mechanisms designed to respond adaptively to recurrent environmental events (the presence of  $p$ 's). The mechanism is entirely modular, designed to deal exclusively with a particular kind of input (domain-relevant information) by encoding the input in a manner that can be processed by the animal's nervous system; and it produces a particular kind of output (e.g., behavior such as eating  $p$ ), thereby solving a very specific problem. Its disadvantage would be that there would be no way to take advantage of nonrecurring information in order to find food, for example, the information that a certain ephemerally available stimulus is a cue for food (classical conditioning), the chance discovery that a certain behavior is a good way to obtain food (operant conditioning), or observing another animal successfully obtaining food (social learning).

Examples of “if  $p$ , then  $q$ ” systems are the modular systems that figure prominently in accounts of general intelligence, such as those enumerated by Geary (2005) (spatial, verbal, visual object recognition, face recognition,

auditory, olfactory, kinesthetic, and gustatory). Nevertheless, despite having specific formatting requirements, the information processed by human modular language systems can be produced voluntarily (i.e., via executive processes) and can be coupled, via learning, to an endless variety of social functions that are not dependent on environmental recurrences. This contrasts with the fixed signaling systems of nonhuman primates and other animals in which signals occur in particular recurrent contexts (e.g., threat, danger, alarm, greeting) and are coupled to the specific circumstances surrounding their use and the functions they serve. Their meaning is therefore fixed. However, the contextual freedom characteristic of humans means that the functions of signals can change quickly over time, making them ideal for dealing with uncertain, novel situations. As in the case of social learning (MacDonald 2013), there is undoubtedly a great deal of specialized neural machinery underlying human language ability. However, like social learning, it functions as a domain-general system, with no evolutionarily fixed inputs or outputs and no fixed relationship to particular environmental regularities. Even infants 3–6 months of age are capable of many-to-many mappings between signal and function; there are a wide variety of signals, many with no social function at all.

Because of the evolution of motivational systems with an affective (reward/punishment) component, a person seeking a warmer or cooler temperature may indeed be confronted with an infinite number of behavioral choices, but the person can narrow down this infinite array by choosing behaviors likely to change the subjective feeling of warmth or coldness. The behaviors that solve the problem may include behavior resulting from ephemeral associations between a previous behavior and reward (classical or operant conditioning) and behavior learned by observing others (social learning), or it may include a mental model that is a part of the evolved machinery of intelligence (developing highly technical plans for building an air conditioner or heating system by taking advantage of knowledge of materials and thermodynamics and making a plan based on

imagining possible outcomes – thus relying on mechanisms of general intelligence).

The point is that this affective motive and the fact that certain behaviors reliably result in getting warmer or cooler give structure to the person's behavior and enable an adaptive choice from among the infinite number of possible behaviors. The resulting behavior is not random because it is motivated by the desire to attain a comfortable temperature. Motivational mechanisms can thus be thought of as a set of adaptive problems to be solved but whose solution is underspecified. Such systems enable the evolution of any cognitive mechanism, no matter how opportunistic, flexible, or domain-general, that is able to solve the problem. None of these ways of solving the problem need to have resulted in solutions that were successful in our evolutionary past.

This fits well with research showing that problem solving is opportunistic: People satisfy their goals, including evolved goals such as satisfying hunger or regulating body temperature, by using any and all available mechanisms. For example, children typically experiment with a variety of strategies and then select the ones that are effective. Children are *bricoleurs*, tinkerers who constantly experiment with a wide range of processes to find solutions to problems as they occur.

These results point to two conclusions: Given that domain generality is evolvable if the animal is equipped with reward-/punishment-type motivational systems, it is not surprising that it is evolutionarily ancient. Indeed, even primitive animals like *Aplysia* (sea slug) possessing very rudimentary nervous systems have associative mechanisms geared to produce adaptive behavior in novel ephemeral environments by pairing a stimulus with a painful unconditioned stimulus (Carew et al. 1981); the conditioned stimulus is limited only by what the nervous system of *Aplysia* can detect and need not be an evolutionarily recurrent stimulus. Secondly, given the rarity of forms of intelligence approaching the human level and even the rarity of sophisticated learning mechanisms, such as social learning, in nature, one must assume that the cost-benefit calculus for elaborating the mechanisms of intelligence and social learning is difficult to overcome.



*Aplysia* is doing just fine without the elaboration of these mechanisms.

As described in section “[Evolution of Intelligence: Theories](#),” there has been considerable debate on what evolutionary pressures resulted in human general intelligence: rapid climactic change, ecological maximization, social competition, or some combination of these. However, given the pervasiveness of domain-general mechanisms in nature and their ancient pedigree, the evolution of intelligence in a sense that would apply to the behavior of New Caledonian crows, rats, humans, and other primates would always be a theoretical possibility. That is, there is no theoretical reason why a very wide range of animals, certainly including birds and mammals, could not have evolved social learning mechanisms or the ability to infer a causal rule from their experience or to visualize and evaluate various hypothetical scenarios in order to satisfy an evolved motive such as hunger or temperature regulation. The affective basis of domain generality is evolutionarily ancient, resulting primitively in simple associative learning mechanisms (classical and operant conditioning), then elaborated greatly with social learning, and finally general intelligence as a suite of mechanisms, particularly the executive processes of working memory (see below) underlying the ability to manipulate information from a variety of sources in order to achieve goals that may or may not be linked with affective motivational systems derived from the evolutionary past.

Although intelligence is usually conceptualized in terms of the ability to solve novel problems, it should also be noted that human general intelligence is adept at finding novel, more efficient ways to solve evolutionarily ancient problems of survival and reproduction (e.g., finding better ways to extract resources from the environment or developing more effective military tactics). The novelty is quite often in the solution, not in the problem itself. Nevertheless, novel problems, as would be presented, for example, in rapidly changing novel environments, certainly pull strongly for intelligence because solutions for these novel problems are necessary for survival.

### Research on Animal Intelligence

As noted above, research on New Caledonian crows has established the existence of problem-solving mechanisms able to produce novel solutions to the ancient evolutionary problem of procuring food. Earlier research by Heinrich (2000) demonstrated the ability of ravens to solve novel problems by using long pieces of string to hang meat from a perch. For ravens, gaining access to this food was a novel problem because it did not occur in their natural environments. The solution involved repeated pulls on the string with the beak while holding and releasing the string with a foot. Though each step in the solution may be innate (e.g., grabbing objects with their beaks or with their feet), assembling these behaviors into a sequence that solves the problem was novel. Not all birds arrived at this solution, indicating individual differences in performance, as there are for general intelligence in humans. The solution did not emerge through a trial-and-error process via learning.

Importantly for conceptualizing the mechanisms underlying intelligence, Heinrich argued that the ravens formulated a goal, built mental models, and evaluated possible sequences of actions without having to endure their consequences. They took into account information from various sources in planning the solution – an obvious drawback to trial-and-error learning. Thus, the ravens did not pull up the string if the piece of meat appeared to be too large, nor did they pull up the string if it was attached to rocks rather than meat. Insightful problem solving involving goals, mental models, and evaluation of possible outcomes has also been demonstrated in apes.

Based on models of human intelligence showing the existence of a *g* factor of general intelligence, several studies have found a general intelligence factor in a wide range of animal species, including a variety of primate species (see Fernandes et al. 2014; Reader et al. 2011), rats, rodents, rabbits, cats, dogs, raccoons, ravens, and pigeons (Galsworthy et al. 2014). Further, tasks that are more *g* loaded are more heritable and are more associated with differences between species and, among humans, among different human

groups (reviewed in Fernandes et al. 2014). Using principal axis factoring, Fernandes et al. found that the  $g$  factor explained 62% of the variance in five cognitive abilities for primates, while, utilizing a different technique, Reader et al. (2011) found a general factor that explained 65% of the variance across diverse cognitive tasks (behavioral innovation, social learning, tool use, extractive foraging, and tactical deception) using data from 62 primate species. Better performance on these tasks was correlated with brain volume. Reader et al. conclude that their results do not support the massive modularity hypothesis and that social intelligence (e.g., tactical deception) is linked to the general factor of intelligence. Fernandes et al. and Reader et al. both found the highest interspecies variation and loadings associated with tool use, while Woodley of Menie et al. (2015) found that tool use was linked to high interspecies variation, high  $g$  loadings, and both additive genetic and phenotypic variance. Tool use is hypothesized to be critical for cognitive control of the environment – that is, species and individuals with higher  $g$  are better able to solve novel problems confronted in their environments. Woodley of Menie et al. concludes that results thus far across a wide range of species support the view that “the  $g$ -nexus should generalize to all taxa for which  $g$  is a central component of cognition, indicating profound homology” (p. 162).

A study by Crinella and Yu (1995) suggests that modular mechanisms can be meaningfully linked to a general intelligence factor in animals. They extracted a  $g$  factor in rats that was based on five tests and accounted for 34% of the variance, a finding that was comparable to studies of  $g$  in humans (Jensen 1998). Solving these problems typically involved combining information from multiple sources, including from modules specialized for processing spatial information. Spatial learning is a modular process in rats, but the frontal cortex uses the information generated by spatial modules to solve novel problems. The frontal cortex is essential to combining information from different experiences but is not essential to spatial learning per se. The ability to integrate this information with other experiences (e.g.,

learned associations) is part of a positive manifold linked to success in solving other novel problems and to brain size. As indicated below, models of human intelligence involve combining information from modular mechanisms, such as spatial information, into solutions to novel problems.

### Intelligence and Explicit Problem Solving in Humans

The animal data fit well with research on humans, which has consistently found that more intelligent people are better at attaining goals in situations of minimal prior knowledge. Of particular importance is fluid intelligence, defined as “reasoning abilities [consisting] of strategies, heuristics, and automatized systems that must be used in dealing with ‘novel’ problems, educating relations, and solving inductive, deductive, and conjunctive reasoning tasks” (Horn and Hofer 1992, p. 88). Tests of fluid intelligence correlate strongly with  $g$  (e.g., Carpenter et al. 1990). Tests such as Raven’s Progressive Matrices and Cattell’s Culture Fair Test tap the capacity “to adapt one’s thinking to a new cognitive problem” (Carpenter et al. p. 404). This highlights the idea that intelligence taps conscious problem solving in situations in which past recurrences, including recurrences over evolutionary time, would be unhelpful, except perhaps by analogy or by induction, to the new situation.

Theories proposing a critical role for domain-general processes in intelligence emphasize two fundamentally different processing mechanisms, implicit and explicit processing. Implicit and explicit mechanisms may be contrasted on a number of dimensions (e.g., Geary 2005; MacDonald 2008; Stanovich 2004). Implicit processing is automatic, effortless, and relatively fast and involves parallel processing of large amounts of information. Implicit processing is characteristic of what Stanovich (2004) terms the autonomous set of systems, which respond automatically to domain-relevant information. For example, the visual systems of monkeys and humans contain numerous areas specialized for different aspects of vision. Areas specialized for color and for motion are sensitive to different aspects of visual stimulation; processing in these different areas

occurs in parallel and results in a unitary image. Other modules proposed in the cognitive literature include modules for social exchange, theory of mind, fear, folk physics, and grammar acquisition.

Although implicit processing is characteristic of evolved modules, it is not restricted to evolved modules. It occurs in a wide range of circumstances, including skills and appraisals that have become automatic with practice or repetition, perceptual interpretations of behavior (e.g., stereotypes), and priming effects. Modules, as defined here, therefore need not be domain specific; they may also result from domain-general processes of associative and implicit learning (Stanovich 2004, p. 39) (Table 1).

On the other hand, explicit processing characteristic of intelligent problem solving is conscious, controllable, effortful, and relatively slow and involves serial processing of relatively small amounts of information. Such processing is characteristic of what Stanovich (2004) terms the analytic system characterized by context-free mechanisms of logical thought, planning, and cognitive control. The analytic system is sensitive to linguistic input that allows for explicit representations of the context, including hypothetical representations of the possible consequences of actions. Explicit processing is typically experienced as an internal linguistic monologue that is associated with the experience of agency or free will. The executive processes of working memory are paradigmatic examples of explicit processing.

As an example of explicit processing, consider the Tower of Hanoi problem in which participants must develop a long-term plan with multiple

subgoals. This problem requires one to be able to activate multiple goals and keep track of the satisfaction of each of the goals in working memory (Carpenter et al. 1990, p. 413). These goals must be consciously and explicitly held in mind while performing the task. Contrast this type of problem solving with examples of implicit processing, such as everyday perception in which, when we look around the room, our brains are automatically carrying out a large number of operations involving many different specialized modules (e.g., mechanisms for perceiving vertical contours, horizontal contours, motion, color, etc.) that allow us to see the objects in the room. The calculations are done very rapidly, and we are not conscious of making them. This latter situation would not count as an example of intelligent problem solving.

**Mechanisms Underlying General Intelligence**

As noted, intelligence involves explicit processing. In particular, intelligence involves central executive processes that focus attention on explicit representations of relevant information in working memory while simultaneously inhibiting information not relevant to the problem. Theories of the mechanisms underlying intelligence posit a central executive capable of explicit processing that receives input from a variety of systems, many of them modular mechanisms characterized by implicit processing, including auditory, visual, spatial, or episodic information (i.e., information from life events involving memories derived from a variety of systems) (Baddeley 2000).

**Evolution of Intelligence, The, Table 1** Characteristics of implicit and explicit cognitive systems

Implicit system	Explicit system
Not reflectively conscious	Conscious
Automatic	Controllable
Fast	Relatively slow
Evolved early	Evolved late
Parallel processing	Sequential processing
High capacity	Limited by attentional and working memory resources
Effortless	Effortful
Evolutionary adaptation or acquired by practice	Acquisition by culture and formal tuition

Working memory capacity has been implicated as an underlying source of individual differences in fluid intelligence as indicated by moderate to strong correlations between fluid intelligence and working memory capacity (e.g., Kyllonen and Christal 1990). Thus Kyllonen and Christal found correlations from 0.80 to 0.90 between working memory capacity (assessed by tasks such as digit span and mental arithmetic) and reasoning ability (assessed by performance on analogies and verbal reasoning). Engle et al. showed that the executive functions of working memory (assessed by tasks involving attentional control) predicted *g*, but that short-term memory capacity (assessed by tasks such as memory for sets of words) did not.

Individual differences in working memory capacity reflect differences in the capacity for controlled attention, including the ability to inhibit irrelevant information. Kane et al. (2001) found that participants with low working memory capacity were less able to inhibit the prepotent response of orienting toward a visual cue in a task that required them to look in the direction opposite the cue (looking toward a visual cue is an automatic response; looking away from a visual cue requires suppression of an automatic response; see MacDonald 2008). This supports the idea that working memory capacity plays a crucial role in controlling attention in situations in which responding does not involve automatic implicit processing – that is, in situations requiring active engagement with task goals and the inhibition of prepotent, automatic responses.

As noted above, goal management is an important feature of animal intelligence. One role of the executive functions in solving novel problems is to manage goals. This involves constructing, executing, and maintaining a mental plan of action during the solution of a novel problem (Carpenter et al. 1990). For example, the Raven's Progressive Matrices fluid intelligence test and the Tower of Hanoi problem (in which participants must develop a long-term plan with multiple subgoals) both require one to be able to activate a goal with multiple subgoals and keep track of the satisfaction of each of the subgoals (Carpenter et al. p. 413).

Executive functions underlying general intelligence are thus involved when problems call for substantial planning and keeping track of various subgoals. They are involved in dealing with situations that are highly demanding of attentional resources, as more aspects of the problem require attention. More complex tasks require more involvement of controlled processes that structure and analyze the problem, assemble a strategy of attack on it, monitor the performance process, and adapt these strategies as performance proceeds. Keeping task-relevant information in active state is particularly challenging in conditions in which distracting information is present (Kane et al. 2001).

### **Is Working Memory a Domain-General Mechanism?**

The executive functions of working memory and the mechanisms of activation and inhibition do not satisfy the criteria for modularity. By definition, mechanisms for solving novel problems have to be unspecialized in the domains for which they provide solutions. Although they may have access to specialized information obtained from the various modules that provide them with inputs, the problem-solving procedures would have to be general enough to allow the solution of novel problems in various domains. For example, there is a substantial correlation between performance on the Raven's Progressive Matrices and performance on the Tower of Hanoi puzzle (Carpenter et al. 1990). Both tasks require goal management, working memory, and inhibition of prepotent responses. However, the types of information used in solving these problems, the specific goals and subgoals, and the specific responses requiring suppression are unique to each task, and the tasks themselves are not problems that were recurrent in the EEA.

Moreover, measures of working memory capacity predict performance across a wide range of tasks. The only common element of these tasks is that they make high demands on attentional resources, indicating that a general capacity is involved. For example, people who did well on a mathematical processing task also tended to do well on a perceptual task requiring

inhibition of prepotent responses (Kane et al. 2001). This is what one would expect if working memory “reflects an abiding, domain-free capability that is independent of any one processing task” (Kane et al. 2001, p. 169).

The executive functions are thus able to access goal-relevant information from a wide range of domains when solving a problem. Indeed, it is in being able to access representations from more modular processes that the executive functions are able to extend cognitive competencies in ways that are unrelated to their evolutionary function. The data on general intelligence in animals is also consistent with this view. For example, Thompson et al. (1990) found that six brain regions were involved in psychometric *g* for the rat, including a visuospatial attentional mechanism, a visual discrimination mechanism, a vestibular-proprioceptive-kinesthetic discrimination mechanism, a place learning mechanism, and a nonspecific mechanism. This is consistent with models of human intelligence (Case et al. 2001).

There is much evidence that general intelligence facilitates the integration of information obtained from modules. Geary’s (2005) distinction between biologically primary and biologically secondary abilities is useful in this regard. Biologically primary abilities are domain specific and include abilities such as language and simple quantitative abilities, which develop universally and spontaneously. Biologically secondary abilities, such as reading and mathematical ability, use these domain-specific modules, but in a novel manner. Rather than seeming to be spontaneous and effortless, biologically secondary abilities typically require practice and tuition, often with coercion, bribery, or exhortation. Learning these biologically secondary abilities involves explicit, conscious awareness rather than implicit awareness. Success at these biologically secondary abilities is strongly correlated with general intelligence (Geary 2005).

As a case in point, human language results from highly dedicated systems that enable children to effortlessly and unconsciously learn extraordinarily complex grammatical rules. However, skill in integrating these language systems as

well as the output of visual processing mechanisms into an evolutionarily novel ability – reading – is strongly linked to general intelligence. Unlike language learning, reading is typically mastered only with a great deal of conscious effort and represents a major hurdle for many schoolchildren. The correlation between IQ and reading skills ranges from about 0.6 to 0.7, even longitudinally (e.g., Stevenson et al. 1976). IQ correlates with reading most when decoding ability – a specialized, likely modular process – is controlled (Jensen 1998). Children at the third- or fourth-grade level are adept at decoding, and individual differences are mainly in comprehension. Reading comprehension is approximately as highly correlated with verbal as with nonverbal IQ.

### Decontextualization as a Function of General Intelligence

Decontextualization enables humans to inhibit the operation of highly context-sensitive, implicit, and automatic heuristics for making inferences, judgments, and decisions (Stanovich 2004). Decontextualization enables dealing with novel and unpredictable environments because a common source of solutions to novel problems involves recognizing similarities between new problems and previously solved problems, as via analogical reasoning (Chiappe and MacDonald 2005).

As noted, logical thought, planning, and cognitive control are fundamental to intelligence, and since they operate in a context-free manner (Stanovich 2004), they are not tied to recurrent contexts but operate to find general rules, as in the example of the New Caledonian crows noted above. IQ researchers are well aware of the centrality of decontextualization for thinking about intelligence.

One of the well-known byproducts of schooling is an increased ability to decontextualize problems. In almost every subject...pupils learn to discover the general rule that applies to a highly specific situation and to apply a general rule in a wide variety of different contexts. The use of symbols to stand for things in reading (and musical notation); basic arithmetic operations; consistencies in spelling, grammar, and punctuation; regularities and

generalizations in history; categorizing, serializing, enumerating, and inferring in science, and so on. Learning to do these things, which are all part of the school curriculum, instills cognitive habits that can be called decontextualization of cognitive skills. The tasks seen in many nonverbal or culture-reduced tests call for no scholastic knowledge per se, but do call for the ability to decontextualize novel situations by discovering rules or regularities and then using them to solve the problem. (Jensen 1998, p. 325).

## Conclusion

As noted above, there is excellent evidence that general intelligence is an adaptation underlying the ability of humans to solve problems where subjects have a minimal amount of prior knowledge. Such problems are novel because they have not been previously encountered by the subject, and thus it is not surprising that more intelligent people are able to create novel solutions to ancient problems of survival and reproduction (Chiappe and MacDonald 2005). Research on human intelligence has shown that the degree to which the *g* factor loads onto cognitive ability measures positively moderates the association between these measures and a variety of biological variables, including brain size, reaction time, and inbreeding-depression effects, and also with phenotypic and genetic characteristics associated with performance on the tests, such as the magnitude of population differences in cognitive performance (Jensen 1998; Rushton and Jensen 2010). This demonstrates that it is the most domain-general measures of intelligence that have the highest validity in predicting biologically meaningful manifestations of cognition. Furthermore, the most domain-general measures of intelligence enjoy the highest criterion validity – meaning that they are better at measuring the real-world advantages that stem from high IQ (Rushton and Jensen 2010). Such individuals tend to make more money, perform better in scholastic and workplace environments, and achieve a higher social status than people on the low end of the IQ distribution. They are also more conscious of personal health and safety. On the job, the *g* factor is the

best single predictor of job performance. Correlations between *g* and job performance range between 0.2 and 0.8, with greater predictive validity achieved for jobs of greater complexity. Thus, people with higher general intelligence are more adept at attaining their evolutionary goals in situations of novelty, complexity, and unpredictability – consistent with the hypothesized functions of *g* as a psychological adaptation designed by selection (Chiappe and MacDonald 2005; Geary 2005).

General intelligence is therefore at the heart of an evolutionary analysis. Although modules designed to process specific types of information are unquestionably important to an evolutionary analysis, evolutionary psychology has over-emphasized modularity and ignored the vast data indicating a prominent role for domain-general mechanisms in human and animal cognition. Indeed, research has uncovered associations between a general intelligence factor and ability to solve problems that have often been advanced as solved by domain-specific modules, such as cheater detection, social exchange, and learning (Chiappe and MacDonald 2005; Fernandes et al. 2014). Fernandes et al. also point out that very similar cognitive abilities have been found in widely divergent species (e.g., various primate species and hyenas) despite very different ecologies. The prediction from massive modularity theory – that the principal source of species differences in intelligence should be unique because each species has its own set of specialized modules that evolved to solve species-specific problems – is not supported.

Domain-general mechanisms are powerful but fallible mechanisms that are the basis for solving a fundamental problem faced by all but the simplest organisms: the problem of navigating constantly changing environments presenting new challenges that have not been recurrent problems in the EEA. Most important, the domain-general mechanisms at the heart of human cognition are responsible for the decontextualization and abstraction processes critical to the scientific and technological advances that virtually define civilization (Chiappe and MacDonald 2005).

## Cross-References

- ▶ [Aurelio Jose Figueredo](#)
- ▶ [Bruce Ellis](#)
- ▶ [Conditioning and Association](#)
- ▶ [Consciousness](#)
- ▶ [Cosmides & Tooby \(1992, 2005\)](#)
- ▶ [David Geary](#)
- ▶ [Domain Generality](#)
- ▶ [Domain Specificity](#)
- ▶ [Evidence of Brain Modularity](#)
- ▶ [Intelligence Versus Ecological Adaptations](#)
- ▶ [Intelligent](#)
- ▶ [J. Philippe Rushton](#)
- ▶ [Massive Modularity in Evolutionary Psychology](#)
- ▶ [Race Differences](#)

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