Review TRENDS in Cognitive Sciences Vol.9 No.5 May 2005

Evolution of the brain and intelligence

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Intelligence has evolved many times independently among vertebrates. Primates, elephants and cetaceans are assumed to be more intelligent than 'lower' mammals, the great apes and humans more than monkeys, and humans more than the great apes. Brain properties assumed to be relevant for intelligence are the (absolute or relative) size of the brain, cortex, prefrontal cortex and degree of encephalization. However, factors that correlate better with intelligence are the number of cortical neurons and conduction velocity, as the basis for information-processing capacity. Humans have more cortical neurons than other mammals, although only marginally more than whales and elephants. The outstanding intelligence of humans appears to result from a combination and enhancement of properties found in non-human primates, such as theory of mind, imitation and language, rather than from 'unique' properties.

Introduction

Animals differ in intelligence, and humans are usually considered to be by far the most intelligent. However, it is unclear which brain properties might explain these differences. Furthermore, the question of whether properties such as a theory of mind, imitation or a syntactical language are uniquely found in humans is hotly debated. Finally, recent reports on high intelligence in animals with relatively small brains, such as corvid birds and dogs, has raised once again the discussion about the relationship between brain and intelligence [1,2].

In this context, we will address the following questions: (1) How can we define and measure animal intelligence? (2) What differences in intelligence are supposed to exist among animals and between animals and humans? (3) When we relate differences in intelligence to brain properties, which properties should we look for? (4) Are differences, especially those between humans and other mammals, quantitative or qualitative in nature?

How do we define and measure intelligence?

There is no universally accepted definition of animal intelligence, or procedure to measure it. Intelligence may be defined and measured by the speed and success of how animals, including humans, solve problems to survive in their natural and social environments (see also [3]). These include, for example, problems related to feeding, spatial orientation, social relationships and intraspecific communication. However, what animals must learn in their environments and how they accomplish this can differ considerably. Accordingly, behavioral ecologists have proposed that intelligence is nothing but an aggregate of special abilities that evolved in response to specific environments [4]. Comparative psychologists disagree by pointing out that we can test animals for *general* problem solving and associative-learning abilities. This should be done with 'unnatural' tasks in 'arbitrary environments', that is, using laboratory tests [5,6]. However, laboratory tests carry the risk of posing problems in an 'unfair' manner, because of certain perceptual or cognitive predispositions of the animals being tested [7].

Recently, several comparative and evolutionary psychologists and cognitive ecologists have converged on the view that mental or behavioral *flexibility* is a good measure of intelligence, resulting in the appearance of novel solutions that are not part of the animal's normal repertoire [8–10]. This can be studied either in the laboratory by measuring changes of tactics in problem solving or by observing 'innovation rates' in the wild [11].

Supposed differences in intelligence

Using mental and behavioral flexibility as a criterion for intelligence, among tetrapod vertebrates, mammals and birds appear (on average) to be more intelligent (cf. [8]). Among birds, corvids, parrots and owls are considered more intelligent [11], and among mammals, primates and cetaceans [12]. Among primates, apes come out as more intelligent than monkeys, and monkeys more than prosimians; and among apes, chimpanzees, bonobos and humans appear to be particularly intelligent [8]. Thus, intelligence as defined above has apparently evolved independently in different classes of vertebrates (e.g. birds and mammals [1]), and in different orders of the same class (e.g. cetaceans and primates), as well as in different families of the same order. This speaks strongly against an 'orthogenetic' view of intelligence, that is, a single evolutionary line culminating, for example, in *Homo sapiens*.

Neural correlates of intelligence

The question arises of how to relate these supposed differences in intelligence to brain properties, and which properties we should compare. These could either be general properties, if we assume that the evolution of intelligence is based on an increase in 'information processing capacities' [13,14]), or specialities of anatomy or physiology of different brains, if we conceive

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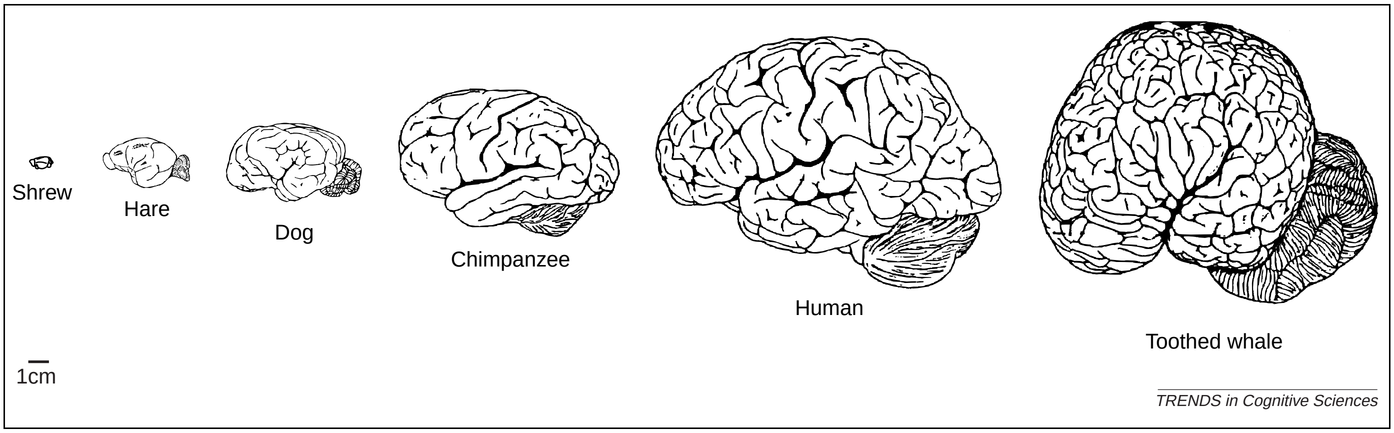

Figure 1. A series of mammalian brains. Humans do not have the largest brain in absolute terms and are exceeded in size by many cetaceans (whales, dolphins, porpoises) and the elephants. They also do not have the most convoluted cortex. With a few exceptions, convolution of the cortex increases in proportion to cortical size.

intelligence as a number of special adaptations to a given environment [3].

General properties

Absolute size is the most general of all brain properties (Figure 1; Table 1), and ranges in mammals from brains of small bats and insectivores (weighing less than 0.1 g) to those of large cetaceans (up to 9000 g). It is assumed that animals with larger brains are more intelligent than those with smaller ones [15]. However, monkeys possess brains that are much smaller than those of ungulates (Table 1), but their higher cognitive and behavioral flexibility is undisputed. Also, the 1.35 kg brain of *Homo sapiens,* supposedly the smartest creature on earth, is significantly exceeded by the brains of elephants and some cetaceans. Thus, a larger brain alone does not necessarily assure greater intelligence.

The next much-discussed general factor is relative brain size (Figure 2). Mammals with relatively larger brains are often assumed to be more intelligent [13]. As body size increases, brain size increases in a negatively allometric way following a power function with an exponent of 0.6–0.8 [13,14]. This means that with increasing body size, brains become *absolutely* larger,

Table 1. Brain weight, encephalization quotient and number of cortical neurons in selected mammals

Animal taxa	Brain weight (in g)[a]	Encephalization quotient[b,c]	Number of cortical neurons (in millions)[d]
Whales	2600–9000	1.8	
False killer whale	3650		10 500
African elephant	4200	1.3	11 000
Man	1250–1450[e]	7.4–7.8	11 500
Bottlenose dolphin	1350	5.3	5800
Walrus	1130	1.2	
Camel	762	1.2	
Ox	490	0.5	
Horse	510	0.9	1200
Gorilla	430[e]–570	1.5–1.8	4300
Chimpanzee	330–430[e]	2.2–2.5	6200
Lion	260	0.6	
Sheep	140	0.8	
Old world monkeys	41–122	1.7–2.7	
Rhesus monkey	88	2.1	480
Gibbon	88–105	1.9–2.7	
Capuchin monkeys	26–80	2.4–4.8	
White-fronted capuchin	57	4.8	610
Dog	64	1.2	160
Fox	53	1.6	
Cat	25	1.0	300
Squirrel monkey	23	2.3	480
Rabbit	11	0.4	
Marmoset	7	1.7	
Opossum	7.6	0.2	27
Squirrel	7	1.1	
Hedgehog	3.3	0.3	24
Rat	2	0.4	15
Mouse	0.3	0.5	4

[a] Data from [13,17,73].
[b] Indicates the deviation of the brain size of a species from brain size expected on the basis of a 'standard' species of the same taxon, in this case of the cat.
[c] Data after [13,73].
[d] Calculated using data from [17].
[e] Basis for calculation of neuron number.

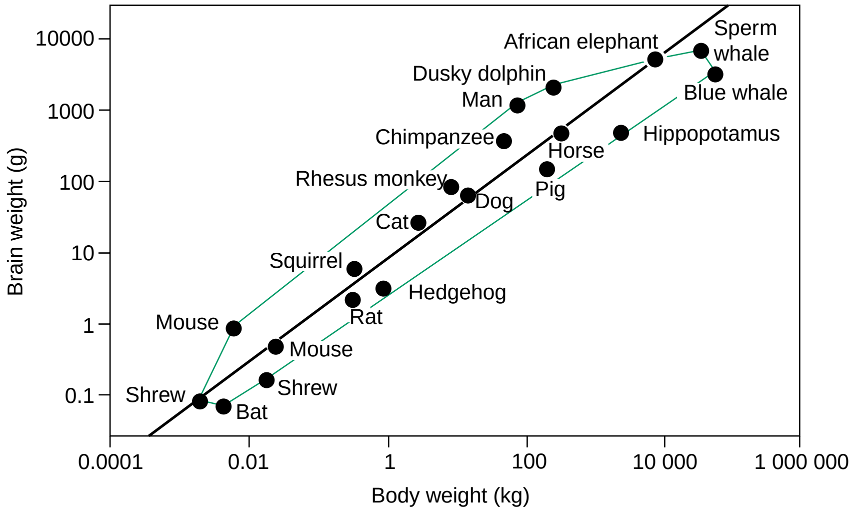

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Figure 2. Relationship between brain size and body size in selected mammals. Brain size (kg) and body size (g) are given for 20 mammals, including those with the smallest and the largest body and brain weights (in the shrew and mouse, two different species are represented). In all vertebrates, brain size increases *negatively allometrically with a power function of exponent 0.6–0.8,* meaning that an increase in brain size lags behind an increase in body size. The data are plotted in log–log coordinates, with a regression line (black line) drawn through the data points. The exponent of the power function is represented by the slope of the regression line. The green line connects the data points that are furthest from the regression line and indicates how much brain size deviates, positively or negatively from average mammalian brain:body ratio. As can be seen, humans as well as dolphins have larger brains, and the hippopotamus and blue whale smaller brains than expected. Modified from [74].

but *relatively* smaller. Among large mammals, humans have the relatively largest brain (2% of body mass), whereas shrews, the smallest mammals, who exhibit supposedly much less cognitive and behavioral flexibility, have brains of up to 10% of their body mass [16] (Figure 3). The relationship between relative brain size and intelligence is therefore inconclusive.

Another much-discussed general factor is encephalization. This is expressed by an ‘encephalization quotient’, $EQ=E_a/E_e$, which indicates the extent to which the brain size of a given species E_a deviates from the expected brain size E_e, based on a ‘standard’ species of the same taxon [13]. With the cat as ‘standard’ for mammals ($EQ=1$; Table 1), humans have the highest EQ of 7.4–7.8, indicating that the human brain is 7–8 times larger than expected. This can be related to an extremely rapid increase in brain size during hominid evolution (see Box 1), which in turn required substantial reorganization of the digestive system and feeding behavior (see Box 2). Humans are followed by some dolphin species with EQs of around 5 [12]. The snag with the EQ as a predictor for greater intelligence is that some New World capuchin monkeys have higher EQs than chimpanzees and gorillas [13,15] (see Table 1) despite their lower intelligence. Thus, EQ is also not the optimal predictor for intelligence.

Perhaps absolute or relative size of the cerebral cortex, as the assumed substrate for higher cognitive abilities, might better predict intelligence. Cortical volume

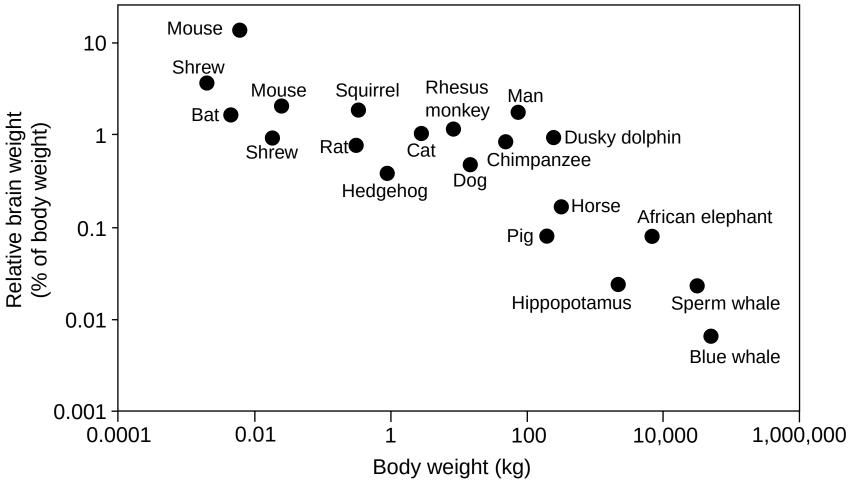

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Figure 3. Mammalian brain size as a percentage of body size. Brain weight is given as a percentage of body weight for the same 20 mammalian species as in Figure 2, again plotted in log–log coordinates. As can be seen, small mammals such as mice and shrews have much larger brains in relative terms (10% or more of body weight) than cetaceans (less than 0.01%). Humans, with a brain representing 2% of body weight, have a much higher relative brain size than would be expected (around 0.3%). Modified from [74].

Box 1. How can brains grow rapidly?

During 3.5 million years of human evolution, an enormous increase in brain size has occurred, from a volume of 450 cm^3 found in Australopithecines to about 1350 cm^3 in modern *Homo sapiens* and 1500 cm^3 in *Homo neanderthalensis*, which is mostly the result of a positively allometric growth of the cortex (Fig. I). Experts agree that such a rapid growth, independent of its evolutionary 'driving forces', must be based on relatively simple genetic mechanisms [65,66]. In the mammalian cortex, neurons are produced at two stages and modes of cell division. First, progenitor cells are formed in a narrow zone around the telencephalic ventricle. By symmetric cell division, this ventricular zone grows exponentially. This is followed by asymmetric cell division, in which one precursor cell gives rise to another precursor cell and a neuron, which then migrates from the ventricle to distant positions forming the cortical plate. According to the 'radial-unit hypothesis' of Rakic [67,68], neurons originating from the same progenitor cell form a cortical column, in which later-born neurons position themselves on top of earlier-born ones. Evidently, the number of cycles of symmetric cell production is most important for the expansion of the cortex, because each cycle doubles the number of precursor cells and with this the number of cortical columns. The number of asymmetric cell divisions, by contrast, controls the number of neurons per column and with this the thickness of the cortex in a linear fashion. This could explain, why there is a roughly 1000-fold difference in cortical surface between mouse and man, but only a two- to threefold difference in cortical thickness [13]. Accordingly, a delay in the onset of the second, asymmetric mode of cell division allowing a few extra symmetric cell divisions would lead to an exponential increase in cortical surface. Furthermore, if onset, rate and cessation of symmetrical cell cycles are identical in all parts of the brain, we get a uniform increase in size; if they differ in different parts of the brain, we get positive or negative allometric growth (that is, some parts of the brain increase in relative size while others fall behind). Both effects could be induced by small modifications of regulatory genes [68].

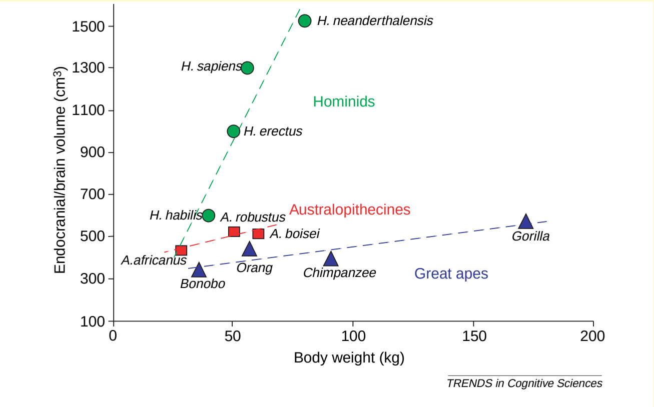

Figure I. The relationship between body size and brain size or endocranial volume (extinct species) in great apes (blue triangles: bonobo, orang-utan, chimpanzee, gorilla), australopithecines (red squares: *Australopithecus africanus, A robustus, A. boisei*) and hominids (green circles: *Homo habilis, H. erectus, H. sapiens, H. neanderthalensis*) (data from [13]). Whereas in the great apes and the extinct australopithecines, brain/endocranial volume has increased only slightly with body size, in hominids a steep increase in brain/endocranial volume has occurred during 2.5 million years culminating in the brain of the extinct *Homo neanderthalensis*, which with a volume of 1200–1750 cm^3 was considerably larger than that of modern *Homo sapiens*.

increases faster than brain volume as a power function with an exponent of 1.13 [13,17]. Consequently, human cortical volume is considerably exceeded by that of the elephants and large cetaceans, both in absolute and relative terms, despite those taxa being considered less intelligent [13,17]. But what about the prefrontal cortex (PFC), as the 'seat' of reason and action planning [18]? It has previously been claimed that the PFC is exceptionally large in humans [19,20], although recent studies contend that the human frontal or prefrontal cortex is *not* disproportionally large compared with other primates [21,22] and may be exceeded by that of elephants and cetaceans. However, these discrepancies might result from the difficulty, among others, of exactly defining the prefrontal cortex in different mammals.

Intrinsic organization of cortex

The number of cortical areas increases with cortex size or surface area [23,24]. Cortical areas are believed to be composed of 'columns' or 'modules' [25,26], recent studies have demonstrated that the volume of a cortical column increases with brain size by an exponent of 0.34 [27]. This is matched, however, by a decrease in neuron density so that the number of neurons per column is nearly constant [27,28]. Average cortical thickness is not correlated with cortical or brain volume; cetaceans and elephants generally have thin cortices (about 1.2 mm) and primates thick cortices (2–3 mm) [17]. Cortical neuronal density varies among mammalian brains, but in general is negatively correlated with brain volume. Humans and the great apes are situated well above and elephants and cetaceans well below the regression line [17].

From cortical volume and cell density, we can calculate the number of cortical neurons (Table 1). It turns out that humans have the largest number of cortical neurons (about 1.2×10^{10}) but are closely followed by large cetaceans and elephants. Although the human cortex is much smaller in surface area than that of these animals, it is twice as thick and has a much higher cell density. A similar situation is found when comparing, for example, dogs and cats (see Table 1): cats have much smaller brains than dogs, but a much higher cell density. Neurons in the human cortex have 29 800 synapses on average [29] resulting in a total of about 3.6×10^{14} synapses. Unfortunately, the number of synapses per neuron is at present unknown in elephants and cetaceans. An important parameter for information processing capacity (IPC) is conduction velocity of cortical fibers. It is mostly determined by the diameter of myelinated fibers. Myelinated cortical fibers are particularly thick in primates and relatively thin in elephants and cetaceans [28,30]. The thinner fibres have a much lower conduction velocity. In addition, the average distance between neurons in elephants and cetaceans is larger, which further impairs their cortical IPC.

Thus, humans do *not* have the largest brain or cortex either in absolute or relative terms. However, owing to the thickness and relatively high cell density in the cortex, humans have the largest number of cortical neurons, although not that many more than elephants and whales. Given the higher conduction velocity and smaller

Box 2. The costs of large brains

The human brain occupies only 2% of body mass, but consumes about 20% of total metabolism. However, heart, liver, kidney and the gastrointestinal tract are equally ‘expensive’. Together with the brain, they consume about 70% of basal metabolism of the human body [69]. According to the ‘expensive tissue hypothesis’ by Aiello and colleagues [69,70], every increase in brain size must be balanced by a reduction of the demands of the other ‘expensive’ organs. The solution for the ‘energy crisis’ of the human brain consisted in a reduction of gut size, which had to be compensated by an increase in the quality of food, that is, higher nutritional value and digestibility. Recently, Fish and Lockwood [71] confirmed that in most primates diet quality and brain size are significantly positively correlated and found that evolutionary changes in diet quality are related to changes in relative brain size. Diet quality is favored by higher motor and cognitive skills, improved recognition of high-quality food, better foraging tactics or better manual processing of food, for example, by means of instruments, which, in turn, is favored by increased manual dexterity and increased action planning abilities. However, Fish and Lockwood discovered deviations from the overall pattern indicating the additional effect of non-dietary constraints. The true bottleneck of energy demand of the human brain appears to lie in its prenatal and early childhood growth. The brain exceeds all other ‘expensive’ organs by its extremely rapid growth that prenatally requires 60% of basal metabolism, and this continues during the first year slowing down until the age of 7 years [69]. According to the ‘maternal energy hypothesis developed by Martin [72], this rapid growth puts a heavy load on the energy budget for both infant and mother before birth and during early childhood. According to Aiello and colleagues [69], besides an increase in food quality, the solution lay in specific social interactions such as grandmothering and food-sharing between unrelated adults of both sexes.

distances between neurons, the human cortex probably has the greatest IPC.

The search for cortical specialties

So far, we have dealt with possible correlations between general problem-solving ability and general brain traits. The alternative is to look for adaptive specializations within the brains of vertebrate or mammalian taxa. In cognitive ecology, some experts view responses to challenges from the environment as a basis for an increase in cognitive capacities and brain complexity, whereas others emphasize a correlation with the complexity of social relationships.

A much cited example for the first view is the relationship between spatial memory and the size of the hippocampus in birds and mammals [6,31,32]. However, Macphail and Bolhuis [33] conclude that empirical evidence for a strict correlation is weak at best. For example, birds with excellent food-storing abilities do not always perform better than other birds when tested for spatial orientation, and they do not always have the largest hippocampi. Shettleworth [7] concurs that no simple relationship exists between these parameters, but argues that species-specific differences in the use of spatial as opposed to non-spatial cues (e.g. color) can explain the observed discrepancies. Furthermore, experience is known to influence hippocampal development, which could explain intra-specific differences in hippocampal volume in relation to spatial memory in both birds and humans.

Dunbar [34,35] as well as Byrne and co-workers [8,36] propose that neocortical enlargement correlates better with social than with environmental complexity. Dunbar found a close correlation between the ratio of isocortex to the rest of the brain on the one hand and social group size and complexity of social relationships on the other. For example, baboons show a remarkably high degree of sociability and have the largest isocortex of Old World monkeys [35]. Byrne and Whiten found a highly significant correlation between isocortical size and the prevalence of tactical deception [36].

More subtle features, for example, differences in cortical cytoarchitecture, have been claimed to contribute to intelligence and IPC. The morphological (and probably functional) diversity of cortical neurons (i.e. number of subtypes) increases with size of cortex (reviewed in [37]). There are differences in the percentage of GABAergic cells in the rat (15%) and primate (20%) cortices, but the significance of this finding is unclear. Only in the primate cortex are large Betz cells found in motor areas, and large Meynert cells in the primary visual cortex, and this has been interpreted as favoring increased sensorimotor abilities, which are typical of primates. In layer 5b of the anterior cingulate cortex of great apes and humans, spindle-shaped cells are found that are four times larger than average pyramidal cells and have widespread connections with other brain areas [38,39], although their specific significance for cognition is unknown.

Recent studies [37,40] have shown that the intracortical organization in mammals regarding density, size and shape of pyramidal cells and spine density is more variable than previously assumed. In the prefrontal cortex of macaque monkeys and humans, respectively, neurons carry up to 16 and 23 times more spines than neurons in the primary visual area [37,41], and dendrites are more branched. These differences are interpreted as indicating a greater IPC of the prefrontal cortex [37].

Do humans and their brains have unique properties?

There is a long tradition that ascribes properties to humans that are supposedly not found in other animals. The most cited are causal understanding of mechanisms of tool use, tool-making, syntactical–grammatical language, consciousness, self-awareness, imitation, deception and theory of mind [9]. There is evidence, however that great apes possess at least some states of consciousness found in humans (reviewed in [42]; see Figure 4). Deception has been widely observed among monkeys; great apes and cetaceans show mirror self-recognition, and great apes and even corvids show an understanding of the mechanisms of tool use and tool-making [1,3,8]. Existence of imitation, theory of mind and syntactical language in non-human animals is under debate and will be briefly discussed in the following sections.

Imitation

The prevalent view is that imitation is found only in humans, and that non-human primates exhibit ‘stimulus enhancement’ and ‘emulation’ rather than true imitation [43–45]. In ‘stimulus enhancement’ an animal watches a conspecific successfully solving a problem (e.g. cracking a coconut). This attracts the new animal’s attention to the object and it will then learn more quickly by trial and error. In ‘emulation’ an animal observes a conspecific

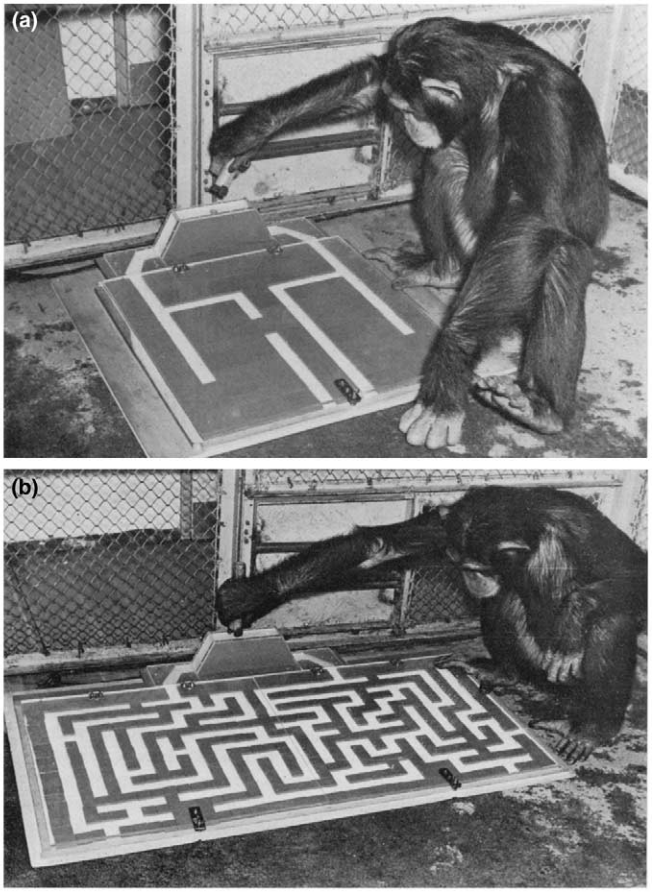

Figure 4. Action planning in apes. The photograph shows the chimpanzee Julia from the zoological institute of the University of Muenster, Germany, being confronted with a simple maze (above) and a complex maze (below). Julia had to decide whether to move the disk (by means of a magnet) either to the right or to the left side of the starting point to find the correct way out of the maze. Julia stared at the maze for a while and then made the correct choice. There can be little doubt that Julia mastered this task with conscious action planning. Reproduced with permission from [75].

reaching a certain goal and tries to act similarly, although not behaving precisely like the conspecific. 'True' imitation is defined as the acquisition of skills by observation, resulting in novel behavior. Byrne and Russon [45] distinguish between 'action-level' imitation, requiring the copying of a certain sequence of actions, and 'program-level' imitation, which is reaching a goal in variable ways. On the basis of food-preparation techniques of gorillas and the imitative behavior of orangutans they argue that these animals show program-level imitation, and that action-level imitation is seldom observed in the great apes as opposed to humans. Recently, Subiaul *et al.* [46] claimed that rhesus monkeys are capable of imitation by copying an expert's use of a rule rather than just copying a certain motor behavior. This again widens the discussion about imitation in non-human primates.

Studies of the macaque brain show that posterior parietal and frontal areas, including the much discussed 'mirror neurons' in frontal area F5, are dedicated to the execution and recognition of meaningful hand-reaching and grasping as well as facial movements [47]. It is, however, unclear to what degree this might form the neuronal basis of imitation.

Theory of mind

It is disputed whether non-human primates possess a theory of mind (ToM), that is, the ability to understand another individual's mental state and take it into account in one's own behavior [48]. A related question concerns the concept of knowledge and the distinction between 'right' and 'false beliefs'. Some experts, such as Povinelli, initially contended that chimpanzees have ToM, but later came to the view that a full ToM is unique to humans [49]. Others, such as Tomasello, initially denied the existence of ToM in chimpanzees, but now see signs of some aspects of it [50]. In humans, ToM and the understanding that a person can hold a false belief develops between the ages of 3–4 years and is fully developed only at the age of 5. In a recent study by O'Connell and Dunbar on false belief [51], chimpanzees, a group of autistic children (assumed characteristically to lack ToM) and children of ages between 3 and 6 years were tested non-verbally. The chimpanzees performed better than both the autistic children and 3-year-old normal children; they were equal to 4–5-year-old children and inferior to 6-year-olds. This would corroborate the idea that chimpanzees exhibit at least some aspects of ToM.

Recent fMRI studies in humans identified cortical areas related to empathy/ToM, imitation and the distinction between self and others (review in [52]). The right inferior parietal and posterior temporal cortex plus the right dorsal lateral, orbital, anterior cingulate and insular cortex showed activations when subjects were asked to focus either on themselves or on others. In this context, 'mirror neurons' in monkey frontal area F5 are viewed by some as 'forerunners' of human cortical areas underlying ToM and the distinction between self and others [47]. This interpretation is weakened by the fact that no signs for a ToM have yet been found in monkeys.

Syntactical–grammatical language

The most-cited example for a unique human ability is syntactical–grammatical language [53–55]. Most authors agree that sentences consisting of up to three words can be understood and used by chimpanzees, gorillas and dolphins. Savage-Rumbaugh and colleagues demonstrated that the 8-year-old bonobo chimp, Kanzi, who was raised in a language environment similar to that of children showed linguistic capabilities including signs of grammar and syntax typical of a 2-year-old girl [56], but Kanzi did not go beyond these abilities despite his long training period.

Wernicke's speech area located in the superior temporal and inferior parietal lobe [57] is apparently *not* unique to humans [58], and the existence of precursors of Broca's area in the frontal lobe in non-human primates is disputed [58,59]. The monkey F5 'mirror neurons' are believed to be partially homologous to Broca's area, particularly because Broca's area in humans is also active during movements of the hand and mouth, as is the case with the mirror neurons [47].

There is a controversy about the roots from which human language evolved (vocal, mostly affective-emotional communication versus visual communication, gestures and mimicry, or a combination of both) [60,61]. It has also been argued that speech and gesture develop in parallel, phylogenetically and ontogenetically [62]. Accordingly, the ability of humans to use language *without* accompanying gestures would just be a further specialization, because under normal conditions humans use both components [62,63].

Conclusions

If we define animal intelligence as the degree of mental or behavioral *flexibility* resulting in novel solutions, either in the wild or in the laboratory, we can conclude that among tetrapods, mammals and birds are more intelligent, and among mammals, humans are more intelligent than members of other taxa. Differences in intelligence among the great apes, cetaceans and elephants are not sufficiently tested, but these taxa all appear to be more intelligent than monkeys, and monkeys more intelligent than prosimians and the remaining mammals. Evidently, among vertebrates, intelligence has not increased in a unilinear or 'orthogenetic' way towards humans, but in a parallel fashion.

Of the more general brain features discussed here, number of cortical neurons combined with a high conduction velocity of cortical fibers correlates best with intelligence. Here, humans win over elephants, cetaceans and the great apes. This would corroborate the view that an increase in 'information processing capacity' is of high importance for intelligence. However, structural and functional specializations in the human prefrontal cortex might also have played an important role.

Corvid birds are astonishingly intelligent when it comes to tool use, flexibility and action planning, and may even rival primates in some respect [1]. The relative size of their brains and pallium (cortex), and particularly of those parts that appear to correspond to the prefrontal cortex of mammals, is much larger than in other birds except parrots, but at about 10 g, corvid brains are rather small in absolute terms. Unfortunately, data about the number of neurons, synapses and connections in their brain or pallium are lacking. As birds generally have much smaller cells than mammals [64], this, combined with higher packing density, could result in a much higher number of pallial/cortical neurons in corvids compared with mammals with the same brain or cortex size.

It remains open whether humans have truly unique cognitive properties. Experts recognize aspects of imitation, theory of mind, grammatical–syntactical language and consciousness in non-human primates and other large-brained mammals. This would mean that the outstanding intelligence of humans results not so much from qualitative differences, but from a combination and improvement of these abilities. This might be specifically true for the human prefrontal cortex, where a combination of an ability for temporal analysis with motor behavior, action planning, thinking and language is evident [18]. In this way, a number of quantitative changes could lead to events that look like 'jumps' in the evolution of brains and intelligence.

Regrettably, truly comparative data about animal intelligence are rare. Hence, we are still far from a full understanding of the neurobiological basis of the differences in intelligence across vertebrates. Future research should investigate the neural basis of high intelligence of some birds, for example, corvids, most desirably the collection of exact data on neuron density. Another unsolved problem is the large difference in EQ between Old World and New World monkeys: is there a parallel difference in intelligence? Finally, it would be useful to develop tests by which the intelligence of members of distantly related taxa, such as corvid birds and primates, can be tested under the same conditions.

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