Chapter 6
Evolution of Cognitive Brains: Mammals

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Abstract In mammals, detailed information about higher cognitive abilities or "intelligence" is restricted to representatives of rodents, artiodactyls, carnivores, cetaceans, elephants, and primates. Tool use as well as "technical" problem-solving is present in most species of these taxa. In string-pulling experiments, apes, monkeys, dogs, and elephants were successful but with no sign of insight into mechanisms. Mirror use is demonstrated in apes, monkeys, and pigs, while mirror self-recognition is found only in the great apes, magpies, and possibly dolphins and elephants. Gaze following is documented in primates, dogs, and wolves. Metacognition was demonstrated in apes, macaques, dolphins, and rats. Finally, signs of a theory of mind are found in chimpanzees and rhesus monkeys and questionable in dogs and wolves. Neither absolute nor relative brain size (uncorrected or corrected for body size) are good predictors for higher cognitive abilities. The number of cortical neurons appears to be a better predictor of intelligence but does not solve the paradox of elephants and cetaceans, which have at least several billion cortical neurons like the great apes, while being less intelligent. The best fit is obtained, when parameters that directly determine neuronal information processing capacity, i.e., cortical interneuronal distance and axonal conduction velocity, are also taken into account. Here, primates excel, followed by carnivores, while the large-brained elephants and cetaceans perform poorly.

Keywords Intelligence • Cognitive abilities • Absolute brain size • Relative brain size • Number of cortical neurons • Information processing capacity

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6.1 Introduction

Mammals have always been considered to be smart. However, while in primates the presence of higher cognitive abilities like tool fabrication, imitation, metacognition and, at least, in the great apes, mirror self-recognition and aspects of a theory of mind are undisputed (cf. Byrne 1995; Roth 2013), the presence of such abilities in "insectivores" (i.e., Afrosoricida, Eulipotyphla), ungulates (i.e., Perissodactyla, Artiodactyla), elephants, and cetaceans (whales, dolphins) is either undocumented or disputed. There is an ongoing debate about higher cognitive abilities in elephants and cetaceans. While some authors attribute astonishingly high mental abilities to these large-brained animals, particularly to the cetaceans (cf. Marino 2004, Marino et al. 2007, 2008; Herman 2012), others come to the conclusion that elephant and cetacean intelligence is modest compared to primates and even carnivores (cf. Byrne et al. 2009; Manger 2013; Guentuerkuen 2014).

There have been and still are many attempts to correlate degrees of intelligence found in mammalian species to properties of their brains, the most popular being absolute brain size, relative brain size (uncorrected or corrected for body size) as well as absolute or relative size of the cerebral cortex (cf. Jerison 1973; Lefebvre 2012). However, none of these approaches have yielded convincing results. More recently, it has been argued that the number of cortical neurons is a more reliable predictor of intelligence (cf. Roth and Dicke 2005; Herculano-Houzel 2012; Roth 2013), but it turns out that even this factor does not fully explain why some monkeys with about one billion cortical neurons in many respects appear to be as intelligent as great apes with five to eight times more cortical neurons and why elephants and cetaceans with numbers of cortical neurons equal to or even higher than those found in great apes exhibit only modest degrees of intelligence—at least in the eyes of many experts (cf. Manger 2013).

In earlier publications, we have argued that in addition to the number of cortical neurons, other parameters relevant for information processing capacities like the speed of interneuronal signal transfer as well as cortical network properties must be taken into consideration (Roth and Dicke 2005, 2012; Roth 2013). In the following article, we will review recent literature on mammalian intelligence and their relationship to brain properties in the light of this hypothesis.

6.2 Phylogeny and Taxonomy of Mammals

Ancestors of mammals appeared about 224 mya in the Triassic. Early mammals conducted an inconspicuous life until the end of the Mesozoic. Around 170 mya, the modern type of mammals, the multituberculates, evolved which had small bodies and conducted a nocturnal and/or arboreal life. The split between the Prototheria (monotremes) and the Theria (marsupials and placental mammals) is believed to have occurred 150 mya, and the split among the Theria between

Metatheria and Eutheria 125 mya or earlier. The great time of mammals began near the end of the Cretaceous, around 70 mya, and particularly with the extinction of the dinosaurs 65 mya.

The first infraclass of mammals comprises the Prototheria with only one order, the monotremes (Monotremata) with the platypus (*Ornithorhynchus*) and echidna (Echidna*,* 12 species). The second infraclass, the Theria, includes the Metatheria or Marsupialia, comprising seven extant superorders with a total of 334 species. The larger metatherian group, Australidelphia (five superorders with 234 species, among them the cangaroos), live in Australia and New Guinea, whereas a smaller group, the Ameridelphia (about 100 species, among them the opossum *Didelphis*) live in North, Central, and South America. The Eutheria or Placentalia originated about 100 mya and for a long time conducted a modest life as insect eaters parallel to the marsupials.

Placental mammals are commonly divided into four superorders. The first group, Afrotheria, includes among others the orders Afrosoricida (tenrecs and golden moles), Macroscelidea (elephant shrews), Tubulidentata (aardvarks), Hyracoidea (hyraxes and allies), Proboscidea (elephants, Elephantidae, as single family with three species), and Sirenia (dugongs and manatees). The second group Xenarthra comprises the group Cingulata (armadillos) and Pilosa (sloths and anteater). The third group, Euarchontoglires, includes the orders Scandentia (treeshrews), Dermoptera (colugos), Primates (lemurs, bushbabies, lorises, monkeys, and apes including humans; more than 400 species), Rodentia (rodents; about 2300 species), and Lagomorpha (pikas, rabbits, hares; about 80 species). Finally, the fourth group, Laurasiatheria comprises the orders Eulipotyphla (hedgehogs, moles, shrews; about 388 species), Chiroptera (bats; about 1100 species), Pholidota (pangolins or scaly anteaters), Carnivora, (dogs, cats, bears, seals etc.; about 270 species), Perissodactyla (odd-toed ungulates like horses, zebras, rhinos and tapirs; about 19 species), Artiodactyla (even-toed ungulates like cattle, pigs, sheep, deer, camels, antelopes; about 260 species), and Cetacea (whales, dolphins, porpoises; about 80 species) (largely after Tarver et al. 2016).

6.3 What Is Animal Intelligence?

In humans, intelligence is commonly defined as the sum of “higher” mental capacities such as abstract thinking, understanding, communication, reasoning, learning and memory formation, action planning, and problem-solving. Usually, human intelligence is measured by intelligence tests and expressed in intelligence quotient (IQ) values related to different contents (e.g., visual–spatial, verbal, numerical). Evidently, such a definition and measurement of intelligence cannot be applied directly to nonhuman animals, because any test depending on verbalization is inapplicable. According to the majority of behaviorists and animal psychologists (cf. Roth 2013), “intelligence” can be understood as mental or behavioral flexibility or the ability of an organism to solve problems occurring in its natural and social environment culminating in the appearance of novel solutions not part of the animal's normal repertoire. A number of authors distinguish between *ecological intelligence* consisting in the ability to master challenges of an environment; *social intelligence* targeting social group size, complexity of social relationships, and means of social communication (gaze following, theory of mind, knowledge attribution etc.); and *general intelligence* consisting in efficient information processing and mental functions like abstract thinking, insight, metacognition, mirror self-recognition, etc. Byrne and Bates (2011) have added *physical intelligence* which includes, among others, tool use and tool fabrication and "technical" problem-solving, e.g., carnivores opening a puzzle box, orangutans using water to fill a tube containing a peanut, and crow using stones to weight a container to get access to food, while others consider these cognitive abilities as part of ecological intelligence. Among authors, there is a great overlap in attributing cognitive functions to these categories of animal intelligence.

6.4 Cognitive Abilities and Intelligence in Mammals

In the following, we will concentrate on frequently used paradigms for measuring intelligence in mammals (as rated in birds), i.e., tool use and tool fabrication, technical problem-solving including understanding of principles, mirror use, gaze following, imitation and observational learning, mirror self-recognition, metacognition, "theory of mind," and mental time travels. Data on primates and birds will be presented only briefly for comparative reasons, because they are presented in more detail in other articles of this volume.

6.4.1 Tool Use and Tool Fabrication

Tool use has been extensively studied in primates and birds, and some of them, e.g., chimpanzees or corvid birds, have been shown to regularly fabricate tools in the wild or in captivity (for an overview see Emery and Clayton 2009; Roth and Dicke 2012; Roth 2013). The first studied case of tool use in non-primate mammals was made in the Californian sea otter (*Enhydra lutris*). Otters were observed to open mussels and sometimes crabs and urchins by pounding them against a stone lying on their breast, and the same stone was used (Hall and Schaller 1964).

In a similar way, wild banded mongooses (*Mungos mungo*) regularly use anvils like rocks or the stems of trees, but also the sidewalls of gullies, to open hard-shelled food objects such as bird eggs or snail shells. It was demonstrated in this context that imitation as well as practicing plays an important role (Müller 2010). Dingoes (*Canis lupus dingo*) have been observed to use a table for getting food (Smith et al. 2012). North American badgers (*Taxidea taxus*), while hunting ground squirrels, often plug openings of ground-squirrel tunnels. They usually take soil from the area around the tunnel opening, but sometimes objects moved from greater distances are used for plugging (Michener 2004). Degus (*Octodon degus*, a rodent) can be trained to retrieve otherwise out-of-reach rewards by using a rake-like tool holding it with their forelimbs (Okanoya et al. 2008). According to the authors, the degus managed to distinguish between useful and nonuseful tools after extensive training.

Elephants use sticks for scratching their body and removing ticks and bushes for fly-switching, which they modify until they are long and effective enough, which is considered by some authors as an evidence for tool fabrication. However, a number of experiments (Hobhouse 1915; Rensch and Altevogt 1955; Hart et al. 2008; Nissani 2004) with captive elephants revealed that the animals did not learn to retrieve food by using a stick. Other experiments, in which elephants had been trained to remove a lid from a bucket in order to retrieve a food reward, revealed great difficulties of the animals with adopting their behavior to slightly different experimental conditions (Nissani 2006). In a similar experiment by Irie-Sugomoto and colleagues (2008), one elephant learned to pull a baited tray in order to retrieve the food. Minuzo et al. (2015) demonstrated that elephants acquire inaccessible food by blowing the food, until it comes in accessible places. In summary, elephants mostly reveal only simple forms of tool use with no or little understanding of the underlying mechanism (Byrne et al. 2009).

Among cetaceans, dolphins may kill scorpion fish in order to use their stingy body to poke after a moray eel hidden in a crevice (Brown and Norris 1956). Dolphins, beluga whales, and humpback whales blow bubble rings, and dolphins seem to do this for amusement or for catching fish (McCowan et al. 2000). One matrilinear group of bottlenose dolphins was observed to use marine sponges while foraging ("sponging") (Krützen et al. 2005; Patterson and Mann 2011). However, the significance of "sponging" for foraging remains unclear (Manger 2013).

6.4.2 *Puzzle Box Problem-Solving*

Problem-solving abilities often have been tested by using puzzle boxes, in which animals had to open a baited box. Such a puzzle box has been used in a recent study by Benson-Amram et al. (2015) in 39 species from nine families of carnivores. The authors measured the time spent by the animal to open the puzzle box as well as changes in work time over successive trials. In addition, body mass, manual dexterity, and absolute and relative brain volume were determined. All subjects except mongooses succeeded in opening the box by manipulating it, and work time significantly decreased, as the number of trials increased. The authors take this as evidence that successful individuals improved their performance with experience on the basis of trial-and-error learning, while there was no sign of insight. The highest success rate was found in the families Ursidae (bears; 69.2% of trial), followed by Procyonidae (raccoons and allies; 53.8%), and Mustelidae (otter, badger, weasels etc., 47.1%), while the members of the family Herpestidae (mongooses) failed. The authors found no correlation between success rate on one hand and social complexity or manual dexterity on the other hand, while there was a significant correlation with relative brain size.

Similar experiments using “puzzle feeders” have been executed with lemurs in the wild (Kendal et al. 2010) as well as in the laboratory. The gray mouse lemur mastered to open boxes in different ways including the use of reversed images and aye-ayes demonstrated basic understanding of features of tools by solving a can-pulling task (Fichtel and Kappeler 2010). All monkey and ape species tested so far likewise succeeded in such tasks, but again evidence for insight into the opening mechanism was either absent or equivocal.

6.4.3 String-Pulling Experiments

Numerous experiments on intelligence in mammals and birds used the string-pulling setup. Recently, Riemer et al. (2014) conducted string-pulling experiments with Border Collies. Previous experiments had revealed that dogs have a tendency to choose the string that is nearest to them instead of the baited string (“proximity bias”). In these experiments, dogs performed above chance when the baited and unbaited strings’ ends were equidistant, irrespective of being straight or curved, but seemed to be unable to overcome their proximity bias in a parallel or diagonal string task, when proximity of the unconnected string’s end to the reward was misleading. The authors conclude that the dogs can learn to pay attention to connectivity of the strings, when proximity is not a confounding factor.

Nissani (2004) reported string-pulling as well as sucking-blowing experiments with Asian elephants. All tested elephants mastered the string-pulling experiment, but they acquired the behavior gradually by trial and error, and most of them seemed unable to transfer their skills to similar tasks. In another series of experiments, elephants learned to remove food from a narrow tube either by sucking or blowing. In a competitive situation (with one elephant on either side of the tube), they always sucked the food in order to get it first. However, they were unable to transfer their experience to a competitive situation, in which they had to remove the food from a wider tube by either pushing or pulling it with their trunk.

Recently, Mayer et al. (2014) conducted string-pulling experiments in different taxa of primates, i.e., capuchin monkeys, bonobos, chimpanzees, and children, with two versions of a broken-string problem. In the standard condition, subjects had to choose between an intact and a broken string as means to a reward. In the critical condition, the functional parts of the strings were covered up and replaced by perceptually similar but nonfunctional cues. Apes, monkeys, and young children at or above an age of 3.5 years succeeded in the standard, but only children at or above an age of 5.5 years mastered the test with covered strings. Interestingly, there was no difference between monkeys and apes. Again, there was evidence for the important role of experience, but not for insight in monkeys, apes, and children younger than 5.5 years.

Corvid birds as well as primates regularly master these tasks quite often. In the experiments with New Caledonian crows by Taylor and colleagues (cf. Taylor et al.

2009), difficulties arose for the otherwise “intelligent” crows, when visual control was restricted or absent. The authors conclude that spontaneous string pulling in New Caledonian crows may not be based on insight but on operant conditioning mediated by a perceptual-motor feedback cycle.

6.4.4 Use of Mirrors

A larger number of mammals are able to use mirrors in order to identify otherwise unobservable objects or body parts or look around a corner. Rhesus monkeys, which failed the standard version of the mirror self-recognition (MSR) test (see below), learn to use mirrors in order to study otherwise hidden parts of their bodies (genitals, head implants). Similarly, Old World mangabeys (*Cercocebus torquatus*) learn to grope for a peanut on the backside of a board, when their hand is guided by a mirror (McKiggan, quoted in Byrne 1995). Pigs learn to turn to an invisible food bowl within 5 h, when they could see it in a mirror (Broom et al. 2009).

6.4.5 Gaze Following

Gaze following has been demonstrated in lemurs, macaques, capuchin, spider monkeys, and marmosets but without signs of understanding visual perspective (Roth and Dicke 2012). Great apes are able to track gaze to hidden targets and look back to the human experimenter, when they do not find a target (Bräuer et al. 2005; Tomasello et al. 2007).

For decades, the only case of gaze following in non-primate animals was demonstrated in dogs. As shown by Miklósi et al. (2003), dogs can understand human pointing and inform humans about hidden objects, look at the faces of humans and follow their gaze, while this ability appeared to be absent in wolves. The authors reported that dogs “look back” to the human face when confronted with unsolvable problems but that wolves do not. Later, however, Range and Virányi (2011) demonstrated that hand-raised wolves develop both the ability of gaze following into distant space and to look behind barriers. The former developed earlier than the latter. This suggests that gaze following and “looking back” in dogs and wolves is strongly dependent on training by humans.

More recently, Téglás et al. (2012) demonstrated that following gaze or directional gestures by their owner requires preceding human communicative signals, e.g., direct gaze or addressing. Wallis et al. (2015) showed that dogs can follow human gaze into distant space. However, with increasing experience and age, dogs prefer fixating the human face instead of distant targets. The authors speculate that with increasing training, the human face becomes more attractive.

6.4.6 Imitation

Imitation has long been considered an inferior kind of learning and was typically called “aping” or “monkeying” in the sense of a meaningless copying of a certain behavior. Only in recent years did it become clear that imitation is a higher cognitive ability. However, to date, there is no universally accepted definition of imitation, and some kinds of behavior previously viewed as imitation are now interpreted differently. One of these imitation-like behaviors is response facilitation or emulation, found in a wide range of animals, which means that seeing an action “primes” the individual to do the same, and the individual, by trial and error, finds the same or a very similar solution to the problem (cf. Byrne 1995; Bates and Byrne 2010).

In primates, imitation and emulation play an important role in social learning. For example, young baboons (*Papio*) quickly learn which kinds of fruit are edible, after one group member has tasted a fruit. Vervet monkeys (*Chlorocebus*), again Old World monkeys, learn this task more slowly, although they live in the same environment as baboons. The greatest imitation abilities appear to be present in dolphins. Bottlenose dolphins spontaneously imitate other dolphins and humans and do this on demand (“elicited imitation”), and they seem to be superior in this respect to all other nonhuman mammals (Kuczaj II and Yeater 2006). This ability apparently plays an important role in social life as well as in coordinated behaviors (e.g., synchronous swimming).

Dogs are highly social animals, and one could expect that imitation of conspecifics or of their owner is well developed. However, there is little evidence for that. In contrast, a recent study by Range and Virányi (2014) demonstrated that wolves are much better than dogs at imitating problem-solving behavior of a conspecific, i.e., the opening of a baited puzzle box. While the wolves readily opened the box after a demonstration by a conspecific, the dogs failed to solve the problem. The authors try to explain these differences by pointing to the fact that the dependency of wolves on close cooperation with conspecifics, including breeding but also territory defense and hunting, created selection pressures on motivational and cognitive processes enhancing their propensity to pay close attention to conspecifics’ actions. In contrast, during domestication, dogs’ dependency on conspecifics has been relaxed, leading to reduced motivational and cognitive abilities to interact with conspecifics.

Learning by observation was demonstrated in mice in an experiment by Carlier and Jamon (2006). Here, female mice performed reliably and immediately a sequence of actions, i.e., pushing a piece of food into a tube attached to the side of a puzzle box and recovering it by opening a drawer in front of the box after having observed a conspecific “demonstrator.” None of the naive mice was able to solve the task. Similar effects of observational learning or “insight” was demonstrated in rats by Blaisdell et al. (2006). According to the authors, the rats were able to make causal inferences by passively observing task-solving conspecifics, which could not be explained by Pavlovian learning.

6.4.7 *Mirror Self-Recognition*

The ability of mirror self-recognition (MSR) is often taken as evidence for "higher" mental states eventually leading to self-consciousness. However, the presence of this ability in nonhuman animals is hotly debated. While the MSR test yields clear results in children at and after an age of 18 months, all tests in nonhuman animals have turned out to be complicated. MSR was first demonstrated by Gallup (1970) in chimpanzees and later by various authors including Gallup in orangutans and bonobos and finally and with great difficulty in one gorilla. Regularly, the tests were successful only in less than half of animals tested and not always in those that passed the test.

Reiss and Marino (2001) succeeded in demonstrating that captive-born bottleneck dolphins (*Tursiops truncatus*) are capable of mirror self-recognition. Hints of MSR were observed in the killer whale, the false killer whale, and the California sea lion (Delfour and Marten 2001). After a number of failures, Plotnik and colleagues demonstrated mirror self-recognition at least in one out of three Asian elephants, *Elephas maximus* (Plotnik et al. 2006). But here again the successful elephant lost interest quickly. Given the very poor visual acuity, the results of these experiments have been questioned (cf. Manger 2013; Guentuerkuen 2014). Interestingly, some years ago the common magpie (*Pica pica*), a corvid, was found to pass the MSR test (Prior et al. 2008).

6.4.8 *Metacognition*

Metacognition is the ability to know what a subject knows and what it does not know. The principle of such experiments is that suitable animal are confronted with tasks, in which they have to discriminate between two tones of different pitch or length or two pictures showing grains of different size. The differences between the two tones or pictures are reduced stepwise such that they become increasingly difficult to distinguish. Correct answers are rewarded; for incorrect answers, there is a "time out." However, in addition to the decision between the two stimuli, there is the possibility to carry out an *uncertainty response (UR*), if animals have great difficulty with choosing the correct answer, and this allows them to immediately perform the next trial (Smith 2009). Foote and Crystal (2007) demonstrated that rats passed an acoustic duration discrimination test, in which animals had to distinguish between short (2–3.6 s) and long (4.42–8 s) noises. The rats increasingly declined the test, when the difference in duration became intermediate, i.e., 3.6–4.42 s, and thus very difficult to distinguish. In experiments with macaques, chimpanzees, and dolphins, URs occurred exactly in moments, when human participants likewise had problems with distinguishing the pattern, and started disappearing, when it became increasingly easy for the human observer to distinguish the patterns. Usually, the URs were preceded by hesitation. Remarkably, capuchin monkeys believed to be highly intelligent, failed in these experiments.

6.4.9 Theory of Mind

Under the topic "theory of mind (ToM)" experts study to which degrees animals are able to understand the intentions and knowledge of others and accordingly are capable of predicting their behavior. Premack and Woodruff (1978) were the first to ask this question with respect to chimpanzees, and despite numerous studies on a variety of species, this topic is still debated. To date, some experts believe that at least some animals understand some mental states, while others find the evidence unconvincing (for an overview see van der Vaart and Hemelrijk 2014; Roth 2013). It appears reasonable to assume that both chimpanzees and rhesus monkeys understand the goals and perceptions of others as well as what others know but not what others falsely believe (Lyons and Santos 2006; Premack 2007; Byrne and Bates 2011; Seed and Tomasello 2010). The same appears to hold for jays and ravens (Emery and Clayton 2009; Byrne and Bates 2011).

There has been an extensive discussion about the presence of ToM in dogs and wolves (for an overview see Horowitz 2011). To date, there is no unequivocal evidence that hand-raised wolves and domestic dogs possess a ToM, although they pass on some trials of a putative theory-of-mind test and fail on others. While some authors argue in favor of a more relaxed or "rudimentary" definition of ToM (cf. Horowitz 2011), others like Udell et al. (2011) argue that the term "theory of mind" has outgrown its usefulness in comparative cognition studies.

6.4.10 Mental Time Travel

Mental time travel (MTT) is the subject's ability to travel backward and forward mentally from the present moment to remember certain past events and to anticipate future activities. The ability to remember *what* happened *when* and *where* (WWW memory) is widespread among birds and mammals (cf. Roberts 2012), for example, in the context of food caching or past experience of places, where food was obtained. There is also evidence in birds as well as mammals (rats, primates) for prospective MTT, because they readily learn to use both time of day and elapsed time intervals as cues for important events such as food delivery. Rats, for example, learned to suppress the immediate intake of saccharine in favor of a later intake of more palatable and nutritive sucrose up to 30 min. Similarly, chimpanzees and orangutans could wait for 3–8 min for a delayed larger reward, and monkeys did so for 15 min (McKenzie et al. 2004). Thus, at least some birds and mammals are able to learn to anticipate the consequences of different choices, e.g., among kinds of food or among useful and nonuseful tools, and some of them (e.g., squirrel monkeys) are even able to anticipate their own future drive states (thirst or hunger) (cf. Roberts 2012).

6.5 Conclusions Regarding Ranks of Intelligence Among Mammals

Insight into higher cognitive abilities in mammals is compromised by the fact that the majority of mammalian taxa have not or only rarely been studied in this respect, e.g., Prototheria, Metatheria, Afrosoricida, Tubulidentata, Xenarthra, Pholidota, Eulipotyphla, Chiroptera, and Perissodactyla. This restricts our knowledge to representatives of rodents, artiodactyls, carnivores, cetaceans, elephants, and above all primates.

Tool use and tool fabrication are extensively present in primates and to a more limited degree in degus, otters, mongooses, badgers, dogs, dolphins, and elephants. Problem-solving by means of a puzzle box is found in all primates tested including lemurs and, among carnivores, in bears, raccoons, otter, badgers and weasel and presumably in dogs and wolves. In string-pulling experiments, apes, monkeys, dogs, and elephants were successful but with no sign of insight into mechanisms. Mirror use was found in apes, monkeys, and pigs but might be more widespread. Gaze following was demonstrated in all primates tested as well as in dogs and wolves. Extensive imitation and learning by observation was found in apes and monkeys as well as in dolphins and to a limited degree in elephants, wolves, dogs, mice, and rats. Mirror self-recognition was found in chimpanzees, orangutans, bonobos, gorillas, magpies, and possibly dolphins and elephants. Metacognition was demonstrated in apes, macaques, dolphins, and rats. Finally, stronger or weaker signs of a theory of mind were found in chimpanzees and rhesus monkeys and questionably in dogs and wolves. Mental time travels appear to be widespread across mammals and were demonstrated in rats, monkeys, and apes.

6.6 The Correlation of Brain Properties and Intelligence in Mammals

Many attempts have been made to correlate intelligence with brain properties, the most influential work being Harry Jerison's book *Evolution of the Brain and Intelligence* (1973). A much discussed brain trait is absolute size, followed by relative brain size, i.e., percent of body size or the relative size of alleged "seats" of intelligence like the cerebral cortex in mammals. Given the fact that much of brain size is determined by body size and therefore represents "confounding factor" (Jerison 1973), a number of authors have tried to determine the degree of "encephalization," i.e., brain size corrected for body size. The best known of such attempts is Jerison's "encephalization quotient (EQ)" (for a critical overview, see Lefebvre 2012). Other authors argued in favor of more "functional" brain properties like the number of neurons in the entire brain or in the pallium or cortex, their packing density, pattern of connectivity, and other parameters relevant for information processing capacity (IPC) (Roth and Dicke 2012; Roth 2013).

In mammals, there is an enormous variation in body size (volume or weight). The smallest mammal is the Etruscan shrew (*Suncus etruscus*) with a body weight of 1.8 g, and the largest mammal and animal is the blue whale (*Balaenoptera musculus*) with a length of 30 m and a body weight up to 180 tons. The largest living terrestrial animal is the African elephant (*Loxodonta africana*) with a body weight up to 7.5 tons. Thus, among mammals there is a range in body size or weight of eight orders of magnitude. The volumes or weights of brains likewise vary enormously. Among mammals, the smallest brain is found in the bat (*Tylonycteris pachypus*) which weighs 74 mg, and the largest brains of all animals are found in the sperm whale (*Physeter macrocephalus*) and "killer whale" (*Orcinus orca*), with up to 9 kg. African elephant brains weigh up to 6 kg. This is again an enormous range, here roughly five orders of magnitude (cf. Table 6.1).

As to the major mammalian taxa, "insectivores" (i.e., the unrelated Afrosoricida and Eulipotyphla) range from about 10 to 600 g in body size and 0.1 to 6 g in brain size. In the order Carnivora, body size varies between 1.5 and 365 kg and brain size between 17 and 460 g; in the order Artiodactyla body size varies between 1.5 kg and 4.5 tons, with brains up to 762 g; Perissodactyla taxa vary in body size between 150 kg and 3.5 tons and have brains up to 540 g. Among cetaceans, body sizes vary between 40 kg and 180 tons and brain sizes between 470 g and 8.2 kg. Primates, with the exception of prosimians and tarsiers, generally exhibit larger brains compared to body size than the other orders. New World monkeys have brains of 7–118 g and Old World monkeys of 36–222 g, with the largest brains found in baboons. Among apes, gibbons have brain sizes of 88–105 g, which lie within the range of Old World monkeys, while the large apes, i.e., orangutans (*Pongo pygmaeus*), gorillas (*Gorilla gorilla*), and chimpanzees (*Pan troglodytes*), have brain weights between 330 and 570 g (males) (cf. Table 6.1).

6.6.1 Absolute Brain Size

Comparing the data on cognition in mammals as presented above, with absolute brain size, we yield no clear-cut correlation. On the one hand, "insectivores" with very small brains on average reveal no signs of higher cognitive abilities, while the order Carnivora, large-brained species like bears and sea lions appear to be more intelligent than small-brained species, which would fit. Within primates, there appears to be a loose correlation between brain weight and intelligence given that small-brained prosimians appear to be less intelligent than Old and New World monkeys with brain weights of 50–220 g, and the great apes with brain weights of 330–570 g are on average believed to be more intelligent than the monkeys, let alone humans with a brain weight of about 1.350 g. However, some monkeys like the capuchin appear to be almost equal in at least some aspects of intelligence with gorillas or chimpanzees, despite a much smaller brain (about 80 g), and the capuchin is believed to be more intelligent than carnivores or ungulates with brains around 500 g. Furthermore, in carnivores and "ungulates" (artiodactyls and perissodactyls), the range of brain size

Table 6.1 Brain weight, encephalization quotient, and number of cortical neurons in selected mammalian taxa

Taxa	Brain weight(in g)[a]	Encephalization quotient[b,c]	Number of cortical neurons (in millions)
Sperm whale	8183	0.45	
African elephant	4200–7500	1.3–2.4	11,000[d]; 5600[e]
Killer whale	4779–5059	2.57–5.55	
False killer whale	3650	4.03[f]	10,500[d]
Blue whale	3636	0.21	
Man	1250–1450	7.4–7.8	15,000[d]
Bottlenose dolphin	1350–1,88	3.61–5.3	5800[d]
Walrus	1130	1.2	
Camel	520–762	0.6–1.2	1700[g]
Ox	490	0.5–0.8	
Horse	510–600	0.9	1200[h]
Gorilla	570	1.5–1.8	4300[d]; 9000[i]
Chimpanzee	430	2.2–2.5	6200[d]
Tiger	279	0.78	
Lion	260	0.6	
Sheep	140	0.8	
Rhesus monkey	88	2.1	840[d;] 1710[j]
Long-tailed monkey	36		840[d]
Gibbon	88–105	1.9–2.7	
White-fronted capuchin	57	4.8	720[d]; 1140[j]
Dog	64–135	0.7–1.6	160[d]
Fox	43–53	0.9–1.6	
Cat	25–37	1.0	300[d]
Squirrel monkey	23	2.3	450[d]; 1340[j]
Rabbit	11	0.4	
Marmoset	7	1.7	
Opossum	7.6	0.2	27[d]
Squirrel	7	1.1	
Hedgehog	3.3	0.3	24[d]
Rat	2	0.4	21[d]; 31[k]
Mouse	0.3	0.5	5[d]; 13,6[k]

[a] Data from Haug (1987), Jerison (1973), and Russel (1979)

[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 Jerison (1973) and Russel (1979)

[d] Roth and Dicke (2012)

[e] Herculano-Houzel et al. (2014)

[f] Manger (2013)

[g] Kazu et al. (2014)

[h] Cozzi et al. (2014)

[i] Herculano-Houzel (2012)

[j] Herculano-Houzel et al. (2007)

[k] Herculano-Houzel et al. (2006)

is nearly identical, while the former are believed to be considerably more intelligent than the latter. Finally, elephants and cetaceans, with brains 5–30 times larger than those of monkeys certainly are less intelligent. Thus, the maxim "bigger is better" appears to hold for comparisons *within* orders like carnivores or artiodactyls at best, but not for comparisons *across* orders of mammals. Furthermore, among cetaceans, dolphins, in general, appear to be more intelligent than the large-brained whales, while many of them have much smaller brains.

6.6.2 Relative Brain Size and EQ

Given these inconsistencies, experts have studied the impact of *relative* brain size, either uncorrected or corrected for body size. As in all vertebrates, brain size generally increases with body size, but in most cases the relationship between brain size and body size (BBR) is negatively allometrical, i.e., at a phylogenetic increase in body size, the increase in brain size "lags behind" and, thus, becomes relatively smaller (for details cf. Jerison 1973). As a consequence of negative brain allometry, with increasing body weight, relative brain weight decreases from more than 10% in very small mammals like shrews to less than 0.005% in the blue whale (van Dongen 1998). The human brain again ranks relatively high with roughly 2% of body weight, but in close proximity to apes and dolphins.

Comparing relative rather than absolute brain size with the ranks of intelligence in mammals, as presented above, yields even worse results, because the relatively largest brains are found in the "insectivores" with up to 12%, while humans have "only" 2% and many cetaceans and the elephants less than 1%. Thus, there is more of an anticorrelation than a correlation due to the fact that small animals tend to have relatively larger brains. For those reasons, Jerison (1973) tried to correct relative brain sizes for body size by his encephalization quotient EQ. This quotient indicates the extent to which relative brain size of a given species deviates statistically from the expected or average relative brain size of the larger taxon (e.g., order) under consideration.

As shown in Table 6.1, the lowest EQs are found in very large cetaceans like the blue whale (0.21). The sperm whale, hares, mice, and rats have an EQ well below average, followed by mice, sheep, and horse. The cat has an average relative brain, while dogs, camels, and elephants have EQs slightly above average. Among primates, Old World monkeys have slightly higher EQs on average (1.7–2.7) than New World monkeys (1.7–2.3), with the exception of the white-fronted capuchin. Gorillas and chimpanzees have astonishingly low EQs, while the highest EQs are found in dolphins and finally humans. While the high EQ of humans is of no surprise, the relatively high EQ (up to 5.3) of dolphins is unexpected compared to the relatively low EQs of chimpanzees and gorilla given the undeniably higher intelligence of the great apes. Thus, Jerison's EQ does not remove major inconsistencies in BBR.

6.6.3 Size of Cortex

An alternative is to look for a correlation between intelligence and absolute or relative cortex size given the reasonable assumption that the mammalian cortex is the site of their intelligence. However, this does not yield better results. With increasing body and brain size, mammalian cortices increase in surface area as well as in volume. The smallest mammals, for example, shrews, have a cortical surface (both hemispheres together) of 0.8 cm^2 or less, and in the rat we find 6 cm^2, in the cat 83 cm^2, in humans about 2400 cm^2, in the elephant 6300 cm^2, and in large-brained cetaceans a maximum of 7400 cm^2. Thus, from shrews to large whales we find a nearly 10,000-fold increase in cortical surface area.

However, the increase in cortical surface area contrasts with a modest increase in cortical thickness, i.e., from 0.4 mm in very small shrews and mice to 2–4 mm in humans and the great apes. Most large-brained cetaceans have surprisingly thin cortices between 1.2 and 1.8 mm (cf. Kern et al. 2011), and even the elephant, again with a very large brain, has an average cortical thickness of 1.9 mm (Haug 1987). In most mammals, the cortex grows somewhat faster than the rest of the brain, whereas in whales as well as in the elephant cortical volume, while increasing in absolute volume, decreases in relative volume. Yet, both elephants and cetaceans possess the largest cortices among mammals, which again is not a good predictor of intelligence.

6.6.4 Number of Cortical Neurons

Some authors argue that, instead of absolute or relative brain or cortical size, a much better predictor of mammalian intelligence is the number of cortical neurons as well as the effectiveness of their wiring and processing speed (cf. Roth and Dicke 2005; Herculano-Houzel 2012; Roth 2013). Brains and cortices of the same volume may contain very different numbers of neurons depending on their neuron packing density (NPD). Cortical NPD of mammalian species is highest in small eulipotyphlans and small rodents but is nearly equally high in small primates, which however are much larger in brain size than the former. In primates cortical NPD ranges from 75,000 neurons/mm^3 in the mouse lemur (*Microcebus* sp.) and the marmoset (*Callithrix jacchus*) to 25–30,000 neurons/mm^3 in gorillas and humans. By contrast, with 6000–7000 neurons mm^3, the cortices of whales and elephants have the lowest NPD among mammals (Haug 1987). Herculano-Houzel et al. (2015) report NPD values that are about half of those reported by Haug, but their measurements included both gray and white matter, while Haug's data are based only on gray matter. Despite this technical difference, the NPD ranking order reported by Herculano-Houzel et al. (2015) is the same as in Haug (1987). Thus, primates including humans stand out by having much higher cortical NPD than non-primate mammals of the same brain and cortex size. In addition, while in nonmammalian taxa cortical NPD strongly decreased with increasing brain and cortex volume with an exponent of −0.5, it decreases only slightly in primates with an exponent of −0.17 (Herculano-Houzel et al. 2015).

The number of cortical neurons of a taxon can be determined either indirectly by calculating it on the basis of the cortex volume and the cortical NPD, as we have done on the basis of the data by Haug (1987), or directly by cytometric techniques like the "isotropic fractionator" method used by Herculano-Houzel and colleagues (cf. Herculano-Houzel 2012) or a "stereological" method used by Pakkenberg and colleagues (cf. Eriksen and Pakkenberg 2007). Due to the differences resulting from the different methods, in a considerable number of cases, the data obtained by the different authors strongly vary.

Mice, rats, and hedgehogs have cortical neurons between 12 and 45 million (Roth and Dicke 2012; Herculano-Houzel et al. 2015). Among "ungulates" studied, we find a range between about 300 million (pig) and 1670 million (giraffe) (Kazu et al. 2014). There are almost no cell counts for carnivores except for the dog (160 million), the cat (300 million), and the raccoon (453 million) (Roth and Dicke 2012). Very large carnivores like the polar bear or the sea lion with brain weights around 500 g are expected to have at least 1000 million cortical neurons. Due to higher NPD, carnivores have more cortical neurons than "ungulates" of the same brain size (Herculano-Houzel 2012; Kazu et al. 2014).

Owing to their small neurons and high NPD, primates have many more cortical neurons than other mammals of the same brain and cortex size. However, here we find large differences in the cell counts. According to Roth and Dicke (2012), based on the NPD data by Haug, the small New World squirrel monkey (*Saimiri sciureus*) has 450 million, the larger New World white-fronted capuchin 720 million. Herculano-Houzel et al. (2007), however, report 1340 million for the former and 1140 million for the latter. For the rhesus monkey (*Macaca mulatta*), Roth and Dicke (2012) calculated 840 million, and Herculano-Houzel et al. report (2007) 1710 million cortical neurons, while in the larger long-tailed macaque (*Macaca fascicularis*) they found "only" 800 million cortical neurons, which would be close to our data concerning the rhesus monkey.

Herculano-Houzel and colleagues (2012) and Roth and Dicke (2012) state that chimpanzees have about 6000 million, while there is a discrepancy concerning the gorilla (4300 million by Roth and Dicke 2012 and up to 9000 million by Herculano-Houzel 2012). As to the human cortex, Roth and Dicke (2012) arrived at 14,000 and Herculano-Houzel (2009) at 16,000 million neurons, while Pakkenberg and Gundersen (1997) counted 19,000 million neurons in women and 23,000 million in men. Herculano-Houzel (2009) as well as Roth and Dicke (2012) consider this value as being too high.

Cell counts in elephants and cetaceans likewise vary widely among authors, again mostly because of different methods applied. While Roth and Dicke (2005) calculated about 11,000 million cortical neurons in the African elephant, Herculano-Houzel et al. (2014) found "only" 5600 million. Both authors, however, agree that elephants have fewer cortical neurons than humans despite their much larger brain. There is likewise debate about the number of cortical neurons in cetaceans. Roth and Dicke had arrived at about 11,000 million in a 7-kg cetacean brain, and in the Minke whale (*Balaenoptera acutorostrata*), with a brain weight of about 6 kg, Eriksen and Pakkenberg (2007) counted 12,000 million cortical neurons. However, in a recent paper published by the Pakkenberg group (Mortensen et al. 2014), the authors reported 37,200 million cortical neurons in the long-finned pilot whale (dolphin) (*Globicephala melas*) at a brain weight of about 3500 g. This would be almost twice as much as the value found by Pakkenberg and Gundersen for the human cortex (23,000 million in men). However, Herculano-Houzel et al. (2014) question these values mostly for methodological reasons. In addition, they argue that cetaceans, as descendants of ungulates—characterized by relatively thin cortices with low NPD—should rather strictly follow their general brain-cortex pattern, and they predict that the number of cortical neurons even in large-brained cetaceans would be well below 10,000 million and, thus, rather conforms to the cell counts made in elephants.

Apart from these discrepancies, in mammals, the number of cortical neurons correlates better with intelligence than absolute or relative brain size or EQ. Carnivores appear to be more intelligent than "ungulates" and these are more intelligent than "insectivores," and this fits nicely the number of cortical neurons. The reason for this is that carnivore cortices have a higher NPD and consequently contain more neurons than ungulate cortices of the same size. Within primates, we again find a positive relationship between numbers of cortical neurons and levels of intelligence. The least intelligent primates, lemurs, have the lowest number of neurons, followed by monkeys and finally by the great apes and humans. Humans appear to have the largest number of cortical neurons (if we disregard the data by Mortensen et al. 2014), because of a large cortical volume combined with a high NPD. The high number of cortical neurons in monkeys (as a consequence of extremely high NPD) reported by the Herculano-Houzel group would further speak in favor of the high degree of intelligence found in the capuchin or squirrel monkeys coming close to that of the great apes.

The opposite is found in elephants and cetaceans, both of which have much fewer cortical neurons than expected based on their large brain and cortex sizes. Apparently, this is a consequence of very low NPD as well as of their relatively thin cortices. In the case of cetaceans, this may be—as Kazu et al. (2014) argue—a consequence of phylogeny: cetaceans are descendants of artiodactyls, which, as mentioned have a much lower NPD than primates, and their strong increase in body and brain size in cetaceans probably led to a further decrease in NPD. Thus, in both elephants and cetaceans, we find the puzzling fact that they have 3–7000 million cortical neurons equal to the great apes, while having modest to moderate degrees of intelligence.

In summary, while there is a relatively good correlation between intelligence and number of cortical neurons within mammalian orders, it breaks down, when we compare numbers of neurons in cortices of the same size in ungulates, carnivores, primates, elephants and cetaceans because of huge differences in NPD. At a given cortical volume, primates including humans have much more cortical neurons than the other mammalian taxa.

6.6.5 Information Processing Capacity

Information processing capacity (IPC) of a cortex is intimately related to signal transmission speed, i.e., how fast cortical neurons "transfer signals to each other." Signal transmission speed is determined by (1) interneuronal distance, (2) axonal conduction velocity, and (3) transsynaptic transmission time. While the latter appears to be rather constant among mammals, factors (1) and (2) vary greatly. Interneuronal distance, trivially, is inversely related to NPD: the higher the NPD, the shorter the interneuronal distance. Conduction velocity is a direct consequence of the thickness of the myelin sheath. The myelin sheath is thickest in primates and thinnest in elephants and cetaceans (Zhang and Sejnowski 2000; Changizi 2001). Thus, while an elephant or dolphin/whale may have the same number of cortical neurons like a chimpanzee (e.g., 4–5 billion), the former has a much lower signal transmission speed than the latter. Thus, a combination of very low NPD and low axonal conduction velocity appears to make information processing capacity of elephants and cetaceans very slow despite a high number of cortical neurons. This could, among others, explain why their cognitive abilities are modest but, also, why in cetaceans we find that the two cerebral hemispheres often work (and sleep) independently.

Conversely, small-sized monkeys like the capuchin monkey, due to their high NPD and high axonal conduction velocity, probably has a very high information processing capacity, which could be equal to that found in larger primates—let alone non-primate mammals—with a higher number of cortical neurons but lower NPD. This could explain why small monkeys with relatively small brains containing little more than one billion cortical neurons are equal, at least in some aspects of cognition, to a chimpanzee or a gorilla with 4–6 times more cortical neurons.

6.7 Conclusions

We found that in mammals neither absolute nor relative brain size nor the EQ are good predictors for higher cognitive abilities. Large-brained ungulates (762 g or more) and even larger-brained cetaceans (8200 g or more) and elephants (up to 6000 g) are of moderate or even very modest intelligence when compared to monkeys with much smaller brains. The latter appear to be almost as intelligent as the apes, while again having much smaller brains. Taking relative brain weight or the EQ into account does not yield better correlations. The number of cortical neurons appears to be a better predictor of intelligence, but here we have the paradox of elephants and cetaceans, which have at least several billion cortical neurons (as many as the great apes), but are very modest in intelligence. The best fit is reached, when we compare degrees of intelligence with a combination of the number of cortical neurons with parameters that directly determine information processing capacity of a brain/cortex, i.e., interneuronal distance (neuron density) and axonal conduction velocity. Here, primates and especially humans excel, while the large-brained elephants and cetaceans perform poorly. Taking IPC into account, we can also explain why small-brained primates can be (almost) as smart as the great apes except humans.

The human brain appears to constitute an optimal trade-off between factors determining neuronal information processing capacity, i.e., absolute and relative brain size, number of neurons, packing density, and axonal conduction velocity (Hofman 2012; Roth 2013). However, we believe that in addition the emergence of a syntactical and grammatical language about 100,000 years ago appears to have functioned as an enormous "intelligence amplifier" making thinking, problem-solving, and communication much easier (cf. Roth 2013). Among nonhuman animals there is a variety of complex and syntactical languages like bird song or dolphin language, but so far, there is no evidence that such a syntax reaches the semantic level (Fitch and Hauser 2004; Berwick et al. 2011). The invention of writing about 5000 years ago certainly has served as a second "intelligence amplifier."

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