Chapter 5 Intelligence: Evolutionary Biological Foundations and Perspectives

Thomas W. Holstein

Abstract Although the term intelligence is now used in a wide variety of felds to explain the emergence of complex causalities, intelligence is understood here primarily as the ability of neural systems to solve problems in cognitive decisionmaking processes. Cognition and intelligent behavior are therefore primary objects, but not subjects, of chance-driven biological evolution. Recent work in neurobiology and comparative genomics has now shown how, starting from simple neural systems, forms capable of solving comparably complex problems in cognitive processes have evolved in all major groups of the animal kingdom. Although this cognition is based on the same basic cellular elements (neurons), it is realized in central nervous structures (brains), some of which have developed quite differently in animal evolution. By comparing the nervous systems of animals capable of higher intelligent sensory performance, the frst common properties and principles are now becoming apparent, which are prerequisites for the emergence of higher intelligent systems (e.g., the density, but not number, of neuronal elements). Such common rules are probably also constraints in the development of artifcial intelligent systems.

1 Introduction

The biological foundations of intelligence and our consciousness are one of the most exciting topics at the interface of biology and psychology, and they are of fundamental importance for the self-understanding of humans and our cognitive ability. For a long time, this topic was treated from an anthropocentric point of view, accepting that humans are a product of biological evolution, but at the same time claiming a special position for humans. An essential prerequisite for intelligence or intelligent cognition and intelligent behavior is without doubt the ability of individuals to develop a form of self-refection and consciousness. For a long time, hominids, primates, and mammals in the broader sense had a unique selling point in

T. W. Holstein (\boxtimes)

Centre for Organismal Studies, University of Heidelberg, Heidelberg, Germany e-mail: holstein@uni-heidelberg.de; https://www.cos.uni-heidelberg.de/index.php/t. holstein?l=#

[©] The Author(s), under exclusive license to Springer Nature 105 Switzerland AG 2022

R. M. Holm-Hadulla et al. (eds.), *Intelligence - Theories and Applications*, [https://doi.org/10.1007/978-3-031-04198-3_5](https://doi.org/10.1007/978-3-031-04198-3_5#DOI)

that it was assumed that only these animals had developed the corresponding correlate for consciousness in the form of the cerebral cortex during evolution.

In a September 2020 editorial in the American journal *Science*, two papers were presented under the title "Shared consciousness" (Nieder et al., [2020;](#page-13-0) Stacho et al., [2020\)](#page-14-0), in which it was shown for the frst time at the level of neuroanatomy and neuropsychology that in birds, when performing a complex "thinking task," neuronal responses are activated in the brain that correlate with the perception of stimuli of problem solving. Such activity appears to be the neural correlate and a marker of both consciousness and long-established cognitive abilities in these birds (Herculano-Houzel, [2020;](#page-12-0) Kabadayi et al., [2016](#page-12-1); MacLean et al., [2014](#page-13-1); Olkowicz et al., [2016](#page-13-2)).

This work raises a number of new questions that are fundamental to our understanding of the biological evolution of intelligence. They also pose the question of the special position of humans on a new basis: What are ultimately the molecular and cellular foundations of human intelligence? Does intelligence exist in other animal groups and on what principles is it based? If consciousness and intelligence have arisen multiple times in the animal kingdom in a convergent evolution, what is the signifcance of this for the development of "artifcial intelligence"? This essay will attempt to provide an overview of recent work on the properties and evolution of neural systems that may provide answers to these questions.

2 Basics of Neuronal Cognition

The epitome of neural cognition is without doubt the human brain. Its immense complexity—it consists of a hundred billion neurons of an as yet unknown number of different types, each neuron capable of connecting to tens of thousands of other neurons—makes a holistic understanding of its functioning extremely diffcult. However, the human brain has evolved from simpler forms in the more than 500 million years of its evolution. Much of current knowledge of the individual elements of our nervous system is therefore based on comparison with simpler and more accessible systems in invertebrates and vertebrates. For example, the large neurons of the marine snail *Aplysia* allow a detailed study of neuronal architecture and physiology during various forms of associative learning (Kandel et al., [2021\)](#page-12-2). Additionally, the importance of ion channels in the formation of the action potential during excitation conduction was discovered in the giant axons of squid (Hodgkin & Huxley, [1952;](#page-12-3) Kandel et al., [2021](#page-12-2)). Although single neurons represent the functional units of nervous systems, they alone cannot explain the specifc properties of neuronal systems; these always rely on multicellular circuits of neurons with emergent functional properties (Bosch et al., [2017](#page-11-0)). Understanding the earliest evolutionary examples of nervous systems is thus essential for understanding their function (Fig. [5.1](#page-2-0)).

Fig. 5.1 A diffuse nervous network without brain and ganglia, like the nervous system of cnidarians, probably stood at the beginning of the evolution of nervous systems. The nerve network of the freshwater polyp *Hydra vulgaris*, shown by expression of a nerve-specifc membrane protein (red) and cell nuclei stained with a DNA dye (DAPI) (blue). In *Hydra*, however, a high density of sensory neurons is established around the mouth opening (hypostome) of the polyp, which are important for the act of capture and feeding. There is a wide spectrum of different neurotransmitters expressed in subpopulations of neurons. Such simple neural networks are capable of complex behavioral patterns, such as the act of capture with cnidocytes or the different forms of locomotion (see Fig. [5.2\)](#page-4-0), and are currently being studied in cellular and neurobiological terms. (Image © Bertulat & Holstein)

3 The First Nervous Systems

Nervous systems appeared very early in the evolution of animals and were certainly present before the emergence of bilaterally symmetrical animals—also known as Bilateria. Of the lineages that diverged prior to the radiation of Bilateria in the Cambrian ("Cambrian explosion"), nervous systems are present only in cnidarians (Cnidaria) and comb jellies (Ctenophora), but not in sponges (Chapman et al., [2010;](#page-11-1) Watanabe et al., [2009\)](#page-14-1). The nervous systems of Cnidaria and Bilateria share many similarities, while there are differences in Ctenophora due to the limited number of neurotransmitters; also, their phylogenetic position is still open (Bosch et al., [2017;](#page-11-0) Moroz et al., [2014](#page-13-3)).

Cnidaria, which include medusae (jellyfsh) and polyp-forming groups (hydras, anemones, corals), possess a nervous system that, unlike the nervous systems of the Bilateria, does not function as a centralized nervous system (CNS), but rather represents a diffuse neuronal network that operates without a brain or ganglia (Fig. [5.1\)](#page-2-0). By comparing this simple neuronal system with the more complex systems, fundamental design principles of a CNS can be explored, including its contribution to higher neural functions such as consciousness and intelligent behavior (Bosch et al., [2017](#page-11-0)).

It is fascinating to see the complex behavioral patterns that Cnidaria already possess. The sophistication of their behavior was frst recognized in the eighteenth century when Abraham Trembley described the locomotion of the freshwater polyp *Hydra* (Trembley, [1744\)](#page-14-2) (Fig. [5.2\)](#page-4-0).

However, medusae also possess a wide variety of behavioral patterns that are used not only for locomotion but also for prey capture and sexual reproduction. How all these behavioral patterns come about via a diffuse network of neurons is currently not understood at all (Bosch et al., [2017](#page-11-0); Rentzsch et al., [2019\)](#page-13-4). It is also entirely counterintuitive that in Cnidaria, the simple neural network exhibits sensory cells and organs comparable in complexity with the sensory outputs of vertebrates. For example, cnidarian cells are highly specialized neuronal cells that, with their nematocysts and ciliary mechano- and chemoreceptors, are among the most complex cell types in the animal kingdom (David et al., [2008](#page-11-2); Holstein & Tardent, [1984;](#page-12-4) Nüchter et al., [2006](#page-13-5)), and cube jellyfsh have evolved lens eyes, known only from the higher Bilateria, for orientation in space.

In recent years, in addition to the classic freshwater polyp *Hydra* and its related marine colonial forms (e.g., *Hydractinia echinata*), medusae (*Clytia hemispherica* and *Aurelia aurita*) and the sea anemone *Nematostella vectensis* have been studied in the laboratory and their genomes have been decoded (Chapman et al., [2010;](#page-11-1) Gold et al., [2019](#page-12-5); Leclere et al., [2019;](#page-12-6) Putnam et al., [2007\)](#page-13-6). As a result, several basal nervous systems are available for functional analyses, which can also be used to understand the origin of complex behaviors at the molecular level. The genomes and transcriptomes that have now been sequenced show that these behavioral patterns are based on an unexpectedly high genetic complexity of cnidarian neural networks. The diversity of synaptic proteins, small neurotransmitters, neuropeptides, as well as their processing machinery is as complex as that we know from "higher" animals, e.g., insects and vertebrates.

Thus, it can be concluded that the cellular and molecular repertoire of our nervous system evolved in the common ancestors of Cnidaria and Bilateria at a very early stage of evolution (>500 million years ago). Yet the primary function of the nervous system was probably "only" used for simple sensory and motor coordination. Nevertheless, given the complex behavioral patterns of these animals, it is currently debated to what extent these simple neural networks have properties beyond neural coordination, or whether higher neural functions require the centralization of the nervous system. The fact that the evolution of the CNS of Bilateria is closely linked to the existence of a second dorso-ventral body axis, which is still lacking in Cnidaria, suggests that certain circuits of the nervous system frst evolved in Bilateria. Here, evolution led to ganglia and central nervous structures, which allowed for a higher neuronal density and thus a higher number of synaptic contacts.

The formation of a CNS can be understood as an evolutionary trend that occurred at the beginning of Bilateria evolution. Comparative genomic studies show commonalities in the ontogeny of the nervous system, including its central nervous elements, in all related groups of Bilateria, including the brain (Hirth et al., [2003;](#page-12-7)

Fig. 5.2 The Geneva naturalist Abraham Trembley meticulously observed the freshwater polyp in its behavior and published his fndings in 1744 in the infuential book "*Mémoires pour servir à l'histoire d'un genre de polypes d'eau douce*." Plate 3 describes various patterns of movement of the hydras, which are about 1 cm long: One is a caterpillar-spinner-like locomotion (Figs. 1–4) in which the animal alternately contracts and stretches while the fxed aboral pole (b) follows the oral end with the tentacles and is thus lifted from one location to the next. The other movement involves summersaulting of the aboral end (foot) (Figs. 5–9). In addition, the animals may move vertically or in a vessel (Fig. 10) and attachment to the water surface (Fig. 11). Trembley was not only an "observational naturalist," but also a founder of experimental biology (discovery of regeneration in *Hydra*) with great impact on the philosophers of his time

Reichert, [2005](#page-13-7)). They fall into three major groups, the Deuterostomia, Lophotrochozoa, and Ecdysozoa. The Deuterostomia, which include vertebrates (vertebrates) as the largest group with humans, form the nervous system on the dorsal side (Notoneuralia), whereas Lophotrochozoa and Ecdysozoa form the

Fig. 5.3 Phylogenetic tree representing the evolutionary relationship between *cephalopods* (Cephalopoda) and corvids (Corvidae) and great apes (Hominidae). (Modifed from: *Biological Reviews 96 (2021) 162–178* © 2020 *The Authors. Biological Reviews published by John Wiley & Sons Ltd on behalf of Cambridge Philosophical Society. Image sources: © CCBY-SA: snail, echinoderm, chiton*; © CCBY-NC-ND*: octopus*; © jenesesimre, *stock.adobe.com*: *octopus, squid, arthropod, clam;* © artbalitskiy, *stock.adobe.com*: *monkey, corvid, fsh, amphibian, reptile*)

nervous system on the ventral side (Gastroneuralia). Recent fndings suggest that forms with a CNS have evolved independently (convergently) in the three major groups, which are capable of higher neuronal outputs and thus intelligent behavior according to behavioral criteria (Roth, [2015;](#page-14-3) Roth & Dicke, [2005,](#page-14-4) [2012\)](#page-14-5) (Fig. [5.3\)](#page-5-0).

4 Cognition in Invertebrates

Insects possess the most complex brains of the Ecdysozoa. They belong to the arthropods, whose nervous system is derived from simple progenitors with an oral nerve ring and ventral nerve cords containing ganglia. The tripartite brain has socalled "mushroom bodies" (*corpora pedunculata*) in its anterior part, which occupy half of the brain volume in honeybees and whose neuronal density is an order of magnitude greater than in vertebrates (Reichert, [2005](#page-13-7); Roth, [2015\)](#page-14-3) (Strausfeld & Hirth, [2013](#page-14-6)). The region has been identifed as a substrate for the evolution of cognitive and social functions and has an impressive repertoire and fexibility of behavioral patterns for foraging, spatial orientation, and social interaction (Roth, [2015\)](#page-14-3). Bees are also characterized by their great learning behavior and appear to be capable of building cognitive maps for spatial orientation that can be retrieved in a contextdependent manner (Roth, [2015\)](#page-14-3), although this is still under debate (Cruse & Wehner, [2011;](#page-11-3) Wehner & Menzel, [1969](#page-14-7)).

The most complex brains of the Lophotrochozoa—and of all animals outside of vertebrates—are found in the cephalopod molluscs, including octopuses (Octopoda),

squids (Theutidae), and cuttlefish (Sepiida) (Albertin et al., [2015;](#page-11-4) Wanninger & Wollesen, [2019\)](#page-14-8). As a member of the large group of molluscs (Mollusca), which also includes bivalves and gastropods, their nervous systems are derived from simple forms with an oral nerve ring and ganglia-containing ventral nerve cords, as found in annelids (polychaete). The nervous system of squid contains approximately 550 million neurons, of which approx. 90% are in the arms and optic nerves and 10% are in the brain proper. The brain is divided into a ventral motor section and a dorsal section, to which sensory information processing and higher cognitive functions are attributed (Albertin et al., [2015;](#page-11-4) Roth, [2015](#page-14-3); Shomrat et al., [2008\)](#page-14-9). The vertical lobe of an octopus brain is its most complex part and key structure for the circuits involved in learning and memory processes (Albertin et al., [2015](#page-11-4); Shomrat et al., [2008](#page-14-9); Young et al., [1971\)](#page-14-10). It contains more than half of the neurons in the brain, with approximately 26 million neurons (Roth, [2015](#page-14-3)). It consists of two types of neurons: interneurons that can form "*en passant*" synapses to primarily visual afferents and projection neurons that connect to the subvertical lobe. This creates a highly ordered network with millions of intersecting fibers.

In the recently published frst description of the genome of *Octopus bimaculoides*, it was shown that the molecular basis of this highly complex brain is based, among other things, on neuronal adhesion proteins that are responsible for the formation of synaptic contacts between neurons (Albertin et al., [2015\)](#page-11-4). In the *Octopus* genome, 168 genes encoding for cell adhesion proteins (protocadherins) are present. They result from tandem gene duplication and an expansion of this gene family that is primarily expressed in neural tissue. The function of protocadherins has been studied primarily in mammals, where they are required for neuronal development and survival as well as synaptic specifcity; however, they arise here by complex splicing rather than gene duplication. The expression of protocadherins in squid neural tissues suggests a central role for these genes in establishing and maintaining the organization of the cephalopod nervous system as known from mammals (Albertin et al., [2015](#page-11-4)).

The highly complex molecular and morphological structure of octopus brains enables us to understand why so many "intelligent" behaviors have been described in these animals. For example, an "*Octopus* is not only good at remembering where tasty food can be found, but after a journey far from home, it often returns home by the shortest route it had never taken before." (Roth, [2015\)](#page-14-3). As with bees, there is debate as to whether squids have a "mental map" (Roth, [2015\)](#page-14-3) and the extent to which they are capable of "learning by observation" (Fiorito & Chichery, [1995;](#page-11-5) Fiorito & Scotto, [1992](#page-11-6); Roth, [2015](#page-14-3)).

However, these reports of intelligent behavior in squid have now taken on a new quality, as it has been shown that squids are also capable of exercising self-control in a reward-delay task (Schnell et al., [2021a,](#page-14-11) [b;](#page-14-12) Schnell & Clayton, [2019](#page-14-13)). The ability to overcome immediate gratifcation in favor of a better but delayed reward is considered an important cognitive skill for effective decision making, goal-directed behavior, and future planning (Mischel & Underwood, [1974](#page-13-8); Santos & Rosati, [2015;](#page-14-14) Schnell et al., [2021a,](#page-14-11) [b](#page-14-12); Schnell & Clayton, [2019](#page-14-13)). In humans, the ability to exercise self-control has been linked to children's cognitive performance: children

who were able to delay a reward longer,¹ also performed better on intellectual tasks (Mischel, [2015](#page-13-9); Mischel et al., [1989](#page-13-10)). To test self-control in squid, Schnell and colleagues gave the animals a task that also measured an individual's ability to forgo immediate reward (Schnell et al., [2021a,](#page-14-11) [b](#page-14-12)). Squid maintained delay times for up to 50–130 s. To test learning performance, squid had to learn to associate the reward with one of two stimuli; they then had to learn to associate the reward with the alternative stimulus. Again, squid that were able to delay their reward longer than others had better learning performance (Schnell et al., [2021a,](#page-14-11) [b](#page-14-12)). The work showed that squid can tolerate delays in order to obtain food of higher quality or quantity, which is ultimately comparable to the situation in mammals (Schnell et al., [2021a,](#page-14-11) [b\)](#page-14-12).

5 Cognition in Vertebrates

Humans (*Homo* sp.) belong to a genus that is member of the family of great apes (Hominidae) and thus to mammals (Mammalia). The study of complex cognition has traditionally been limited to hominids and related groups within primates, as these have been considered the pinnacle of cognitive complexity, although there has been increasing evidence that there are other mammals, as well as birds (Aves), that possess brains capable of cognitive performance comparable to that of primates (MacLean et al., [2014;](#page-13-1) Olkowicz et al., [2016\)](#page-13-2). Examples include cetaceans (Fox et al., [2017;](#page-12-8) Marino, [2002](#page-13-11)), elephants (Plotnik et al., [2006,](#page-13-12) [2011\)](#page-13-13), or parrots (Pepperberg, [2006](#page-13-14); Pepperberg et al., [2013\)](#page-13-15) and corvids (Boeckle & Bugnyar, [2012;](#page-11-7) Emery $\&$ Clayton, [2004\)](#page-11-8). The fact that corvids possess cognitive abilities equivalent to those of monkeys (Clayton & Emery, [2005;](#page-11-9) Emery & Clayton, [2005;](#page-11-10) Güntürkün & Bugnyar, [2016;](#page-12-9) Kabadayi et al., [2016](#page-12-1)) has therefore raised the question of whether complex cognition has evolved repeatedly and independently in vertebrates (Roth, [2015\)](#page-14-3).

Mammalia and Aves diverged into two distinct groups of amniotes^{[2](#page-7-1)} approximately 300 million years ago, and their brains—like the nervous systems of all vertebrates—can be traced back to the simplest precursors of chordates 550 million years ago (Fig. [5.3](#page-5-0)). According to general doctrine, however, there are fundamental differences in brain anatomy and neuroarchitecture between apes and corvids (Jarvis et al., [2005](#page-12-10)). According to this view, the mantle layer (pallium) of the cerebrum in birds does not possess layering as in mammals (this powerful layering has earned the mammalian pallium the name "cerebral cortex"), and therefore birds would not possess a cerebral cortex (Güntürkün & Bugnyar, [2016;](#page-12-9)

¹Children were presented with one marshmallow and given a choice—eat it immediately or wait to get two later. The experiment also became known as the Marshmallow Test (Walter Mischel 2014, Settlers, ISBN 9783827500434).

²Amniotes are terrestrial vertebrates that can reproduce independently of water through embryonic shells, whereas amphibians depend on it for embryonic development and produce tadpoles as larval stages postembryonically.

Herculano-Houzel, [2020\)](#page-12-0). However, this assumption of an absent cerebral cortex has been challenged because, like our cerebral cortex, the pallium of birds also derives embryonically from the same section of the developing brain with all molecular markers, and it has a comparably high number and density of neurons (Güntürkün & Bugnyar, [2016](#page-12-9); Herculano-Houzel, [2020;](#page-12-0) Puelles et al., [2013\)](#page-13-16). In the new work, it is now shown that the avian pallium has a similar neuronal organization and layering as the mammalian cortex and has neurons (Stacho et al., [2020](#page-14-0)) that can neurophysiologically represent what is perceived (Nieder et al., [2020\)](#page-13-0), which is a hallmark of consciousness (Herculano-Houzel, [2020](#page-12-0)).

Therefore, an intriguing question is to what extent within vertebrate cognition and the capacity for consciousness already existed in the common ancestor of birds and mammals (Bshary & Brown, [2014;](#page-11-11) Herculano-Houzel, [2020;](#page-12-0) Nieder et al., [2020\)](#page-13-0). Although the evolution of squid and comparison with other animal groups suggests that there was convergent evolution of higher cognition and consciousness (Roth, [2015\)](#page-14-3), there do appear to be certain structural and embryological commonalities within vertebrates that resulted in the evolution of neuronal structures with particularly high neuronal density being built only in certain regions, which then enabled the emergence of higher intelligent systems. Therefore, in addition to birds, the biological foundations of cognition in primates/hominids, the group of mammals to which we humans belong, will be conclusively addressed.

6 Hominid Cognition

It has long been assumed that the high cognitive performance and intelligence that characterize hominids and humans are closely related to, or even explained by, the size and complexity of the brain and cerebral cortex (*cortex cerebri*) (Fig. [5.3\)](#page-5-0). Indeed, within hominids there has been an extremely rapid increase in brain size since the split of the great apes and genus *Homo* in the late Miocene 6–7 million years ago (Harrison, [2010](#page-12-11)), particularly in human evolution, while brain size has changed less among the different great ape groups within hominids.

The large increase in size of the human brain was accompanied by signifcant restructuring of the digestive system and feeding and social behaviors (Fonseca-Azevedo & Herculano-Houzel, [2012;](#page-12-12) Roth & Dicke, [2005,](#page-14-4) [2012\)](#page-14-5).

Repeated attempts have been made to correlate high cognitive performance in mammals in general with brain size. In 2005, Roth and Dicke determined the available data on brain size in various mammals and examined the correlation to brain cognitive performance (Roth & Dicke, [2005,](#page-14-4) [2012](#page-14-5)). This showed that while absolute brain size can vary by up to fve orders of magnitude within mammals (ranging in weight from 0.1 g for the smallest brains in insectivores and bats to 9000 g in large whales), the human brain is far from the largest (weighing slightly less than 1.35 kg). This is also true when considering the relative size of the brain (brain size/

body size), thereby compensating for allometric effects,³ again hominids are in the middle range (Roth & Dicke, [2005,](#page-14-4) [2012\)](#page-14-5). The data therefore do not allow for a simple correlation between brain size and cognitive performance.

A clearer picture emerges for the structures of the cortex relevant for cognition, where the most neurons among recent primates are found in humans (Sousa et al., [2017\)](#page-14-15). The neurobiological substrate of general intelligence in mammals is considered to be the frontal lobe (prefrontal cortex) located at the front of the brain (Duncan et al., [2000\)](#page-11-12). It is directly involved in linking sensory information to the cognitivemental processes of thinking, action planning, and decision making (Roth & Dicke, [2005,](#page-14-4) [2012\)](#page-14-5). Although the human prefrontal cortex is particularly large (Roth $\&$ Dicke, [2005](#page-14-4), [2012\)](#page-14-5), recent comparative studies in primates have fundamentally questioned the disproportionate size of the human prefrontal cortex (Roth & Dicke, [2005,](#page-14-4) [2012](#page-14-5); Semendeferi et al., [2002](#page-14-16)), an issue that remains the subject of current research (Hayashi et al., [2021\)](#page-12-13).

Since neither absolute nor relative brain size is a unique feature of the human brain, the question arises as to what biological properties of the brain distinguish humans from their closest recent hominid relatives, the chimpanzees (*Pan troglodytes*) and pygmy chimpanzees or bonobos (*Pan paniscus*). Thus, the view is gaining ground that the key to the unique capabilities of the human brain is expressed less in its absolute or relative size, or even in the number of neurons and glia, but rather in more subtle components such as a greater diversity of neuronal cell types or more complex patterns of neuronal connectivity (Sousa et al., [2017\)](#page-14-15). Moreover, these changes must be evolutionarily young, i.e., they must have started at the earliest with the strong brain development of hominids in the early Miocene (15–18 million years ago) and at the latest with the split of the genus *Homo* from the rest of the hominids, the great apes, in the late Miocene 6–7 million years ago.

At this point, comparative genomic studies have been crucial to a better understanding of possible factors in brain evolution within mammals. Direct comparison of the now fully sequenced great ape genomes (Chimpanzee & Analysis, [2005;](#page-11-13) Kronenberg et al., [2018](#page-12-14); Locke et al., [2011;](#page-13-17) Mao et al., [2021;](#page-13-18) Scally et al., [2012](#page-14-17)) with that of humans allows the identifcation of relevant neuronal genes that are exclusive to humans and that have newly formed during this time window, e.g., through gene duplication. This approach has been used to identify primate-specifc genes that are particularly active in the neural stem and progenitor cells of the developing neocortex (Florio et al., [2018](#page-11-14)). The number of strictly human-specifc genes is limited $(n = 15)$, have emerged within the last 6–7 million years, and contain regulatory genes involved in neuronal proliferation and expansion of the neocortex (Florio et al., [2015](#page-11-15), [2018\)](#page-11-14). Other neocortex-specifc genes present in other primates

³Allometry relates organ size to body size; the brain follows a power function with an exponent of 0.6–0.8, meaning that as body size increases, brains become larger in absolute terms but smaller in relative terms (Roth, G., and U. Dicke. 2005. Evolution of the brain and intelligence. Trends Cogn. Sci. 9:250–257, Roth, G., and U. Dicke. 2012. Evolution of the brain and intelligence in primates. Prog Brain Res. 195:413–430).

or mammals were higher in number $(n = 3458)$ but also contribute to neocortical development (Florio et al., [2018](#page-11-14)).

Of particular interest here is the *SLIT-ROBO GTPase 2* (*SRGAP2*) gene, whose expression is also enriched in the developing neocortex (Charrier et al., [2012;](#page-11-16) Dennis et al., [2012](#page-11-17)). It is known that SRGAP2 is involved in brain development (Guerrier et al., [2009](#page-12-15)) and that humans carry at least three similar copies of the gene, whereas non-human primates carry only one. Humans have been shown to carry four non-identical copies (termed A–D) of *SRGAP2* at different locations on chromosome 1 (Geschwind & Konopka, [2012\)](#page-12-16). By comparing the gene sequences to those of the orangutan and chimpanzee *SRGAP2 genes*, the authors estimated that *SRGAP2* was duplicated in the human lineage approximately 3.4 million years ago, resulting in *SRGAP2A* and *SRGAP2B* (Geschwind & Konopka, [2012](#page-12-16)).

Further duplications of *SRGAP2B* led to *SRGAP2C* approximately 2.4 million years ago and to *SRGAP2D* approx. 1 million years ago, and *SRGAP2C* in particular may have played an important role 2–3 million years ago when human cognition evolved (Geschwind & Konopka, 2012). A further study shed light on the mechanism of the *SRGAP2 gene* (Charrier et al., [2012\)](#page-11-16). The formation of dendritic protrusions (*spines*) on the surface of neurons is essential for the formation of synaptic contacts. Here, SRGAP2A has been shown to promote the formation of spines and slow the migration of neurons within the developing cerebral cortex, while the human-specific SRGAP2C promotes the formation of more spines.

This results in a higher density of *spines* and a slowdown in cortical development, allowing for greater brain plasticity, i.e., the ability to change neuronal connections in response to new experiences (Geschwind & Konopka, [2012\)](#page-12-16). Duplication of *SRGAP2C* has also been found in Neanderthals and Denisova humans. Interestingly, the *FOXP2* gene, which is associated with the establishment of some aspects of our brain's language ability as well as language disorders, also has the same mutations in Neanderthals and humans that the great apes lack (Krause et al., [2007](#page-12-17)).

7 From Homo Sapiens Intelligence to Artifcial Intelligence?

The aim of this work was to show how the simplest stages of a neural network gave rise to complex nervous systems that are very likely convergent with each other in a wide variety of animal groups over the $>600-500$ million years of evolution. Humans therefore no longer appear to be the only species to possess intelligence. However, a comparison of the different systems shows that the high cognitive performances that enable intelligent behavior are always tied to a specifc environment and context. These contexts are at the same time linked to millions of years of evolution of biological "cognition systems." Artifcial intelligence is therefore only conceivable as an extension of human intelligence, albeit with the inclusion of all the sophistication that made the emergence of higher cognition possible in evolution.

Acknowledgements Many thanks to Rainer M. Holm-Hadulla, who gave the impulse for this work and enabled me to look beyond the "edge of my nose" of our research on the nervous system of the Cnidaria.

References

- Albertin, C. B., Simakov, O., Mitros, T., Wang, Z. Y., Pungor, J. R., Edsinger-Gonzales, E., Brenner, S., Ragsdale, C. W., & Rokhsar, D. S. (2015). The octopus genome and the evolution of cephalopod neural and morphological novelties. *Nature, 524*, 220–224.
- Boeckle, M., & Bugnyar, T. (2012). Long-term memory for affliates in ravens. *Current Biology, 22*, 801–806.
- Bosch, T. C. G., Klimovich, A., Domazet-Loso, T., Grunder, S., Holstein, T. W., Jekely, G., Miller, D. J., Murillo-Rincon, A. P., Rentzsch, F., Richards, G. S., Schroder, K., Technau, U., & Yuste, R. (2017). Back to the basics: Cnidarians start to fre. *Trends in Neurosciences, 40*, 92–105.
- Bshary, R., & Brown, C. (2014). Fish cognition. *Current Biology, 24*, R947–R950.
- Chapman, J. A., Kirkness, E. F., Simakov, O., Hampson, S. E., Mitros, T., Weinmaier, T., Rattei, T., Balasubramanian, P. G., Borman, J., Busam, D., Disbennett, K., Pfannkoch, C., Sumin, N., Sutton, G. G., Viswanathan, L. D., Walenz, B., Goodstein, D. M., Hellsten, U., Kawashima, T., … Steele, R. E. (2010). The dynamic genome of hydra. *Nature, 464*, 592–596.
- Charrier, C., Joshi, K., Coutinho-Budd, J., Kim, J. E., Lambert, N., de Marchena, J., Jin, W. L., Vanderhaeghen, P., Ghosh, A., Sassa, T., & Polleux, F. (2012). Inhibition of SRGAP2 function by its human-specifc paralogs induces neoteny during spine maturation. *Cell, 149*, 923–935.
- Chimpanzee, S., & Analysis, C. (2005). Initial sequence of the chimpanzee genome and comparison with the human genome. *Nature, 437*, 69–87. <https://doi.org/10.1038/nature04072>
- Clayton, N., & Emery, N. (2005). Corvid cognition. *Current Biology, 15*, R80–R81.
- Cruse, H., & Wehner, R. (2011). No need for a cognitive map: Decentralized memory for insect navigation. *PLoS Computational Biology, 7*, e1002009.
- David, C. N., Ozbek, S., Adamczyk, P., Meier, S., Pauly, B., Chapman, J., Hwang, J. S., Gojobori, T., & Holstein, T. W. (2008). Evolution of complex structures: Minicollagens shape the cnidarian nematocyst. *Trends in Genetics, 24*, 431–438.
- Dennis, M. Y., Nuttle, X., Sudmant, P. H., Antonacci, F., Graves, T. A., Nefedov, M., Rosenfeld, J. A., Sajjadian, S., Malig, M., Kotkiewicz, H., Curry, C. J., Shafer, S., Shaffer, L. G., de Jong, P. J., Wilson, R. K., & Eichler, E. E. (2012). Evolution of human-specifc neural SRGAP2 genes by incomplete segmental duplication. *Cell, 149*, 912–922.
- Duncan, J., Seitz, R. J., Kolodny, J., Bor, D., Herzog, H., Ahmed, A., Newell, F. N., & Emslie, H. (2000). A neural basis for general intelligence. *Science, 289*, 457–460.
- Emery, N. J., & Clayton, N. S. (2004). The mentality of crows: Convergent evolution of intelligence in corvids and apes. *Science, 306*, 1903–1907.
- Emery, N. J., & Clayton, N. S. (2005). Evolution of the avian brain and intelligence. *Current Biology, 15*, R946–R950.
- Fiorito, G., & Chichery, R. (1995). Lesions of the vertical lobe impair visual discrimination learning by observation in Octopus vulgaris. *Neuroscience Letters, 192*, 117–120.
- Fiorito, G., & Scotto, P. (1992). Observational learning in Octopus vulgaris. *Science, 256*, 545–547.
- Florio, M., Albert, M., Taverna, E., Namba, T., Brandl, H., Lewitus, E., Haffner, C., Sykes, A., Wong, F. K., Peters, J., Guhr, E., Klemroth, S., Prufer, K., Kelso, J., Naumann, R., Nusslein, I., Dahl, A., Lachmann, R., Paabo, S., & Huttner, W. B. (2015). Human-specifc gene ARHGAP11B promotes basal progenitor amplifcation and neocortex expansion. *Science, 347*, 1465–1470.
- Florio, M., Heide, M., Pinson, A., Brandl, H., Albert, M., Winkler, S., Wimberger, P., Huttner, W. B., & Hiller, M. (2018). Evolution and cell-type specificity of human-specific genes preferentially expressed in progenitors of fetal neocortex. *eLife, 7*, e32332.
- Fonseca-Azevedo, K., & Herculano-Houzel, S. (2012). Metabolic constraint imposes tradeoff between body size and number of brain neurons in human evolution. *Proceedings of the National Academy of Sciences, 109*, 18571–18576.
- Fox, K. C. R., Muthukrishna, M., & Shultz, S. (2017). The social and cultural roots of whale and dolphin brains. *Nature Ecology & Evolution, 1*, 1699–1705.
- Geschwind, D. H., & Konopka, G. (2012). Neuroscience: Genes and human brain evolution. *Nature, 486*, 481–482.
- Gold, D. A., Katsuki, T., Li, Y., Yan, X., Regulski, M., Ibberson, D., Holstein, T., Steele, R. E., Jacobs, D. K., & Greenspan, R. J. (2019). The genome of the jellyfsh Aurelia and the evolution of animal complexity. *Nature Ecology and Evolution, 3*, 96–104.
- Guerrier, S., Coutinho-Budd, J., Sassa, T., Gresset, A., Jordan, N. V., Chen, K., Jin, W. L., Frost, A., & Polleux, F. (2009). The F-BAR domain of srGAP2 induces membrane protrusions required for neuronal migration and morphogenesis. *Cell, 138*, 990–1004.
- Güntürkün, O., & Bugnyar, T. (2016). Cognition without cortex. *Trends in Cognitive Sciences, 20*, 291–303.
- Harrison, T. (2010). Anthropology. Apes among the tangled branches of human origins. *Science, 327*, 532–534.
- Hayashi, T., Hou, Y., Glasser, M. F., Autio, J. A., Knoblauch, K., Inoue-Murayama, M., Coalson, T., Yacoub, E., Smith, S., Kennedy, H., & Van Essen, D. C. (2021). The nonhuman primate neuroimaging and neuroanatomy project. *NeuroImage, 229*, 117726.
- Herculano-Houzel, S. (2020). Birds do have a brain cortex-and think. *Science, 369*, 1567–1568.
- Hirth, F., Kammermeier, L., Frei, E., Walldorf, U., Noll, M., & Reichert, H. (2003). An urbilaterian origin of the tripartite brain: Developmental genetic insights from Drosophila. *Development, 130*, 2365–2373.
- Hodgkin, A. L., & Huxley, A. F. (1952). Propagation of electrical signals along giant nerve fbers. *Proceedings of the Royal Society of London - Series B: Biological Sciences, 140*, 177–183.
- Holstein, T., & Tardent, P. (1984). An ultrahigh-speed analysis of exocytosis: Nematocyst discharge. *Science, 223*, 830–833.
- Jarvis, E. D., Güntürkün, O., Bruce, L., Csillag, A., Karten, H., Kuenzel, W., Medina, L., Paxinos, G., Perkel, D. J., Shimizu, T., Striedter, G., Wild, J. M., Ball, G. F., Dugas-Ford, J., Durand, S. E., Hough, G. E., Husband, S., Kubikova, L., Lee, D. W., … C. Avian Brain Nomenclature. (2005). Avian brains and a new understanding of vertebrate brain evolution. *Nature Reviews. Neuroscience, 6*, 151–159.
- Kabadayi, C., Taylor, L. A., von Bayern, A. M., & Osvath, M. (2016). Ravens, New Caledonian crows and jackdaws parallel great apes in motor self-regulation despite smaller brains. *Royal Society Open Science, 3*, 160104.
- Kandel, E. R., Koester, J. D., Mack, S. H., & Siegelbaum, S. A. (2021). *Principles of neural science* (6th ed.). McGraw-Hill Education.
- Krause, J., Lalueza-Fox, C., Orlando, L., Enard, W., Green, R. E., Burbano, H. A., Hublin, J. J., Hanni, C., Fortea, J., de la Rasilla, M., Bertranpetit, J., Rosas, A., & Paabo, S. (2007). The derived FOXP2 variant of modern humans was shared with Neandertals. *Current Biology, 17*, 1908–1912.
- Kronenberg, Z. N., Fiddes, I. T., Gordon, D., Murali, S., Cantsilieris, S., Meyerson, O. S., Underwood, J. G., Nelson, B. J., Chaisson, M. J. P., Dougherty, M. L., Munson, K. M., Hastie, A. R., Diekhans, M., Hormozdiari, F., Lorusso, N., Hoekzema, K., Qiu, R., Clark, K., Raja, A., … Eichler, E. E. (2018). High-resolution comparative analysis of great ape genomes. *Science, 360*, eaar6343.
- Leclere, L., Horin, C., Chevalier, S., Lapebie, P., Dru, P., Peron, S., Jager, M., Condamine, T., Pottin, K., Romano, S., Steger, J., Sinigaglia, C., Barreau, C., Quiroga Artigas, G., Ruggiero, A., Fourrage, C., Kraus, J. E. M., Poulain, J., Aury, J. M., … Copley, R. R. (2019). The genome of the jellyfsh Clytia hemisphaerica and the evolution of the cnidarian life-cycle. *Nature Ecology & Evolution, 3*, 801–810.
- Locke, D. P., Hillier, L. W., Warren, W. C., Worley, K. C., Nazareth, L. V., Muzny, D. M., Yang, S. P., Wang, Z., Chinwalla, A. T., Minx, P., Mitreva, M., Cook, L., Delehaunty, K. D., Fronick, C., Schmidt, H., Fulton, L. A., Fulton, R. S., Nelson, J. O., Magrini, V., et al. (2011). Comparative and demographic analysis of orangutan genomes. *Nature, 469*, 529–533.
- MacLean, E. L., Hare, B., Nunn, C. L., Addessi, E., Amici, F., Anderson, R. C., Aureli, F., Baker, J. M., Bania, A. E., Barnard, A. M., Boogert, N. J., Brannon, E. M., Bray, E. E., Bray, J., Brent, L. J., Burkart, J. M., Call, J., Cantlon, J. F., Cheke, L. G., … Zhao, Y. (2014). The evolution of self-control. *Proceedings of the National Academy of Sciences of the United States of America, 111*, E2140–E2148.
- Mao, Y., Catacchio, C. R., Hillier, L. W., Porubsky, D., Li, R., Sulovari, A., Fernandes, J. D., Montinaro, F., Gordon, D. S., Storer, J. M., Haukness, M., Fiddes, I. T., Murali, S. C., Dishuck, P. C., Hsieh, P., Harvey, W. T., Audano, P. A., Mercuri, L., Piccolo, I., … Eichler, E. E. (2021). A high-quality bonobo genome refnes the analysis of hominid evolution. *Nature, 594*, 77–81.
- Marino, L. (2002). Convergence of complex cognitive abilities in cetaceans and primates. *Brain, Behavior and Evolution, 59*, 21–32.
- Mischel, W., & Underwood, B. (1974). Instrumental ideation in delay of gratifcation. *Child Development, 45*, 1083–1088.
- Mischel, W. (2015). *The Marshmallow test: Why self-control is the engine of success*. Little, Brown.
- Mischel, W., Shoda, Y., & Rodriguez, M. I. (1989). Delay of gratifcation in children. *Science, 244*, 933–938.
- Moroz, L. L., Kocot, K. M., Citarella, M. R., Dosung, S., Norekian, T. P., Povolotskaya, I. S., Grigorenko, A. P., Dailey, C., Berezikov, E., Buckley, K. M., Ptitsyn, A., Reshetov, D., Mukherjee, K., Moroz, T. P., Bobkova, Y., Yu, F., Kapitonov, V. V., Jurka, J., Bobkov, Y. V., … Kohn, A. B. (2014). The ctenophore genome and the evolutionary origins of neural systems. *Nature, 510*, 109–114.
- Nieder, A., Wagener, L., & Rinnert, P. (2020). A neural correlate of sensory consciousness in a corvid bird. *Science, 369*, 1626–1629.
- Nüchter, T., Benoit, M., Engel, U., Ozbek, S., & Holstein, T. W. (2006). Nanosecond-scale kinetics of nematocyst discharge. *Current Biology, 16*, R316–R318.
- Olkowicz, S., Kocourek, M., Lucan, R. K., Portes, M., Fitch, W. T., Herculano-Houzel, S., & Nemec, P. (2016). Birds have primate-like numbers of neurons in the forebrain. *Proceedings of the National Academy of Sciences of the United States of America, 113*, 7255–7260.
- Pepperberg, I. M. (2006). Grey parrot numerical competence: A review. *Animal Cognition, 9*, 377–391.
- Pepperberg, I. M., Koepke, A., Livingston, P., Girard, M., & Hartsfeld, L. A. (2013). Reasoning by inference: Further studies on exclusion in grey parrots (Psittacus erithacus). *Journal of Comparative Psychology, 127*, 272–281.
- Plotnik, J. M., de Waal, F. B., & Reiss, D. (2006). Self-recognition in an Asian elephant. *Proceedings of the National Academy of Sciences of the United States of America, 103*, 17053–17057.
- Plotnik, J. M., Lair, R., Suphachoksahakun, W., & de Waal, F. B. (2011). Elephants know when they need a helping trunk in a cooperative task. *Proceedings of the National Academy of Sciences of the United States of America, 108*, 5116–5121.
- Puelles, L., Harrison, M., Paxinos, G., & Watson, C. (2013). A developmental ontology for the mammalian brain based on the prosomeric model. *Trends in Neurosciences, 36*, 570–578.
- Putnam, N. H., Srivastava, M., Hellsten, U., Dirks, B., Chapman, J., Salamov, A., Terry, A., Shapiro, H., Lindquist, E., Kapitonov, V. V., Jurka, J., Genikhovich, G., Grigoriev, I. V., Lucas, S. M., Steele, R. E., Finnerty, J. R., Technau, U., Martindale, M. Q., & Rokhsar, D. S. (2007). Sea anemone genome reveals ancestral eumetazoan gene repertoire and genomic organization. *Science, 317*, 86–94.
- Reichert, H. (2005). A tripartite organization of the urbilaterian brain: Developmental genetic evidence from Drosophila. *Brain Research Bulletin, 66*, 491–494.
- Rentzsch, F., Juliano, C., & Galliot, B. (2019). Modern genomic tools reveal the structural and cellular diversity of cnidarian nervous systems. *Current Opinion in Neurobiology, 56*, 87–96.
- Roth, G. (2015). Convergent evolution of complex brains and high intelligence. *Philosophical Transactions of the Royal Society B, 370*, 20150049.
- Roth, G., & Dicke, U. (2005). Evolution of the brain and intelligence. *Trends in Cognitive Sciences, 9*, 250–257.
- Roth, G., & Dicke, U. (2012). Evolution of the brain and intelligence in primates. *Progress in Brain Research, 195*, 413–430.
- Santos, L. R. & Rosati, A. G. (2015). The evolutionary roots of human decision making. *Annual review of psychology 66*, 321–347.
- Scally, A., Dutheil, J. Y., Hillier, L. W., Jordan, G. E., Goodhead, I., Herrero, J., Hobolth, A., Lappalainen, T., Mailund, T., Marques-Bonet, T., McCarthy, S., Montgomery, S. H., Schwalie, P.-C., Tang, Y. A., Ward, M. C., Xue, Y., Yngvadottir, B., Alkan, C., Andersen, L. N., … Durbin, R. (2012). Insights into hominid evolution from the gorilla genome sequence. *Nature, 483*, 169–175.
- Schnell, A. K., & Clayton, N. S. (2019). Cephalopod cognition. *Current Biology, 29*, R726–R732.
- Schnell, A. K., Amodio, P., Boeckle, M., & Clayton, N. S. (2021a). How intelligent is a cephalopod? Lessons from comparative cognition. *Biological Reviews of the Cambridge Philosophical Society, 96*, 162–178.
- Schnell, A. K., Boeckle, M., Rivera, M., Clayton, N. S., & Hanlon, R. T. (2021b). Cuttlefish exert self-control in a delay of gratifcation task. *Proceedings of the Biological Sciences, 288*, 20203161.
- Semendeferi, K., Lu, A., Schenker, N., & Damasio, H. (2002). Humans and great apes share a large frontal cortex. *Nature Neuroscience, 5*, 272–276.
- Shomrat, T., Zarrella, I., Fiorito, G., & Hochner, B. (2008). The octopus vertical lobe modulates short-term learning rate and uses LTP to acquire long-term memory. *Current Biology, 18*, 337–342.
- Sousa, A. M. M., Meyer, K. A., Santpere, G., Gulden, F. O., & Sestan, N. (2017). Evolution of the human nervous system function, structure, and development. *Cell, 170*, 226–247.
- Stacho, M., Herold, C., Rook, N., Wagner, H., Axer, M., Amunts, K., & Güntürkün, O. (2020). A cortex-like canonical circuit in the avian forebrain. *Science, 369*, eabc5534.
- Strausfeld, N. J., & Hirth, F. (2013). Deep homology of arthropod central complex and vertebrate basal ganglia. *Science, 340*, 157–161.
- Trembley, A. (1744). *Mémoires pour servir à l'histoire d'un genre de polypes d'eau douce à bras en forme de cornes*. J. & H. Verbeek.
- Wanninger, A., & Wollesen, T. (2019). The evolution of molluscs. *Biological Reviews of the Cambridge Philosophical Society, 94*, 102.
- Watanabe, H., Fujisawa, T., & Holstein, T. W. (2009). Cnidarians and the evolutionary origin of the nervous system. *Development, Growth & Differentiation, 51*, 167–183.
- Wehner, R., & Menzel, R. (1969). Homing in the ant Cataglyphis bicolor. *Science, 164*, 192–194.
- Young, J. Z., Young, J. Z., & Boycott, B. B. (1971). *The anatomy of the nervous system of octopus vulgaris*. Clarendon Press.

Thomas W. Holstein studied biology at the University of Vienna (1973–1980) (Dr. phil.). Afterwards he was at the University of Zürich (1980–1983) and University of Munich (1983–1993) (Dr. rer. nat. habil). He was associate professor at the University of Frankfurt (1993–1998) and full professor at the Technical University of Darmstadt (1998–2004). He declined offers to the Universities of Karlsruhe and Vienna, and joined the University of Heidelberg in 2004, where he has been teaching and researching ever since. Here, he was managing Director of the Zoological Institute (2004–2011), Dean of the Faculty of Biosciences (2007–2012), Fellow at the Heidelberg Marsilius-Kolleg (2011–2014), and President of the Heidelberg Academy of Sciences (2015–2020). He is a member of the DFG's SFB 1324, who's spokesperson he was in the frst funding period (2017–2021). His feld of work is molecular cell and developmental biology with a focus on questions in evolutionary biology. With his research group, he works on stem cells and the nervous system of the freshwater polyp *Hydra* and the sea anemone *Nematostella*.