Wolfgang Welsch · Wolf Singer
André Wunder *Editors*

# Interdisciplinary Anthropology

## Continuing Evolution of Man

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*Editors*
Prof. Dr. Wolfgang Welsch
Universität Jena
Institut für Philosophie
Zwätzengasse 9
07743 Jena
Germany
wolfgang.welsch@uni-jena.de

Prof. Dr. Wolf Singer
MPI für Hirnforschung
Abt. Neurophysiologie
Deutschordenstr. 46
60528 Frankfurt/Main
Germany
singer@mpih-frankfurt.mpg.de

André Wunder, M.A.
Universität Zürich
Philosophisches Seminar
Zürichbergstrasse 43
CH-8044 Zürich
andre.wunder@philos.uzh.ch

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# Preface

This volume is the result of a research project entitled "Evolutionary Continuity – Human Specifics – The Possibility of Objective Knowledge" that was carried out by representatives of six academic disciplines (evolutionary biology, evolutionary anthropology, brain research, cognitive neuroscience, cognitive psychology, and philosophy) over a period of three-and-a-half years starting July 1, 2006, and ending December 31, 2009.

The starting point for the project was the newly emerging riddle of human uniqueness. Formerly, people believed it possible to determine which features distinguish humans from other animals. Rationality, i.e., the possession of mind, reason, language, logical thinking, etc., was thought to be *the* unique characteristic of human beings. This is precisely what the old definition of the human as *animal rationale* suggested: only human beings possess rationality and this sets them apart from all other creatures. But the results of scientific research fundamentally questioned this view in recent decades. With regard to the dimensions of rationality (possession of concepts, arithmetic, reasoning, etc.), it was found that they not only exist in us humans, but that at least early forms can be found in our close and distant relatives in the animal world. Not a single element of rationality is really exclusive to humans. For example, all mammals are capable of elementary categorizations; pigeons are experts in abstraction and generalization; chimpanzees and bonobos do not only understand causal relationships in the physical world but are also able to understand what their conspecifics think; finally, chimpanzees and orangutans are able to act on the basis of prior reasoning. Certainly, most of these skills are more perfectly developed in us than in our relatives. Yet, they are – and this precisely is the new insight – in no way exclusive to humans. Rather, our rationality constitutes an advancement of animal rationality.

Alarmed by these results and in order to adhere to the exclusivity of humans, many attempts were made to come up with other human specifics. However, all of the alternatives turned out to be untenable in the light of recent research. The making and use of tools, for example, are common in the animal world; aesthetic judgment can already be observed in animals; the same applies to altruism, or to walking upright, grasping hand, premature birth, and neoteny. Even sadism can be found sporadically among our closer relatives. In short, nothing in humans can be considered an absolute novelty, spontaneously occurring when humans appeared on the earth. Rather, we have to see these traits as advancements of prehumanly existing characteristics.

On the other hand, it goes without saying that we humans are quite extraordinary beings doing things without simile in the animal kingdom. No species among the higher organisms is so widely spread all over the world, constructs cathedrals, surfs the web, and engages in space travel. Only humans have developed poetry, philosophy, science, and technology. We humans clearly differ from other creatures in our achievements. The common denominator for all of these distinctly human accomplishments is "culture." Humans are cultural beings par excellence and that is what renders humankind distinct from any other species.

Of course, certain preforms of culture can be found in the animal world as well: from the formation of colonies over sophisticated forms of communication up to the invention of tools. In chimpanzees, we can even observe cultural diversity between different populations as one population might use different cultural practices than another but in very similar contexts. Yet, what animal culture (even in chimpanzees) lacks is cumulative cultural development, the ongoing procession of developments in which all achievements constantly form the basis for further steps. This is typical of humans, and this has brought about the gigantic cultural evolution that so obviously distinguishes humans from their fellow beings.

Hence, this is the situation: though the uniqueness of human beings is undisputable, all explanations for this fact successively got lost in recent decades. There is no special factor that could explain the particularities of human existence. Rather, all human skills derive from a continuous relation to prehuman skills, that is to say elements that have been developed earlier in phylogeny and have been inherited therefrom. But starting from abilities that are anything but special, how could the particularity of human beings have come into being? This is the modern riddle of human uniqueness.

The only possible explanation is that our uniqueness must have *emerged* from our evolutionary heritage. Since in human evolution our ancestors had to start with the same endowment as our closest relatives, it obviously is the case that in hominization the use of this heredity must have acquired a direction considerably different from that of our animal companions – which finally led to the impressive achievements of cultural evolution. Our ancestors must have been seized by a special dynamic development or used their endowment in a specific way that the uniqueness of humankind emerged and animal-like humans became fully fledged human beings.

This was the issue underlying the project. Starting from this point, the following research questions were formulated: How strong is evolutionary continuity in human beings? How can we understand that it gave way to cultural discontinuity? Which aspect of cultural existence is really unique to humans? Can the possibility of objective knowledge be seen as an (admittedly extreme) case in point?

These research questions were first developed by Prof. Dr. Wolfgang Welsch (Friedrich-Schiller-University, Jena). To realize the project he invited five research partners: Dr. Julia Fischer (German Primate Center, Göttingen), Dr. Hannes Rakoczy (Max Planck Institute for Evolutionary Anthropology, Leipzig), Prof. Dr. Wolf Singer (Max Planck Institute for Brain Research, Frankfurt/Main), Dr. Ricarda I. Schubotz (Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, later Max Planck Institute for Neurological Research, Köln), and Prof. Dr. Rainer Mausfeld (Institute of Psychology at Christian Albrecht University of Kiel). Jointly, six areas of research were defined that addressed different aspects especially productive with regard to the overall question. The results of three-and-a-half years of research are now presented in the six chapters of this volume. They document a combination of meticulous empirical studies with theoretical and meta-theoretical thinking. The final Overview (Forster/Welsch) summarizes the results once more with regard to the leading research questions.[1]

It is and always has been the persistent conviction of all authors that the ship of research has to pass the Scylla of a simply naturalistic reductionism and the Charybdis of an abundant supranaturalism to sail past a one-sided orientation on merely physicist and neurobiological issues on the one hand and an ignorant rejection of empirical research results on the other and finally enter the open sea of evolutionary enlightenment. We hope that this volume will help us to take the ship forward some distance and that it presents aspects apt to determine our future understanding of evolution and of humankind's position in it.

Finally, we would like to add some words of thanks. We are very much obliged to the German Federal Ministry of Education and Research that has financed this project and the German Aerospace Center that has proved to be a helpful and competent partner in all phases of research. Furthermore, we would like to thank Friedrich-Schiller-University, Jena, which has given us the opportunity to introduce the project in a lecture series in the winter semester 2006/2007 and also to present the results in a closing conference in December 2009. Thanks are also due to the Springer publishing company for its spontaneous interest in the project and for the careful and accurate design of the volume. Finally, we would like to thank all other research partners and their staff (Julia Fischer, Maria Golde, Rainer Mausfeld, Reinhard Niederée, Hannes Rakoczy, Elisabeth Scheiner, Ricarda I. Schubotz, Christian Spahn, Peter Uhlhaas, and Emily Wyman) for their dedicated cooperation, as well as the various honorable international colleagues (Merlin Donald, Christopher Frith, Ruth Millikan, Joëlle Proust, and Evan Thompson) for their contribution to the discussions. Last but not least, we are very much obliged to Michael Forster who, using his stupendous understanding of latest results in

[1]With regard to the general question of how animal-like humans became really human, see Wolfgang Welsch's explanations concerning the origin of human uniqueness during the proto-cultural period (starting 2.5 million years ago, when the evolution of humankind took up momentum, and lasting until 40,000 years ago, when the takeoff of cultural evolution took place): "Das Rätsel der menschlichen Besonderheit," in: Jahrbuch 2009 der Deutschen Akademie der Naturforscher Leopoldina (Halle/Saale), LEOPOLDINA (R.3) 55 (2010).

research on the one hand and his excellent philosophical reflections on the other, lead us back on productive paths time and again and also drew up the closing overview.

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Wolfgang Welsch
Wolf Singer
André Wunder

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# Contents

# Contributors

**Julia Fischer** Cognitive Ethology Lab, German Primate Center, Kellnerweg 4, 37077 Göttingen, Germany, fischer@cog-ethol.de

**Michael Forster** Department of Philosophy, University of Chicago, Stuart Hall 203, Chicago, IL, USA, mnforster@uchicago.edu

**Rainer Mausfeld** Department of Psychology, Christian Albrechts University Kiel, Olshausenstr. 62, 24098 Kiel, Germany, mausfeld@psychologie.uni-kiel.de

**Hannes Rakoczy** Institute of Psychology & Courant Research Centre "Evolution of Social Behavior", University of Göttingen, 37077 Göttingen, Germany, hannes.rakoczy@psych.uni-goettingen.de

**Elisabeth Scheiner** Cognitive Ethology Lab, German Primate Center, Kellnerweg 4, 37077 Göttingen, Germany, elisabeth-scheiner@cog-ethol.de

**Ricarda I. Schubotz** Max Planck Institute for Neurological Research, Gleueler Str. 50, 50931 Köln, Germany, schubotz@nf.mpg.de

**Wolf Singer** Department of Neurophysiology, Max Planck Institute for Brain Research, Deutschordenstr. 46, 60528 Frankfurt am Main, Germany; Frankfurt Institute for Advanced Studies, Johann Wolfgang Goethe-Universität, Ruth-Moufang-Str. 1, 60438 Frankfurt am Main, Germany, singer@mpih-frankfurt.mpg.de

**Christian Spahn** Department of Philosophy, College of Humanities, Keimyung University, 100 Sindang-Dong, Dalseo-Gu, Daegu 704-701, South Korea, christian.spahn@googlemail.com

**Peter J. Uhlhaas** Department of Neurophysiology, Max Planck Institute for Brain Research, Deutschordenstr. 46, 60528 Frankfurt am Main, Germany, uhlhaas@mph-frankfurt.mpg.de

**Wolfgang Welsch** Institute of Philosophy, Friedrich-Schiller-University Jena, Zwätzengasse 9, 07743 Jena, Germany, wolfgang.welsch@uni-jena.de

**Emily Wyman** Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103, Leipzig, Germany, wyman@eva.mpg.de

# Brain Evolution and Cognition: Psychosis as Evolutionary Cost for Complexity and Cognitive Abilities in Humans

**Peter J. Uhlhaas and Wolf Singer**

**Abstract** Cognitive functions correlate with the organization and complexity of neural networks. During the evolution of mammalian brains, basic algorithms for neural computations have largely remained unchanged while between species comparisons reveal marked differences in the volume of neocortex. Accordingly, the specific cognitive functions found in humans need to be considered as the product of the iteration of basic cortical algorithms. In humans, one characteristic feature of cortical organization is the addition of strategically important areas that serve as nodes for additional interactions between phylogenetically conserved brain regions. These novel processing structures serve multimodal integration and the generation of metarepresentations. The novel cognitive functions that have emerged from this increase in complexity comprise multiperspectivity, creativity, language, and theory of mind. We propose that certain mental disorders, such as schizophrenia, are a consequence of this evolutionary trend towards complexity whereby the increasing prevalence of self-referential internal computations enhances the risk of specific disturbances in higher cognitive functions. These pathological phenomena of human cognition can thus be considered as specific side effects of the evolution of human capabilities.

P.J. Uhlhaas (✉)
Department of Neurophysiology, Max Planck Institute for Brain Research, Deutschordenstr. 46, 60528 Frankfurt am Main, Germany
e-mail: uhlhaas@mph-frankfurt.mpg.de

W. Singer
Department of Neurophysiology, Max Planck Institute for Brain Research, Deutschordenstr. 46, 60528 Frankfurt am Main, Germany
and
Frankfurt Institute for Advanced Studies, Johann Wolfgang Goethe-Universität, Ruth-Moufang-Str. 1, 60438 Frankfurt am Main, Germany
e-mail: singer@mpih-frankfurt.mpg.de

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# 1 Introduction

With the advances in the cognitive neurosciences in the last two decades, the prospect for a unified framework for understanding mind and brain has increased tremendously. Numerous studies have shown close correlations and also causal relationships between neural events and mental phenomena that clearly support the view that the human mind is an emergent property of neural events, leaving little room for ontological dualism (Singer, in press). Accordingly, this evidence suggests the view that human mental operations as well as their dysfunction are intimately tied to the architecture and function of the biological hardware that supports cognition and action.

While these data clearly place the mind within nature, there are several issues that are still largely unresolved. For example, what are the unique capabilities that characterize the human mind? For long it has been assumed that there is a clear distinction between the supposedly "unique" cognitive abilities of humans and the cognitive functions in "lower" organisms. Yet, recent research suggests that certain abilities that were formerly considered specific to humans, such as theory of mind, shared attention, and use of symbols, can also be found in primates and other species such as birds, albeit in rudimentary forms (Prior et al. 2008; Tomasello et al. 2003).

In this chapter, we attempt to identify cognitive processes that are specific to humans by drawing on studies that have examined the structure, function, and organization of nervous systems in organisms of different complexity. In the second step, we relate these differences to cognitive processes that may be considered characteristic of *Homo sapiens*. Finally, we argue that these specific human functions predispose for certain malfunctions that manifest themselves predominantly in neuropsychiatric disorders, such as schizophrenia.

# 2 Evolution and Cortical Circuits

The relationship between evolution and the organization and function of central nervous systems had already received attention by Charles Darwin. In the *Descent of Man* (Darwin 1871, p. 10), he suggests that "It is notorious that man is constructed on the same general type or model with other mammals. All the bones in his skeleton can be compared with corresponding bones in a monkey, bat, or seal. So it is with his muscles, nerves, blood-vessels and internal viscera. The brain, the most important of all the organs, follows the same law as shown by Huxley and other anatomists". According to Darwin, the origin of the human brain has to be sought in the precursors of *Homo sapiens* and there is an evolutionary continuity in terms of organization and structure of the human brain.

In the history of evolutionary neuroscience, this perspective has not always been the dominant approach with some positions emphasizing species differences in brain organization while others have subscribed to the opposite view [for a review see Striedter (2005)]. The perspective we adopt in this chapter is to emphasize that the basic building blocks of the human brain are evolutionarily conserved, suggesting that the principles and mechanisms for the encoding, processing, and transmission of information in cortical circuits have largely remained unchanged. In contrast, there are important differences in the complexity and organization of cortical circuits that have lead to unique properties of the human brain.

## *2.1 Basic Building Blocks of Cortical Circuits: Evidence for Evolutionary Continuity*

The transmission of information in neural circuits of the vertebrate brain depends mainly on the generation and propagation of action potentials (APs) that represent the fundamental unit of neural coding. A brief survey reveals that the transmission of signals via APs is a universal feature of all vertebrate nervous systems. In addition, APs are present in invertebrates, such as insects, and even in simple nervous systems, such as that of *Caenorhabditis elegans* (Mellem et al. 2008). However, in all systems, and in particular in simple organisms, signals are also exchanged between nerve cells by direct coupling and by voltage-dependent release of transmitter without APs. The crucial advantage of AP coding is that signals can be propagated over longer distances without attenuation. Important electrical properties of the AP, such as the resting potential, the size, and duration of the AP, have largely remained constant across species (Bullock and Horridge 1965), suggesting that APs represent an energy efficient way of transmitting information in nervous systems.

Similarities extend to the mechanisms underlying intercellular communication. Synapses convert electrical signals into chemical messages that diffuse across a gap, the synaptic cleft, and then are converted into de- or hyperpolarizing synaptic potentials (EPSPs or IPSPs). This type of electro-chemical transmission is a universal feature of vertebrate nervous systems and has possibly evolved around 900 million years ago (Hedges et al. 2006). Synaptic signalling can also be found in invertebrates with the difference that signalling complexity is somewhat lower, while the overall structure and function of synaptic mechanisms are preserved (Ryan and Grant 2009). Similarly, the neurotransmitters that convey signals across the synaptic cleft have largely remained unchanged during evolution [for a review see Venter et al. (1988)]. For example, acetylcholine, serotonin, and other catecholamines are not only found in the animal kingdom but also in plants.

However, differences between species exist with respect to the expression patterns of neurotransmitter receptors, the prevalence of certain cell types and the composition of ion channels in their membrane. For example, the *N*-methyl-D-aspartic acid (NMDA) receptor differs in vertebrates and invertebrates. It is a specialized glutamate receptor that acts as a coincident detector and plays a crucial role not only in signal transmission but also in use-dependent synaptic plasticity and memory formation. Ryan et al. (2008) showed that NMDA receptors in vertebrates possess a specific NR2 subunit that is not present in invertebrates.

In addition, there is evidence that specific neuron types vary with species. The von Economo neuron (VEN) is a large bipolar neuron that was first described in humans and in certain great apes (Allman et al. 2010). As these cells occur in the frontal and anterior cingulate cortex, VENs have been related to social and emotional functions. However, more recent work has shown that VENs can also be found in elephants and whales (Butti et al. 2009). These data indicate that selective pressures have led to the evolution of this type of neuron in phylogenetically unrelated groups. However, other more common types of neurons, such as pyramidal cells, stellate cells, and the different populations of inhibitory interneurons, have remained highly conserved in vertebrates (Kaas 2010).

Similarities across species extend to properties of network activity, such as neural oscillations. Neural oscillations are a fundamental mechanism for enabling coordinated activity in nervous systems (Uhlhaas et al. 2009). They occur in different frequencies from 1 to 400 Hz and are present in simple organisms, such as the olfactory systems of insects (Stopfer et al. 1997), as well as in all cortices of vertebrates (Buzsaki 2006). Moreover, the mechanisms generating neural oscillations, such as the pacemaker neurons and specific networks that couple inhibitory GABA ($\gamma$-aminobutyric acid)-ergic interneurons with each other and with excitatory glutamatergic neurons, are highly preserved.

In conclusion, while certain differences in cellular structures and transmitter systems exist between species, it appears that overall the “basic” building blocks that are fundamental for the coding and transmission of information in nervous systems have remained highly conserved across species and in particular among vertebrates. This suggests that unique cognitive capabilities are not the result of differences in these parameters.

## 3 Changes in Brain Size and Organization During Evolution

### *3.1 Does Size Matter?*

While nervous systems in vertebrates exhibit a rather similar organization across species, there are major differences in size and in particular in the organization of cortical circuits. Across mammalian species, brain size varies by a factor of 100,000 (Herculano-Houzel 2009), indicating that the size of the brain may be a critical determinant of cognitive abilities. This is supported by the fact that species with the largest brains, such as cetaceans and primates, display a greater behavioural repertoire than species with smaller brains (Marino 2002).

However, the relation between brain size and cognitive abilities is not straightforward. For example, elephants have a similar brain size as humans, yet lack several of the higher cognitive functions. Accordingly, it has been proposed that what matters is brain size relative to body mass. Jerison (1973) developed the encephalization quotient (EQ), which is defined as the ratio of the actual brain weight over the expected brain weight given the size of the animal ($EQ = w(\text{brain})/Ew(\text{brain})$). Thus, an EQ of 1 indicates that the brain mass matches the expected value; an $EQ > 1$ means that the brain size in that species is larger than expected given its body weight. Indeed, humans are characterized by the largest EQ in the animal kingdom with a value of approximately 7–8, while chimpanzees, the closest living primate relative, have only an EQ of 2.8 (Jerison 1973). Accordingly, the human brain also contains among primates the largest number of neurons, around 100 billion.

Several factors have been proposed for the disproportional enlargement of the human brain. The first major increase in brain size in hominid evolution occurred possibly when bipedal apes diverged from other apes about 6 million years ago and these increases were probably related to diet (Leonard and Robertson 1994). The second major increase is associated with the emergence of *Homo sapiens* about 100,000 years ago, which has reached the current volume of 1,200–1,800 $cm^3$ (Lee and Wolpoff 2003). Dunbar (1993) has proposed a quantitative relationship between brain size and social group size. According to her perspective, one possible role of brain enlargement could be to increase the competence for social negotiations, for the adjustment of appropriate social behaviours and for the generation of historical memories of contextualized behaviour of particular individuals. It has been argued that these differentiated cognitive abilities may require more complex networks and as a consequence more neurons and connections and hence larger brains.

## 3.2 *Changes in Structure and Connectivity*

The evolutionary increase in brain size is mainly due to a volume increase of layered structures that evolved fairly recently, such as the neocortex, the hippocampus, and the cerebellum. The neocortex, one of the distinguishing features of mammalian brains, consists of a six-layered cellular sheet composed of pyramidal cells and interneurons that are arranged in horizontal layers, which in turn show a modular substructure of vertical columns the neurons of which that share distinct afferent and efferent connections and have similar functional properties (Rakic 2009). Evidence suggests that the neocortex evolved from a trilaminar reptilian precursor by adding several cellular layers (Reiner 1993).

Cortical circuits are fundamentally related to all aspects of higher cognitive and executive processes. In humans, this structure is disproportionally larger than in any other species and makes up 90% of the overall size of the brain, suggesting that the enormous expansion of neocortex may be causally related to the evolution of the specific cognitive abilities that characterize humans.

The expansion in size is due to the addition of novel, cytoarchitectonically distinguishable cortical areas and the myriads of connections that link these areas with the phylogenetically ancient cortical and subcortical structures. In early mammals, only 20–25 cortical areas can be distinguished. In contrast, the human neocortex has been estimated to contain ~150 cortical areas (Kaas 2010). Reasons for the increased parcellation of human neocortex into functionally specialized modules are related to the need to maintain effective connectivity patterns. As the cortex grows in size, more neurons have to communicate with one another. Since the dynamic range of neurons is limited, fully connected networks become impossible because they lead to a combinatorial explosion of input.

One solution is to implement a small-world architecture that represents an optimal compromise between nearest neighbor and strategic long-range connections. Such parcellated networks comprising nodes of variable sizes can carry out local computations and through long-distance connections can self-organize towards globally ordered states (Sporns et al. 2004). Comparative evidence suggests that small-world architectures are found in various primate brains as well as in other mammals, suggesting a general design principle of cortical networks (Striedter 2005).

Although the human neocortex contains the largest number of cortical areas, there is little evidence that any of these areas are unique to *Homo sapiens*. The frontal and especially the prefrontal cortex are considered to be crucial for higher cognitive processes, yet even rodents have a prefrontal cortex, albeit in rudimentary form. In humans, the frontal lobes are the single largest partition of the cortex and relative to other primates have expanded disproportionally (Semendeferi et al. 2002). Furthermore, cross-species comparisons of the effects of lesions have shown that in humans frontal lesions entrain a wide range of severe cognitive deficits, whereas in cats, for example, there is little change of overt behaviour (Mesulam 1998).

The increase in the size of neocortex goes along with a shift in the prevalence of intrinsic over extrinsic connections. Most of the connections a cortical neuron receives come from other cortical neurons rather than from subcortical relays and sensory organs. In the human cerebral cortex, 90% of connections are established with other neocortical pyramidal cells, i.e., not input or sensory neurons (Buzsaki 2006). This architecture results in an immense number of reentrant loops that is reflected in the fact that over 80% of the pathways leaving the cortex are directed to other areas of the cortex.

The addition of new areas and the concomitant increase in neuron numbers and connections necessarily also led to an expansion of white matter that harbors cortico-cortical long-range connections. Thus, in complex brains, there is a disproportionate increase in long-range connections leading to an increase in white matter at four-third power of the volume of grey matter during the course of the evolution (Zhang and Sejnowski 2000). This developmental trend is most pronounced in regions that are crucial for human-specific cognitive functions, such as language. One example is the arcuate fasciculus that links auditory areas in the temporal lobe (Wernicke) with executive areas in the frontal lobe (Broca). Thus, in humans, but not in chimpanzees or macaques, frontal cortices are strongly connected via the arcuate fasciculus with the left medial temporal gyrus and inferior temporal gyrus, areas that are critical for language (Rilling et al. 2008). These findings highlight the