Preface

Looking at the extraordinary overlap between human and chimpanzee genomes, one might expect equally extraordinary overlap in their thoughts, sensations, perceptions, and emotions. Yet there are both considerable similarities and differences between human and nonhuman primate brains and minds. It is not yet clear how to capture these interesting patterns of convergence and divergence, especially in terms of identifying the relevant neural structures and the selective pressures that helped shape each species' psychological signature. In what ways are our minds and brains similar to those of other primates? And where do the critical differences lie? New advances in cognitive psychology, comparative biology, and neuroscience have created an opportunity to take a fresh look at these complex and fascinating problems. It therefore seemed timely to assemble a panel of distinguished researchers in those fields, with the goal of presenting a state-of-the-art comparative perspective on primate cortical organization and function. Such was the aim of the ninth Fyssen Symposium, entitled "From Monkey Brain to Human Brain," which was held at the Pavillon Henry IV in St-Germain-en-Laye from 20 to 23 June 2003, and of which the present volume constitutes the report.

The first part of the meeting was dedicated to an examination of the potentials and limits of the modern techniques for studying primate brains. Discussion focused largely on neuroimaging methods, but other approaches were also examined, including those provided by recent advances in genetics and computer-based reconstructions. These methods can now be applied identically across different species of primates, including humans, and may thus serve as a starting point for the definition of cross-species homologies.

Neuroimaging, in particular, offers a diversity of means to compare human and nonhuman primate brains. At the anatomical level, macroscopic images of brain volume or surface can be warped onto each other, thus allowing for precise measurements of the amount of regional distortion. A comprehensive approach to this problem is presented in David Van Essen's chapter. At the functional level, the response profile of different brain areas to the same stimuli can be measured and compared across species using functional magnetic resonance imaging (fMRI). Ultimately, fMRI should provide a strong connection to single-cell recordings in the behaving monkey, although there are important caveats that are discussed by Zoe Kourtzi and Nikos Logothetis. Anatomical and functional MRI results can be integrated within computerized atlases that, increasingly, also incorporate detailed postmortem data. For instance, Karl Zilles describes how the regional and laminar distribution of various types of neurotransmitters and receptors provides a rich source of comparative data across species.

Karl Zilles and Jean-Jacques Hublin also examine the extent to which measures of brain size, shape, gyrification, and vascularization shed light on the evolution of the human brain and the major factors that shaped its organization. As described by Jean-Pierre Changeux, advances in genomics have merely strengthened, rather than resolved, the paradox of the nonlinearity of primate evolution, which is the fact that major changes in brain size and functional complexity resulted from small changes in the genome. This paradox raises many unsolved questions, which are explored in the first chapters:

- Was human brain evolution driven mostly by a change in cortical surface?
- What is the meaning of the ten- to twenty-fold variation in relative size between different cortical areas of the human and macaque brains?
- Does a single deformation field suffice to account for cross-species differences in cortical maps? Or is there also evidence that new cortical areas have appeared? Might even more radical forms of reshuffling of the cortical layout have occurred?
- Have basic units such as cortical layers and columns been preserved in evolution, or did their functionality change?
- Were there also major changes in microcircuitry, for instance in axonal arborization and long-distance connectivity? What is their significance?

A second section of the meeting examined particular domains of human competence and their possible precursors in primates. We intentionally focused first and foremost on cognitive functions that appear to be particularly developed in our species, to such an extent that they initially appear unique and devoid of precursors: arithmetic, reading, theory of mind, cooperation, and altruism. Remarkably, in all of these domains, some plausible analogs or even homologs have begun to be identified in nonhuman primates. In arithmetic, for instance, a coherent story is emerging that relates the human capacity for symbolic calculation to a more primitive form of numerosity processing, available to primates as well as to many other species including rats and pigeons. As reviewed by Elizabeth Brannon, behavioral studies in primates have revealed a competence for discriminating and comparing the numerosity of sets of dots. This competence for nonsymbolic arithmetic is also present in preverbal human infants, and may thus be part of our evolutionary heritage at birth. A very exciting development is that its neurobiological bases in monkeys have begun to be identified. Based on electrophysiological recordings, Andreas Nieder and Earl Miller identify a population of single neurons tuned to approximate numerosity. They demonstrate that the properties of these neurons explain the distance effect and Weber's law that characterize monkey and human number-processing behavior. Using fMRI and anatomical warping methods, Stanislas Dehaene proposes that the parietal areas that have been identified as the substrates of numerosity processing in humans and macaques are plausible homologs. Only humans, however, have the ability to access this numerosity representation through written and spoken symbols, which allows them to develop a full-fledged system of exact arithmetic. More generally, Dehaene proposes that human cultural inventions such as reading and arithmetic rely on a "recycling" of existing cerebral areas (a minimal conversion to a novel use) rather than the *de novo* creation of cultural cortical circuits through an all-purpose learning system.

David Perrett and his colleagues tackle the issue of whether only humans have a capacity to understand the actions, intentions, and minds of others. Behavioral experiments, mostly from chimpanzees, converges with recent single-cell recordings in macaques to suggest that primates possess a remarkable degree of competence for inferring the intentions of other congeners from their actions, with neural substrates in the superior temporal sulcus. In related work, Giacomo Rizzolatti and Giovanni Buccino examine the power and limits of the parieto-frontal "mirror neuron" systems, which provides a joint representation of the actions of oneself and of others. They demonstrate that a homologous parietofrontal mirror system is present in humans, and speculate that this system, common to production and comprehension of actions, could have played a crucial role in the emergence of language. Giuseppe Luppino describes in great detail the anatomy of parietal and frontal connections on which the action system is founded. He presents new anatomical findings on visual connections of the posterior parietal cortex and discuss the homologies between monkey and human parietal lobe organization. Atsushi Iriki further describes how part of these circuits are modified when macaque monkeys learn to use a tool in order to reach for objects. This innovative behavioral paradigm, which lends itself to basic neurophysiological, neuroimaging, and gene expression experiments, provides a new standpoint from which to speculate about the evolution of human toolmaking ability.

The issue of action understanding is taken one step further by Jeffrey Stevens and Marc Hauser, who ask how primates evolved the ability to cooperate with one another. They outline a series of constraints that any biological species must meet in order to develop cooperation, and specifically reciprocal altruism. Furthermore, they describe a new behavioral task in which multitrial reciprocation develops or fails to develop between two tamarin monkeys as a function of whether the initial acts of cooperation are intentional or not, thus revealing some of the behavioral mechanisms of cooperation in nonhuman primates. These studies open the door to future neurobiological assays of cooperation in human and nonhuman primates.

Cognitive control constitutes an essential element of cooperation as well as any other form of complex behavior extending over a period of time. Michael Petrides considers how the primate prefrontal cortex contributes to elaborate tasks that require cognitive control over the contents of working memory. Céline Amiez, Jean-Paul Joseph, and Emmanuel Procyk extend this analysis to the anterior cingulate cortex, which in humans appears as an essential element of many cognitive control tasks such as the Stroop test. They review anatomical, single-cell, and lesion studies that indicate that rewards and errors may be processed similarly by the anterior cingulate in both human and nonhuman primates.

Beyond these high-level cognitive functions, it is also essential, and perhaps simpler, to examine to what extent basic functions such as visual recognition and visual attention are also significantly related in humans and in other primates. Elinor McKone and Nancy Kanwisher review human neuroimaging evidence in favor of the hypothesis that a subpart of the ventral visual system houses mechanisms evolved for face recognition, as opposed to more general forms of expertise for within-category variation. This face recognition system may also be present in other primates. More generally, as discussed by David Van Essen, the primate inferotemporal cortex may constitute a plausible homolog of the human visual fusiform region for visual recognition, although the amount of cortical distortion and reorganization in this area remains to be fully understood. The inner workings of the primate inferotemporal cortex are analyzed in detail by Manabu Tanifuji, Kazushige Tsunoda, and Yukako Yamane. They describe convergent single-cell and optical imaging studies that begin to reveal how visual objects composed of multiple parts are coded by neural populations. Stanislas Dehaene argues that those populations of neurons may constitute an evolutionary precursor of the human reading system, since they require only minimal modification to be reconverted into an invariant visual letter and word recognition device.

Finally, Claire Wardak, Suliann Ben Hamed, and Jean-René Duhamel ask whether the macaque parietal lobe houses a visual attentional system comparable to the one observed in human neuropsychological and neuroimaging experiments. Parietal lesions in macaques lead to extinction and lesion orienting deficits comparable to those observed in human neglect patients, thus lending credibility to the hypothesis of a strong cross-species homology at this level, too.

The analysis of precursors of human abilities raises many further questions that cut across domains of cognitive competence. When does evidence of behavioral homology imply neurobiological or computational homology? To what extent do uniquely human cognitive abilities such as mathematics and reading rely on evolutionary ancient mechanisms? How can work on the evolutionary function of particular cognitive abilities integrate with work at the level of mechanism? None of the chapters provide any definitive answers to these difficult issues. Yet, by giving some concrete examples of possible homologies between human and nonhuman primates, this book as a whole sets the stage for any further attempts to characterize human nature.

In closing this preface, we would like to express our profound gratitude to the Fyssen Foundation for making this symposium possible. The topic of the symposium coincided nicely with the aim of the Fyssen Foundation, which is "to encourage all forms of scientific inquiry into cognitive mechanisms, including thought and reasoning, underlying animal and human behaviour, and their ontogenetic and phylogenetic developments." The symposium was organized by two members of the Scientific Committee of the Foundation, Stanislas Dehaene and Giacomo Rizzolatti, with the help and advice of a previous member, Marc Hauser, and an external expert, Jean-René Duhamel (who was also one of the first to receive a Fyssen fellowship in 1985).

Unfortunately, a shadow was cast on our scientific discussions by the sad news of the death of Madame Fyssen, only a few days before the meeting. Since 1982, Madame Fyssen had been the president of the Foundation, which she had created together with her husband in 1979. In spite of her age, she attended every meeting of the Scientific Council, and she had been looking forward to this symposium. Her personality and presence were driving forces that helped maintain the Foundation's focus throughout the years. Thanks to her generosity, the Foundation continues to play an important role in the development of brain and cognitive sciences, particularly in France, by awarding fellowships and grants to young researchers as well as a renowned international prize.

We are extremely grateful to the staff of the foundation, Nadia Ferchal, Fanny Bande and Julie Rubin for their efficacious support of both the organization of the meeting and the publication of this book.