

## Preface

This volume deals with a simple question: How does the brain choose efficiently and adaptively among available options to ensure coherent, goal-directed behavior? Hidden behind this question are many problems that necessitate a multidisciplinary approach. Indeed, to understand how humans and other animals solve this problem, we need answers from researchers versed in anatomy, traditional psychology, learning theory, neuroimaging, and mathematical modeling. The goal of this book is to provide the reader with an overview of key approaches that researchers are currently pursuing in this quest.

### **How This Volume Came About**

This volume was inspired by a meeting of the same name held at St. John's College, Oxford, June 2 through 4, 2010. The meeting was the fourth in a series that started around the turn of the century with a meeting in Jena, Germany, organized by Michael Coles and Wolfgang Miltner. That first meeting was motivated by an upsurge of research interest in the error-related negativity (ERN), a component of the human event-related brain potential that is elicited in the anterior cingulate cortex following errors in simple choice reaction-time tasks. The discovery of the ERN by Michael Falkenstein and colleagues in the early 1990s provided a clearly observable neural correlate of a key aspect of cognitive control: the ability to monitor ongoing thought and action to identify situations in which effortful, intelligent control is required.

The Jena meeting was followed in 2003 by a meeting in Dortmund, Germany, organized by Markus Ullsperger and Michael Falkenstein. By the time of this meeting, two prominent theories of the ERN had been proposed—the reinforcement learning theory of Holroyd and Coles, and the conflict monitoring hypothesis of Botvinick, Carter, and Cohen—giving rise to the meeting's title: "Errors, conflicts, and the brain." Both theories were grounded in formal computational models that could account for a number of behavioral and physiological phenomena observed in the psychological literature and that proposed possible underlying

neural architectures. Meanwhile, the ERN was being investigated in an increasing number of research fields, extending from traditional cognitive neuroscience to developmental psychology and psychopathology. This meeting resulted in a book edited by the organizers and published by the Max Planck Institute for Human Cognitive and Brain Sciences.

A third meeting, “Errors, conflicts, and rewards,” was organized in 2006 in Amsterdam, the Netherlands, by Richard Ridderinkhof, Sander Nieuwenhuis, and Rogier Mars. Reflecting the growing scope of research on cognitive control and performance monitoring, this meeting also included researchers working on nonhuman primate and rodent models of control. The title of the meeting also featured the word “reward,” signifying the increasingly evident convergence between research on performance monitoring and cognitive control, on the one hand, and studies of reward-guided learning and decision making on the other. Ridderinkhof, Nieuwenhuis, and Todd Braver edited a special issue of the journal *Cognitive, Affective, and Behavioral Neuroscience* (2007, 7:4) with contributions from speakers at this meeting.

The fourth meeting, held in Oxford in 2010, followed these trends of increasing the scope of the research presented while maintaining an emphasis on conceptual and methodological convergence in studies of the motivational and cognitive control of behavior. In addition to psychologists and cognitive neuroscientists, the speaker list included a zoologist, a behavioral economist, an anatomist, and a number of researchers with a background in engineering and machine learning. From a meeting focused on developments around a small number of event-related potentials, the meeting has expanded into a medley of approaches, each addressing the same underlying question: How does the brain choose efficiently and adaptively among available options to ensure coherent, goal-directed behavior? We have invited contributions to this volume from researchers working in a wide range of fields, reflecting the spectrum of approaches present at the meeting.

### **Organization of the Book**

This book is aimed at a graduate audience in all fields of research that deal with motivational and cognitive control. We hope that, besides providing an overview of cutting-edge research in the area, the volume will serve as a handbook that can be used by psychologists, biologists, economists, and neuroscientists alike. The contributors have been asked to situate their own findings and theories in the context of authoritative overviews of the relevant fields. For ease of further study, each chapter includes boxes with suggestions for further reading and questions that are outstanding in the field. In addition, interim summaries between the parts aim to integrate their contents into the wider literature.

The book begins with a consideration of the anatomical basis of control. The three chapters in part I each deal separately with one core component of the control system: the mechanisms of high-level control within the prefrontal cortex; the mechanisms of motivated action selection and learning in the basal ganglia; and the mechanisms of modulatory control by monoamine neurotransmitter systems. In the first chapter, Sallet and colleagues focus on anatomical aspects of the interaction between lateral and medial prefrontal cortex, a prominent feature of many models of cognitive control. The chapter by Haber focuses on the connectivity of basal ganglia circuits, which are increasingly recognized as providing a crucial point of convergence between cognitive and motivational influences on behavior. Haber describes the various pathways of communication within reward circuits of the brain and between reward and association circuits, and the interactions among these networks. In the third chapter, Ullsperger describes the role of modulatory neurotransmitters in control, focusing primarily on dopamine, serotonin, and norepinephrine.

Part II addresses the contributions of the cerebral cortex to control. Building on the anatomical perspective taken in the first section, these chapters focus on the functional architecture of cortical control. The chapters by Boorman and Noonan and by Kennerley and Tobler provide complementary perspectives on the contributions of subregions within prefrontal cortex to action selection and choice based on reinforcement value. Laubach focuses on the frontal cortex in rats, providing a basis for the expanded cortex in human and nonhuman primates discussed in the following chapters. Mars and colleagues look at how the prefrontal cortex exerts control via modulation of activity in posterior brain areas. Pearson and colleagues extend the field of focus from the frontal lobes to the posterior cingulate cortex, a region of the brain often seen in imaging experiments of control but thus far largely neglected in the literature.

Part III considers the many ways in which subcortical brain regions underpin the control functions of the cortex. Two of the contributions focus on the role of the basal ganglia: Liljeholm and O'Doherty review evidence on the role of the basal ganglia in instrumental behavior, while Greenhouse and colleagues discuss the contribution of these structures to a hallmark feature of cognitive control: response inhibition. In the other chapters in the section, the focus is on the role of monoamine neurotransmitter systems: Walton and colleagues provide an in-depth look at the most widely studied neurotransmitter in the field of motivational control, dopamine. In the final chapter, Nieuwenhuis reviews work on the locus coeruleus norepinephrine system, which influences cortical functioning through its widespread network of cortical connections.

Whereas most chapters in this volume focus on group-averaged data, assuming that the neural systems in question operate in a similar manner across individuals,

the contributions in part IV focus on three types of individual differences in control. First, Van den Bos and Crone look at changes in neural control of social decisions during the development from adolescence into adulthood, showing how neural functioning and behavior undergo substantial changes during this period. Ridderinkhof and colleagues then review evidence regarding individual differences in control in the adult population. Their chapter specifically focuses on how incorporating individual differences into one's research can shed new light on the interface between motivational and cognitive control. Finally, De Bruijn and Ullsperger discuss performance monitoring in patient populations, showing how various neurological and psychiatric conditions are associated with specific and identifiable disturbances in cognitive control.

Research on cognitive and motivational control has historically benefitted greatly from the use of explicit computational models of neural functioning. Part V takes a closer look at recent developments in computational approaches that have been particularly influential in this regard. Ribas-Fernandes and colleagues provide an overview of formal models of learning, proposing a hierarchical reinforcement model of behavior. This focus on reinforcement learning is followed in chapters by Cockburn and Frank and by Holroyd and Yeung. Both chapters consider the relationship between the basal ganglia and prefrontal cortex in motivational and cognitive control, while presenting somewhat contrasting accounts of the respective roles of the basal ganglia and anterior cingulate cortex. The chapter by Khamassi and colleagues provides a complementary perspective on "meta-control" and the mechanisms by which the control system is itself optimized. Once again, the focus is on lateral and medial prefrontal regions. Finally, Shenoy and Yu adopt a Bayesian approach that considers paradigmatic response inhibition tasks within a rational decision-making framework.

The concluding part VI comprises three chapters that highlight recent overarching trends in the literature. Chierchia and Coricelli discuss the influence of concepts and methodologies from economic decision theory on theorizing and experiments in the study of control. Hunt and Behrens discuss how the approaches apparent in this volume are now starting to be used to solve problems in more complex and applied domains, focusing in particular on the neuroscience of social decision making. Finally, Bestmann and Mars look at how computational models such as those proposed in part V can be formally linked to the experimental data obtained in neuroimaging and electrophysiology experiments.

## **Acknowledgments**

As Jared Diamond and James Robinson state in their recent edited volume (*Natural Experiments of History*, Harvard University Press, 2008), completing an edited book

costs each editor on average two friends, because of the various levels of stress involved in the process. We are grateful that this has not proven true in our case. We thank all of our contributors, as well as the speakers and attendees of the Oxford meeting, for making both the meeting and this book a success. We are tremendously grateful to the International Brain Research Organization, the UK Neuroinformatics Node, the Guarantors of Brain, and the McDonnell Network of Cognitive Neuroscience at the University of Oxford for their generous financial support, and to the staff at St John's College, Oxford, for their warm hospitality at the June meeting. We thank MaryAnn Noonan, Laurence Hunt, and Vanessa Johnen for their able assistance in organizing that meeting. We are delighted to be able to publish this book with MIT Press, and would like to thank specifically Susan Buckley and Robert Prior, who have provided unwavering support to a group of first-time editors. Finally, we would like to thank our colleagues, friends, and families for their support during periods of stress and strain as we worked on this volume deep into the night.