Preface to the Second Edition

In this second edition of *Exploring the Thalamus and Its Role in Cortical Function* we have brought some of the material up to date, modified some of the illustrations, and addressed several issues that arose in discussions with colleagues, students, and each other. Whereas for the first edition we deliberately kept the focus on the thalamus, in this edition we explicitly recognize that new knowledge gained about the thalamus will play an increasingly important part in the way we think about cortical functions. We have extended the title of the book to reflect this and have introduced an additional chapter that deals with action and perception, functions that are recognizably cortical. Growing knowledge of thalamic functions will force a reappraisal of the way in which we think about the cerebral cortex and its interactions with the rest of the nervous system.

Current views of cortical function and experimental approaches to understanding the cerebral cortex are heavily dominated by what can best be described as a corticocentric view. In this edition we explicitly challenge this view more strongly than we did in the first edition. The dominance of the view appears to us to be more obvious now than it was when we were writing the first edition. It is a point we consider more fully in chapter 10. Essentially, the view represents a failure to recognize that all neocortical areas receive important inputs from the thalamus and send important outputs to the motor centers of the brain. There is probably no area of cortex that lacks direct input from the thalamus and output connections with other subcortical centers. The contemporary view that dominates the literature ignores these connections. Over and again cortical function is analyzed in terms of hypothetical messages that pass from one cortical area to another, going through a complex hierarchy of corticocortical connections, from the "lowest" centers that receive sensory messages through a series of higher centers that eventually connect to motor actions or to memory storage, without any communication with subcortical centers until a final cortical decision for output has been reached. The nature of the message is left unexamined, and the intermediate stages of processing are thought of as being primarily, or more often entirely, parts of cortical mechanisms for producing an elaboration of receptive fields at early stages or of motor commands higher in the hierarchy. The extent to which even the "highest" cortical areas have thalamic inputs and the "lowest" have motor outputs is simply not recognized.

If we aim to understand how thalamic functions relate to cortical functions, we have to understand the circuitry that links each cortical area not only to other cortical areas but also to thalamic inputs and motor outputs, and we have to understand how any particular cortical cell is linked into these pathways. Much contemporary research involves imaging methods for localizing cortical activity in awake human or experimental subjects, or recording the activity of single cortical nerve cells in awake experimental animals trained to undertake tasks designed to reveal the perceptual or motor capacities of the nervous system. Neither of these approaches is suited to exploring the nature of the circuitry that links cortical areas or connects nerve cells within cortical areas. The functional connections must be hypothesized, but cannot be experimentally demonstrated by these methods. As a result we have a plethora of fascinating results about what particular cortical areas (or nerve cells within particular areas) can do, with no analysis of, and often no questions about, the circuitry that leads to these capacities. Some of this circuitry may well be primarily focused in the cortex, but much must involve the thalamus, forcing us to think of the thalamus as a key player in cortical function.

In the past few years it has become clear that many and perhaps virtually all of the inputs to the thalamus are copies, through branching axons, of motor instructions. Some are motor instructions that are being issued by ascending afferents, others are instructions issued by a lower cortical area and copied through an axonal branch via a thalamocortical link to higher cortical areas. That is, the information that the cortex receives from the thalamus is primarily information about ongoing motor instructions. Cortical functions, which have been analyzed in the past in terms of hierarchical links that carry sensory messages about external events, can instead be viewed in terms of corollary links, or efference copies that carry information about instructions for action, and these can be seen as providing the neural basis of perceptual processing.

This book was first conceived as an exploration of the thalamus itself, and in the first edition we attempted to define some of the functional categories that might prove critical in understanding thalamic functions. These categories included the distinctions between drivers and modulators, first order and higher order thalamic relays, and bursting and tonic discharge patterns. Some of these distinctions can be taken further now than was possible in the first edition. They are explored in the chapters that deal with thalamic organization itself, and it is our hope that they will serve as key categorizations for an understanding of the thalamus. As we look ahead, the role of the thalamus will necessarily become more entwined with the cortex; as we stressed in the first edition, the two are intimately related, and in this second edition we have started to explore not just the thalamus but, more than before, its role in cortical function.

Apart from these considerations, the general aims of the book and our purpose in writing it are as stated in the preface to the first edition. There is nothing to add other than to thank Mriganka Sur, Peter Ralston, and Gary Matthews for commenting on a draft of the second edition, and Marjorie Sherman for careful proofreading. During the period of preparation of the second edition both authors received support from the National Institutes of Health (grants EY03038 and EY11409 to S.M.S. and EY012936 to R.W.G.).

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