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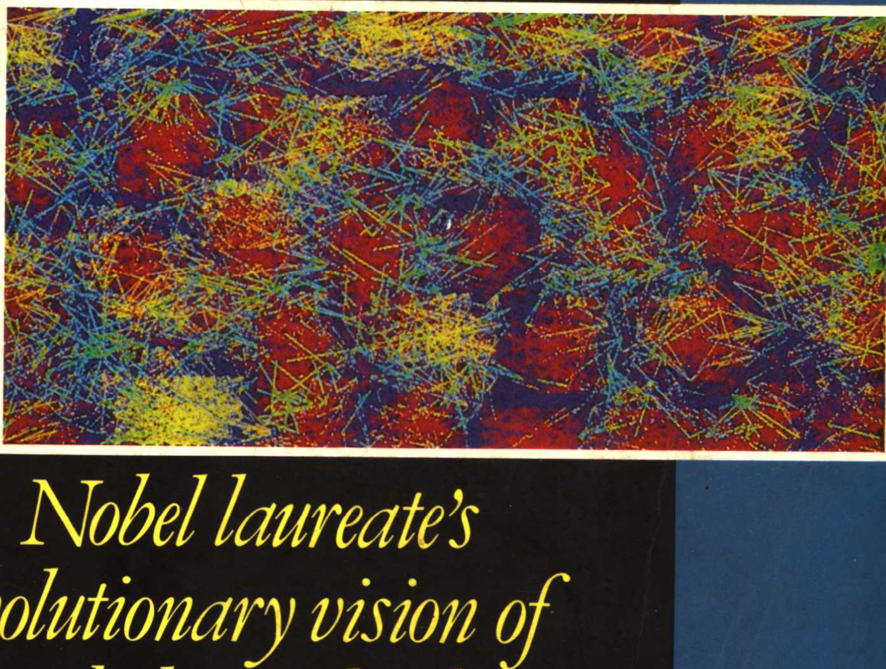
NEURAL DARWINISM

The Theory of Neuronal Group Selection



A Nobel laureate's revolutionary vision of how the brain develops and functions

GERALD M. EDELMAN

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To suppose that the eye with all its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration, could have been formed by natural selection, seems, I freely confess, absurd in the highest degree. When it was first said that the sun stood still and the world turned round, the common sense of mankind declared the doctrine false; but the old saying of "Vox populi, vox Dei," as every philosopher knows, cannot be trusted in science.

—CHARLES DARWIN
The Origin of Species, Sixth Edition
Organs of Extreme Perfection and Complication

And in the midst of this wide quietness
A rosy sanctuary will I dress
With the wreath'd trellis of a working brain,
    With buds, and bells, and stars without a name,
With all the gardener Fancy e'er could feign,
    Who breeding flowers, will never breed the same

—JOHN KEATS
Ode to Psyche

PREFACE

The purpose of this book is to describe a theory of brain function aimed mainly at an understanding of the biological bases of perception. The theory of neuronal group selection addresses this problem by attempting to answer several key questions. How are connections specified in large neuronal populations? What principles determine the organization of representations and maps in the nervous system? What are the bases in neural structure of perceptual categorization and generalization? The theory proposed to answer these questions is cast in terms of a rigorously selectionist view relating brain development and evolution to structure and function. In the theory, population thinking, the central theoretical mode of biology itself, is applied to individual brains functioning in somatic time. The theory insists that an adequate explanation of higher brain functions first requires an explanation of those developmental constraints on evolution that lead to somatic variation in both brain structure and brain function. Selection of functional variants from neural populations that emerge as a result of this variation during an individual's development is held to be the central principle underlying behavior. This approach is not at present accepted, nor does it have strong antecedents in the history of a science replete with speculations in other categories of ideas.

To be scientifically sensible at this stage of our knowledge, certain constraints must be put on any attempt to relate the brain to psychological activity. In undertaking this theoretical task, I have therefore limited myself stringently to what might seem to a cognitive psychologist to be a very restricted set of psychological functions. I hardly touch upon some of the grand themes that run through William James's (1890, republished 1950) magnificent *Principles.* Consideration of a more modern list (Norman 1981) of the "essential twelve issues"—belief systems, consciousness, development, emotion, interaction, language, learning, memory, primary perception, performance, skill, and thought—will illustrate how narrow is my sweep. The key list I shall consider is: development, perception (in particular, perceptual categorization), memory, and learning, and I will take up these subjects in that order. My hope is that once a constrained theory adequate to link these processes is built, it may become possible to construct a more comprehensive description, not just in terms of perceptual categorization but also in terms of perceptual experience.

It appears to me that such restraint is necessary if we are ever to get anywhere in the extraordinarily challenging domain of understanding the biological bases of psychology. At the same time, no such limitation must be placed on subject matter: a net must be cast broadly over many fields in search for evidence that may be pertinent. This is the strategy I have used here, in the belief that a sound theory must be consistent with the central principles of developmental and evolutionary biology. One of the implicit assumptions I have made is that, to be successful, the theory must confront several central unsolved problems of these fields, particularly those concerned with the relationships between developmental genetics, epigenesis, and morphologic evolution. Accordingly, in providing support for the theory, I have ranged from molecular biology to ethology and back again.

Some further words about the order of topics may prove useful to the reader. The first part of the book is devoted to a general description of neuronal group selection in somatic time. The second part considers in a rather rigorous fashion the two main epigenetic mechanisms governing such selection during embryogenesis and behavior. These mechanisms are embedded in the context of salient facts of developmental biology and evolution. Because of the generality of the embryogenetic events considered in chapter 4, it may seem to deviate from the central subject of the nervous system. Nevertheless, that chapter describes the first of the epigenetic mechanisms that account for the origin of anatomical diversity, and I therefore deemed it particularly important to connect the central principles of nonneural development to neural development. The second epigenetic mechanism of the theory (that which results in synaptic selection) must be presented in formal terms to be truly convincing. Those readers who find this tedious upon a first reading of chapter 7 may ignore the mathematics; they will find qualitative descriptions of various changes in synaptic efficacy and their consequences interspersed in the material of that chapter. The third part of the book is devoted to an understanding of the integration of the two epigenetic mechanisms within phenotypes capable of motor action, categorization, and learning. Its main aim is to define the smallest selective unit capable of such global functions.

Many recent subjects of central neurobiological significance have not been accorded major treatment. These include, among others, the detailed analysis of the visual system, the regional mapping of neurotransmitters, the endocrine modulation of neural function, and various features of invertebrate nervous systems. The guideline used in choosing the examples that I have discussed is whether they embody evidence relating directly to critical points of the theory. The result may appear at first glance to be a rather unconventional assembly of examples from various biological disciplines. I can only hope that the reasons for my choice will become evident as the reader gains further comprehension of a theory that is itself unconventional. In any case, I have made efforts wherever possible to provide detailed models of particular ideas or processes, in the expectation that the hazards that this procedure entails are more than compensated for by its heuristic value. I believe this approach to be useful at an early stage of understanding of any subject and in particular when confronting the intricacies of brain function.

Because this is both a complex and an unfamiliar subject, I have also used an unconventional device in an effort to help the reader. At the head of each chapter is a running list of the key subjects, examples, or ideas presented in that chapter; main examples that contradict received ideas or that are particularly salient to the theory are italicized. These lists were designed to be useful in anticipating and reviewing the chapter contents, but they are *not* keyed to the section headings, which are listed in the table of contents proper. A short introduction containing a précis of the theory and a brief history of population thinking in neurobiology have been placed in chapter 1, prior to the evidential arguments and the deeper considerations of central ideas that are presented in subsequent chapters. At best, this terse description can give only a hint of what is to come. After having provided a more thoroughgoing description of the theory of neuronal group selection in the main body of the text, I offer a number of specific predictions at the end of the book in an attempt to define the limits of the theory and to show that it is empirically testable.

This book barely touches upon the psychologically important issue of social transmission, but I have been constantly aware of that process in writing it. The frequent interactions with my colleagues at the Neurosciences Institute (NSI), particularly its research director, Dr. W. Einar Gall, have provided a sustaining force for which I am

grateful. I am also grateful to Susan Hassler, editor at the NSI, for her help. It has been a privilege to work at the Institute with Dr. Leif Finkel and Dr. George N. Reeke, Jr., on several models that are important to the theory. The opportunity to share ideas with them within the scholarly atmosphere of the NSI encourages me in the hope that the Institute will continue both to support the development of theoretical work in the neurosciences and to encourage younger scientists in its pursuit.

New York, 1986

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PART ONE

SOMATIC SELECTION

1

A Summary and Historical Introduction

INTRODUCTION

It is difficult to imagine the world as it is presented to a newborn organism of a different species, no less our own. Indeed, the conventions of society, the remembrances of sensory experience, and, particularly, a scientific education make it difficult to accept the notion that the environment presented to such an organism is inherently ambiguous: even to animals eventually capable of speech such as ourselves, the world is initially an unlabeled place. The number of partitions of potential "objects" or "events" in an econiche is enormous if not infinite, and their positive or negative values to an individual animal, even one with a richly structured nervous system, are relative, not absolute.

Whether richly structured or simple, nervous systems evolved to generate individual behavior that is adaptive within a species' econiche in relatively short periods of time. Such behavior in a phenotype requires initial categorization of salient aspects of the environment so that learning can occur on the basis of the resultant categories. A fundamental task of neuroscience is thus to show how, in a particular species, the structure and function of the nervous system permit perceptual categorization to occur as a basis for learning and meaningful adaptive behavior. Ultimately, this comes down to the question: How can we relate perceptual psychology to neural structure and function? Many previous attempts to provide an answer to this question have relied on various theories that are based on the notion of information processing. In this book, I shall suggest instead that a satisfactory answer to this question requires a new theory, one that has widespread consequences for neuroscience as well as for our understanding of our own place in nature. In this introductory chapter, I shall outline this theory and briefly consider its historical antecedents. My hope is that this may ease the reader's later course through the various lines of evidence adduced in its support. At the same time, I recognize that this outline has the deficiencies of being overly abstract and that a fuller comprehension of the main ideas of the theory will require a detailed consideration of that evidence.

A Brief Outline of the Theory

The theory of neuronal group selection was formulated to explain a number of apparent inconsistencies in our knowledge of the development, anatomy, and physiological function of the central nervous system. Above all, it was formulated to explain how perceptual categorization could occur without assuming that the world is prearranged in an informational fashion or that the brain contains a homunculus. The reasons for abandoning information processing as the primary mode of brain function will be presented in detail in the next chapter; my main purpose here is to outline the central ideas of an alternative view.

To account for categorization without assuming information processing or computing, the theory proposes that the key principle governing brain organization is a populational one and that in its operation the brain is a selective system. According to the theory (Edelman 1978, 1981; Edelman and Reeke 1982; Edelman and Finkel 1984), the brain is dynamically organized into cellular populations containing individu-