

# NEURAL DARWINISM

The Theory of  
Neuronal Group Selection

---

GERALD M. EDELMAN

Basic Books, Inc., Publishers

New York

# CONTENTS

---

LIST OF ILLUSTRATIONS	xiii
LIST OF TABLES	xvii
PREFACE	xix

## PART ONE

### SOMATIC SELECTION

1. A Summary and Historical Introduction	3
Introduction	3
A Brief Outline of the Theory	4
Population Thinking in Neurobiology	8
Natural Selection and Population Thinking in Relation to Behavior	10
Decline and Reinstatement of Selectionist Ideas	11
Ideas of Somatic Selection	14
Critical Distinctions among Selectionist Ideas	17
Selection and Instruction in Global Brain Theories	20
2. Structure, Function, and Perception	23
Introduction	23
Perceptual Categorization and Generalization	26
Diversity and Overlapping Connectivity in Neural Structures	33
Critical Challenges to Instructionist or Information Processing Models	37

3. Neuronal Group Selection	43
Introduction	43
Degeneracy and the Definition of a Group	46
Sites of Variability	57
The Need for Reentrant Structure and Function	60
Explanatory Power of the Theory	64
The Adaptive Significance of Neuronal Group Selection	67

## PART TWO

## EPIGENETIC MECHANISMS

4. Developmental Bases of Diversity: The Primary Repertoire	73
Introduction	73
CAMs and Cell Surface Modulation in Morphogenesis	74
CAM Expression Sequences in Embryogenesis and Neurogenesis	83
Causal Significance of CAM Function	88
The Regulator Hypothesis	93
Variability and Constancy of Pattern in Neural Structure	100
5. Cellular Dynamics of Neural Maps	105
Introduction	105
Representation and Mapping	107
Developmental Constraints on Map Formation	110
Cellular Primary Processes and Selection	117
Map Ordering in Development	121
Adult Maps: Stabilized Competition within Fixed Circuitry	126
<i>Variability in Functional Maps and Map Reorganization</i>	127
<i>Arborization and Overlap</i>	133
<i>Map Changes Linked to Critical Periods</i>	136
Conclusions	138
6. Evolution and Function of Distributed Systems	140
Introduction	140
Evolutionary Change in Neural Networks	143
A Network Example	148

- Interspecies Variability: The Evolutionary Origin of Nuclei,  
Laminae, and Parallel Circuits 151
- Developmental Constraints and Evolutionary Change: The  
Relationship of the Regulator Hypothesis to Heterochrony 156
- Evolutionary Maintenance of Degeneracy in Distributed  
Systems 162
- Overlapping Arbors and Reentrant Maps 163
- Group Confinement* 166
- Group Selection* 169
- Group Competition* 170
- Map Function and Heterochrony 173
7. Synapses as Populations: The Bases of the Secondary  
Repertoire 178
- Introduction 178
- Background for a Population Model 180
- A Formal Example of the Postsynaptic Rule and an Application to  
    Mapping 183
- A Formal Treatment of Presynaptic Modifications 192
- Population Effects Arising from Dual Rules in a Network 195
- Consequences of a Population Model Obeying Dual Rules 198
- Transmitter Logic 203
- The Relation of Synaptic Change to Memory 204

## PART THREE

## GLOBAL FUNCTIONS

8. Action and Perception 209
- Introduction 209
- The Motor Ensemble 212
- Evolutionary Considerations 213
- Functional Bases of Gestures 221
- Gestures and Neuronal Group Selection 226
- Motor Activity Affecting Sensory Sheets: Feature Correlation and  
    Parallel Sampling 231
- Global Mappings 236
- Summary 238

9.	Categorization and Memory	240
	Introduction	240
	Restrictions and Definitions	243
	Categorization	244
	Perceptual Categorization	247
	<i>Generalization in Pigeons</i>	247
	<i>Object and Auditory Recognition in Infants</i>	251
	Critical Summary	256
	Neural Organization and the Process of Generalization	259
	The Problem of Memory Reconsidered	265
10.	Selective Networks and Recognition Automata	271
	Introduction	271
	The System Design of Darwin II	272
	The Responses of Darwin II	279
	Performance Limitations and Prospects	288
11.	Selection, Learning, and Behavior	291
	Introduction	291
	The Modern Interpretation of Learning Experiments	293
	Learning and Surprise	295
	Behavior and Conditioning	297
	Hierarchies of Selection in Developmental Learning: Bird Song	300
	Neuronal Group Selection in Learning	303
	From Selective Reentrant Networks to Information Processing	308

## CONCLUSION

12.	Summary, Predictions, and Implications	315
	Introduction	315
	Adequacy	321
	Predictions	323
	<i>Selection Mechanisms</i>	323

*Mapping Arrangements and Reentry* 325  
*Perceptual Categorization and Learning* 326  
Unfinished Business and General Implications 328

REFERENCES 331  
ABBREVIATIONS AND MATHEMATICAL SYMBOLS 355  
CREDITS 357  
INDEX 359