Preface

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In the thirty years since identified neurons became a subject of serious attention in neuroscience its accomplishments have become too diverse to be reviewed in any meaningful way in a single volume. The goal of this volume is to be a milestone, which both indicates the distance we have traveled and points out the long road ahead, without attempting to provide the detail of a road map or travel guide; John Fentress's classic volume in 1976, 'Simpler Networks and Behavior' was perhaps the last real overview of the whole field. The four authors here (Theodore H. Bullock, James L. Larimer, Janet L. Leonard, and George J. Mptso) present individual views of the role of identifiable neurons in the organization and control of behavior. Since 1967, when Felix Strumwasser contributed a chapter entitled 'Types of information stored in individual neurons' to C.A.G. Wiersma's classic volume, 'Invertebrate Nervous Systems' and identified eight types of information, it has become very clear that identifiable neurons (and probably all neurons) are much more flexible and multifunctional than we once assumed and/or hoped. As Ted Bullock's overview points out, the last twenty years have seen a more or less geometric increase in the number of known neurotransmitters, neuromodulators, ion channels, second messengers, etc. As the arsenal of neurobiological techniques increases, so do the opportunities to identify neurons individually. Jim Larimer's review of the classic system of 'command neurons', the abdominal positioning interneurons in the crayfish abdomen, shows that essentially all of the neurons involved are potentially identifiable and that understanding the neuronal control of behavior in this system requires consideration of large numbers of neurons and a statistical approach. This approach involves a novel application of techniques and statistics to neuroscience, such as

mark-recapture studies and the Lincoln index, which are standard techniques in population biology but are used here to estimate the size of populations and functional groups of neurons involved in behavior. These techniques should have a wide application in neurobiology and will help identify the boundaries between 'simple' and more complex systems. In fact, one of the striking new developments over the last 20 years is a blurring of the lines between studies of 'simple' systems of identifiable neurons on the one hand and more complex neuronal networks involving large numbers of more or less anonymous neurons. Ted Bullock uses the term 'addressable' to describe both individually identifiable neurons and identifiable sets of neurons, and one wonders whether the study of identifiable neurons per se will remain a distinct subdiscipline. Just as Linnaeus's theory of the 'fixity' of species was a necessary precursor to Darwin's theory of the mutability of species, so the concept of the invariant neuron and the fixity of circuits, along with the existence of identifiable neurons, has made it possible to document the intrinsic variability of individual neurons and the dynamic interactions that form circuits.

By the mid-1980's, Graham Hoyle and his students, working in insect locomotion, Getting and Dekin working on swimming in the marine mollusc *Tritonia*, and the crustacean stomatogastric ganglion community (Selverston, Moulins, Harris-Warrick, Marder, etc.) [for references and discussion see Leonard, 2000] had all developed the hypothesis that individual identified neurons can have multiple functions and that simple circuits composed of a small number of identifiable neurons can be 'polymorphic' to use Getting and Dekin's term [discussed also in this volume by Bullock, 2000; and Larimer, 2000]. Jim Larimer's discussion of the classic identified neuron system, the abdominal posi-

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0006-8977/00/0555-0233\$17.50/0

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tioning system of the crayfish, shows that individual neurons once thought to be dedicated to abdominal positioning are also involved in swimmeret movements and steering behavior. The picture of the neural control of the movements of crayfish abdomen that is emerging from the work of Jim Larimer's laboratory is one of hierarchical organization of behavior that seems very reminiscent of the ethological hypotheses of G.P. Baerends [1976; discussed in Leonard, 2000].

By the early 1990's there was increasing interest in the analysis of simple circuits from the standpoint of dynamic systems theory and/or from a computational point of view [cited and discussed in the papers by Leonard, 2000 and Mpitsos, 2000]. This interest seems to be based on the realization, emerging more or less simultaneously from data in several systems, that even in small systems of identifiable cells, function and processing are distributed among several neurons. Even the classic 'command neurons' of the crayfish are shown in this volume by Jim Larimer to be better described as 'command elements' according to the Kupfermann-Weiss [1978] model. As George Mpitsos demonstrates [2000], recent progress in the analysis and description of complex and nonlinear systems, and the development of neural network models in artificial intelligence and biological systems have shown that it is in principle possible for complex, patterned activity to be 'self-organized' from the nonlinear behavior of an ostensibly simple system or circuit. His discussion of the complex self-organizing properties of even simple systems gives a sobering view of the limitations of a strictly deterministic approach and a look forward at the concepts and methods that we are starting to need in order to understand even very simple circuits.

Another reason for the use of a more computational approach is that in many cases the nature and strength of connections between neurons is plastic and can be modulated by local environmental conditions. These results make the identified neuron a more important tool than ever, because, without identified neurons the task of identifying and describing the types and sources of variability in a circuit is virtually impossible. There is also increasing evidence that specific motor patterns may be produced in more than one way [see Bullock, 2000; Leonard, 2000]. Knowing that self-organization is possible in principle, it becomes necessary to attempt to determine whether this does or does not occur in the systems we are studying. In the interest of providing new generalizations to guide our thinking and/or new dragons to slay, the paper by Leonard provides: (a) two alternative models of the production of identifiable motor patterns by multifunctional circuits; one based on Hoyle's orchestration model [Sombati and Hoyle, 1984], but gener-

alized to fit cases such as the crayfish abdominal positioning system, and the other, a simplistic but testable model of a self-organizing system, and (b) a brief discussion of the relationship of neural architecture to circuit function.

Ted Bullock, Janus-like, looks simultaneously forward and backward, in his overview of identifiable neurons, identifying not only the progress that we have made but also persistent areas of ignorance that will need to be cleared up before we can understand the general principles by which behavior is produced by nervous systems. As Jim Larimer demonstrates, as systems of identifiable neurons become larger, new techniques and concepts need to be employed so that a picture of the functional forest emerges from the identifiable trees. The last twenty-five years has seen the spectacular development of improved techniques for multi-unit recording (cuff electrodes, optical recording techniques, computer techniques for spike train analysis, etc.) along with the increasing understanding of the subtleties in the activity of identified neural circuits that have the potential to allow us to test the models presented in this volume in intact, freely-moving animals and/or more intact preparations. One can predict that in next decade at least one of the important uses of identified neurons and simple circuits will be as models for understanding the ways in which neuromodulators act to perform computations in parallel distributed circuits, store and address distributed representations in Hopfield networks, and/or adjust synaptic weights in feed-forward networks during associative learning [Mpitsos, 2000]. While identifiable neurons may be disappearing as an independent field, their usefulness in understanding the principles that govern nervous systems is undoubtedly going to blossom.

In a companion volume ('Simpler systems in comparative and integrative neurobiology'), that will appear as a special Festschrift issue of *Progress in Neurobiology* for the 85th birthday of Ted Bullock, reviews of the control of behavior in a variety of model systems (leech swimming by Peter Brodfuehrer and Maria Stella Thorogood; gastropod feeding by Don Murphy; insect behavior by Chris Comer and Mel Robertson; Mauthner cells by Robert Eaton, R.K.K. Lee and Mark Foreman; and lamprey swimming by Jim Buchanan) demonstrate the power and potential of identifiable neurons and addressable units in both documenting the dynamic properties that are most likely characteristic of all neurons and understanding how the networks of such dynamic units act to produce behavior. The ideas contained in the present volume will, we hope, serve to stimulate further research, offering ideas for experimentation with simpler systems and perhaps, explanations for the behavior of more complex systems.

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