Neuroscience: a new era?

H. B. Barlow


The power of Darwinian selection is much in evidence these days, especially after the success of the clonal selection theory in immunology; it has, for instance, been applied to the travelling salesman problem by Brady (Nature 317, 804–806; 1985) and to the learning of temporal sequences such as bird song by Dehaene and colleagues (Proc. natn. Acad. Sci. USA 84, 2727–2731; 1987).

The basic idea of Gerald Edelman’s book is stated in the title: neurons are organized into groups, and these groups are subject to a selection process which forms the anatomical and functional patterns of connection that are responsible for the astonishing performance of the brain. Assessment of the merit and originality of the idea depends upon the specifics of these proposals: what are neuronal groups, what are the selective processes applied to them, and where is the potential for exponential growth that is so essential for a Darwinian process to have the power it does? Finding answers to these questions is not easy, for although the distinguished author has obviously made desperate efforts to explain himself clearly, this is an exceedingly difficult book to read and understand.

One of the difficulties is stylistic. In discussing the localization of function in the brain, Edelman says (pp. 141–142): “The position taken here (and the only one consistent with neuronal group selection theory) is that the real basis for overall functional responses is the dynamic interaction of specific individual components arranged in repertoires of neuronal groups or populations within different mapped reentrant structures rather than the fixed assignment of function to anatomically distinct regions”. That sentence is hard to understand, and so are many others in the book.

A second difficulty lies in the lack of clarity and completeness in the definitions. For example, it is crucial to understand exactly what Edelman means by the term “neuronal group”, which figures so prominently in his thinking. Perhaps the simplest question to ask is: are the groups overlapping, or non-overlapping? If a given neuron can belong to more than one group the number of possible groups is virtually unlimited and it might be possible to devise a rule for group reproduction that would give the potential for exponential growth. Both Darwin and Wallace appreciated that it was the potential Malthusian population explosion that gave natural selection its immense power, and the glimpse of neuronal groups with these properties makes one say to oneself “Aha, this idea might work”. If, on the other hand, the groups are non-overlapping, then reproduction and selection can merely shuffle neurons from one group to another, and it is hard to believe that this contains any such exciting potential.

Eagerly turning to the book, one finds the primary definition of a neuronal group on pp. 46–47, as follows: “... a collection of cells of similar or variant types, ranging in number from hundreds to thousands, that are closely connected in their intrinsic circuitry and whose mutual dynamic interaction may be further enhanced by increases in synaptic efficacy”. This does not resolve the issue, and it is not for another 150 pages or so that it becomes reasonably clear that, alas, the groups do not overlap. Such an elementary point upon which so much hinges should have been resolved with the first definition.

It is disappointing that groups appear to be non-overlapping, but it is hard to see the merit of the overall concept for other reasons as well. Edelman says (pp. 164–165): “According to the model, a neuronal group in the cerebral cortex is functionally defined as an ensemble of cohesively interconnected cells, all of which express the same receptive field”. In the visual cortex there are no reports of two or more different cells having identical receptive fields. But apart from the lack of experimental evidence for such groups, what theoretical or practical advantage could be conferred by having a set of cells with identical function?

The selection process is the next hurdle. This depends upon synaptic modification according to a Hebbian rule, as in so many current neural network models (for example, Longuet-Higgins et al. Q. Rev. Biophys. 3, 223–244; 1970 and Parallel Distributed Processing, by McClelland, Rumelhart and the PDP research group, MIT Press; 1986). What is curious, however, is that in Edelman’s version the result of positive selection is to incorporate more and more cells into the same group. What is the benefit of this? It is not like the increase in population of a species, which implies that they have successfully competed for a larger fraction of the available primary resources so that the genes responsible for the success have multiplied. For more and more cells in one group to belong to the same structure seems to confer no particular advantage either to the cells, or to the group, and nothing corresponding to the genes has been proposed. Such a process would probably wreck the function of the whole brain, for if the cells in a group respond to a larger fraction of the sensory stimuli being received, this implies that they are becoming less selective. Thus Edelman’s type of selection does not seem to happen, and it is hard to see how it would confer any advantage if it did.

The book contains an interesting section on cell adhesion molecules and their effects in development, but this is not a complete review of all the work in the field. There are also accounts of two computer simulations of the processes Edelman thinks are at work in the brain, and these have the merit of trying to give greater precision to the ideas that his words leave unclear.

This is not a book for the faint-hearted, because of its difficulty and obscurity, nor is it for the untutored, because it gives such an incomplete and one-sided account of brain development and function. But epoch-making books are often panned unfairly by bigoted reviewers, so readers are strongly urged to study “this magisterial work” (as the publisher’s blurb calls it) and decide for themselves whether it ushers in a new era in neuroscience, or whether it’s just a hopeless muddle.

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Groups and grandmothers in neuroscience

Sir,—In his review of Neural Darwinism: The Theory of Neuronal Group Selection (Nature 331, 571; 1988) Horace Barlow has made several factual errors and has misrepresented the theory by misinterpreting the nature of neuronal groups. Barlow’s chief objection is that neuronal groups cannot carry out the functions proposed by the theory. This misinterpretation arises because he does not understand that the major mechanism of selection acts upon synapses in populations1. Barlow says that the theory uses Hebb’s rule for synaptic plasticity. In fact, the book states explicitly (p.201) that these populations do not, in general, obey hebbian rules. This misunderstanding by Barlow invalidates all of his dependent arguments: in fact, increasing numbers of cells do not have to be incorporated into groups, experience makes the cells in a group more selective not less, and neuronal group selection confers a number of advantages that have been clearly outlined in the book. Not the least of these is that it accounts for the dynamic organization of topographic maps3.

Barlow is also confused about how receptive fields are represented by cells in groups. Receptive fields are similar within a group but not identical. Moreover, the purpose of cooperativity within a group is to provide sharp functional boundaries in an otherwise diverse and overlapping anatomy. The combinatorics afforded lead to an immense diversity: admittedly, the diversity is not as immense as would obtain from permuting individual neurons, but it is overwhelmingly larger than could be represented by Barlow’s concept that individual neurons each “correspond[s] to a pattern of external events of the order of complexity of the events symbolized by a word”4 — the infamous ‘grandmother’ neuron.

Every reviewer has an inalienable right to sins of omission. This perhaps accounts for Barlow’s overlooking the main themes of the book — the central importance of perceptual categorization, the constraints of development and evolution on brain function, the role of variability in the nervous system, and the various mechanisms of re-entry between maps. One can only suspect that his actual sins of omission in the review are motivated less by the presumption that the theory “ushers in a new era in neuroscience” than by the premonition that an old one is about to be ushered out.

Barlow replies—I found the book hard to understand, and the extravagant claims made for it perplexing, so I cannot dismiss the possibility that I failed to pick up some important messages. I am not convinced that this is so, but if it is I apologize and we must leave it to other, unbiased, readers to decide whether this was entirely my fault, or whether the book itself was to blame.

There are other bits of my review for which I do not apologize. Part of the book is concerned with background material which is unoriginal and adds no new insight, so I did not draw attention to it. I did mention the review of Edelman’s own book (p.470). 

In the section on development there is no mention of work such as that of Willshaw, von der Malsberg or Swindale, which is certainly relevant to any discussion of the factors moulding the brain during development. It is perhaps unfair to expect an account of the spatial organization of the neuronal network, but an uninformative reviewer might gain the impression that Edelman and his colleagues are the only ones with interests in this area, and that is unfortunate.

Finkel implies that I am wedded to, or even responsible for, the notion of ‘grandmother’ neurons. If he would re-read the article he quotes he would find that its ideas are less restrictive than he thinks: the cells postulated are thought to owe their properties partly to modification by experience, and room is left for cooperative or connectionist factors to mould the neurons that categorize perceptions. Room is also left for neurons that are selectively sensitive to highly specific stimuli, such as the faces of particular individuals. Finkel has a right to regard such neurons as “infamous”, but I hope this does not blind him to the experimental evidence of Gross, Rolls, Perrett and their colleagues1,2,3 that they exist.

Although I do not agree with the ideas in Neural Darwinism I think the title is splendid, and it should encourage all of us to seek a role for selection in neurobiology. Experimental techniques are developing rapidly, and we need as many clearly expressed theories as possible about the way the brain performs its remarkable functions; the facts elicited by testing them will then weed out errors and select the fittest ideas with greater finality than any amount of discussion in these columns.

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