

BOOK REVIEWS

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DARWINIAN SELECTION IN THE BRAIN¹

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In this book, Gerald Edelman explains how a process akin to natural selection, but one which operates in somatic time on the interactions between neurons, is responsible for order in the brain. The theory of neuronal group selection was proposed by Edelman over ten years ago and has since been developed by Edelman and his colleagues at Rockefeller University, Leif Finkel and George Reeke, into a well-posed and synthetic theory of nervous-system development. In this review, I will focus on the issues of most concern to evolutionary biologists: in what sense is the brain a selective system, and what are the similarities and differences between neuronal group selection and the genetical theory of evolution.

There are two basic aspects to any selective system: variation in fitness and heritability. Consider first variation in fitness. In genetic evolution, the word "fitness" is used in at least two different senses: the first in an operational sense and the second in a design or engineering sense. There are several measures of operational fitness, including the per capita rate of increase (first used by Fisher [1930]) and expected reproductive success. Fitness in the sense of better design (often referred to as *adaptedness*) is far more difficult to define in genetic evolution, and there is no universal definition, since it depends on the specifics of the species and its environment. In neuronal group selection, "fitness" is also used in the operational and engineering senses as discussed shortly. What sort of entities possess fitness? Again, this depends upon the problem of interest, but candidates in genetic evolution include bits of DNA, genes, chromosomes, organisms, populations, and possibly whole species. A final point to realize about fitness in evolution is that it is always dependent on the environment. What is fit in one environment may be unfit in another.

In neurobiology, candidates for units of selection are the synapse, neuron, neuronal group, nuclei, and whole cortical columns. It is basic to the theory of neuronal group selection that groups of neurons function as units of selection. A neuronal group is defined as "a set of more or less tightly connected cells that fire predominantly together" (p. 198). With terms appropriately translated, this definition of a group corresponds nicely to the definitions of group structure used in population genetics (see, for example, Uyenoyama and Feldman [1980]). In neuronal group selection, fitness also has an operational and a design sense, referring either to

the likelihood of response of a neuronal group or to the design features that affect its likelihood of response, such as a group's receptive field or connectivity.

In Edelman's view, differences in fitness result from the competition of groups for the capture of cells and for input. It is worth commenting on the ecological and "neuroecological" causes of differences in fitness, since this has been a source of confusion in discussions of Edelman's theory by neurobiologists (see, for example, Barlow [1988]). Darwin, reasoning from Malthus, identified the capacity for exponential growth in a world of finite resources as a fundamental cause of fitness differences in the biota (the so-called "struggle to survive"). However, resource limitation is by no means the only cause of fitness differences, and even Darwin discussed others. There is much interest today among evolutionary biologists in the evolution of intraspecific interactions in which fitness effects result from interactions between conspecific individuals. The logic of fitness interactions is perhaps as relevant as competition to the differences in response generated in an interacting neural network. Whatever the case, there are no conditions in a selective theory concerning the local causes of fitness differences, only that such differences must exist for selection to occur.

Now consider the issue of heritability. In evolution, DNA replication is the ultimate cause of parent-offspring correlations at all levels. An important point to realize is that there is no requirement in genetical evolution that parent entities exactly copy themselves. Sexually reproducing organisms certainly do not copy themselves (although their DNA does), and yet they can be units of selection. What is necessary in a selective system is that there be some correlation (higher than the background noise) between the fitnesses possessed by parent and offspring entities. Edelman proposes that the groups that respond initially to a stimulus (by virtue of their receptive fields and connectivity) respond better to the same stimulus after the rules of synaptic change operate. Conversely, groups that initially responded poorly may not respond at all after the rules of synaptic change operate. In other words, in neuronal group selection, it is the effects of one neuron on another (synaptic efficacies) that change under specified rules, and this produces a correlation between the likelihood of responses of a group before and after selection.

We can now state the basic parallels between selection in genetic evolution and neuronal group selection. In genetic evolution, differences in *adaptedness* to an environment lead to differences in reproductive success, which, when coupled with rules of genetic transmission, lead to a change in frequency of genotypes in

¹ *Neural Darwinism. The Theory of Neuronal Group Selection*. Gerald M. Edelman. Basic Books, N.Y. 1987. xxii + 371 pp. \$29.95.

a population. In neuronal group selection, differences in receptive fields and connectivity between neuronal groups lead to differences in initial response of groups to a stimulus, which, when coupled with rules of synaptic change, lead to a change in probabilities of further response to the stimulus.

Although it is clear that neuronal group selection can increase the likelihood of response of certain groups, what guarantees that the selected groups produce output or behavior that is adaptive to the organism? I think that this question can be viewed as one concerning levels of selection. Note that there is no requirement in selective systems that selection at one level increase the fitness of higher, more inclusive, levels. Whether or not this occurs depends on how the system is organized. If there is one thing that has been continually emphasized in current studies of levels of selection in genetical evolution, it is that there is usually a conflict between levels in the direction of selection. How are such conflicts resolved? If more inclusive levels are to evolve adaptations at their level, they must evolve a means of regulating the selfish tendencies of their component entities.

Consider, for example, individual organisms. Organisms can be viewed as collections of cooperating genes. We know that there are powerful selective forces which favor genes that can pursue their own interests, and we know of examples of this in the cases of segregation-distorter genes and transposable elements. What maintains the generally cooperative nature of the genome and makes the genes produce effects that benefit the whole organism? In eukaryotic organisms, meiosis usually ensures that the two alleles at a locus have equal chances of ending up in a gamete. Therefore, if an allele is to increase its frequency in the next generation, it must do so by benefiting the whole organism. Because of meiosis, selfishness does not benefit the individual gene. Let us return now to the question of neuronal group selection and adaptive behavior. What guarantees that the outputs of the selected groups are adaptive to the goals of the organism?

In Edelman's view, neuronal group selection occurs in the context of larger selective loops, including that of genetic evolution. Edelman hypothesizes that genetic evolution has led to the establishment of repertoires of neuronal groups that monitor the state of the organism with regard to important parameters associated with genetic fitness, such as appetite, safety, and mating, to name a few. In humans, there is clearly some flexibility in the values that can be established during the lifetime of an individual, and even values that decrease genetic fitness can become established. In neuronal group selection, such value-laden groups feed into the neuronal-selection process so that the selected group has output that is appropriate to the goals of the organism. This provides a neural basis for learning.

The basic problem in brain theory and psychology to which Edelman applies neuronal group selection is that of *category formation* in perception and motor activity. How is it that an initially naive brain comes to recognize objects and divide an ambiguous world into categories? The problem of category formation should be a familiar one to the evolutionary biologist. Darwin (1859 p. 462) asked "why is not all nature in confusion instead of the species being, as we see, well-defined" and "why are not all organic beings blended

together in an inextricable chaos" (Darwin, 1859 p. 171). In other words, the problem of categories in evolutionary biology is the problem of the existence of distinct species. This problem can be restated as follows. There are infinitely many possible niches in nature, so why are there relatively few distinct species? There are two views of this problem in biology. The first is that distinct niches really do exist in nature and that species adapt to them. The second is that the evolving population creates its own distinct niche even in an environmental continuum (for an example of this view, see Bernstein et al. [1985]). The first view is basically instructive, and the second is selective (see below).

Edelman recognizes that the category problem is the fundamental problem with which brain theory must deal. Categorization is basic to all subsequent perceptual activity. Indeed, the category problem is a basic problem for all selective theories, as the above-mentioned example of the species problem in evolutionary biology should indicate. There are infinitely many possible categories/objects in the world. How does the brain create the ones to which it responds? Most of the book deals with this problem in one way or another. As with the species problem in biology, there are two possibilities, the first instructive and the second selective. Either categories exist in nature and the brain is somehow instructed as to their existence, or a process operating in the brain in somatic time creates categories. One of the accomplishments of the book is its treatment of category formation by neuronal group selection.

Basic to Edelman's view of category formation is the idea of a classification couple, which should be viewed as the minimal unit capable of classification. In a classification couple, there are two disjunctive pathways operating in parallel which might, for example, sample the environment. It is easy to see how the principles operating in a classification couple might be generalized to classification n -tuples. As a simple example of a classification couple, consider the following one, which samples input from the outside world. Such a couple might consist of two parallel paths, each containing i) a sensory level at the periphery of the organism ("recognizers" denoted R) and ii) a level in which neuronal groups differentially respond to the sensory input ($R \times R$), and connections between each of the two $R \times R$ levels. The latter connections are termed "reentry," a process which plays a fundamental role in category formation in neuronal group selection. The kinds of properties recognized at the R level of sensory input will of course be something that is set by genetic evolution, depending on the niche of the species.

Consider the following simple example of a classification couple operating in a universe composed of character objects. Similar classification couples are at the basis of a classifying automaton named *Darwin II*, described in the book. The two disjunctive pathways are assumed to be a local feature-detection pathway and a tracing routine. The R level of the local feature-detection pathway of the couple responds to various specific features of an object, for example whether in any given region of space there is a bend, a vertical, horizontal, or angular line, a cross, etc. The $R \times R$ level of the tracing routine responds to overall properties of the object, such as shape, curvature, numbers

of crosses, bends, etc. The key property of the classification couple is that the two disjunctive sampling paths reenter one another at the $R \times R$ (or higher) level.

How might such a classification couple work so that, say, \times and $+$ could become associated as belonging to the same category, say, the category of objects with pairs of lines that cross in the middle. For these two characters the groups responding in $R \times R$ of the local feature detector will be quite different. However, the groups responding in the $R \times R$ of the tracing pathway will be similar for these two characters, because they each consist of a pair of lines crossing near their center. Let us label the groups responding in $R \times R$ for the tracing pathway as A (these are the same groups for both an \times and a $+$), and let us label the different set of groups responding to \times and $+$, respectively, in the $R \times R$ of the local feature pathway as 1 and 2 . If, in the past, the automaton has experienced both an \times and a $+$, the reentrant connections between A and 1 and between A and 2 will have been strengthened by neuronal group selection. This association can be tested in the following way. Turn off any sensory input into the tracing pathway, so that any association observed depends upon past experience (through memory as recategorization [discussed next]) and not as a result of any immediate correlation. With the tracing pathway turned off, present the automaton with \times . Groups 1 will respond in $R \times R$ of the local feature detector. Because of the strengthened reentrant connections, groups A will respond in the tracing $R \times R$ (even though no tracing has occurred, since it has been turned off), and groups 2 will then also respond in the $R \times R$ of the local feature-detector pathway (even though $+$ is not part of the current input).

Thus \times and $+$ will have become associated as belonging to the same class as a result of neuronal group selection and reentry between two disjunctive sampling paths. This simple example also illustrates the role of memory in neuronal group selection. In the experiment with the simple automaton just described, in which a \times and $+$ are first presented and then the tracing input turned off, memory exists as strengthened reentrant

connections between groups A and 1 and 2 . These strengthened connections lead at a later time to the recategorization of \times as belonging to the class of objects with a cross near the center. Thus, memory is viewed in neuronal group selection not as a storage of information but, rather, as a process of recategorization. Providing a theory of memory based on mechanistic principles of neuronal group selection is a major accomplishment of the book.

In this review, I have discussed only those issues of most direct relevance to evolutionary biologists, and there is much in the book that I have left out. There can be no question that this is a work of grand scope written by a brilliant and creative mind. Edelman attempts to bridge many disciplines from molecular biology to perceptual psychology. In so doing, Edelman has established a new framework for interpreting and conducting neurobiology. As this framework gains maturity, it is to be expected that certain details of the book will prove to be incorrect. Nevertheless, as I have tried to show, at its most basic level the theory of neuronal group selection is well-posed logically, and the conceptual issues addressed in the book come naturally out of the view that the brain is a selective system.

LITERATURE CITED

- BARLOW, H. B. 1988. Neuroscience: A new era? *Nature* 331:571.
- BERNSTEIN, H., H. C. BYERLY, F. A. HOPF, AND R. E. MICHOD. 1985. Sex and the emergence of species. *J. Theoret. Biol.* 117:665-690.
- DARWIN, C. 1859. *The Origin of Species by Means of Natural Selection*. Murray, London, U.K. [Facsimile. 1964. Harvard Univ. Press, Cambridge, MA]
- FISHER, R. A. 1930. *The Genetical Theory of Natural Selection*. Oxford Univ. Press, Oxford, U.K.
- UYENOYAMA, M. K., AND M. W. FELDMAN. 1980. Theories of kin and group selection: A population genetics perspective. *Theoret. Popul. Biol.* 17:380-414.

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