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Autor(en): **Olby, Robert**

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RECEPTIVE FIELDS: A KEY CONCEPT IN NEUROBIOLOGY

BY

Robert OLBY*

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This essay forms part of a larger work given to a study of inter-disciplinarity in post-World War II neurobiology. The suggestion for such a study came from the debates that have taken place over the nature of the cross-disciplinary movement from which arose the molecular biology we know so well. The standard view has it that molecular biology was the fruit of the intellectual migration of physicists into biology and of the impact upon biology of the theory and technology of information science which military science had promoted.[1] Because I suspect both claims have been somewhat overstated[2] I decided to look more closely and critically at the manner in which scientists from different disciplines converge on a problem. Such an exercise should not be conducted in the air. Therefore I selected an example – neurobiology – because, like molecular biology, it has involved intellectual migrations, this time from molecular genetics to neurobiology, and a determined influence from computer science and artificial intelligence. In the time at my disposal I have severely restricted my agenda by concentrating on three case studies – those of memory molecules, receptive field, and parallel distributed processing. Today I will concentrate attention on receptive fields – in itself a very large subject.

It has been generally assumed that in the present century, when scientific disciplines have multiplied and training in science has become more and more specialized, efforts to bridge disciplines by instituting inter-disciplinary activities – conferences, research programs, and publications – offer the best strategy for making progress in science. This should not be taken as a forgone conclusion. Thus J.D. Watson remarked recently:

> "The physicists don't bring anything but intelligence and arrogance. For the most part physicists are lost souls when they come to biology. They think they don't need to know anything. Most interdisciplinary efforts in universities are failures. They bring together people who cannot do either of the subjects. It is assumed that if we brought them together they would suddenly be worth their salaries."[3]

And when Walther Rosenblith wrote the preface to the proceedings of one of the many interdisciplinary symposia that took place in the 1950s he brought a breath of scepticism

* Department of History and Philosophy of Science, University of Pittsburgh, 1017 Cathedral of Learning, Pittsburgh, PA 15260, USA.

to our high expectations. There had, he complained, been a "surfeit" of such events. True, many fields of the life sciences had been "profoundly affected by the technological advances that had their origin in the physical sciences." But experts in these technologies acquired a taste for the challenges of these less structured fields," unfortunately they "sometimes lacked perspective and respect for the toughness of the problems that they proposed to tackle." He went on:

> Responsible workers in the behavioral and life sciences became increasingly squeamish about the one-day symposium in which mathematicians, physicists, and engineers vented frequently the belief that the intelligent application of some rather elementary notions from mathematics and physics should yield spectacular results in the solution of a variety of thorny problems. The brain, perception, learning, thinking, that is to say, all topics that in Warren Weaver's phrase are characterized by "organized complexity," were the explicit target of these optimistic predictions.
>
> The biological scientists who had been trained in the more traditional approaches adopted a retaliatory stance in which they were only too often satisfied to point to the truly appalling complexities of their experimental data. The two parties separated, leaving behind numerous volumes that were represented to be high-fidelity transcriptions of the tape recordings of these encounters. Relatively few among the symposaists got beyond the *hors d'oeuvres* and stayed, as it were, to dinner.[4]

I want to look at the history of the concept of the receptive field, with a view to exposing what seems to me some significant features of this productive concept.[5] One is the continuity in commitment to the tradition of neurophysiology, another is the collaborative association that developed between neuroanatomy and neurophysiology at the level of the laboratory – and not just at symposia. Finally I wish to comment on the impact of mathematical and informational approaches.

The receptive field can be traced back as a concept to the writings of Sherrington. He spoke of "the whole collection of points of skin surface from which the scratch-reflex can be elicited..."[6] In 1931 Lord Adrian applied it to the area of the frog's skin innervated by a single afferent fibre.[7] Keffer Hartline six years later applied the concept to the retina. It was for him the region of the retina within which the stimulus must fall in order to obtain a response from the cell to whose axon the microelectrode was applied, Hartline wrote:

> This region will be termed the receptive field of the fiber. The location of the receptive field of a given fiber is fixed; its extent, however, depends upon the intensity and the size of the spot of light used to explore it and upon the conditions of adaptation.[8]

Hartline discovered three kinds of cells – **On** cells, **Off** cells and **On/Off** cells. He plotted the change in sensitivity as the light spot was moved out from the center of the field where it was at a maximum, and he noted the effect of the light level in the surrounding environment. Particularly striking was his demonstration of inhibition when light was shone at a region adjacent to the field being studied. Hartline's demonstrations of the application of well-known laws from photometry and psychophysics at the level of single cells was very rewarding and offers us an eloquent testimony to the marriage of physics and physiology which he achieved in his own intellectual development.

Stephen Kuffler applied Hartline's system to the ganglion cells of the cat and discovered receptive fields which combined all three of Hartline's types of cell – that is the receptive field was itself divisible into three regions – the **center-surround** pattern. **On** cells had a central region that responded when illuminated, a penumbra which responded when the light was turned off, and a border between them which responded both when the light was turned on and when it was turned off. The phenomenon of inhibition which Hartline had discovered between different receptive fields, Kuffler found operated between the penumbra and the center. This important discovery suggested that the spatial discrimination of the visual system was very precise.

Now Kuffler was less interested in vision in its own right than in general principles of nervous activity. Wiesel, on the other hand, was fascinated by the problem of perception. He had been trained in medicine and psychiatry, and had assisted Carl Gustaf Bernhard in his application of drugs to prevent fits in epileptics. He had also carried out parallel studies of the action of drugs on cats. These studies were monitored by tracing the brain waves with the EEG apparatus. In America as in Europe there was still considerable enthusiasm for EEG studies in the early fifties. Single cell recording seemed to offer a tool to locate the source of these waves. Wiesel was put to help in Ken Brown's study of the relation between single cell excitation and the waves produced from the retina – the **Retinogram (ERG)**. At this point I should emphasize my impression that the great hope was the EEG rather than single cell recording in its own right. The International Society for Electroencephalography had been established in 1947, and held symposia through the 50s. Alexander Forbes, President in 1953 explained:

> Neurophysiology may be likened to a tree, and the highly specialized application of it called EEG to a flower that has recently blossomed on that tree. It call it flower rather than fruit, for it is spectacular, but still so new, so empirical and so little understood, that it needs to mature through years of patient research before it has the solidity and substance that merits analogy to fruit.[9]

And Adrian, addressing the same international symposium remarked:

> The gray matter of the cortex is a three-dimensional jungle of every kind of nervous growth and we have only just arrived at a technique for studying single units. This was far simpler when we had to deal with medullated nerve fibres, so robust that they could be isolated without appreciable damage.[10]

The reasons for this enthusiasm stem in part from the fact that until Hans Berger announced his discovery of the EEG in 1929[11] and Adrian and Matthews had confirmed it in 1934[12], there was considerable scepticism concerning the possibility of exploring the cerebral cortex at the level of individual neurons with the same chance of success as was being achieved at the neuro-muscular junction and with spinal axons. Sherrington in his most important work eliminated the cerebrum as a "complicating and disturbing affair" by using decerebrate animals, and thus concentrating on the spinal cord. Many thought that all you would get from the cortex in the form of electrical phenomena would be a confused buss. The confirmation of the EEG by two of the most respected collaborators in neurophysiology had a dramatic impact. The subsequent history of the attempts to locate the source of the EEG and of the ERG reveal that this was a false dawn, and only the untiring efforts of men like Tomita many years later produced positive results.

While EEG held the limelight singlecell recording remained a byway for the those dedicated physiologists who were not afraid of the esoteric world of axonology, or of the demands that surgical skill placed upon those who wanted to study the activity of the sensory activity of the intact animal. Once Wiesel was able to leave on one side the retinogram studies of his more senior co-worker, Ken Brown, he adopted a direct approach applying Kuffler's technique for the retina to the first region of the brain that processes visual information – the **Striate Cortex** (Area 17 or V1). He emphasizes that this was a very simple try-and-see approach. He had no predictive theory to tell him what to expect.

The results of the work of Hubel and Wiesel are well known. They found that the same very specific spatial organization was present in the cat cortex that had been noted by Kuffler in the cat's retina. To their surprise Hubel and Wiesel discovered cortical cells which displayed even more specificity than Kuffler had observed. These cells responded only to edges; furthermore, for any given cell the orientation had to be specific. The cells of the striate cortex were organized in a sequential manner. Starting from a given point there was an organized array of cells responding to a range of orientations through 180 degrees.

They used the single cell recording system with the cat striate cortex to investigate its columner organization, to assess the effects of visual deprivation, to establish the presence of left/right ocular dominance, and much more. In their hands the receptive field revealed a hierarchy of stages in processing, for cells in different layers. Moreover, different regions of the brain were activated by more and more complex receptive fields. Perception, it seemed, consisted of a series of processing stages starting in the retina as an outpost of the brain, going on to the lateral geniculate nucleus and on to the cortex in an hierarchical sequence.[13]

Alongside these studies of the visual system Patrick Wall, Michael Merzenick, and others were applying the concept of the receptive field to the somatosensory modality. Their work led to the discovery of the reorganization of receptive fields following injury. This yielded a wealth of evidence that cortical reorganization in both its acute and chronic forms is a widespread occurrence. The recognition of this fact has resulted in a significant modification to the so-called "classical" concept of the receptive field making its geography much more variable, its functioning dynamic, and its response to peripheral and central injury active rather than passive. The story of the emergence of these unexpected effects of injury is a striking case of the role which pathological phenomena often plays in physiological research.[14]

Criticism of the Receptive Field

Following the use of lesions and evoked potentials, single-cell recording proved a powerful tool in probing the deeper levels of the sensory equipment of the brain. It has revealed specific functional localizations at the level of individual ganglion cells. The associated concept of the receptive field has offered an organizing principle of fundamental importance in all sensory modalities save that of taste. It has been claimed that its very success has stifled other approaches. Does the experimental system of single-cell recording itself "manipulate" the organism to yield discrete receptive fields. Are they an artifact of this manipulation?

Those with a preference for holistic and systems approaches have suggested that the "classical" receptive field is an outmoded concept which should be banished. Instead they see the receptive field as a local expression of more fundamental properties of nerve nets for which Fourier methods are the appropriate tool. The concentric surround structure of simple neurons is only one outcome of an interactive process involving sets of neurons. Critics have argued that it is fundamentally erroneous to ascribe psychological roles – feature extraction – to neurons. Others have questioned the Hubel/Wiesel scheme of serial information processing – from spots to edges to slits – and have suggested that these cortical cells may be carrying out a more general analysis of visual space rather than simply extracting one or another of these features in a piecemeal fashion. The effect of surrounding regions of the retina upon a receptive field[15] has led to a new interpretation of the receptive field in terms of the summation of two Gaussian surfaces – one called the center response mechanism, the other the surround response mechanism – hence the name "difference of Gaussians model" (DOG model). This model was based on results from recording from more than 100 sites in the same receptive field.[16] This reinterpretation of the center-surround receptive field treated it as a system of elements – receptors – its response to the visual input being an expression of the response of the system.

The Gene Analogy

These alternative interpretations of the receptive field remind one of similar issues which arose in the development and acceptance of the gene concept in genetics. The concept of the receptive field has been in existence long enough for one to be able to draw some parallels regarding their respective histories. The gene was at first defined purely in terms of its functional role in the distribution of hereditary traits to offspring. Its definition was phenotypic, i.e., in terms of the traits to which it gace rise. The concept began its life as a simple independent unit. Then genic interaction was discovered, and following that came linkage and the association of genes with chromosomes, and finally its definition in terms of the chemistry of DNA. The result was the existence of **several** different definitions of the gene – a unit of function, or of recombination, or of mutation, and as a specific sequence of nucleotide bases in DNA. Geneticists have continued to use the term "gene" in all these different ways because they had agreed what they considered was the relationships between them. Consequently there has been no serious objection to the continued use of the term gene although it has been transformed and developed to yield a variety of definitions.

When we reflect on the history of the receptive field, a number of parallels with the gene come to light. Just as the gene was originally defined in terms of its phenotypical manifestation, so a receptive field in the cortex was defined in terms of the region of the sense organ from which it receives stimulation. A particular locus of a chromosome determines the production of a specific molecular product. A specific cell of the striate cortex "determines" the "signification" to be given to stimulation of a specific set of retinal cells. Like genic interaction in genetics whereby one gene influences the expression of another, so we find in sensory physiology the phenomenon of inhibition of excitation in one receptive field by theat in a neighbouring one. As higher levels of sensory processing were discovered the determination of the meaning of sensory information was seen to depend on several superimposed fields. If the classical receptive field is now seen as just one way and not the only one to define the fundamental unit of sensory perception, we should not worry that all definitions are not equivalent, as long as we know the nature of the foundations of those differences.

Other Approaches

The study of the neurophysiology of vision owes its success to the combination of physiological, anatomical and pathological approaches that have been used in concert. The knowledge thus gained has been recognized as of general importance for the nervous system as a whole. The eye, after all, is an "outpost" of the brain. We may ask what general features of nerve organization and function has it revealed? First, it exemplifies the Sherringtonian principles of convergence and divergence – the output from many rods and cones in the retina converging on fewer ganglion cells, and the subsequent divergence of paths from cells in the striate cortx to many other cells in various parts of the brain. Second there is clear anatomical evidence of feed-back from higher centers in the brain to lower ones. Third comes the recognition of the existence of parallel processing of information by ganglion cells – some operating by linear summation, others by non-linear summation.[17]

All this was known before the recent excitement over parallel distributed processing, or PDP, surfaced in the 1980s.[18] This could hardly have been otherwise, for the idea of parallel rather than serial processing first arose out of considerations of the architecture of the central nervous system! The idea was "neurally inspired." Nor did the concept of learning by training as in the training of a network, rather than by the imposition of a "program" as in serial processing, teach the neurophysiologist something new. Even the notion of memory as a "distributed" function of many neurons can be found in a primitive form in the writings of Karl Lashley[19] and in Donald Hebb's speculative concept of a "cell assembly."[20] Consequently it has not been difficult for neurophysiologists to be sceptical concerning the achievements of PDP. The units of a PDP model do not accurately represent neurons, nor do the patterns of connection in the network of a such a model represent those found in the brain. On the other hand PDP modelling, as Terry Sejnowski remarked, "offers one of the few ways that neuroscientists can test qualitative ideas about the representation and processing of information in populations of neurons."[21]

Another resource that has found a place in the neurosciences is that of information theory. The nervous system is treated as an input/output system in which a signal (the stimulus) is transduced in a receiver (the receptor), and transmitted through a channel (the nerve fibre) to a particular source of sources in the brain, where the signal is decoded. Treating the visual system as an information system, Joseph Atick has assessed its approach to optimum design for efficiency of information representation. He has shown how the center/surround structure of the receptive fields manifests optimization of information representation.[22] Information theory, it seems, offers yet another resource to guide the neurophysiologist in his search for the significance of the structure he uncovers, and at the same time serves to emphasize the dynamic and holistic nature of the neural network. Viewed in this way the classical receptive field is a construct from the localized form of the stimulation of retinal cells. Even here, however, it was the neurophysiologists who detected the powerful effects upon the receptive field of areas surrounding but outside it. Thus from the record of history, it appears that the experimental tradition of neurophysiology closely associated with descriptive anatomy and clinical pathology have represented the cutting edge. Information theory and PDP have been the assistants.[23]

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