A Brief History of the "Feature Detector"

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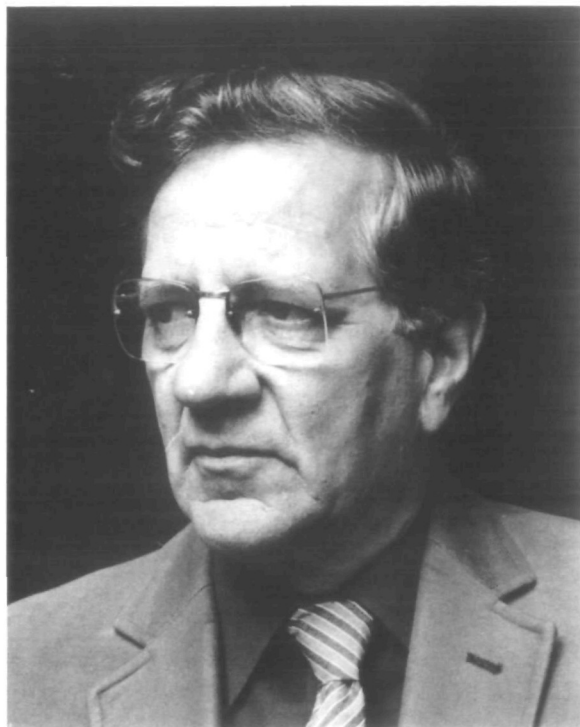Kevan Martin
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A Brief History of the "Feature Detector"

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H. B. Barlow

The feature detector hypothesis, and its subsequent development into the doctrine that single neurons code for perceptually significant events, has been the *leitmotiv* of most work on sensory systems. In the face of strong competition from the alternative theories of neural networks and oscillating ensembles of neurons, the single neuron doctrine retains its grip on the imagination of those working on the neural mechanisms of perception.

The year 1953 was an *annus mirabilis* for Cambridge University. Not only did a short letter by J. D. Watson and F. H. C. Crick appear in *Nature* on 25 April, but *The Journal of Physiology* published a paper on 28 January bearing the laconic title, "Summation and Inhibition in the Frog's Retina," by H. B. Barlow. Against the advice of his supervisor, E. D. Adrian, Barlow had taken on the task of repeating some early work by Hartline (1938, 1940a,b) on the ganglion cells of the frog's retina. Adrian had told him, "I wouldn't do that—Hartline's a very clever chap you know" (quoted in Barlow, 1990). However, the results of the graduate student's persistence were to become a landmark. Barlow's exacting experiments on the frog's retina *in vitro* demonstrated for the first time the presence of an inhibitory surround in the ganglion cell's receptive field. In the same year, Kuffler (1953) independently discovered surround inhibition in ganglion cells of the mammalian retina *in vivo*. With Fitzhugh, Barlow and Kuffler later extended their work on the retinal ganglion cell's receptive field (Barlow et al., 1957). However, the conceptual significance of Barlow's paper lay hidden in the discussion, which began conventionally, but then shifted to an ethological perspective to consider how a ganglion cell's response might be useful for the frog:

> an optic nerve fibre is the final common path for activity aroused in a considerable region of the retina, and if some purposive integration has taken place, it should be possible to relate this in the visual behaviour of the frog. According to Yerkes (1903) the frog uses its eyes mainly in feeding; it also escapes from large moving objects. . . . When feeding, its attention is attracted by its prey, which it will approach, and finally strike at and swallow. Any small moving object will evoke this behaviour, and there is no indication of any form discrimination. In fact, 'on-off' units seem to possess the whole of the discriminatory mechanism needed to account for this rather simple behaviour . . . [and] it is difficult to avoid the conclusion that the 'on-off' units are matched to this stimulus and act as fly detectors. (Barlow, 1953)

So a powerful and unifying idea—that single neurons are detectors that code for perceptually significant events—was born into a neuroscientific world of equipotential nerve nets, electrical field effects, and mass-

action. Like many influential ideas, it was both ahead of its time and a development of older ideas. Barlow's insight that evolutionary processes had resulted in a match of detector and stimulus might have been a predictable consequence of his own descent from Darwin. But he had been fortunate on at least two additional counts. First, E. D. Adrian was his supervisor, and it was he who had made the fundamental observation that sensory nerves signaled the intensity of a stimulus by their rate of firing (Adrian and Zotterman, 1926). Second, Lorenz (1952) and Tinbergen (1953) were at that time developing the embryonic field of ethology and were also popularizing the ideas of "innate releasing factors" to explain the stereotyped species-specific behavior of animals (see Barlow, 1985). Later, Barlow (1961a) himself pointed to the influence of Mach (1886) and Pearson (1892), whose ideas on the "economy of thought" were antecedents for his central thesis that the brain had evolved to represent and recognize objects as efficiently as possible. For Barlow (1961a,b, 1972, 1981) one important facet of efficient coding was that objects be represented by the fewest possible active neurons.

There are other antecedents for this idea. Ramon y Cajal (1892) suggested that pyramidal cells of the neocortex were "psychic cells." This notion was taken further by Sherrington (1940):

"We might imagine this principle [of convergence] pursued to culmination in final supreme convergence on one ultimate pontifical nerve-cell, a cell the climax of the whole system of integration. Such would be a spatial climax to a system of centralization. It would secure integration by receiving all and dispensing all as unitary arbiter of a totalitarian State. But convergence towards the brain offers in fact nothing of that kind. The brain region which we may call 'mental' is not a concentration into one cell, but an enormous expansion into millions of cells. They are it is true richly interconnected. Where it is a question of 'mind' the nervous system does not integrate itself by centralization upon one pontifical cell. Rather it elaborates a million-fold democracy whose each unit is a cell." (p. 277; this passage was cut from the extensively revised 1951 edition—perhaps the image of a totalitarian state had, by then, taken on too dark a hue)

Barlow rejected Sherrington's view of a millionfold democracy, and ultimately opted for something just short of a pontifical cell. Sherrington was primarily a motor physiologist, hence his view: "Behaviour is rooted in integration" (1940, p. 221). He saw the evolution of the mind as something that was driven by the motor system, not by the sensory system, so it is not surprising that he and Barlow should arrive at diametrically opposite views. These divisions remain in current literature, and it seems certain that, had Barlow studied motor rather than sensory pathways, his view of the role of single neurons in perception would not have taken the form it did.

Barlow (1961a) saw the relevant sensory stimuli as "passwords," which served as "releasers" of specific responses. Single neurons were detectors of these passwords, or "trigger features" as they came to be known. Messages that were not passwords were rejected by the detectors. This view also had a Sherringtonian antecedent. In considering the evolution of the function of human neocortex from simple invertebrate nervous systems, such as that of medusa, Sherrington (1940, p. 213) had written, "The trigger-organ [sense-organ] remains what primordially it was, a means of releasing a motor act, but it gets secondary connections with the nerve-lines from other trigger-organs doing likewise." Barlow showed how selective in its stimulus requirements the trigger-organ could be. Yerkes (1903) had concluded that frogs did not use vision to locate themselves in their habitat, nor did they use form discrimination, or learn visual reactions. This made frogs seem less visually competent than their prey, although later studies by Ingle (1968) and Ewert (1970) showed that evolution had provided batrachians with a far richer behavioral repertoire than Yerkes had given them credit for. But in 1953, Barlow was able to use Yerkes' evidence of limited competence in support of his idea that the responses of single ganglion cells could be the triggers of specific behaviors.

Barlow (1961a) drew a moral from his notion of passwords. This *moral* was that the experimenter needs to know what behavior their chosen stimulus elicits. Equally they must use stimuli that have some specific behavioral consequence. His *moral* seems often to have been forgotten by neuroscientists over the decades, but it was heeded by a group at MIT who provided a powerful extension of the feature detector hypothesis. In 1959, they published an article with the eye-catching title, "On What the Frog's Eye Tells the Frog's Brain." Their basic finding, presented to the electrical engineering world (Lettvin et al., 1959) and later to the world of general physiology (Maturana et al., 1960), was the existence of five classes of retinal ganglion cells in the frog that responded to different, specific spatiotemporal patterns of excitation. Their claims were conveyed to Barlow by Hartline and, as Barlow later recalled, "At first I don't think either of us believed much of what Lettvin and his co-workers reported. Hartline had worked on movement sensitivity and was particularly surprised by 'unidirectional rate sensitivity—the claim that some ganglion cells responded to movement in one direction and not the other" (Barlow, 1969).

It is true that, by modern standards, the protocols of the MIT group were unconventional: "Early in our work we found that taking records hindered rather than helped this kind of research by leading to premature standardizing of method" and so "we took no records except those needed to illustrate our papers" (Lettvin et al., 1961). Their preparation differed from Barlow's and Hartline's in that they left the frog's eye intact and connected to the frog's brain, and recorded from the optic nerve or optic tectum. They took the notion of using natural stimuli seriously, to the extreme of using "a delightful exhibit . . . a large color photograph of the natural habitat of the frog from a

frog's eye view, flowers and grass" (Lettvin et al., 1959). They were also unusual in drawing into their considerations a lot of anatomy, even electron microscopic studies by Maturana. However, it was not their technical advances that allowed them to find something that both Barlow and Hartline had missed; it was simply a different way at looking at the problem, as Barlow (1985) later acknowledged: he "was fixated on the difficulty and the importance of signal/noise discrimination in sensory systems." The MIT group's concerns lay elsewhere.

In their paper entitled "How We Know Universals: The Perception of Visual and Auditory Forms," Pitts and McCulloch (1947) had sketched, in unusual biological detail, a neural mechanism that would enable a given shape to be recognized regardless of its size or orientation, or a particular chord to be recognized regardless of its pitch. Their circuit was designed to extract the universal, or invariant, properties of the stimulus. In their experiments, Lettvin and Maturana were thus primed to look for invariance in the responses of the ganglion cells (Lettvin, 1988). So where Hartline and Barlow had seen On–Off receptive fields, Lettvin and Maturana recorded from the same cell type and had seen direction selectivity that was invariant with contrast and speed. They found three other classes of ganglion cells that seemed to give invariant responses to different trigger features despite changes in illumination and background (the fifth type was a "dimming detector"). They suggested that "in a system like this, a unique combination of the four qualitative contexts in a certain spatial relation may define a class of objects. . . .Obviously this is a way in which the universals 'prey' and 'enemy' can be recognised" (Maturana et al., 1960). They thought they had discovered Kant's synthetic a priori (Lettvin, 1988).

The MIT group had made a significant push forward in understanding the link between single units and perception. Their emphasis on the invariance of responses to trigger features also marked a divide between the issues of signal processing and the issues of the representation of symbols and their manipulation that became a central concern in the field of artificial intelligence. This divide remains in contemporary theories of vision. Barlow, characteristically, saw it differently. For him, pattern recognition and its implications of invariance could not be separated from the problems of signal:noise discrimination. As he put it, "There is no difficulty about pattern recognition in the absence of noise, but there are great difficulties in the presence of noise" (Barlow, 1969). The system had to ensure that it did not respond to false targets— to inappropriate stimuli that coincidentally contained some features in common with the trigger stimulus. The frog's bug detectors provide a good demonstration of the problem of noise. A frog shows no form discrimination, so it can be fooled easily into striking at any moving small object as if it were prey. It cannot discriminate the false target from the real prey; its feature detectors cannot discriminate signal from noise. To be fair, the experimenter only succeeded in confusing the laboratory frog by artificially intro-

ducing noise into the frog's environment. In the frog's natural environment, most bug-sized moving objects are bugs, so the limited language of the frog's ganglion and tectal cells may have evolved to be well-matched to the frog's world. Subsequent behavioral and electrophysiological work showed that the tectum of the frog must be involved in some additional form processing, because, as Ingle (1968) concluded, the behavior of frogs indicates that they possess abilities such as perceptual constancy and gestalt processes, which would not be predicted from known retinal physiology.

Concurrently, similar ideas were being introduced into the literature on the mammalian visual cortex by Hubel and Wiesel. The story of their serendipitous discovery of orientation sensitivity is well known (Hubel, 1988). Before that, however, Hubel (1959) had already observed direction-selective cells in the visual cortex of the awake cat. By mapping the receptive fields of cortical cells in great detail, Hubel and Wiesel were able to define precisely the trigger features of neurons in the primary visual cortex of the cat and monkey (Hubel and Wiesel, 1959, 1962, 1965, 1968). At that time, much of the work on visual cortex used stimuli that were either small circles of light, as in the perimetric studies of Daniel and Whitteridge (1959), or large-field stimuli, as used by the Freiburg group (Jung, 1960). Had Kuffler (1953) used large-field stimuli in studying the cat's retinal ganglion cells, he would have shown how ineffective large-field stimuli were. Although the work of Barlow et al. (1957) on cat ganglion cells convincingly demonstrated the importance of the intensity and dimensions of the stimulus, perhaps more attention should have been given by visual physiologists to Barlow's *moral* that the stimuli used must have some specific behavioral consequence. At the time, Bullock (1961) commented, "It is curious that we think nothing of stimulating the eye with a large sudden 'on' but would not do the equivalent to the vestibular system—a blow to the head or a shock to the whole vestibular nerve." The great leap forward came with the realization by Hubel and Wiesel that more natural stimuli had to be used if progress was to be made in defining the functional architecture of visual cortex.

Given the mood of the times, and the revolution in sensory physiology that they were leading, Hubel and Wiesel (1962, 1965, 1968) were curiously circumspect when they discussed the role of their simple, complex, and hypercomplex cells in perception. They were clearly reluctant to assign specific functions to the different cell classes and avoided calling them detectors of any sort. They recognized that hypercomplex cells, which respond only to short stimuli, could serve as "curvature detectors," but they suggested that such a term would be unwise because it did not encapsulate other essential properties of the neuron, such as its orientation sensitivity. In their seminal 1962 and 1965 papers they compared their results with those obtained from lower vertebrates. This was most unusual for a mammalian experimental paper. In 1962, for example, they reiterated the point made

by Lettvin et al. in 1959, that "it is not enough to know the reaction of his visual system to points of light.... When one inspects responses that are a few nervous transformations removed from the receptors, as in the optic nerve, that same choice of stimulus is difficult to defend." Like the frog's array of detectors, the complex cells discovered by Hubel and Wiesel in the cat and monkey visual cortex also had receptive field properties that could not be predicted from their responses to small spots of light. Like simple cells, complex cells were sensitive to the orientation and width of the stimulus, but gave invariant responses for changes in the absolute position of a stimulus, over several degrees of the visual field. After their discovery of the hypercomplex cells, Hubel and Wiesel (1965) made the interesting speculation that inactive units may provide important signals about the form of objects in the world. They emphasized that a simple description of the cell's responses to sensory stimuli was insufficient for a proper understanding of the role of that cell in perception. Such understanding could only arise if we knew how that information was used at higher levels. This seems a deep insight that has been largely ignored.

In these studies of cat and monkey visual cortex, Hubel and Wiesel did not mention invariance, although the orientation-, color-, and motion-sensitive cells they found clearly had qualities that Lettvin and colleagues would have called invariant. However, when Creutzfeldt and Sakmann reviewed the field in 1969, they concluded that "no convincing correlations have yet been found between certain optimal stimuli of higher order neurones and correspondent 'units of perception'. Therefore the question arises as to whether the hypothesis is correct that different stimulus aspects ('invariants') are processed in different channels. . . . This hypothesis is often not stated clearly and is only implicit in the methods of investigation and presentation of data." Stronger support for the hypothesis was to come later (see below). The enduring conceptual contribution of Hubel and Wiesel's work of the 1960s was their idea that the visual processing in the cortex was hierarchical, with progressively higher-order cells coding for more abstracted functions and being more selective in their stimulus requirements. This, of course, raised the specter of Sherrington's pontifical cell. How far did the hierarchy go? Was it possible that the cortex contained neurons whose responses were so specific that they would fire only when one's grandmother came into view? Hubel's (1988) answer was plain enough: "This notion, called the *grandmother cell theory*, is hard to entertain seriously."

In 1972 Barlow reentered the forum with an ingenious and Solomonic compromise: "Single Cells and Sensation: A Neuron Doctrine for Perceptual Psychology?" He was impressed by the power that the Central Dogma had had in accelerating the progress of molecular biology. What he wanted was an equivalent central dogma for neurobiology. In the end he had to settle for five dogmas, which together formed a single neuron doctrine. Like the Turin shroud, the

single neuron doctrine wove together fact and speculation in a way that challenged believer and sceptic alike. Like most doctrines, it was open to many interpretations, but Barlow was able to bring back to center stage the whole notion of invariance and a new emphasis on the indivisibility of signal processing and feature detection:

> The central proposition is that our perceptions are caused by the activity of a rather small number of neurons selected from a very large population of predominantly silent cells. The activity of each single cell is thus an important perceptual event and it is thought to be related quite simply to our subjective experience. The subtlety and sensitivity of perception results from the mechanisms determining when a single cell becomes active, rather than from complex combinatorial rules of usage of nerve cells. (Barlow, 1972)

It was not the grandmother cell theory, but it was conceptually a million miles from Sherrington's "millionfold democracy," or "town-meeting model" as Lettvin (1988) phrased it. Barlow's concept, following Hubel and Wiesel's lead, was firmly hierarchical. In place of pontifical cells he had cardinal cells, which were high-level neurons that coded for patterns as complex as those contained in a face. These neurons, he supposed, formed a substantial fraction of the cells of the neocortex, although only a small fraction needed to be active to represent any given scene. That only a few active neurons may be responsible for a percept, takes us full circle to Ramon y Cajal's "psychic cells." Indeed, the power of the doctrine was that everything essential to the neural basis of perception could be understood at the level of single cells. The doctrine eased the burden on experimentalists enormously. It was not necessary for them to look for more global, or more molecular, properties of the brain. The tool for the job, the microelectrode, was at hand and had already proven its worth.

Ironically, the strongest opposition to the neuron doctrine came from "young Turks" within MIT and Cambridge University, the same two institutions that had seen the birth and nurture of the trigger feature hypothesis. At MIT, a group in the Artificial Intelligence Laboratory was promoting a strategy of investigation whose origins were logic, metaphysics, and computer science, not neuroscience (see Marr and Poggio, 1977). In their view, visual processing was a highly symbolic activity and thus one could not begin by describing the responses of single neurons, which was Barlow's starting point. The first stage was to define the computational problem (e.g., motion detection, or stereovision) and develop a computational theory to solve the problem. This stage formed the top level of their hierarchy. Only when the computational theory was in hand could one begin to study the next level: the nature of the representation of the input and output, and the algorithm by which the transformation between input and output would be accomplished (see Marr, 1982). The third and lowest level concerned the actual machinery on which the

algorithms would be implemented. Thus, in the MIT group's formulation of levels-of-explanation, the development of the computational theory was completely disconnected from any of the concerns of neurobiology. Even the algorithms that emerged were for implementation on digital computers, not brains. As the MIT group saw it, most of the early processing in vision was to compute a representation, which was a necessary preliminary to the task of object recognition. This stands in marked contrast to the process of pattern recognition conceived by Barlow, where object representation and object recognition were inextricably bound together in the feature detector (Barlow, 1991).

On the other side of the Atlantic Ocean, Campbell and Maffei (1974) were suggesting that neurons in the visual pathways were not feature detectors at all, but linear filters, each selective for different spatial and temporal frequencies. They suggested that, since any spatial or temporal stimulus can be characterized by its Fourier transform, the visual system was actually designed to deconstruct the visual scene into its Fourier components. The great attraction of Fourier analysis was that it seemed to provide a solution to the problem of representing objects in the brain: each active neuron contributed its component of spatial or temporal frequency to a Fourier synthesis. The application of Fourier theory to the visual system, however, eschewed Barlow's *moral* that the stimulus used must have some specific behavioral consequences. The Fourier transform was measured by presenting the neuron with sine wave gratings of varying fineness and contrast. Through the 1970s, an enormous research effort was spent in defining the spatial and temporal filter characteristics of single neurons along the visual pathways. Rather less effort was devoted to explaining how these individual neurons acted together to enable an object to be represented and recognized.

Paradoxically, Barlow (1961a) himself was one origin of this "sea-change" in ideas. In his discussion of passwords he had explicitly introduced the notion of the receptive field as a filter of information, although the selective response of feature detectors to their trigger stimulus meant that they had to be very nonlinear filters. Although a Fourier-like representation of the visual scene was costly in active cells, it had the great advantage that the same linear filters could be used for any arbitrary stimulus. Thus, the linear systems approach could avoid the combinatorial explosion of cells that would result if each object had to be represented by the activity of a particular single neuron. Barlow (1972) estimated that only about 1000 active cardinal cells were needed to code for the whole visual scene. He supposed that most of the neurons of the neocortex were cardinal cells. Different scenes would be represented by a different combination of cardinal neurons. Perhaps, as in Goethe's aphorism, "If the eye were not sunlike, it could never see the sun," the process of evolution had matched feature detector to stimulus feature, and in so doing had already defined the limits of the possible worlds

that could be represented in the brain. Maturana eventually arrived at a much more neo-Kantian position—that perception specified external reality (see Maturana and Varela, 1980). Nevertheless, solving the computational problems of representation and recognition is not sufficient in itself, for perception must eventually lead to the release of some action. Here both linear systems theory and feature detection theory fall silent.

In the 1970s, linear systems theory, with its concept of neurons as filters, came to dominate experimental and machine vision research. The linear filter approach also was perceived as being antithetical to the concept of trigger feature detectors. Marr, in particular, was strongly opposed to Barlow's idea of feature detectors and thought "that the time has now come to abandon those older ways of thinking." He preferred to think of cells as signaling no more than a convolution, but this led to further problems, because "people thought of them [Hubel and Wiesel's simple cells] simultaneously as linear convolvers and as feature detectors, and that is criminal, intellectually" (Marr, 1982). In fact, Barlow's approach was, in many ways, parallel to that of the MIT Artificial Intelligence Laboratory. Both saw vision, from its earliest processing stages, as essentially a symbolic operation, and both used the metaphor of language and symbolic logic to describe this operation. The efforts of MIT group were devoted to the problems of computing a representation, whereas Barlow was less concerned with defining high-level computational theories and more concerned with the problem of how pattern recognition could be implemented using the noisy hardware of the brain (Barlow, 1969). Unlike the MIT group, he incorporated into his models the statistical methods of signal processing and information theory developed by Attneave (1954) and Shannon and Weaver (1949; see Barlow, 1961a,b). His goal was the richest representation by the fewest number of active neurons. It was left to others to explore the general filter properties of neurons using abstract stimuli, ranging from sine waves through Gabor functions to Lie transformation groups (see Hoffman, 1984). But the lines between filters and feature detectors were never clearly drawn. Today, the debate has taken another twist as new, "kinder, gentler" versions of grandmother cells (Hurlbert, 1993) are promoted by Marr's erstwhile colleagues (e.g., Poggio, 1990).

In the two decades since the neuron doctrine for perceptual psychology was proposed and the four decades since the appearance of the feature detector, much of the thinking in the field has moved strongly away from single units and hierarchies toward neural networks, parallel distributed processing, and more molecular approaches to neuronal function. Indeed, there is even a *Rana computatrix*—a set of models that attempt to define the processes underlying the visuomotor behavior of batrachians, such as the frog—implemented on neural networks (Arbib, 1991). In mammals, solving the problem of how the different features of objects—their color, motion, depth, and

shape—are bound together after they are initially processed separately seems to require more than the neuron doctrine can provide (see Hurlbert, 1993). This has led some to believe that the hegemony of the single neuron is over (Douglas and Martin, 1991; see Hurlbert and Derrington, 1993). Nevertheless, Barlow's doctrine has remained the philosophical substrate and prime justification for single-unit recordings in awake behaving monkeys. There have been major successes for the neuron doctrine: Gross et al. (1969) discovered hand and object selective neurons in the inferotemporal cortex; Hawken and Parker (1987) found neurons in area 17 of monkey whose acuity matched that seen in psychophysical experiments; Newsome et al. (1989) discovered neurons in area MT of monkeys whose performance on a motion discrimination task matched that of the monkey's psychophysical performance—these neurons surely come close to being "units of perception." The experiments on primate area MT have received considerable attention, because they are seen by many to provide the substance behind Barlow's neuron doctrine for perception, and to provide a model example for future investigations of the identity between neuronal firing and perception (Albright, 1991; Hurlbert and Derrington, 1993). Most recently, neurons with selective responses to pictures of faces or objects that hold this information "on line" in working memory tasks have been documented in the inferior prefrontal regions of the macaque cortex (Wilson et al., 1993). Such neurons may qualify as "units of cognition" and thus represent the ultimate expression of the concept of cardinal cells.

The enduring success of the feature detector hypothesis is surely due to its essential simplicity. Even though Barlow's neuron doctrine may have been redefined or misinterpreted over the years, it provided a stable and unifying conceptual framework within which a new understanding of the functions of the visual system could emerge. The doctrine has been sufficient to guide visual physiologists to the outer reaches of the known "sensory" cortex, where they are now confronted with the great artificial divide between sensory and motor, between trigger and releaser. Neuroscientists face some uncertain times as they begin to grapple with the problems of bridging this gap. In his 1972 paper, Barlow predicted this eventuality. And today his ultimate goal of a unifying principle, a central dogma for neurobiology, seems more urgently required than ever. He understood, better than most, that "new facts make no sense without fitting them together with old facts, and then what matters is whether they change people's ideas" (Barlow, 1990). The history of neuroscience over the past four decades shows that both his facts and his ideas mattered a great deal.

Notes

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