

Vision Fin de Siècle

A Reductionistic Explanation of Perception for the 21st Century?

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The 20th century has been one of triumph, at least for science. In its explosive growth, myriad fields have been created, others have been altered beyond recognition. At the very beginning of the century, classical physics was considered by some to be exhaustive and complete. Yet almost immediately these foundations were shaken and superseded by strange and jarring ideas, special and general relativity, quantum mechanics, and so on. In biology, residual vitalistic thinking gradually gave way to a mechanistic conception of life, a consequence, in part, from Darwin's influential theory. A century later, this view was vindicated with Watson and Crick's structure for DNA and the subsequent rise of molecular biology. This reductionistic achievement provided a simple model accessible even to the layperson, explaining how a molecule could replicate itself, how it could also code for specific proteins. Thus, the central dogma of molecular biology (DNA→RNA→protein) provided a key insight about life. Much of course had to be done and significant questions still remain. Yet almost overnight there was no longer a "secret of life." No longer could one stare at the cell's protoplasm and see it as the mysterious life substance. Now within each cell, one could imagine a mixture of specific molecules with particular shapes and affinities.

The explosion of new concepts and findings resulting from the growth of molecular biology has been phenomenal; its ideas have completely transformed most areas of biology and medicine. Yet none of these subsequent developments can even be remotely compared to the discovery of DNA and the delineation of the genetic code when considered against a yardstick measuring the deepest of mysteries solved.

To be challenged by comparable mysteries, an increasingly diverse number of scientists are drawn to the brain, the most complicated physical and biological object known. Here the gulf between what is taken to be the outward phenomena and the possible explanation is the very widest. How does the brain, a physical object, go about the process of mediating complex behavior and conscious experience? More to the point for this chapter, how does the nervous system allow us to experience the visual world as we do? With the most talented scientists and armed with the most advanced technical instruments, is there any chance that we can understand seeing in such dramatic reductionistic terms? Will we, say in a generation or two hence, marvel at the definitive advance in understanding of perception at a mechanistic level?

Of course, this is a premature question, given the present state of knowledge. Yet even framing such a question may have some value in providing a different context to imagine what kinds of information are needed to envision goals. To even consider an answer, one must start at least briefly with some history.

I. ANTECEDENTS

First, I should note that the experimental study of visual perception was already very well developed during the earlier part of the 19th century, certainly well before the proclaimed birth of experimental psychology by Wundt in 1879. Several achievements stand out. Thomas Young's (1802) surprising and correct promulgation of the trivariant nature of color vision, followed by Helmholtz's (1909/1962) codification provided secure foundations for the science of color. Wheatstone's (1838) invention of the stereoscope provided a dramatic example of how the presentation of two flat images could give rise to the perception of three dimensions. Methodologically, there were important advances as well; in particular, the psychophysical methods developed by Fechner (1860) were foundational.

Alongside these more tangible advances, there was a broad current of theoretical assumptions about perception inherited from an earlier period when perception was mainly the province of philosophy. Two broad perspectives are discernible. First is a strong empiricist tradition, related to British associationism, assuming that the contents of perception, and particularly vision, are the consequence of learned associations of elementary sensations, coupled with motor-action and tactile feedback (Berkeley, 1709). For example, Helmholtz comments that as a child his mother took him to the town square where he thought he saw miniature puppets on the church tower which were really fully grown persons. According to Helmholtz, he had yet to learn that small figures (in terms of visual angle) at great distance were really full-sized persons. Thus, he argued that our perceptions require unconscious inferences, linking the elementary sensations through locomotor experience to acquire the correct perception of size and distance. An opposing line of thinking in a more nativist tradition, exemplified by Hering (1868), was more sympathetic to the idea of inborn characteristics of the organism, developing more or less independent of

experience. Depth for Hering (1868) was indicated by the stimulation of various retinal loci in the two eyes according to the geometry of binocular vision (see Turner, 1994).

A novel and later much vilified approach was the program of the structuralists, an attempt to discern the relation between elementary sensations and perception. Much depended on introspection, a procedure requiring trained observers who could isolate their sensations for later understanding of how they contributed to perception. Most treatments consider this to be a somewhat misguided chapter in the history of experimental psychology, one that provides an object lesson of failed goals and methods. Flawed as it was, the underlying motivation did not seem out of step with the times. The modern science of chemistry was in its infancy (John Dalton proposed his theory earlier in the century) and Mendeleev was just proposing the periodic table. So, why shouldn't the new science of psychology make an attempt along a parallel track to delineate the basic constituents of sensation and to see how they formed perception? Reasonable as it may have seemed then, it failed the ultimate of scientific tests. It didn't work, and it didn't lead anywhere except to provoke reaction. The detractors were many—William James (1892) in America, the Gestalt psychologists in Germany, and later and most enduringly, the behaviorists.

The Gestalt revolution launched against such structuralist thinking began with Wertheimer's (1912) famous paper on apparent motion (see also Hochberg, chap. 9, this volume). Although apparent motion was noted much earlier by Exner, also forming the basis of cinema, Wertheimer's contribution was still memorable because he was able to show in addition to seeing two stationary flashes, there was something not present in the stimulus: "phi," the perception of motion. Particularly significant to Wertheimer, there was a restricted range of spatial and temporal relations between the flashes where the stationary flashes themselves were invisible, yet vivid motion was still seen. One could experience pure "phi" without seeing the constituents that evoked it. Thus, argued Wertheimer, one simply could not analyze perception into its elementary sensations. To explain these phenomenon, Wertheimer suggested that there was, related to the presentation of the two successive flashes, a "short circuit" in the brain that was related to the perception of motion. The existence of this supposed physical phenomenon was a brain correlate of perception.

Other important phenomenon were quickly identified by the Gestalt psychologists and their numerous contemporaries. Most important was the phenomenon of perceptual grouping as well as the figure-ground distinction, highlighted most dramatically in Rubin's (1915) classic face-vase demonstration. The Gestalt psychologists saw these new phenomena as reflecting autonomous laws of perception, not determined by learned associations acquired through experience. Rather, they saw the phenomenon as revealing some as yet unspecified holistic physical process taking part in the medium of the brain. Kohler in particular was taken with brain field theory very early on and continued this line of thinking for many decades (Kohler, 1924, 1947).

Such ideas, however, were not enthusiastically received by those in the newly emerging behavioristic tradition. Developing at about the same time in the United States, behaviorism eventually became the reigning approach to psychology, largely stimulated by animal learning experiments conducted decades earlier (by Morgan, Thorndike, etc.), also buttressed by Pavlov's studies on conditioned reflexes. The latter did not shrink from the task. "Now, gentleman, we shall pass from peaceful affairs if we may so so, to matters of war, to Mr. Kohler. We are at war with him" (Pavlov, 1935, 1957, p. 599). Based on his own work and the prevailing *Zeitgeist*, he stated,

Are not Helmholtz's famous "unconscious conclusions in his *Physiological Optics*—in reality conditioned reflexes? We may take as an example the case of a drawing imitating the visual character of a relief. In actual experience, of course, the tactile and muscular stimuli proceeding from a relief represent the initial and fundamental stimuli . . . which only subsequently obtain a vital significance by being constantly reinforced by tactile and muscular stimuli. (Pavlov, 1957, p. 215)

In America, Hull's (1943) axiomatic behavioral theory linked stimuli in the animals environment to responses that could be selectively strengthened during drive reduction. Obviously in hindsight there were many shortcomings of Hull's connectionistic theory and its immediate successors. Interestingly, even Hull acknowledged his own theory's limitations. He postulated somewhat surreptitiously the concept of "afferent neural interaction" to account for the organism's tendency to respond to Gestalt-like relations, for example, to the brighter of two lights, rather than to absolute luminance.

Hebb (1949) in his seminal book articulated the complementary strengths of earlier Gestalt theory and the behavioristic approach. Noting the extremes of each, he writes,

Two kinds of formula have been used, leading at two extremes to (1) switchboard theory, and sensori-motor connections (2) field theory. . . . In the first type of theory . . . cells in the sensory system acquire connections with cells in the motor system, the function of the cortex is that of a telephone exchange. Connections rigidly determine what animal or human does and their acquisition constitutes learning. . . . (2) theory at the opposite extreme denies that learning depends on connections at all, and attempts to utilize instead the field conception that physics has found so useful. The cortex can be treated as a statistically homogeneous medium. (p. xvii)

Gestalt theory and related formulations (Lashley's theory of mass action) were more suited to handle the organizational aspects of vision, providing at least the beginnings of an explanation of how the relations between individual stimuli could play a role. Yet, Gestalt theory was silent in dealing with how such relational factors could be causally related to behavior. There was no mechanism in Kohler's brain state theory of how the global electrical pattern would plausibly actuate the specific nerves that would cause motor behavior. Gestalt theory with its preoccupation with dynamic states ignored the possible role of specific neural connections. In Hebb's terminology, distributed systems (i.e., brain state theories) were able to han-

dle the problems of stimulus equivalence (that a triangle remained a triangle under various size changes, viewpoints, positions, colors, etc.) but were not able to deal with behavior.

Hebb's, frankly, speculative theory was able to provide at least a plausible account of how very specific neural circuits (cell assemblies and phase sequences) might actually respond to stimulus relations, and by virtue of their embodiment in a neural circuit, they had the potential to influence motor behavior.

Even though the specifics of Hebb's formulations were based on some outdated concerns (he needed to postulate reverberatory circuits to deal with short-term memory phenomena), his monograph was a milestone. Although in hindsight it provided no specific research agenda, it provided something of perhaps greater significance. It suggested a plausible and respectful reconciliation of the seemingly contradictory posturing of the Gestalt tradition and the behaviorists, acknowledging the contributions of each by presenting a speculative brain theory that would overcome their respective weaknesses. As such, Hebb's theory at mid-century provided hope and inspiration to serious workers in the still undeveloped brain sciences, giving them the courage to pursue their own research agendas with the expectation of future progress, overcoming what seemed like the current stagnation and futile debate.

II. VISUAL RECEPTIVE FIELDS

Single-unit visual electrophysiology emerged against this background in the 1950s. Before reviewing its development, however, we need to consider, at least briefly, some key concepts about brain tissue as it developed over the past 150 years.

In the 19th century scientists began to understand brain structure, which reflected a general growth in biological knowledge. For example, Schwann's (1839) cell theory marked the beginning of the modern era of histology, indicating that the constituents of biological tissue were made up of tiny repeating elements. Because the nervous system was so much more complex and the variation and tortuosity of neurons was so much greater, cell theory did not seem immediately applicable. Many thought the nervous system was formed by a complex continuous reticulum: that there were no elementary units. It was only after Ramon y Cajal perfected Golgi's technique that Waldeyer-Hartz (1891) was able to argue with force that nerve cells (neurons) were separate entities, that they made contact at specific points (the word synapse was not coined as yet), and that neurons were likely to form the elementary constituents of the brain (see Finger, 1994). Later, Sherrington was able to hypothesize mainly from behavioral experiments that the points of contact (synapses) were likely to be both excitatory and inhibitory, an intellectual leap later confirmed by Eccles (Sherrington's student) recording from within single neurons themselves. Presynaptic neurons could excite or inhibit neighboring cells, and the net result could be an action potential, the all-or-none impulse that was specialized for long-distance communication. The action potential represented a neural decision as to the sum total of excitatory and inhibitory influences. Thus,

neurons could be conceived as having an integrative role, not simply being passive connectives, but more flexibly combining influences from many other neurons.

At this point, we begin our description of the transformative role played by the visual neurophysiologist at midcentury. The development of a very simple technique, the recording of neural impulses using the microelectrode was crucial. Eventually it was possible to simply insert a tiny probe into the tissue with little apparent damage, allowing investigators to "eavesdrop" on individual neurons one at a time during normal visual stimulation. Kuffler (1953) and Barlow (1953) were the first to truly exploit the technique, showing clearly that "on" and "off" responses were actually caused by light falling on different areas of the retina. Although anticipated by Barlow (1953), Lettvin and colleagues (Lettvin, Maturana, McCulloch, & Pitts, 1959) went much further to capture the imagination of a new generation, outlining properties of cells in the frogs retina that began to look startlingly like what was most important for the frog: little bugs to eat, growing shadows indicating predators looming closer.

The investigations of Hubel and Wiesel (1959, 1962) were the most systematic, comprehensive, and had the most lasting impact. Confirming Kuffler, they found concentric receptive fields in the retina and lateral geniculate nucleus. In the primary visual cortex they found something entirely different. Each cell required that light or dark regions be oriented. With a genius both for observation and taxonomy, they classified the cells into discrete categories of ascending complexity. Simple cells summed the excitatory and inhibitory effects of light from differing portions of the receptive field. Complex cells preserved the properties of orientation selectivity yet allowed oriented stimulus to vary in its exact position. Even higher order cells were also noted. Hypercomplex cells were orientation selective and responded, but only if the line did not spill over into more distant retinal regions. Hypercomplex cells of higher order generalized this property of line length limitation by not firing for any line that exceeded a certain length independent of the retinal area stimulated. Along the way Hubel and Wiesel also noted that many cells were direction selective, giving vigorous response for movement of an oriented bar in one direction but little or no response for movements in the opposite directions. Later studies by Barlow and colleagues demonstrated how specific these selectivities would be. For example, motion-selective cells in the rabbit's retina were selective to the direction of motion independent of shape, contrast, or contrast polarity (Barlow & Hill, 1963).

The combination of specificity and abstractness of the receptive fields was astonishing. Rivaling the autonomous relational processes posited by Gestalt psychologists 50 years earlier, cortical neurons were sensitive to "relations," not absolutes. Each individual cell seemed to be triggered by its own preferred local Gestalt, a very specific relation of dark, light, and even movement. Most impressive was the order and succession of taxonomic categories. The remarkable properties of each successive stage in the cortex was seen as the result of simple neuronal convergence from the previous stages. Linearly aligned receptive fields of neurons in the lateral genic-

ulate nucleus were hypothesized to converge on cortical cells with excitatory connections bestowing orientation selectivity to simple cells (Hubel & Wiesel, 1962). Consequent convergence of aligned simple cell receptive fields were thought to comprise the input to complex cells and so forth. So the most remarkable visual properties of single neurons could arise from the most simple and successive application of excitatory and inhibitory processes, mechanisms proposed decades earlier by Sherrington and Eccles. The result of such simple combinations was indeed grand—units that seemed to mimic some of the as yet poorly understood elements of visual intelligence. Lettvin, Maturana, Pitts and McCulloch (1961) noted that there “was an odd discrimination in these cells, which, though we would not be surprised to find it in the whole animal, is somewhat startling in single units so early behind the retina,” (p. 774). This was a far cry from the simple type of “atomic” psychophysics developed by Fechner, Wundt, et al., clearly more similar to Gestalten than to little patches of light. Specific neuronal connections, so dismissively rejected by the Gestalt psychologists (with their interest in brain fields) were capable of mediating patterns as or even more holistic than the simple Gestalten postulated years earlier.

III. BARLOW'S NEURON DOCTRINE

That these remarkable findings were obtained from just one class of physical brain signals, action potentials, is significant. Many techniques have been developed to measure brain activity before and since. Electroencephalograms (EEGs) and evoked potentials emerged before the advent of single-unit recording; MEG, positron emission tomography (PET), and functional magnetic resonance imaging (fMRI), emerged later. Yet the identities, or worse the multiple identities, of the sources of these signals remain obscure. Extracellular recorded action potentials, with their very brief durations, unvarying size, and short propagation distances leave little uncertainty regarding their distinct identity. In addition, spikes are not simply epiphenomenal complexities but the very signals that are presumably read by the most understood elements of brains, (i.e., neurons). As Horace Barlow once put it to me “action potentials are the fire, all else is . . . smoke.”

Provoked by the central dogma of molecular biology, Barlow (1972) suggested a set of principles to link the activities of single neurons to sensation:

1. To understand nervous function one needs to look at interactions at a cellular level, rather than either a more macroscopic or microscopic level, because behavior depends upon the organized pattern of these intercellular interactions.
2. The sensory system is organized to achieve as complete a representation of the sensory stimulus as possible with the minimum number of active neurons.
3. Trigger features of sensory neurons are matched to redundant patterns of stimulation by experience as well as developmental processes.

4. Perception corresponds to the activity of a small selection from the very numerous high-level neurons, each of which corresponds to a pattern of external events of the order of complexity of the events symbolized by a word.
5. High-impulse frequency in such neurons corresponds to high certainty that the trigger feature is present.

Yet despite Barlow's bold claims, this neuron doctrine for perception has not had the same finality of DNA→RNA→protein nor has there been a comparable achievement like the cracking of the genetic code. Yes, the legacy of single-unit recording is still very strong. The same approach of recording from one neuron at a time in ever more complex visual displays and in behaving animals continues.

But the conceptual momentum behind Barlow's idea did not increase nor was there a subsequent expansion or codification of Hubel and Wiesel's tightly linked hierarchy. In fact, there has been slippage rather than advance (Cleland, Dubin, & Levick, 1971; Lennie, 1980). The reasons perhaps are many. First and perhaps even *a priori*, it would be difficult to imagine how Hubel and Wiesel's already stunning achievements could be further extended to a description of successive stages in their hierarchy given the forbidding combinatorics of the visual stimulation required. Wisely, Hubel, and Wiesel sidestepped the issue and devoted subsequent studies to other topics, including a masterful description of how various simple attributes get partitioned in the cortical tissue (functional architecture). Second, the findings since Hubel and Wiesel have shown the existence of separate parallel streams of information processing and connectivity running from retina to cortex. The existence of a slow parvo and a separate more rapidly conducting magno pathway begins in the retina and is evident even beyond the striate cortex (Cleland et al., 1971; Shapley, 1990; Stone, 1972). Each stream shows some degree of differential sensitivity, with the parvo system more sensitive to chromatic differences, and the magno system to motion. Instead of a convergent succession of connections arranged hierarchically, these results argue for separate parallel streams, inherently differentiated in function as early as the retina, and maintaining separate identities up through the cortex.

Yet despite these obvious shortcomings regarding the details of Hubel and Wiesel's hierarchy and residual skepticism regarding the extremes of Barlow's neuron doctrine, nothing since has had the force to displace the status of the single neuron as the basic unit of vision. And as we shall see, the newly emerging field of visual psychophysics would only strengthen this outlook.

IV. PSYCHOPHYSICS OF RECEPTIVE FIELDS

For a generation, starting approximately in the 1930s, visual psychophysics, in keeping with its roots in the 19th century, was concerned with detecting small patches of light, with stimuli varying along the simplest physical dimensions, such as inten-

sity or wavelength. In the right hands such simple stimuli were to reveal important properties of early vision; for example, that one quantum is sufficient to activate a single photoreceptor (Hecht, Shlaer, & Pirenne, 1942), and that the detailed spectral characteristics of chromatic mechanisms could be discerned (Stiles, 1959). That one could learn about the properties of the retina at such a microscopic level of detail simply by asking a subject whether he saw something or not, contributed in no small measure to the growing respect accorded to visual psychophysics.

Later, stimulated by the new discovery of visual receptive fields, there was greater interest in a more broadened practice of visual psychophysics. In keeping up with these new results from physiology, the stimuli were to become much richer and more complex. Striking progress was made using new methods and stimuli in the area of depth and motion processing. Julesz's random dot stereogram was perhaps the most dramatic example. Using the new power of the modern digital computer, Julesz's (1961) ingenious demonstration confirmed Wheatstone's observation, but more important, it raised the hope that the brain's representation of space (encoding the third dimension) could be isolated from higher-order cognitive processes and understood as a separate and tractable problem. This view was strongly reinforced by the subsequent discovery of neurons specifically tuned to binocular disparity in the visual cortex (Barlow, Blakemore, & Pettigrew, 1967; Pettigrew, Nikara, & Bishop, 1968). Also evident was a set of findings connecting motion perception to the properties of motion-selective cells. For example, the motion aftereffect and other effects of prolonged stimulation (Barlow, 1963; Barlow & Brindley, 1963; Sekuler & Ganz, 1963) were conceived of as the selective adaptation of hypothesized motion-selective cells in the human visual system.

As a consequence of these and other findings, there developed at least implicitly the notion of the visual system as a set of filters or detectors tuned to very specific sets of features. In each part of the visual field, there were receptors or detectors tuned to orientation, motion, bar width, and even depth. Vision, instead of being a hierarchical process, was conceived of as a set of separate dimensions, mapped onto the topographic map of the visual cortex.

Heretofore, visual stimuli had been described in fairly conventional terms; spatial extent, intensity, movement, and so on. This was soon to be replaced or at least temporarily overshadowed by descriptions less familiar, borrowing heavily from ideas developed in optics and electrical engineering, and in the process the idea of parallel channels became reinforced even further.

Perhaps the best example was the appropriation of linear systems analysis (including Fourier analysis) to describe visual function both psychophysically at the level of the whole organism and through electrophysiological experiments measuring the sensitivity of neurons in response to sine wave gratings. F. W. Campbell and colleagues argued that the contrast sensitivity curve obtained from human observers was the envelope of sensitivities of an underlying set of "channels," each sensitive to different ranges of spatial frequencies (Blakemore & Campbell, 1969; Campbell & Robson, 1968). The detection of a complex pattern could be predicted not by

the peak-to-trough variations in luminance, but only by whether a given narrowly tuned mechanism had received sufficient contrast above its contrast threshold (Graham & Nachmias, 1971). The acceptance of these otherwise novel findings was strongly reinforced by an analysis of receptive field characteristics using linear theory. Thus, spatial-frequency tuning could be explained via the Fourier transform as the simple consequence of the spatial layout of Hubel and Wiesel's receptive fields, with their elongated strips of excitatory and inhibitory regions. These neurons were the same channels that determined the overall contrast sensitivity function. As such, the consequences of systems theory were significant. First, it provided a common metric or method of stimulus description that enabled one to link the behavior of single cells to the behavior of the whole organism. Second, it provided a rather different alternative to Hubel and Wiesel's conception of the receptive field.

Yet to those of us who had gratefully accepted Hubel and Wiesel's hierarchical edifice and who at least implicitly acknowledged at least some of the tenets of Barlow's neuron doctrine, these results seemed alien. For what possible reason could the visual system require such a coding scheme? The most extreme interpretation rested its case on Fourier's fundamental theorem. All functions, including the visual image, can be regarded as sums of sines and cosines. Thus, visual neurons could be conceived of as re-representing the image in terms of Fourier coefficients. This interpretation could not be strictly true, however, because even the narrowest receptive fields were localized and not fully distributed across the whole visual field as required. Less extreme is the now current idea of the representation of images in terms of wavelets, essentially Gabor functions, a hybrid representation, partaking some aspects of frequency analysis but also more localized in space. Such an interpretation suggested the utility of such units as a recoding of the image at different spatial scales, to enable the visual system to process different levels of spatial detail in an image. For example, for motion and stereopsis, there was some evidence that processing for low spatial frequencies had special precedence, and it was even argued that some types of object recognition also had preferential access to restricted sets of spatial frequency mechanisms (Parish & Sperling, 1991). More recently, Field (1994) has suggested that this narrow band tuning is the predicted outcome of a set of engineering constraints, the need to most efficiently code natural scenes (with their particular statistics) using a sparse code (where the majority neurons are inactive at any given moment).

Whatever the interpretation of these results, it appears that early visual receptive fields are indeed relatively narrowly tuned to spatial frequency. As such they are very much less selective to wide-band stimuli such as lines, bars, or gratings (DeValois, Albrecht, & Thorell, 1978). No longer could one regard Hubel or Wiesel's now classical receptive fields as detectors of the obvious visual elements in a scene, which are so evident to observers. One could not therefore regard receptive fields as the building blocks of our ordinary conscious visual perception, say as an artist or cartoonist would use lines and edges.

Thus greater currency of the visual system as a set of parallel channels continued to gain ground, and the spatial frequency findings only reinforced this view. Again, according to this view, each portion of the visual field was populated by so-called feature detectors or channels, each coding a different attribute of the image. Now it also included spatial frequency. Given this assortment of elementary units or "atoms" of vision, it would seem reasonable to see if one could understand the many phenomenon of visual perception in terms of receptive fields. Given some simple ways in which such channels might interact (either showing independence or coupled via inhibition), a wide range of applications of the receptive field concept to perceptual and cognitive phenomenon were attempted. Most successful were accounts about the visibility of fairly simple stimuli (Graham, 1989). As mentioned earlier, if the stimulus amplitude of the components of all possible neurons or channels were below their own individual thresholds, the pattern would remain invisible. This reinforced the view that visual sensitivity as measured by detection could be accounted for by the envelope of best sensitivity of all of the underlying neuronal receptive fields (Barlow, 1972).

The existence of cells with spatial frequency-selective cells sensitive to varying degrees of binocular disparity appeared to provide the beginnings of an explanation for the perceptual phenomenon of stereopsis. It also explained how perceived differences in depth in random dot stereograms could occur. Also satisfying was Adelson's missing fundamental illusion (Adelson & Bergen, 1985), where observers see motion in the direction of the most salient Fourier component rather than the motion of the overall pattern, which argued persuasively for the perceptual role of receptive fields. This coupled with the well-known waterfall effect (motion aftereffect) provided some of the strongest relations between perception and underlying mechanisms. Other equally ambitious but perhaps more ambiguous successes have been attempts to explain fine pattern discrimination (hyperacuity as coined by Westheimer, 1979) in terms of populations of receptive fields (Wilson, 1991). Even more ambitious efforts were seen in attempts to explain the characteristics of visual illusions (Wenderoth, 1992) and visual search behavior (Julesz, 1991; Treisman & Gelade, 1980) in terms of presumed elementary units. Here, however, the attempt was far less successful. Interactions of presumed visual channels could not explain the specific characteristics of visual illusions (see Gillam, chap. 5, this volume), and such channels were also found to lack any explanatory power in understanding visual search (Nakayama & Joseph, 1997). Also there was obvious failures in understanding what some might consider the simplest of visual domains, the perception of brightness. Originally, lateral inhibition, so closely related to the idea of receptive field surrounds was invoked (echoing Mach) in explaining various brightness and lightness illusions, such as simultaneous contrast and Mach Bands (see Ratliff, 1965). This approach has been largely abandoned, as there have been numerous demonstrations of much more powerful and more global influences (Adelson, 1993; Gilchrist et al., 1997; Land & McCann, 1971).

V. A VISUAL TAKEOVER: REDRAWING THE BRAIN

In the late 1970s a quiet revolution suddenly expanded the anatomical domain of vision. For many years, primary or striate cortex was deemed the presumed receiving area for vision, after which it would send its projections to "association" cortex. This fit well with the then current ideas of vision, inherited from British associationism, that a "picture of the world" was formed in the visual cortex. This was associated with other kinds of mental events in the brain (touch, sound, words, etc.), thus establishing the need for a large association cortex for the various connections to higher portions of the brain. Hubel and Wiesel (1962, 1965) largely confined their studies to the striate cortex but did confirm the existence of retinotopic areas anterior to and outside of striate cortex reported 20 years earlier using evoked potential methods (Talbot & Marshall, 1941). As such, there was an awareness of the existence of parastriate visual areas, but the full force of this realization was yet to come. This was to change dramatically, thanks to the pioneering efforts of a number of anatomically oriented neurophysiologists (Allman & Kaas, 1975; Zeki, 1975) and later Felleman and van Essen (1991). Using a variety of mapping techniques and drawing on several species of primate, it became clear that instead of 1 or perhaps 2 additional visual areas, at least 20 distinct areas could be identified. Not only were there many more distinct areas but, more importantly, the total cortical area devoted to vision expanded dramatically. It now comprised half of the brain, at least for the macaque monkey. The full consequences of these new findings cannot be exaggerated.

Within a few years, the relative importance of vision had increased dramatically, particularly when stacked against all other conceivable brain functions. Vision, which earlier was considered to deliver a mere picture of the world to be interpreted by other higher parts of the brain, had in itself become something much more. The enormous size and complexity of even half of the brain hinted to a comparable enormity for vision. The inevitable consequence of this territorial expansion was a much wider definition of what constituted vision. With this new visual "conquest" came an altered awareness of what this takeover had secured. For example, there had been a long tradition of painstaking analysis of degraded performance on various cognitive tasks following selective cerebral ablations in primates (Mishkin, 1982). These were originally considered to be explorations as to the physiological substrates of memory. Now with an expansion of vision extending well into the temporal lobe, the meaning of these studies changed in subtle but significant ways. Thus, the temporal lobe became identified not just with memory but was now linked to something more specifically visual, to a role in mediating visual object recognition. This realization in turn then supported otherwise puzzling and initially discounted findings, for example, that neurons in the temporal lobe selectively fired for specific high-level objects, particularly to faces (Gross, Rocha-Miranda, & Bender, 1972).

So, instead of considering vision as the simple creation of a picture projected

onto the visual cortex, the existence of a greatly enlarged visual brain suggested that vision was not a single function but a staggering conglomerate of functions. This in turn led to a more systematic attempt to categorize such functions more globally. As an example, Ungerleider and Mishkin (1982) suggested that the many visual areas could be conceptually grouped in terms of gross anatomy, into a dorsal and a ventral system. They suggested a dorsal system projecting to the parietal lobes mediating functions related to spatial localization and a ventral system projecting to the temporal lobes mediating object recognition. More recently, this dichotomy has been further confirmed, although in a revised manner (Goodale, 1995), suggesting for the dorsal system, functions more closely related to visuomotor behavior.

In addition to the enlarged scope for vision, there was also a growing awareness as to vision's greater autonomy. Although not denying the connections of vision to other important functions, vision was now conceived as operating by rather vision-specific processes not so closely tied to other functions, particularly language (see Fodor, 1983).

VI. MARR'S INCLUSIVE FRAMEWORK

An important synthetic commentary on vision came from yet another quarter, primarily from artificial intelligence. Before describing David Marr's distinctive contributions, we mention some antecedents arising partly as a consequence of the mobilization of scientists for the war effort. These were the new disciplines of operations research, cybernetics, and information theory that emerged in the late 1940s. Physical systems were now described at a higher level of mathematical abstraction. Thus the concepts of feedback, information, stability, and so on, provided a language that could describe such systems in ways that were not closely tied to the physics of the machinery. As such, it also became a natural language to describe physiological as well as psychological systems. Thus by the mid-1970s there was already a long history in treating the brain more formally, independent of its physical characteristics. In psychology, the mind was now considered as an information-processing device, analogous to a computer (Neisser, 1967; Simon, 1968).

Against this background, Marr's (1982) contributions were more specifically inspired by early advances in artificial vision. Most critical was the work of a small group of founding pioneers who solved a restricted yet significant problem—that of correctly identifying the surfaces of multiple polyhedral objects represented in line drawings (Guzman, 1969; Huffman, 1977; Waltz, 1975). They noted that there was a limited number of line junctions (L, T, fork, arrow, etc.) in such drawings. The interpretation of each junction considered by itself was ambiguous because multiple sets of three-dimensional (3D) surface configurations could have given rise to them (see Cutting & Massivoni, chap. 6, this volume). Nevertheless, if one considered the possible interpretation of line junctions in relation to neighboring junctions, recognizing that there must be consistency in the 3-D interpretation of the line joining neighboring junctions, a general solution to the polyhedral line

drawing could be found. Line drawings of such objects could be correctly interpreted as 3-D scenes.

Critical for this early success was the notion of constraints. Line drawings of polyhedral objects are not arbitrary assemblages of lines but are the consequence of a lawful process of image formation dictated by the projection of 3-D scene onto a 2-D drawing surface. The understanding of this inherent grammar of junctional relations provided a powerful new way to understand vision *independent of the visual apparatus itself*. Recognizing the novel power of this approach, Marr's motivation was to adapt this way of thinking more broadly.

In generalizing beyond this artificially restricted world, Marr and colleagues followed the path parallel to that traversed earlier by J. J. Gibson (1950, 1966). Attempting to understand natural scenes instead of artificial and contrived visual worlds, Gibson's ecological optics provided an imaginative and rigorous analysis of the properties of the optic array as a potential carrier of information about the terrestrial world. Gibson's contribution was to see a rich underlying mathematical order in the optic array (see Cutting, chap. 4, this volume; Proffitt & Kaiser, chap. 7, this volume). Thus for Gibson there was much to be learned about vision from a purely optical analysis of the rules of image formation because the regularities and invariances here provided the key information about scenes and the observers relation to them (see also Nakayama, 1994).

Marr adopted this style of thinking and incorporated it as a key idea in his comprehensive framework to understand all of vision. Explaining vision, however, for Marr was a more complex affair than suggested by his predecessors; understanding could not come from a single perspective. For Marr it was critical to recognize the full scope of the endeavor—that vision required an explanation at many levels. Marr argued that a distinction between three separate levels of explanation was necessary—the computational, the algorithmic, and the level of implementation. The computational level—the most neglected and yet the most fundamental—rested on the type of analysis advocated by Gibson. It required the rigorous analysis of information available in the optic array in relation to the specific visual task. For example, from a mathematical analysis, it can be proven that if one assumes rigid motion, the full 3-D structure of an object can be computed given the image positions of points in three views (Ullman, 1979).

Having understood the computational problem there arises the need for an algorithmic explanation. How is the computation to be realized in a formal sense? For example, if the task were to compute the local motion of an image region a variety of algorithms could be considered based on the elementary operations of multiplication (Reichardt, 1961), addition (Adelson & Bergen, 1985), or division (Horn & Schunk, 1981). Marr suggested that the highly developed discipline of visual psychophysics was well suited to evaluate various candidate algorithms because each might fail in characteristic ways when subjected to the widest range of stimulus conditions.

A final level of description is that of neural implementation. How are the algorithms that solve the computational problem to be realized in neuronal hardware? For example, if the detection of motion requires the formal operation of multiplication or division (as required by Reichardt's model or gradient models) is there evidence that shunting inhibition is present in the cortex, and could it then mediate such an operation?

Over 10 years later, there has been much to criticize regarding these distinctions. Some have suggested that it proposed an optimality or grand design that was simply a hope rather than a scientific theory. Vision, rather than being a supremely adapted system, might be a series of adventitious processes that simply work well enough (see Kitcher, 1988; Ramachandran, 1985). Others, considering scientific tactics, have noted that advances rarely proceed by such a programmatic approach. Rather, knowledge about vision might bubble up in many unforeseen ways not along the route prescribed by Marr. Yet, the overall effect of these distinctions was positive, helping to delineate the various types of endeavors that had already emerged in the study of vision and to more clearly highlight the complementary rather than the competitive nature of various efforts.

In addition to distinguishing three different levels of explanation, Marr made another triple distinction, this time between different levels of visual representation. Acknowledging a greatly expanded visual system, Marr outlined three broad levels of analysis that vision must comprise. First was the level of the image or the primal sketch. This was perhaps the most familiar to physiologists and psychophysical workers and could be understood as mediated by receptive fields. Second was a viewpoint-specific intermediate level, the 2.5-D sketch where for each point in the visual field a surface-normal vector was represented. Third was a viewpoint independent level of visual object representation, where a full 3-D representation of the object resided.

The distinctions with different levels of processing were not unique to vision. In linguistics for example, the delineation between phonology, syntactics, and semantics was a crucial and influential one, clarifying the efforts required by keeping processes and questions distinct. With the explicit postulation of different levels of processing, one could more clearly see how specific research agendas could fit into a larger whole, even if Marr's particular levels would require substantial redefinition. Thus, the endeavor to understand vision as a series of filters was a reasonable way to examine early vision, say at the level of the image or primal sketch but perhaps not appropriate for the analysis of later representations. For example, there may exist visual processes related to object recognition that have little to do with the filtering aspects of earlier stages (see Ullman, 1995). My colleagues and I have been encouraged by Marr's distinctions and have postulated a distinct intermediate level of surface representation interposed between early vision and higher-level vision (Nakayama, He, & Shimojo, 1995). We argue that the encoding of surfaces has its own properties, not readily understood as emerging from the simple combi-

nation of cells with particular receptive fields. Thanks in part to Marr's distinction of separate levels, many researchers with very different interests and talents have been able to coexist almost peaceably, now recognizing their own efforts as a distinct part of a much larger endeavor.

In addition to these important distinctions, Marr and colleagues are also known for their more specific theories of visual processing, for motion, for edges and for stereo (Marr & Hildreth, 1980; Marr & Poggio, 1976; Marr & Ullman, 1981). These studies, important as they were at the time, have not had the same obvious influence. Yet here too, there have been indirect consequences. These papers attracted, perhaps by style as much as by substance, the attention of a wide range of scientific onlookers from the "hard" sciences, eager to test their mettle in a new field. Thus Marr and colleagues, like Hubel and Wiesel a generation earlier, captured the imagination of new talent.

VII. VISION FIN DE SIÈCLE

So where do researchers now find themselves at century's end? The picture I have painted so far has brought us up to the mid-1980s, shortly after Marr's posthumous publication (Marr, 1982). Because it is harder to capture events in the moment, I must be more cursory and yet cover a range of new developments.

A. Attention

First, there has been little said so far about the role of attention in vision. In fact, until fairly recently, it could not be easily observed in the laboratory and was not regarded as a major factor in perception. At best attention was seen as modulating vision, decreasing reaction time by a few tens of milliseconds. Only very recently has there been evidence, and it is now very compelling, that attention is not just a minor biasing factor in visual perception but that it is absolutely critical (see also Doshier & Sperling, chap. 8, this volume; Hochberg, chap. 9, this volume). In fact, evidence indicates that without attention, conscious perception simply does not occur (Mack, Tang, Tuma, & Kahn, 1992; Nakayama, Chun, & Joseph, 1997; Rensink, O'Regan, & Clark, 1997) confirming recent theoretical views (Nakayama, 1990; O'Regan, 1992) (for additional discussion to this point, see Hochberg, chap. 9, this volume). This suggests that the process of vision is a far more active one, perhaps more like exploratory touch as advocated earlier (Gibson, 1950; MacKay, 1973). Also related are new ideas suggesting that attention has an indexing or pointing function, marking items that are to be acted on or singled out for action (Allport, 1993; Ballard, Hayhoe, & Pelz, 1995). Along these lines, Cavanagh (1992) has suggested that the perception of motion can be understood as the active tracking of objects by attention. Such new findings and ideas about the indispensable role of attention provide the beginnings of an alternative view of vision, against the notion that vision is simply a sophisticated "picture."

B. Neuroimaging

One of the most significant developments in the last decade has been the explosive growth of the science of brain imaging in human subjects. After the initial discovery of X-rays, the most exciting advance came long after with computerized-axial-tomography (CAT), resting on a remarkable mathematical technique to reconstruct 3-D density map from a series of successive scans. This technique revolutionized the practice of clinical neurology and neuropsychology, which heretofore had to be satisfied with indirect behavioral testing. Later, and with an almost reckless invasiveness, PET emerged, using the brain itself as the source of some of the highest energy radiation ever used in a medical or biological setting. The addition of radioactive isotopes to the blood would lead to different image intensities depending on the brain's local need for more or less oxygen. Thus, those areas having the highest neural activity would have the greatest concentrations of gamma rays emerging from them. PET's promise was truly revolutionary for psychology and the brain sciences because it also provided a way to capture brain activity, not just structure.

Just as the virtues (and the dangers) of PET were to become more fully appreciated, MRI and fMRI superseded it. Based on radiation inherently less dangerous, it has more virtues than PET (much higher spatial and temporal resolution) but without the obvious risks. Presently, there are indications that eventually the resolution will be on a millimeter scale, such that one will be able to see selective activation of the ocular dominance columns of the striate cortex. Thus far most of the results from such methods have been largely confirmatory, but the promise of new and exciting findings is palpable. Potentially far reaching are successful efforts to make a map of the human visual system comparable to that outlined in the primate (Tootell, Dale, Sereno, & Malach, 1996).

C. Neuropsychology

Related to advances in neuroimaging are new developments in the examination of brain-damaged patients. Much of the recent impetus comes from new efforts to apply methods and concepts derived from cognitive psychology and visual psychophysics to disordered function. This has attracted new investigators to complement existing neuropsychological efforts. Moreover, the new techniques of brain imaging allow independent assessment as to the site of brain damage, enabling a stronger cross-comparison of so many of the new and specific deficits. Over the past few years clinical cases have been reported that demonstrate the existence of extremely specialized deficits—the inability to recognize faces, colors, as well as deficits in seeing motion. Each has its likely brain locus as well. These dramatic findings add weight to the emerging view that the visual system is indeed a very separate set of brain functions, and that even within vision itself there might be countless more specialized modules.

D. A Possible Rebirth of Gestalt Psychology?

As mentioned earlier in regard to psychophysics of receptive fields, the attempt to link receptive field characteristics to perception was strongly tied to the idea of the visual system as a series of passive filters analyzing the image at all portions of the visual field. Thus, the study of vision became a problem of systems engineering, trying to adduce the identity and characteristics of the fundamental filters using rigorous/quantitative psychophysics and quantitative modeling (see Doshier & Sperling, chap. 8, this volume). Regrettably, this significant yet specialized approach greatly overshadowed a richer and once vigorous tradition of research initiated by the Gestalt psychologists and their followers in Germany and Europe (Ash, 1995).

Even though all three leaders of the Gestalt movement were able to migrate to America at the peak of their influence (Koffka came to Smith College in 1927, Wertheimer to the New School in 1934, Kohler to Swarthmore in 1935), their trans-Atlantic move was largely a failure, particularly considering the great strength of their movement in Germany. In part this was the result of America's succumbing to behaviorism and positivism. Perhaps as decisive was the problem of scientific lineage and renewal. Few graduate students were trained to take up positions of needed leadership (Swarthmore and Smith were undergraduate institutions). Also significant was the ideological corner that Kohler permitted himself to become painted into (he alone survived into the postwar years). Kohler was seen to be a defender of a defunct global brain field theory which treated the brain as a more or less homogeneous, self-organizing, physical media, ignoring the role of specific neuronal connections. As such, proper credit for the more solid achievements of the Gestalt tradition in fundamental perceptual research was lost amidst the distaste for Kohler's Gestalt theory. By midcentury, the Gestalt tradition of vision research in America was essentially extinct (cf. Hochberg, chap. 9, this volume).

It is fortunate that Gestalt psychology still had a few vigorous and active adherents in Europe, among them Metzger (1936) in Germany and Kanizsa in Italy. The work of Kanizsa represents perhaps the best example of a continuing Gestalt tradition in perception (see Kanizsa, 1979). In contrast to Kohler, who was preoccupied with philosophical issues relating brain states to perception, Kanizsa followed a more phenomenological approach, carefully crafting sets of demonstrations to make important theoretical points about perception. One of his greatest contributions was his work on perceptual completion, the automatic visual propensity to complete figures either in back of occluding figures (amodal completion) or in front of them (modal completion) forming the now well-known illusory contours. Kanizsa suggested that these processes were exclusively visual, distinct from higher-order thinking despite the fact that such processes also seemed to show "intelligence," enabling the visual system to encode the world from sparse information. As such, Kanizsa's approach was an advance over the preceding Gestalt tradition, which was more static, preoccupied with "laws" linked perhaps to internal states rather than towards the goal of picking up information (see also Hochberg, chap. 9, this vol-

ume, for additional discussion of Gestalt psychology). Kanizsa's demonstrations now grace textbooks and contemporary research papers and form the foundation of a growing emphasis on midlevel vision, roughly analogous to Marr's 2.5-D sketch but based on a richer empirical data base (see also Nakayama et al., 1995).

Along with the greater recognition of Kanizsa's work came the implicit acceptance of visual phenomenology. After years of generalized suspicion associated with the results of Gestalt psychology, even the most tough-minded temperaments could not fail to be moved by a compelling perceptual demonstration. It helped, of course, that one of the most dramatic demonstrations, the Julesz random dot stereogram, could be interpreted at a mechanistic level. Strong demonstrations by Ramachandran and Gregory (1978) were soon to follow, showing a curious disassociation of color and motion. So, phenomenology, one of the staples of Gestalt psychology, is again back, popular, and nearly respectable. It has worked mainly for studies of early and midlevel vision, but there are also hopeful indications that it may be useful for higher-order vision, say object recognition (Thompson, 1980; see also Nakayama et al., 1995 for some additional justifications for the phenomenological method).

E. Dissociation of Conscious Visual Perception and Behavior

The Gestalt psychologists insisted that the phenomenology of visual experience must be the starting point to understand vision. Behavioristically oriented psychologists on the other hand were happy to ignore the issue of conscious experience, asking human observers or animals to make differential responses. Already limited as these traditions were, each would be even further taxed when confronted by a new disassociation—between conscious phenomenal experience and visuomotor behavior. First are examples of patients with brain lesions who are deficient in the conscious perception of a visual stimulus but act appropriately when urged to perform a motor response. Thus patients with hemianopia (resulting from striate cortex damage on one side) can reach appropriately for targets in the blind hemifields showing the phenomenon of blind sight. Milner and Goodale (1995) report the case of an agnostic patient who cannot consciously report the orientation of a large bar but who can correctly orient their hand when asked to regard it as a mail slot and to post a letter.

Against the possibility that these clinical cases represent rare curiosities, analogous phenomenon can also be seen in healthy human subjects. These have taken a number of forms. First are situations where persons perceive a visual configuration erroneously, whereas their motor system acts otherwise. One of the early studies indicated that the pattern of eye movements to misperceived spatial positions (occasioned by induced movement) was normal (Wong & Mack, 1981). Other studies show that observers did not perceive shifts of simple visual scenes during eye movements, but their subsequent unnoticed fixations belied this (Bridgeman, Hendry & Stark, 1975). More convincing perhaps are extended behaviors that have little opportunity for correction after repeated errors. Loomis, da Silva, Fujita, and

Fukushima (1992) show that observers consistently misjudge the distances of objects along a ground plane when queried by various psychophysical methods yet show veridical representation, at least implicitly, by walking blindfolded to distant points with surprising accuracy and ease.

The issue of dissociation between conscious perception and behavior has had a long history in psychology, going back to early studies on subliminal perception (McGinnies, 1949). Reviving this seemingly discredited topic, Marcel (1983) reported that observers cannot "see" a very short-duration stimulus that is quickly followed by a mask. Yet such stimuli facilitate the recognition of semantically related words presented subsequently. Although this finding has not been replicated, more recent studies using a wide variety of different methods argue for some form of dissociation. These studies report repeatable instances where observers cannot report the presentation of a particular stimulus, but there is evidence that it has been encoded rather fully. An interesting example is the phenomenon of repetition blindness, where observer's cannot report the presence of a repeated stimuli in an overlapping succession of letters, words, or pictures (Kanwisher & Potter, 1990). The "attentional blink," another form of "blindness" occurs after observers identify a critical target in a stream of letters or words (Raymond, Shapiro, & Arnell, 1992), yet show (via event-related potentials) that semantic processing of the unreported word occurs nevertheless (Luck, Vogel, & Shapiro, 1996). These are surprising and as yet controversial findings. If replicated and more fully described, they would force us to rethink vision both methodologically and conceptually. First, it suggests that the traditional methods of visual perception and psychophysics are probably too restrictive and may conceal what may be some of the most important factors in determining what aspects of a scene we visually encode. Using an unusual paradigm where observers do not expect additional visual stimuli, Mack and Rock (in press) show a surprising degree of inattentional blindness to what would seem to be the most obvious stimuli, including large shapes and moving patterns in a relatively uncluttered field. What is of particular interest is the fact that highly significant patterns requiring visual coding at rather semantic levels (one's own name, a happy face) appear to break through this inattentional blindness. This implies that a high level of semantic analysis can determine what is seen. Continuing the point regarding vision's analogy with touch (as originally outlined by Gibson and MacKay and mentioned earlier) and regarding the deployment of attention as analogous to a motor response, we might profitably regard the direction of attention as another example of motor responses controlled without visual awareness.

Taken together, the foregoing results indicate the possibility of a very different conception of vision and action from that currently conceived (see also the discussion of Hochberg, chap. 9, this volume). Our commonsense view is that we see and then we act. If the foregoing results are more representative of our normal vision and motor behavior, we may require some rather drastic reworking of our basic metapsychological and philosophical assumptions to move forward.

VIII. A REDUCTIONISTIC EXPLANATION FOR PERCEPTION IN THE 21ST CENTURY?

In surveying the achievements of the past 100 years, one cannot help being impressed by the tremendous progress yet also be aware of how limited our fundamental understanding is. Part of the reason of course has been the “growth” of the visual system, now comprising so much more of the brain’s territory and with it so many more functions. The sheer size of the visual system should be our constant reminder as to the enormity of vision. Marr suggested at least three levels of visual representation, yet there may be many more. Yet even this idea of levels, especially if conceived of as a simple serial process, is bound to be wrong or, perhaps even worse, misleading. With so much of the brain devoted to vision and with the growing appreciation of new and unforeseen specializations as well as the humbling recognition of our own conceptual shortcomings, it would seem short-sighted to demand or to seek exclusively for reductionistic explanations. Yet, we must not rule out the possibility of substantial progress even here. The “single-unit” receptive field notion, worn though it is, has survived because there has been no evident replacement. It has not been for a lack of effort and some specific proposals are fairly well known. If some other more compelling unit of analysis were to emerge, say at a larger scale than single neurons themselves (Abeles, 1991; Edelman, 1987) or even smaller ones, the field could be transformed. Thus, we should salute valiant attempts to understand vision reductionistically, but we should also be mindful that the most important insights about vision are likely to come from almost any quarter. Large integrative theories in sciences can have an equal or even greater impact than mechanistic ones. Darwin’s theory of evolution and Wegener’s theory of continental drift are diverse examples. If the present is any guide, the next century promises riches to those of many persuasions. In a generation hence, I have the hopeful confidence that many will marvel at the achievements of the recent past.

Acknowledgments

Supported in part from grants from the Air Force Office of Scientific Research, the McKnight Foundation, and the Human Frontier Science Project. Thanks to Charles F. Stromeyer for critical reading of an earlier version of this chapter.

References

- Abeles, M. (1991). *Corticonics: Neural circuits of the cerebral cortex*. New York: Cambridge University Press.
- Adelson, E. H., & Bergen, J. (1985). Spatiotemporal energy models for the perception of motion. *Journal of the Optical Society of America*, 2, 284–299.
- Adelson, E. H. (1993). Perceptual organization and the judgment of brightness. *Science*, 262, 2042–2043.
- Allman, J. M., & Kaas, J. H. (1975). The dorsomedial cortical visual area: A third tier area in the occipital lobe of the owl monkey (*Aotus trivirgatus*). *Brain Research*, 100, 473–487.

- Allport, A. (1993). Attention and control: Have we been asking the wrong questions? A critical review of twenty-five years. In D. E. Meyer & S. Kornblum (Eds.), *Attention and performance XIV: Synergies in experimental psychology, artificial intelligence and cognitive neuroscience* (pp. 183–218). Cambridge, MA: MIT Press.
- Ash, M. G. (1995). *Gestalt Psychology in German culture 1890–1967: Holism and the quest for objectivity*. New York: Cambridge University Press.
- Ballard, D. H., Hayhoe, M. M., & Pelz, J. B. (1995). Memory representations in natural tasks. *Journal of Cognitive Neuroscience*, 7, 66–80.
- Barlow, H. B. (1972). Single units and sensation: A neuron doctrine for perceptual psychology? *Perception*, 1, 371–394.
- Barlow, H. B. (1963). Evidence for a physiological explanation of the waterfall phenomenon and figural after-effects. *Nature*, 200(4913), 1345–1346.
- Barlow, H. B. (1953). Summation and inhibition in the frog's retina. *Journal of Physiology*, 119(1), 69–88.
- Barlow, H. B., Blakemore, C., & Pettigrew, J. D. (1967). The neural mechanism of binocular depth discrimination. *Journal of Physiology*, 193, 327–342.
- Barlow, H. B., & Brindley, G. S. (1963). Inter-ocular transfer of movement after effects during pressure blinding of the stimulated eye. *Nature*, 200, 1346–1347.
- Barlow, H. B., & Hill, R. M. (1963). Selective sensitivity to direction of movement in ganglion cells of the rabbit retina. *Science*, 139(3443), 412–414.
- Blakemore, C., & Campbell, F. W. (1969). On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. *Journal of Physiology*, 203, 237–260.
- Berkeley, G. (1709). *An essay towards a new theory of vision*. Dublin: Aaron Rhames.
- Bridgeman, B., Hendry, D., & Stark, L. (1975). Failure to detect displacement of the visual world during saccadic eye movements. *Vision Research*, 15, 719–722.
- Campbell, F. W., & Robson, J. G. (1968). Application of Fourier analysis to the visibility of gratings. *Journal of Physiology*, 197, 551–566.
- Cavanagh, P. (1992). Attention-based motion perception. *Science*, 257, 1563–1565.
- Cleland, B. G., Dubin, M. W., & Levick, W. R. (1971). Sustained and transient neurones in the cat's retina and lateral geniculate nucleus. *Journal of Physiology* (London), 217, 473–496.
- DeValois, R. L., Albrecht, D. G., & Thorell, L. G. (1978). Cortical cells: bar and edge detectors, or spatial frequency filters? In S. J. Cool & E. L. Smith (Eds.), *Frontiers of visual science* (pp. 544–556). New York: Springer-Verlag.
- Edelman, G. M. (1987). *Neural Darwinism: The theory of neuronal group selection*. New York: Basic Books.
- Fecher, G. T. (1860). *Elemente der Psychophysik*. Leipzig.
- Felleman, D. J., & van Essen, D. C. (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cerebral Cortex*, 1, 1–47.
- Field, D. J. (1994). What is the goal of sensory coding? *Neural Computation*, 6, 559–601.
- Finger, S. (1994). *Origins of neuroscience, a history of explorations into brain function*. New York: Oxford University Press.
- Fodor, J. (1983). *Modularity of mind: An essay on faculty psychology*. Cambridge, MA: MIT Press.
- Gibson, J. J. (1966). *The senses considered as perceptual systems*. Boston: Houghton-Mifflin.
- Gibson, J. J. (1950). *The perception of the visual world*. Boston: Houghton-Mifflin.
- Gilchrist, A., Kossyfidis, C., Bonato, F., Agostini, T., Cataliotti, J., Li, X., & Spehar, B. (1997). *A new theory of lightness perception*. Unpublished manuscript.
- Goodale, M. A. (1995). The cortical organization of visual perception and visuomotor control. In S. M. Kosslyn & D. N. Osherson (Eds.), *Visual cognition*. Cambridge, MA: MIT Press.
- Graham, N. (1989). *Visual pattern analyzers*. New York: Oxford University Press.
- Graham, N., & Nachmias, J. (1971). Detection of grating patterns containing two spatial frequencies: A comparison of single-channel and multiple-channel models. *Vision Research*, 11, 251–259.
- Gross, C. G., Rocha-Miranda, C. E., & Bender, D. B. (1972). Visual properties of neurons in inferotemporal cortex of the macaque. *Journal of Neurophysiology*, 35, 96–111.

