Brain and Perception

Holonomy and Structure in Figural Processing

Karl H. Pribram

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One must conclude, as a firmly fixed scientific generalization, that the properties of the external world are rarely represented in a straight-forward way in the human responses triggered in that world. Should perception therefore be expected to be disorganized and chaotic? Not at all. . . . The reason for the apparent disjunction between external stimulus properties and those of the final percept is not hard to find. The physiological organism, standing between these two end terms, has dimensions of its own to contribute, makes its own transformations and creates its own . . . functional relationships in the devious paths from peripheral receptor processes to final response mechanism.

Frank Geldard, pp. 20–21
Sensory Saltation, Inaugural
MacEachran Memorial Lecture, 1975

There are two unavoidable gaps in any behavioral account: one between the stimulating action of the environment and the response of the organism and one between consequences and the resulting change in behavior. Only brain science can fill those gaps. In doing so it completes the account; it does not give a different account of the same thing.

B. F. Skinner (p. 18, 1989)

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John M. MacEachran Memorial Lecture Series

The Department of Psychology at the University of Alberta inaugurated the MacEachran Memorial Lecture Series in 1975 in honor of the late Professor John M. MacEachran. Professor MacEachran was born in Ontario in 1877 and received a Ph.D. in Philosophy from Queen's University in 1905. In 1906 he left for Germany to begin more formal study in psychology, first spending just less than a year in Berlin with Stumpf, and then moving to Leipzig, where he completed a second Ph.D. in 1908 with Wundt as his supervisor. During this period he also spent time in Paris studying under Durkheim and Henri Bergson. With these impressive qualifications the University of Alberta was particularly fortunate in attracting him to its faculty in 1909.

Professor MacEachran's impact has been signficant at the university, provincial, and national levels. At the University of Alberta he offered the first courses in psychology and subsequently served as Head of the Department of Philosophy and Psychology and Provost of the University until his retirement in 1945. It was largely owing to his activities and example that several areas of academic study were established on a firm and enduring basis. In addition to playing a major role in establishing the Faculties of Medicine, Education and Law in this Province, Professor MacEachran was also instrumental in the formative stages of the Mental Health Movement in Alberta. At a national level, he was one of the founders of the Canadian Psychological Association and also became its first Honorary President in 1939. John M. MacEachran was indeed one of the pioneers in the development of psychology in Canada.

Perhaps the most significant aspect of the MacEachran Memorial Lecture

Series has been the continuing agreement that the Department of Psychology at the University of Alberta has with Lawrence Erlbaum Associates, Publishers, Inc., for the publication of each lecture series. The following is a list of the Invited Speakers and the titles of their published lectures:

1975	Frank A. Geldard (Princeton University) "Sensory Saltation: Metastability in the Perceptual World"
1976	Benton J. Underwood (Northwestern University) "Temporal Codes for Memories: Issues and Problems"
1977	David Elkind (Rochester University) "The Child's Reality: Three Developmental Themes"
1978	Harold Kelley (University of California at Los Angeles) "Personal Relationships: Their Structures and Processes"
1979	Robert Rescorla (Yale University) "Pavlovian Second-Order Conditioning: Studies in Associative Learning"
1980	Mortimer Mishkin (NIMH-Bethesda) "Cognitive Circuits" (*unpublished*)
1981	James Greeno (University of Pittsburgh) "Current Cognitive Theory in Problem Solving" (*unpublished*)
1982	William Uttal (University of Michigan) "Visual Form Detection in 3-Dimensional Space"
1983	Jean Mandler (University of California at San Diego) "Stories, Scripts, and Scenes: Aspects of Schema Theory"
1984	George Collier and Carolyn Rovee-Collier (Rutgers University) "Learning and Motivation: Function and Mechanism" (*unpublished*)
1985	Alice Eagly (Purdue University) "Sex Differences in Social Behavior: A Social-Role Interpretation"
1986	Karl Pribram (Stanford University) "Brain and Perception: Holonomy and Structure in Figural Processing" (*in press*)
1987	Abram Amsel (University of Texas at Austin) "Behaviorism, Neobehaviorism, and Cognitivism in Learning Theory: Historical and Contemporary Perspectives"

1988 Robert S. Siegler and Eric Jenkins (Carnegie-Mellon University)
"How Children Discover New Strategies"

1989 Robert Efron (University of California at Davis & Veterans Administration Medical Center)
"The Decline and Fall of Hemispheric Specialization"

Eugene C. Lechelt, Coordinator
MacEachran Memorial Lecture Series

Sponsored by The Department of Psychology, The University of Alberta with the support of The Alberta Heritage Foundation for Medical Research in memory of John M. MacEachran, pioneer in Canadian psychology.

Preface

Do not bite my finger, look where I am pointing
—(Warren McCulloch, quoted by Seymore Papert
in McCulloch, 1965, pp. xx).

Motive

These lectures are motivated by several considerations. First among these is the desire to present in an integrated fashion the results of research in my laboratory as it applies to pattern perception. There are a considerable number of perceptual psychologists who feel that the results of brain research are still too crude to help understand the sophisticated issues that define problems in figural perception. At the same time, perceptual psychology texts often rely on incomplete and outdated findings obtained by neurophysiologists. These lectures review the current state of the art in brain research to show that several lines of inquiry have been converging to produce a paradigm shift (Kuhn, 1962) in our understanding of the neural basis of figural perception.

The second motivation that has produced these lectures is the desire to update the holographic hypothesis of brain function in perception as developed in my laboratory (Barrett, 1969, 1972, 1973a, 1973b, 1973c; Pribram 1966, 1971, 1982b; Pribram, Nuwer, & Baron 1974). The earlier formalisms of the theory have been enriched by new neurophysiological data and by the emergence in the field of artificial intelligence of parallel distributed processing architectures (Rumelhart, McClelland, and the PDP Research Group, 1986). These "neural networks" or "connectionist" models are similar to OCCAM, a content addressable computational model that we (Pribram, 1971; Spinelli, 1970) developed in the late 1960s and stem directly from the content addressable parallel distributed procedures that characterize optical information processing such as holography (see e.g., Hinton, 1979; Willshaw, 1981).

A third motivation for the lectures stems from the desire to emphasize the fact that *both* distributed (holistic) *and* localized (structural) processes characterize brain function. For almost two centuries scientists have squabbled as to whether brain processes are localized (e.g., Broca, 1863; Ferrier, 1886/1978; Gall & Spurtzheim, 1809/1969; Munk, 1881) or distributed (e.g., Flourens, 1846/1978; Lashley, 1942; Walshe, 1948). The facts always have been and still are that both localized and distributed processing takes place in the brain and that it is our job to discern which processes are distributed and which are localized (see e.g., Pribram, 1982b).

A final motivation for these lectures is the desire to portray a neural *systems* analysis of brain organization in figural perception by developing sets of quasi-quantitative models; that is, to describe processing in terms of formalisms found useful in ordering data in 20th-century physical and engineering science. It is my conviction that it is only through the use of these formalisms that the psychological and neurological levels of inquiry regarding perception can become related. The relationship entails sets of transformations which, unless they are described precisely and formally, are apt to be misunderstood by both psychologists and neuroscientists. Chances of misunderstanding are less when communication takes the form of mathematics.

The lectures are divided into three parts. A Prolegomenon outlines a theoretical framework for the presentations; Part I deals with the configural aspects of perception, Part II with its cognitive aspects. There is therefore a considerably different tone to the three sections and the reader must be prepared to "shift gears" from (1) processing theory to (2) perceptions (such as color, form, motion) largely immune from intrusions by what the perceiver has come to know and lastly, to (3) those aspects of perception which entail such knowledge (tableness, flowerness, personness). Critical to understanding is the acceptance of evidence that brain perceptual systems operate as top-down as well as bottom-up processors. It is this evidence that my colleagues and I have spent almost a half century in amassing. Some 1,500 nonhuman primates, 50 graduate students, and an equal number of postdoctoral fellows have participated. The results of these researches have cast doubt on viewing brain perceptual processing as elementaristic, bottom-up, reflex-arc, stimulus-response—views that still characterize many texts in neurophysiology, psychology, and perception.

For the most part, tenets based on these exclusively bottom-up views are held implicitly and therefore felt to be fact rather than theory. Such opinions are thus extremely difficult to modify by only presenting evidence against them. The lectures are therefore composed in terms of an alternative theoretical structure which is presented in the Prolegomenon. This theoretical structure is, however, based on the rich set of data presented in the lectures composing Parts I and II.

There is too much here, and yet not enough. The lectures present a point of view, they review some data ordinarily secluded under the rubrics of memory research or the neurophysiology of attention. Still, many relevant psychophysical experiments and data gathered by studying illusions are barely mentioned. But as I have found no text that explains neural processing in perception in terms of the primate brain as I have come to know it—although bits and pieces of explanation abound—I have written down these lectures. As all authors are, I have been plagued by alternations of mood ranging from exhilaration as the text reflects insights previously barely acknowledged, to despair that these insights will not be shared because of inadequacies in my writing style or lack of an interested audience.

The term for the theory, *holonomic,* was first used by Hertz to describe linear transformations when they are extended into a more encompassing domain. I have here extended its meaning to cover the spectral domain. Holos refers to this domain and Nomos to the naming of the generalization. My greatest trepidation has been caused by the attempt to present the outlines of a formal holonomic theory, a set of models of brain processing in perception. I have, therefore, collaborated with Kunio Yasue and Mari Jibu who became intrigued by the theory and are far more coversant with mathematical modeling than I am. The results of our collaboration make up seven appendices that illustrate facets of the theory.

Clearly neither these mathematical models nor the theory as a whole are in any sense conceived to attempt a "final word" regarding brain processing in figural perception. A story best illustrates the actual purpose of the attempt: At the time of the 3rd neuroscience conference in Boulder, Colorado, Donald Broadbent, Colin Blakemore, Fergus Campbell, and I had climbed high into the Rocky Mountains. Coming to rest on a desolate crag, a long meditative silence was suddenly broken by a query from Campbell: "Karl, do you really believe it's a Fourier?" I hesitated, then replied, "No Fergus, that would be too easy, don't you agree?" Campbell sat silently awhile, then said, "You are right, its probably not that easy. So what are you going to say tomorrow down there?" I replied, this time without hesitation, "That the transform is a Fourier, of course." Campbell smiled and chortled, "Good for you! So am I." We needed no further explanation for our mutually chosen course of action. As scientists we shared Popper's (1962) injunction that scientific propositions need to be falsifiable. And we knew the Fourier relation, because of its relative simplicity, to be the most vulnerable to disproof. Thus far, however, nature has surprised us—she may well be more tractable than we dared hope.

The lectures therefore address those who are deeply interested in understanding how brain processes configure perception. Because of the transdisciplinary nature of the lectures, a number of language systems are inolved in integrating current knowledge: neurophysiological, perceptual, computational, and mathematical. The reader must therefore have the patience to become familiar with what to him is unfamiliar terminology—*Languages of the Brain,* Pribram, 1971 can be of help. As important, is a tolerance for naiveties in descriptions in the disciplines in which the reader is expert: As in parallel distributed processing networks, the tension (error signals) between these naiveties and expertise in each of the disciplines being integrated should improve the models presented in the lectures and therefore our understanding of brain organization in perception.

These lectures are thus but a beginning. The next step is to simulate computationally some of the models composing the theory as outlined mathematically in the Appendix. Insights obtained from the simulations should provoke new directions in brain research and as a consequence sharpen and modify the theory or even replace it with a more comprehensive one. To that end, these lectures are dedicated.

Acknowledgments

No man is an island: My first thanks go to Diane McGuinness without whose penetrating criticism of early drafts of the manuscript and painstaking help with later drafts, this book would certainly fail to communicate. As well, my heartfelt thanks go to Eloise Carlton who accompanied me in all the adventures that led to Part I and initially provided the mathematics necessary to make the theory formally realizable.

Herbert Bauer, Don Doherty and especially Niklas Damiris helped set the tone of the published lectures. They also fed me current articles ranging from quantum physics to neuro- and neurocomputer sciences which considerably sharpened my thinking and consequently the text. Brooke Armstrong, Lauren Gerbrandt, Alastair Harris, William Hudspeth, and Sam Leven contributed in a similar fashion at a later date, especially to Part II. Helga Wild, Helgi-Jon Schweizer, Ivan Blair, and Ray Bradley made the manuscript understandable by their careful attention to the language used and the concepts it represents. Jack Hilgard, Wayne Shebilski, and Brooke Armstrong provided much needed emotional support.

The roots of the ideas presented in these lectures, and therefore my indebtedness, extend deep into this century. Ralph Gerard introduced me to monitoring the electrical responses of the brain to sensory stimulation when as an undergraduate, I attended some of the earliest experiments in which such responses were obtained (Gerard, Marshall, & Saul, 1936). As a medical student I helped record the effects of transecting brain tissue on the transmission of D.C. currents (Gerard & Libet, 1940).

Karl Lashley was, of course, responsible for introducing me, in the course of a decade of close association, to the necessity for the flexibility that comes with

distributed processing. He also introduced me to the possibility of cortical interference patterns (Lashley, 1942), a concept central to the theory developed in these lectures. When, therefore, Wolfgang Kohler asked me to record D.C. currents in monkeys and humans during sensory stimulation an opportunity was provided to examine in the laboratory several of Gerard's and Lashley's unorthodox ideas regarding cortical function. The results of these experiments (Kohler & Held, 1949; Stamm & Pribram, 1961) showed perception to be so resistant to disruption of brain electrical organization that repeated efforts toward understanding failed. Despite joint teaching seminars with Walter Miles and Lloyd Beck (where we actually considered a frequency based mechanism for figural perception) and intensive conversations with Jerome Bruner, Warren McCulloch, and Floyd Allport no plausible neurological frame for understanding perception emerged. Nonetheless, Allport's penetrating review of perceptual theory and his ideas on cyclic event structures (Allport, 1955) kept alive my interest in what at the time seemed an unfathomable mystery.

A series of encounters at the University of Alberta's Center for Theoretical Psychology with Karl Metzger and James Gibson sparked my interest in realism and renewed for me the issue of isomorphism which had occupied many evenings with Kohler and Lashley. This interest was pursued further in conferences (see e.g., *Cognition and Symbolic Processes, Vol. 2,* edited by Weimer & Palermo, 1982) with Robert Shaw, Michael Turvey and Walter Weimer as well as with Gibson himself (see Pribram, 1982a).

It took the advent of optical holography in the early 1960s to dispel the mystery for me (Pribram, 1966). Even then, the complex mathematical nature of the explanation posed difficulties: I recall an earlier seminal conversation with Georg von Bekesy where he characterized the explanation as some newfangled mathematics invented by Hilbert which defies understanding. A session with Dennis Gabor—over an excellent dinner and a memorable bottle of Beaujolais—regarding this mathematics while we both attended a UNESCO meeting in Paris produced three napkins full of equations that described a stepwise procedure for attaining a Fourier transformation, a procedure that I later used to describe processing stages from receptor to cortex (Gabor, 1968; see Lecture 4). The Fourier relation per se was not the answer Gabor warned me, as did Donald MacKay, in repeated further discussions on the topic. The warnings were heeded and I gathered groups of investigators of various persuasions to debate the issues at a series of symposia. For instance, William Uttal, Otto Creutzfeld, William Hoffman and I sought common ground at an international psychological congress in Paris in 1976 and thereafter.

The Boulder Neuroscience Conference of 1974 gave Fergus Campbell, Donald Broadbent, Daniel Pollen, and Colin Blakemore and me a unique opportunity to take a close look at "the state of the art." One of my graduate students, Terrence Barrett (1969b, 1972, 1973b&c) had made forays into Gaborian territory, had grappled with the problem of efficient processing and in general had developed the theme of cortical function as interferometry. All of these developments made it possible to openly discuss a radically different view of the perceptual process at a Neuroscience meeting in Minneapolis (1982) where Karen and Russel DeValois, Horace Barlow, David Hubel, and I aired our intuitions and presented the evidence on which they were based. The heat and light provided by these interactions began to mature my earlier formulations.

However, more complete understanding of the warning given by Gabor and MacKay had to await yet another set of circumstances: Frane Marcelja, a computer scientist working in my laboratory shared the enthusiasm generated by the formal presentation of the holographic hypothesis as an explanation for certain facets of perception and memory as put forward by Robert Baron, Marc Nuwer, and myself (Pribram, Nuwer & Baron, 1974). Unbeknownst to me, he transmitted this enthusiasm to his brother, a mathematician at the National University in Canberra, Australia. The mathematician-brother went to see for himself what visual processing entailed by attending experiments in Peter Bishop's excellent vision research laboratory in the same institution. The result was that he realized that a Gabor elementary function better described the cortical process initiated by sensory stimulation than did the Fourier relation (Marcelja, 1980).

Shortly thereafter, Daniel Pollen—who had in the early 1970s come to Stanford for a few months to teach us his techniques for recording Fourier-like visual responses from cells in the visual cortex (Pollen, 1974)—asked me to address his laboratory group at the Barrows Institute in New Mexico. After the lecture he showed me his "sine-cosine" recordings from neighboring cells in a cortical column—and also introduced me to Stepjan Marcelja, the mathematician, who, with his brother the computer scientist, came to visit me at Stanford a week later. If there is an episode that marks the inception of these lectures, it is this visit.

I first presented the ideas generated by these encounters in 1985 at the Center for Interdisciplinary Research (ZIF) of the University of Bielefeld, Germany. I had been invited by a former student, Bruce Bridgeman, to a meeting on the subject of Perception and Action honoring Ivo Kohler. Together with Eloise Carlton, a formal publication in Psychological Research was forged (Pribram and Carlton, 1986). However, the opportunity to fully realize and bring to completion the expression of these ideas, I owe to Terrence Caelli who initiated the invitation to present the MacEachran lectures and provided immeasurable help not only with data from his laboratory but by critically reading drafts of the manuscript. In this vein, I also acknowledge my indebtedness to those who worked behind the scene at the University of Alberta and its center for Theoretical Psychology, to Diane Kohlman, Barabara Smith, and Deborah Akers who typed and typed and typed once more the various revisions of the manuscript, and again to Deborah Akers and to Pierre Bierre and Lawrence Erlbaum and his staff who smoothed the way to publication.

Viewpoint

Before discussing the details of neural processing in perception, it is important to pause for a moment to consider how best to think about and address the contents of our awareness. More fundamental disagreement has plagued this issue than almost any other topic affecting the mind-brain relationship. At one extreme, is the common sense feeling that the contents of perception can be trusted to reliably inform the perceiver about the world in which he navigates—in philosophy this position is called naive or, when bolstered by evidence, direct realism (Gibson, 1979; Shaw, Turvey, & Mace, 1982).

At the other extreme is the feeling that we can never "really" be sure of anything, including the validity of our perceptions—in philosophy this position is called solipsism, or when specified by evidence, autopoiesis. Autopoieses is the view that our perceptual apparatus operates autonomously as a closed system (Maturana, 1969; Varela, 1979).

In between are compromise views and these also range from various materialisms (e.g., Bunge 1980) to phenomenalist, mentalist (e.g., Sperry, 1980; Searle, 1984) and constructional (e.g., Maxwell, 1976; Pribram, 1971) positions. A recent brief review of these issues is given by Epstein (1987).

When intelligent and deeply thoughtful scientists and scholars come to such disparate conclusions it is often fruitful to search for the specific data on which the conclusions are formed. When this is done it can usually be shown that each "position" has intrinsic merit when limited to its data base but becomes untenable when extended beyond these limitations (Pribram 1986a). What remains is the view that brain processes undergo a dynamic matching procedure until there is a correspondence between the brain's microprocesses and those in the sensory input.

The current lectures review evidence which indicates that the sensory aspects of perception entail brain processes separable from those involving the cognitive aspects. Realism fits the data that deal with sensory driven aspects of percepts; constructivism characterizes cognitively driven processes. Ordinarily the cognitive operations (noumena) operate back onto those (phenomena) that are sensory driven: Kant (1965 edition) was not far off in his constructional realism.

Within the province of realism a critical issue surfaces with regard to how the sensory array, the input to receptors, becomes processed. The difficulty arises in an attempt to specify how the input to the senses is related to receptor processing. In figural vision the issue comes center stage when scientists try to specify the nature of a "retinal image."

Many difficulties are resolved by focusing on the single fact that everyone agrees to: when a diffracting object is placed in the front focal plane of the optical apparatus (pupil, and converging lens), a Fourier transform exactly describes the optical "image" at the back focal plane within the eye (e.g., Taylor, 1978, p. 37). Thus the optical apparatus (especially the lens) operates as a phase adjuster integrating interference patterns among wave forms (due to diffraction) into an optical image. As discussed in detail in Lecture 3, taking this anchor of agreement as a starting point allows the concept of a retinal image to be separated into an "optical image" or "flow" and a "retinal process." From this beginning, clearcut differences can be readily identified in the organization of optic array, optical flow, and retinal process.

Taking the transformation performed by the sensory apparatus—the lens in the case of vision—as a starting point for the analysis of perception and other psychological functions is not new. Egon Brunswick (1966) based his probabilistic functionalism on what he called a "lens model." Patterns of energy become "scattered" in the environment and the sensory receptors "recombine" the scatter:

> The . . . strategy of the organism is predicated upon the limited ecological validity or trustworthiness of cues. . . . This forces a probabilistic strategy. . . . To improve its bet, it must accumulate and combine cues . . . Hence the lens . . . model . . . may be taken to represent the basic unit of psychological functioning. (1966, p.37)

As indicated by the vague wording "limited ecological validity or trustworthiness of cues," Brunswick did not have available the evidence presented in these lectures to analyze in depth the various sensory and neural systems and microprocesses that comprise his "lens-like" operation. Nor did he have available the ecological analyses in depth of the environmental patterns reaching the senses performed by Gibson, Johannsen, Cutting, Turvey, and Shaw. Moreover there was no formal theory available to relate these domains. However, Brunswick was a staunch advocate of such explorations into the more remote causal interrelations among layers of variables composing "manifolds" both external to and within the organism.

A good place to begin the study of these interrelations is Gibson's suggestion that we consider brain processes to resonate to the patterns that stimulate the senses, a suggestion in keeping with the harmonic analyses undertaken in the holonomic brain theory presented in these lectures. As will be detailed, taking Gibson's suggestion seriously commits one to realism. But the commitment entails accepting the full implication of the ecological, "layered," approach to perception by including the layers of brain processes largely ignored by Gibson.

REALISM

There are, therefore, areas of close agreement between Gibson's ecological approach and that taken in the holonomic brain theory. For example, Shaw, Turvey, and Mace indicate the broad implications of taking a realist stance:

> What are the major conceptual barriers to a successful realism? . . . [It is} the assumption . . . [(a)] that the mapping of distal object properties onto proximal stimulus properties is destructive; [(b) that] the structuring of the light by the laws of reflection does not preserve the structure of the environment. On this assumed failure of the proximal stimulus to specify the distal object, it is a simple matter to generate skepticism about an animal's knowledge of what is real. Given the non-specificity assumption, perception must be a matter of making propositions (about what the proximal stimulus stands for) with neither a guarentee of their truth nor any apparent way to determine their truth.
>
> A second related barrier to realism is raised by the mind-body subtheme of animal-environment dualism. It is the promotion of . . . two different and irreducible languages. . . . skepticism arises about the animal's ability to perceive what is real, because the perception of reality depends on . . . the physical and the mental being coordinated. It has seemed in the past a relatively trivial matter to show slippage between the object of reference and the object of experience.
>
> Animal-environment dualism thwarts realism in another, though more subtle, way: It invites a science of psychology largely separate from a science of physics and vice versa . . . Realism is hamstrung to the extent that the sciences hold distinct the knower and that which is known.
>
> Consider, however, a program of theory and research committed to realism. . . . Such a program would have to seek a definition of reality that would be animal-relative, but no less real for being so. (Shaw, Turvey, & Mace, 1982, pp. 160–161)

Taking the stance implied by realism ("a program of theory and research committed to realism") is akin to an act of faith: The initial sensory experiences of infants are disparate; even as adults, introspection yields perceptions differing in kind according to the sense involved. When we identify what we hear, see, and touch as referring to the "same" event, we resort to consensual validation. In humans this procedure is repeated when we identify "a red winged black bird," as the "same" object with the "same" attributes referred to by someone else. One makes a pragmatic existential choice early on, either to distrust the process of consensual validation and retreat into soipsism, or to trust and embrace a realist philosophy, and act accordingly.

Ecological psychology and the holonomic brain theory are both eminently compatible with a realist position. However, to state simply that perception is "direct" skips over several steps in the perceptual process that cannot be ignored.

One *must* confront the fact that the senses are stimulated by patterns of energy perceived as "light," "sound," and "touch" which do not have the same configural properties as do the objects with which they interface. This, however, does not mean that these patterns are composed of elements. Rather, a different process is at work: The configural properties that define objects become distributed and enfolded in the process of interfacing. They are thus *transformed* into an order which, as in a hologram, is recognizably different from the perceived configuration of objects but which, in some non-trivial sense, "contains" those configurations. More on this in Lecture 3.

COMPUTATION AND REPRESENTATION

Given the transformational aspect of the realist stance, the next issue that needs to be discussed concerns the nature of cognitive influences on percepts. This topic is best addressed under the heading "representations." Representation literally implies hierarchical levels of processing in which what is processed becomes "re-presented" at another level. A level or *scale* of processing can be defined as a presentation, a description of an *entity* that is simpler than if it were made in terms of the collection of constituents of that scale or level. Thus the entity at each level can be characterized by a description that is a presentation. Components are described in some different fashion than the entity as a whole. Furthermore, there would be no need for a presentation of the entity as a whole were it not in some basic sense, simpler, that is, more efficient in processing than that available to the components (see e.g., Pribram, 1971, chapters 4 & 13). For example, bytes are more efficient in use than the equivalent description in bits. A presentation of a program in Fortran is much more efficient than a presentation of the successive switch settings that form the hardware equivalent of the program. The question is whether psychological processes can, in the same manner, be considered to be re-presentations of functions of the brain.

In the sense of hierarchical levels of presentation, the analogy between computer software (programs) and hardware serves well. The psychological, mental level is described in presentations that are analogous to presentations at the program level. The "wetware" of the brain can be thought of as analogous to the hardware of the computer (Miller, Galanter, & Pribram, 1960; Pribram, 1986a). There is an equivalence between program and successive hardware switch settings. Can we say therefore that in some real sense the switch settings are re-presented in the program? If this is so, then in the same sense psychological processes re-present brain function.

This leads to a most tantalizing question: To what extent are the re-presented entities configured in a fashion similar to the entities they re-present? In other words, to what extent are presentation and re-presentation isomorphic to one another? The answer to this question obviously depends on reaching some consensus on the definition of isomorphic. Processes that map into each other in such a way as to preserve structure can be said to be either geometrically or algebraically isomorphic. For instance, although the Gestalt psychologists thought that the electrical fields of the brain have a geometric *shape* resembling that of perceived objects, evidence shows that perspective transformations display algebraic (i.e., secondary) not geometric isomorphism (Shepard & Chipman, 1970).

Isomorphism is a non-trivial problem when one assesses the nature of brain representations. Wolfgang Köhler (1964) attempted to show that the geometry of cortical electrical activity conforms not only to the geometry of the physical events that produce sensory stimulation but to the perceptions experienced by the organism. This line of reasoning suggested that brain representations literally "picture" the significant environment of the organism or at least caricature it. Experiments by Lashley (Lashley, Chow, & Semmes, 1951), Sperry (Sperry, Miner, & Meyers, 1955) and Pribram (reviewed in 1971) created a severe disturbance of the geometry of cortical electrical activity without disrupting behavior dependent on perception. Thus, geometric isomorphism between the gross aspects of brain electrical activity and perception has been ruled out.

By contrast, the computer program-hardware analogy suggests that significant *transformations* can occur between levels of presentation: indeed that the utility of re-presentations is derived from these transformations. According to the holonomic brain theory developed here, algebraically linear isomorphic (i.e., isoformal), nonlinear or paralinear transformational processing characterize the relations among brain representations. The computer analogy helped make understandable the results of neuropsychological research which showed that the search for "pictures" in the brain (e.g., Kohler's D.C. potentials, Kohler & Held, 1949) was misplaced. Understanding comes when the neurophysiologist searches for algorithms, such as computable transforms of sensory input.

In the same vein, Gibson (1966), and Shaw, Turvey, & Mace (1982), among others, have proposed that as the organism becomes attuned to its environment, the relationship between the two is one of "complementation," not representation. Thus, musical instruments "complement" the fingers of the hand, yet piano keyboards, violin strings, and clarinet stops have completely different configurations. Complements share common procedures, common functions, and there has been considerable debate (see Vol. 3, No. 1; 1980 of the *Behavioral and Brain Sciences* especially Fodor, pp. 63–110) as to whether the modeling of psychological processes should be complementary and functional (computational and procedural) or structural (representational).

The holonomic brain theory defines its formalism in terms of *transformational* procedures that specify the relationships among complements—presentations—*and* between re-presentations of these presentations. For instance, neuroscientists talk of the "representation" of the spatial ordering of receptors and effectors in the ordering of cortical inputs and outputs—this, despite considerable distortion.

Furthermore, there is good evidence from the work of Sokolov (1963) that brain events "model" sensory input patterns. When a sensory input recurs repeatedly, an organism habituates, that is, fails to react overtly to that input. Sokolov found that when he omitted a stimulus in a regularly recurring series, the organism dishabituates; an orienting reaction occurs. Similarly, if suddenly a signal of reduced intensity is presented within a series of signals of greater intensity, an orienting reaction marks the reduced signal. There must be some enduring brain process that is produced by an input if subsequent variations of that input are "sensed" (although this does not mean that the geometries of input and brain process are isomorphic). Reducing or omitting a signal produces a mismatch, which results in an orienting reaction. During habituation a "neuronal model," a "representation" of the input appears to be constructed and subsequent inputs are matched to this representation. More on this in Lecture 8.

Still, the representation need not be an immutable structure. Rather, re-presentation must be a process, the re-construction of a presentation. (For a sophisticated analysis of what is involved, see Hochberg, 1984). The issue can perhaps be grasped most readily by focusing on memory. Is memory structural in the sense that one may find in the brain an isomorphic form or figure corresponding to a subjectively remembered experience, or is such a "memory" the result of processing neural events stored in some other form? By using primes and probes, Fergus Craik in an elegant program of experiments (Craik, 1988), has shown that disturbances in remembering are almost always due to interference with process and not with a loss of stored items. Neuropsychological evidence (e.g., Pribram, 1986b; Weiskrantz, 1986) has also repeatedly demonstrated that "engrams" are not "lost" as such as a result of brain damage. Rather engrams are reconstructions that can appear as intrusion errors when amnesics are examined in a systematic fashion: that is, during recall, reconstruction of an engram occurs but in an inappropriate context.

The holonomic brain theory thus holds that the "deep structure" of memory (in Chomsky's 1965 sense which distinguishes deep from surface structure) is distributed, as in current image processing and PDP neural network computational models; that this distributed, dismembered store must be re-membered, assembled into an experienced "memory" by a content-addressable process. The process can be triggered internally or from a sensory input. In short, re-membering is a process that depends on *transforming* a deep structure, a dis-membered re-presentation, which is holonomically organized and thus of a form different from either the experienced memory or the sensory array that originated the process.

Formally, in terms of the holonomic brain theory developed in these lectures, the re-presentation occurs as a dynamical transformation in a distributed network of dendritic microprocesses. Smolensky captures the essence of this formalism as follows:

> The concept of memory retrieval is reformalized in terms of the continuous evolution of a dynamical system towards a point attractor whose position in the state space is the memory; you naturally get dynamics of the system so that its attractors are located where the memories are supposed to be; thus the principles of memory storage are even more unlike their symbolic counterparts than those of memory retrieval.

It is these dynamical transformations, these *transfer functions,* that critically distinguish current theories (including the holonomic brain theory) from earlier formalisms such as those of General Systems Theory.

Thus, the holonomic brain theory incorporates "representations" not as pictorial forms but as self-maintaining structures that act somewhat like the setpoints of thermostats. These setpoints serve as "attractors" in more or less temporary stable configurations which are subject to continuous adaptive change. Holoscapes defined in Lecture 2—mapping of isopotential dendritic polarizations—are such configurations. Physiology is replete with examples of self-maintaining structures: the skin remains "the same" despite constantly shedding cells which are replaced with new ones; red blood cells last only a month, yet the red blood cell count remains stable. You as a person, a structure, are recognizable over the years despite the fact that every cell in your skin, hair, and so forth has probably been repeatedly exchanged during the period of observation. Certainly every molecule in your body has been exchanged several times. This self-maintenance of structure is often called self-organization, autopoiesis (Maturana, 1969; Varela, 1979) because the organizing propensity generates the organization since it is genetically specified.

According to the views expressed in these lectures, structure and process are distinguished more by the level or scale of observation than by any intrinsic difference. At the seashore, breakers are processes; they exert considerable force, can move objects, and upset bodies. When viewed from 10,000 feet these same breakers appear as standing waves, a structure that delimits and represents the boundary between open sea and land.

In the holonomic brain theory, when viewed closely the "representations" that are coordinate with perceptions (or memories) are composed of fluctuating polarizations within the dendritic network—probablility amplitude modulated Fourier coefficients. At close range they, like the seashore at hand, are seething with activity that, however, exhibits structure (coordinate with images, objects, etc.) when viewed from the distance of sentient observation.

IN SUMMARY

The holonomic brain theory espouses a *transformational* and *constructional* realism and thus goes beyond the direct realism proposed by Gibson in specifying the ecological details of the sensory and brain processes involved in perceiving. Specification devolves on recognizing *transformations* that occur between *bottom-up levels* among brain systems. *Top-down* influences on processing procedures provide *structural constraints* on processing. That is what these lectures are about.

PROLEGOMENON

Before the connection of thought and brain can be explained, it must be stated in elementary form; and there are great difficulties about stating it. . . . Many would find relief at this point in celebrating the mystery of the unknowable and the "awe" which we should feel. . . . It may be constitutional infirmity, but I can take no comfort in such devices for making a luxury of intellectual defeat. . . . Better live on the ragged edge, better gnaw the file forever! (William James, 1950, pp. 177–179)

. . . it is entirely possible that we may learn about the operations of thinking by studying perception. (Irvin Rock, 1983, p. 1)

1 Aims and Origins

There is good evidence for the age-old belief that the brain has something to do with. . . mind. Or, to use less dualistic terms, when behavioral phenomena are carved at their joints, there will be some sense in which the analysis will correspond to the way the brain is put together. . . . In any case each time there is a new idea in psychology, it suggests a corresponding insight in neurophysiology, and vice versa. The procedure of looking back and forth between the two fields is not only ancient and honorable—it is always fun and occasionally useful (Miller, Galanter, & Pribram, 1960, p. 196)

AN INTRODUCTION

The explosion of data in the behavioral and neural sciences has made the study of the correspondence between the way the brain is put together and the carving behavioral phenomena at their joints even more intriguing and rewarding than when the introductory quotation was written. Exploring the way the brain is put together provides insights into how experience becomes processed. When the evidence from the brain sciences is ignored, the experiential phenomena guiding behavior are found to be so richly structured, and carving can proceed in such a multitude of ways, that the result has often been a purely descriptive phenotypical science in which descriptions constitute a tower of Babel. This is especially true of perception, which of necessity must come to grips with the simultaneity, subjectivity, and relative privacy of what is being experienced.

By contrast, as developed in these lectures, a neural systems analysis of the brain-behavior relationship, which takes into account processing levels, allows the perceptual experience to be analyzed into basic functional modules that are at the same time separable and interpenetrating.

However, care needs to be maintained when identifying the functions of separate neural systems. It seems deceptively easy, but is inadmissable to completely identify neural system function with behavioral system function. The mistake of slipping into a category error plagues all of physiology. The function of the lungs is readily identified as respiration; but respiratory functions include those of red blood cells and the membrane exchange of O_2 and CO_2, as well as the lung's inspiratory/expiratory cycles that make the other aspects of respiration possible. The models that describe inspiration/expiration by the lungs are considerably different from those describing oxygen transport by the hemoglobin of red blood cells.

The issues are the same when it comes to relating the physiology of receptors and the nervous system to behavioral functions including those reported as perceptions. Perception entails the functions of receptors, primary sensory receiving stations, and those brain systems associated with them. There can be no simple model of "perception" or even "pattern recognition," any more than there can be a simple model of "respiration."

In the current lectures these issues are handled in two ways: (a) An attempt is made to sharply distinguish models based on observations made at the behavioral level of psychophysics and perception from those at the neural systems, neuronal and subneuronal levels. The distinction is implemented according to whether models describe *what* is being processed or whether they describe *how* processing is carried out by the nervous system; and (b) whenever possible, transformations, transfer functions, are described that relate the models at different levels to one another. It is the specification of these transfer functions that distinguishes current from earlier mathematical and general systems approaches. The nature of the transfer functions is adduced from data obtained in neuropsychological observations in which both the brain and the situational variables controlling the behavioral reports of perceptual experience are specified.

NEURAL SYSTEMS

When the neurophysiology of perception is considered, a set of processes emerges, each served by a separate neural system. These systems are shown to act in concert with other neural systems anatomically and/or biochemically related to them. Three major divisions can be discerned (see Fig. 1.1) in the sets of primate brain systems relevant to perception. The division is made on the basis of sense modality. In the posterior convexity of the cerebrum, processing is anchored in visual and auditory inputs ("distance" processing); in the frontolimbic forebrain, processing is anchored in olfactory/gustatory and in pain/temperature stimulation (thermochemical processing); midway, surrounding the central

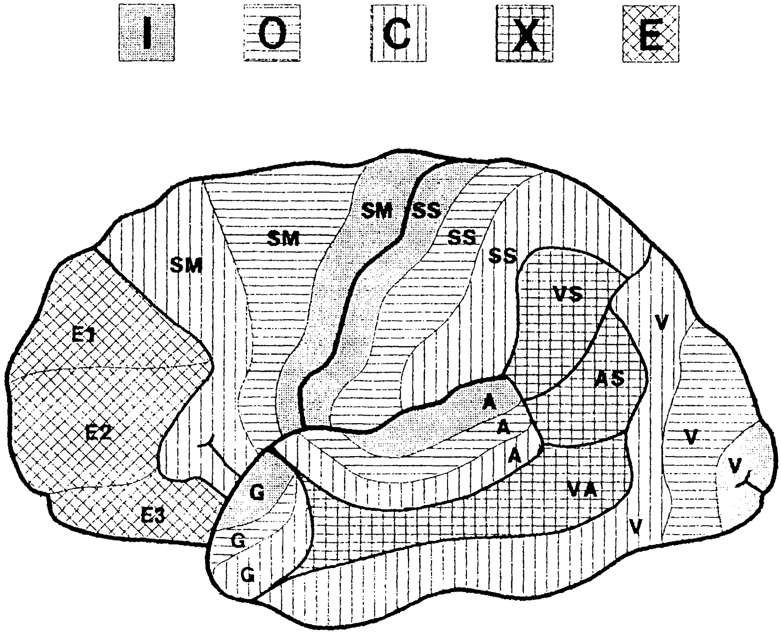


FIG. 1.1. Systems of cerebral structures which are coordinate with cognitive functions. The hierarchical organization is arranged in a top-down manner and designated by the indicated textures for: Executive (E), Cross-Modal (X), Cognitive (C), Object (O) and Image (I) functions. The image, object and cognitive functions apply to the sensory and motor processes such as Vision (V), Audition (A), Gustation (G), and the Somatic divisions. The Somatic division is partitioned into predominantly Motor (SM) and Somaesthetic (SS) compartments. Intrinsic cross-modal processes are represented by regions within which the principle sensory systems interact: Visuospatial (VS), Visuoauditory (VA) and Acousticosomatic (AS). The frontal executive functions are interconnected to other systems so that they can be regulated by Priorities (E1), Practicalities (E2) and Proprieties (E3). From: Hudspeth, W. J. and Pribram, K. H. (1990).

(Rolandic) fissure, processing is anchored in somatic sensibilities that allow the organism to be in proximate *touch* with the environment and, even more important, to directly *act* on, and thus alter it.

Within each division, there is a core of projection systems connected extrinsically, rather directly, with the receptors of the modality: these systems provide for sensory imaging. Surrounding these projection systems are perisensory systems that process the input by controlling movements related to that input: it is these systems that allow figure to be extracted from ground. Beyond these systems are others intrinsic in their connections, that is, they primarily receive their input from and operate back on the sensory-motor systems. The intrinsically connected systems themselves are hierarchically organized: One set of intrinsic systems is sensory-mode specific, extracting invariants from iterated images to produce object-forms. Another, still sensory-mode specific, makes categorizations possible. Yet another is involved in setting up computational spaces which relate processing in various sensory modes to one another. Finally, in humans, systems entailing language have developed as another intrinsically connected complex.

As reviewed in the body of these lectures, the systems responsible for extracting the invariances (constancies) that characterize object-forms, interpenetrate in a top-down, corticofugal fashion, those systems responsible for imaging. This top-down interpenetration is implemented by parallel connections. Such connections, now at a new level in the hierarchy, are found again when systems responsible for stimulus sampling and categorizing are considered, and once more when the systems concerned with relevance and inference are studied. Each level entails both feedforward and feedback operations: thus, the paradox of the separable yet unitary nature of the perceptual experience can be accounted for.

This characterization of the relations between brain systems differs from the traditional view that has been limited to bottom-up, forward propagation from sensory projections to higher order "associative" systems. In the nineteenth century, Flechsig (1900) had suggested that cognitions are derived exclusively by a process in which input from various senses becomes associated in the cortex of the posterior cerebral convexity—thus the term *association cortex*. Flechsig's view is still widely held despite overwhelming evidence (reviewed in Lecture 7) against it. (See e.g., Kuffler and Nichols, 1976; Luria, 1973; Mishkin, 1973; Shepherd, 1988).

As noted, in the alternative view the results of computation at the later level of processing are fed back to the earlier levels. These lectures are based on evidence for such *reciprocal* connectivity between hierarchically ordered neural systems, by means of which processing leads to a *selection* procedure in which input is matched against a resident microstructure (genetically or experientially produced memory). The result of the match acts like a set point on a thermostat (or homeostat) to *instruct* further processing. Of course the set point is not a point or single number as it is on a thermostat; rather, it is a set of "attractors" developed in a multidimensional complex, a temporary stable state, (Prigogine & Stengers, 1984) often referred to as an Image (e.g., a "motor image"). At the same time, the details of processing need not be specified in the match, a great savings in memory storage. Von Foerster (1965) described such operations as providing memory without record. Nonetheless, memory storage is involved, but it consists more of refining Images (Gibson & Gibson, 1955) than of detailing procedures.

In such a reciprocally acting set of systems, input *triggers* an operation that at any moment is largely self-determining. Further, the larger the amount of experience stored in the systems operating in a top-down fashion, the greater the self-determination. Thus Beethoven could compose the late quartets and the Eighth and Ninth Symphonies despite the fact that he was completely deaf at the time of composition.

In short, in systems characterized by bottom-up, top-down reciprocity, selection characterizes a microprocess in which sensory and central inputs are matched with a resident microstructure. The results of the match instruct and direct further processing. In systems endowed with memory storage, these interactions therefore lead to progessively more self-determination. Momentary input serves to trigger rather than specify the process.

NEURONS

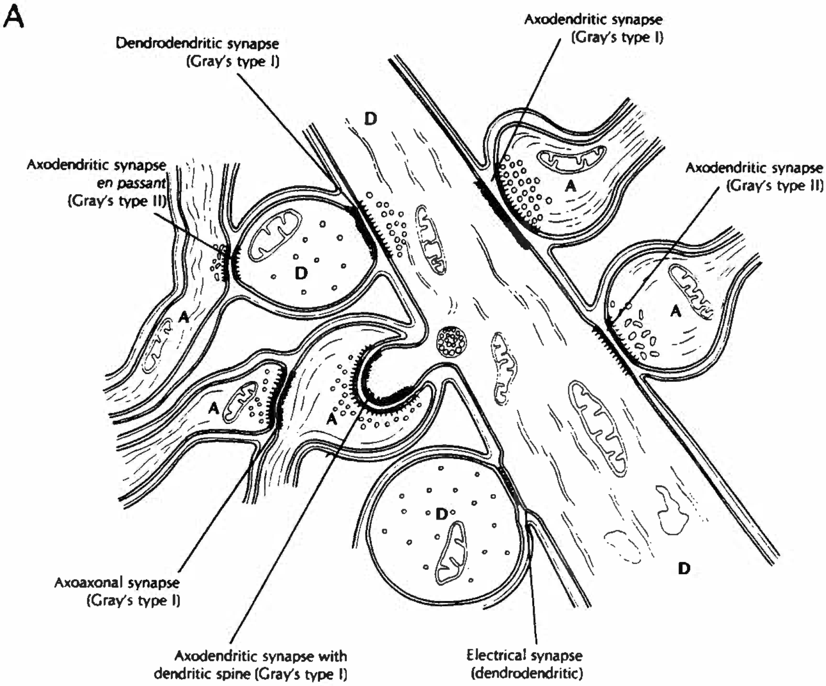
Neurons are ordinarily conceived to be the computational units of the brain. Thus the majority of processing theories since the seminal contribution of McCulloch and Pitts (1943) have taken the axonal discharge of the neuron, the nerve impulse, as the currency of computation.

However, this framework for computational theory has led to considerable misunderstanding between neuroscientists and those interested in computational processing. Successful computational networks depend on highly—often randomly—interconnected elements. The more complex the computation, the more connections are needed: the law of requisite variety (Ashby, 1960). Neuroscientists know that neurons are connected nonrandomly, often sparsely, and always in a specifically configured fashion (see Crick & Asanuma, 1986, for a neuroscience view of connectionist computational theory). In short, current computational processing emphasizes a minimum of constraints in the processing wetware or hardware; in the current neuroscience framework wetware is highly constrained.

Misunderstanding is alleviated when the computational framework is broadened to include the microprocessing that takes place within dendritic networks. Not only are axonal-dendritic synapses that connect neurons subject to local influences in these networks, but innumerable local circuit operations provide the unconstrained high connectivity needed in computational procedures (Bishop, 1956; Pribram, 1960, 1971; Schmitt, Dev, & Smith, 1976). Local circuit neurons are found in many locations in the sensory and central nervous system (see Table, p. 9, in Shepard, 1981). The processing capability of such neurons (primarily inhibitory) is often dendro-dendritic. (See e.g., Rakic, 1976; Sloper, 1971.)

Junctions (axodendritic and dendo-dendritic) between neurons in the form of chemical synapses and electrical gap junctions occur within overlapping dendritic arborizations (Fig 1.2). These junctions provide the possibility for processing as opposed to the mere transmission of signals. The term neurotransmitters applied to chemicals acting at junctions is, therefore, somewhat misleading. Terms such as neuroregulator and neuromodulator convey more of the meaning of what actually transpires at synapses.

Nerve impulse conduction leads everywhere in the central nervous system to such junctional dendritic microprocessing. When nerve impulses arrive at syn-


A
Dendrodendritic synapse
(Gray's type I)
Axodendritic synapse
(Gray's type I)
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en passant
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D
A
D
A
A
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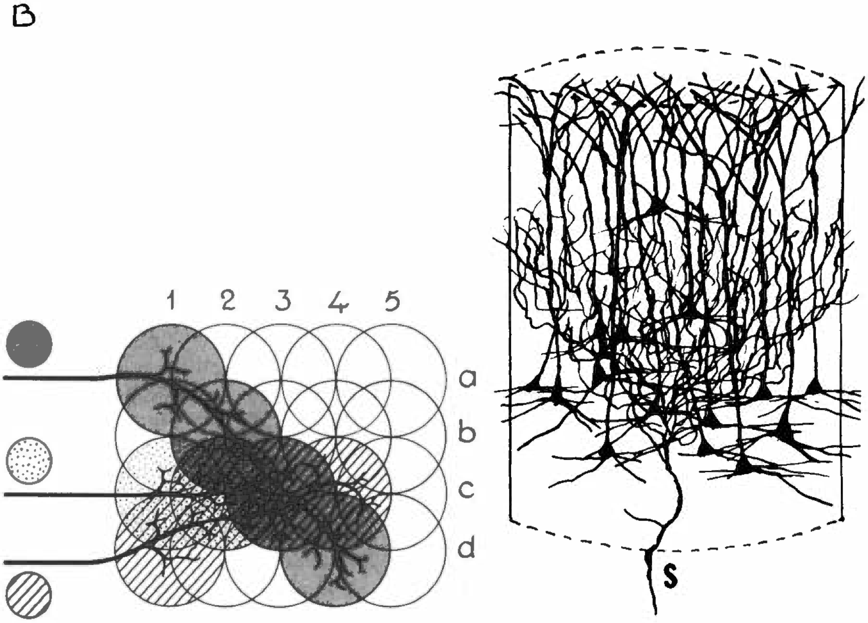
Axodendritic synapse with
dendritic spine (Gray's type I)
Electrical synapse
(dendrodendritic)


B
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apses, presynaptic polarizations result. These are never solitary but constitute arrival patterns. The patterns are constituted of sinusoidally fluctuating hyper- and depolarizations which are insufficiently large to immediately incite nerve impulse discharge. The delay affords opportunity for computational complexity.

The dendritic microprocess thus provides the relatively unconstrained computational power of the brain, especially when arranged in layers as in the cortex. As developed in the next lecture, this computational power can be described by linear dynamic processes, in terms of quantum field neurodynamics.

Neurons (Fig. 1.3) are thresholding devices that spatially and temporally segment the results of the dendritic microprocess into discrete packets for communication and control of other levels of processing. These packets are more resistant to degradation and interference than the graded microprocess. They constitute the channels of communication not the processing element.

Communication via neurons often consists of dividing a message into chunks, labelling the chunks so that they are identifiable, transmitting the chunked message, and reassembling it at its destination. Neurons are labelled by their location in the network. This form of labelling is highly efficient because of the essentially parallel nature of neuronal connectivities.

Neuronal channels constrain the basic linear microprocess. These structural constraints can be topologically parallel, convergent, and divergent. An instance of a combination of these forms of constraint is the connectivity between retina and cerebral cortex, which is expressed as a logarithmic function of distance from the foveal center. Other constraints shape the time course of computations and lead to learning. Unveiling the manner in which constraints are imposed in the natural brain is the work of the neurophysiologist. Much of what is contained in these lectures describes the results of this work.

DENDRITIC MICROPROCESSING

Recognizing the importance of dendritic microprocessing allows a coherent theory to be framed regarding the neural functions responsible for perception. As Pribram (1971) initially stated in *Languages of the Brain*:

> Any model we make of perceptual processes must thus take into account both the importance of Imaging, a process that contributes a portion of man's subjective

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FIG. 1.2A. Ultrastructure of various types of synapse. (A) Axons. (D) Dendrites. From: Barr, M. L. & Kiernan, J. A. (1983). *The Human Nervous System,* Fourth Edition. Philadelphia, PA: Harper & Row.

FIG. 1.2B. Diagram of microstructure of synaptic domains in cortex. The ensemble of overlapping circles represents the junctions between branches of input axons and cortical dendrites. Redrawn after Scheibel and Scheibel in Chow and Leiman, 1970. From Pribram, 1971.

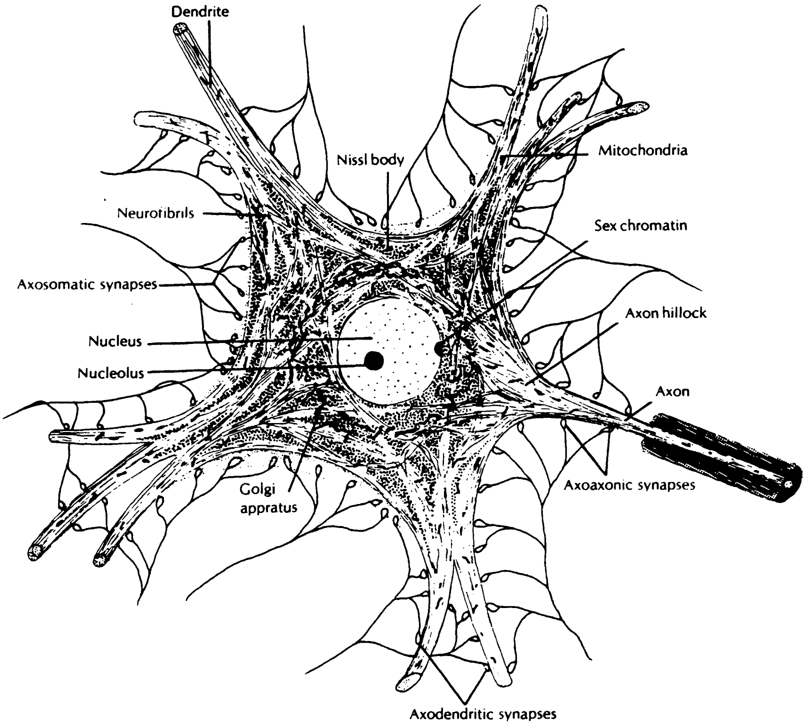

FIG. 1.3. Semidiagrammatic representation of the constituents of a nerve cell. From: Barr, M. L. & Kiernan, J. A. (1983). *The Human Nervous System,* Fourth Edition. Philadelphia, PA: Harper & Row.

> experience, and the fact that there are influences on behavior of which we are not aware. Instrumental behavior and awareness are often opposed—the more efficient a performance, the less aware we become. Sherrington noted this antagonism in a succinct statement: "Between reflex action and mind there seems to be actual opposition. Reflex action and mind seem almost mutually exclusive—the more reflex the reflex, the less does mind accompany it." (p. 104)

Languages then proceeds to detail the fact that nerve impulses in axons and junctional microprocessing in dendrites function reciprocally. An hypothesis was formulated to the effect that when habit and habituation characterize behavior that has become automatic, there is efficient processing of dendritic "arrival patterns into departure patterns." On the other hand, persisting designs of junctional patterns are assumed to be coordinate with awareness. The hypothesis is consonant with the view that we are cognizent of some, but not all of the events going on in the brain.

Nerve impulses arriving at junctions generate dendritic microprocesses. The design of these microprocesses interacts with that which is already present by virtue of the spontaneous activity of the nervous system and its previous experience. The interaction is modulated by inhibitory processes and the whole procedure accounts for the computational power of the brain. The dendritic microprocesses act as a "cross-correlation device to produce new figures from which the patterns of departure of axonic nerve impulses are initiated. The rapidly paced changes in awareness could well reflect the [pace of] duration of the correlation process." (Pribram, 1971).

Historically the issues were framed by Lashley, Kohler, and Hebb. Donald Hebb (1949) summed up the problem by pointing out that one must decide whether perception is to depend on the excitation of *specific cells*, or on a *pattern of excitation* whose locus is unimportant. Hebb chose the former alternative: "A particular perception depends on the excitation of *particular cells at some point* in the central nervous system."

As neurophysiological evidence accumulated (especially through the microelectrode experiments of Jung (1961); Mountcastle (1957); Maturana, Lettvin, McCulloch, and Pitts (1960); and Hubel and Wiesel (1962) this choice, for a time, appeared vindicated: Microelectrode studies identified neural units responsive to one or another feature of a stimulating event such as directionality of movement, tilt of line, and so forth. Today, textbooks in psychology, in neurophysiology, and even in perception, reflect this view that one percept corresponds to the excitation of one particular group of cells at some point in the nervous system.

Profoundly troubled by the problem, Lashley (1942) took the opposite stance:

> Here is the dilemma. Nerve impulses are transmitted over definite, restricted paths in the sensory and motor nerves and in the central nervous system from cell to cell through definite inter-cellular connections. Yet all behavior seems to be determined by masses of excitation, by the form or relations or proportions of excitation within general fields of activity, without regard to particular nerve cells. It is the pattern and not the element that counts. What sort of nervous organization might be capable of responding to a pattern of excitation without limited, specialized paths of conduction? The problem is almost universal in the activities of the nervous system and some hypothesis is needed to direct further research. (p. 306)

Wolfgang Kohler also based his Gestalt arguments on such "masses of excitation. . . within generalized fields of activity" and went on to prove their ubiquitous existence in the decade after the publication of Hebb's and Lashley's statements. A series of experiments in which I was involved established the existence of generalized fields but showed that, although they were related to the speed with which learning took place, they were unrelated to perception as tested by discrimination tasks (see *Languages of the Brain*, chap. 6, for a review of these studies).

Lashley was never satisfied with either Hebb's or Kohler's position. His alternative was an interference pattern model which he felt would account for perceptual phenomena more adequately than either a DC field or a cell assembly approach. He did not, however, have a clear idea of how the process might work. He never specified the fact that the interference patterns were generated by arrivals of nerve impulses nor how such patterns provide a computational scheme for perception. Thus he never developed an argument for the existence of a dendritic microprocess responsible for the computational power of the neuronal mechanism.

According to the views presented here and in keeping with Lashley's intuitions, this computational power is not a function of the "particular cells" and the conducting aspects of the nervous system (the axonal nerve impulses), nor is it necessarily carried out within the province of single neurons. At the same time, the theory based on these views does not support the notion that the locus of processing is indeterminate. Rather the locus of processing is firmly rooted *within regions of dendritic networks* at the junctions between neurons.

As summarized by Szentagothai (1985, p. 40):

> The simple laws of histodynamically polarized neurons . . . indicating the direction of flow of excitation . . . came to an end when unfamiliar types of synapses between dendrites, cell bodies and dendrites, serial synapses etc. were found in infinite variety. . . . A whole new world of microcircuitry became known. . . culminating in a new generalized concept of local neuron circuits (Rakic, 1976; Schmitt et al., 1976).

The ubiquity of such local circuit neurons indicates that computation is strongly influenced by local circuit interactions that modify the postaxonal dendritic processes. Perceptual processing depends therefore on network properties that extend beyond the purview of the dendrites of a single neuron. It is the synaptic event, rather than the neuron per se, that serves as the computational element.

The sub- and superneuronal aspect of the dendritic microprocess, its potential to extend beyond the single neuron, provides explanatory power for both older and recently accumulating evidence that brain processes coordinate with perception are *distributed*. This evidence is reviewed in lectures 2 and 4. In a distributed process, perceptual events are represented not by single neurons but by *patterns of polarization* across ensembles of synapses.

On the basis of their extensive studies Thatcher & John, (reviewed in 1977) came to a similar conclusion:

> The spatiotemporal patterning of these cooperative processes . . . [involve] ionic shifts . . . with extrusion of potassium ions and ionic binding on extracellular mucopolysaccharide filaments. If we focus our attention not on the membranes of single neurons, but upon charge density distributions in the tissue matrix of neurons, glial cells, and mucopolysaccharide processes, we can envisage a complex,

> three-dimensional volume of isopotential contours, topologically comprised of portions of cellular membranes and extracellular binding sites and constantly changing over time. Let us call this volume of isopotential contours or convoluted surfaces a *hyperneuron*. (pp. 305–306)

Basic to this new view of the neurology of perception is the fact that propagated nerve impulses are but one of the important electrical characteristics of neural tissue. The other characteristic is the microprocess that takes place at the junctions between neurons. Hyper- and depolarizations of postsynaptic dendritic membranes occur at the junctions between neurons where they may even produce miniature electrical spikes. However, these minispikes and graded polarizations also differ from axonal nerve impulses in that they do not propagate. As discussed in Lecture 4, the influence of these minispikes and graded polarizations on further neuronal activity is by way of *cooperativity* among spatially separated events. Cooperativity is mediated by the cable properties of dendrites and the surrounding glia (see e.g., Poggio & Torre, 1980) This type of interaction is called nonlocal because the effect is exerted at a distance without any obvious intervening propagation. By analogy the effect is also called *jumping* or *saltatory* as in saltatory conduction by myelinated nerve fibers. It is this saltatory nature of the interactions as captured by perceptual experiences that fascinated Frank Geldard, experiences so clearly described in his inaugural MacEachran Memorial Lecture (1975).

RECEPTIVE FIELDS

The neurophysiologist can readily study the output—spike trains—of neurons when they act as channels, but he has only limited access to the functions of the interactive dendritic junctional architecture because of the small scale at which the processes proceed. A major breakthrough toward understanding was achieved, however, when Kuffler (1953) noted that he could *map* the functional dendritic field of a retinal ganglion cell by recording impulses from the ganglion cell's axon located in the optic nerve. This was accomplished by moving a spot of light in front of a paralyzed eye and recording the locations of the spot that produced a response in the axon. The locations mapped the extent of the responding dendritic field of that axon's parent neuron. The direction of response, inhibitory or excitatory, at each location indicated whether the dendrites at that location were hyperpolarizing or depolarizing.

The resulting maps of dendritic hyper- and depolarization are called *receptive fields*. The receptive fields of retinal ganglion cells are configured concentrically: a circular inhibitory or excitatory center surrounded by a penumbra of opposite sign. This center-surround organization has been shown to be due to the operation of horizontally arranged dendritically endowed neurons that produce "lateral" inhibition in the neighborhood of excitation and vice versa. The center-surround organization thus reflects the formation of a spatial dipole of hyper- and depolarization, an opponent process fundamental to the organization of the configural properties of vision.

Utilizing Kuffler's techniques of mapping, Hubel and Wiesel (1959) discovered that at the cerebral cortex the circular organization of dendritic hyper- and depolarization gives way to elongated receptive fields with definite and various orientations. They noted that oriented lines of light rather than spots produced the best response recorded from the axons of these cortical neurons. They therefore concluded that these cortical neurons were "line detectors." In keeping with the tenets of Euclidean geometry where lines are made up of points, planes by lines and solids by planes, Hubel and Wiesel suggested that line detectors were composed by convergence of inputs from neurons at earlier stages of visual processing (retinal and thalamic—which acted as spot-detectors due to the circular center-surround organization of the receptive fields.)

The Euclidean interpretation of neuronal processing in perception became what Barlow (1972) has called the neurophysiological dogma. The interpretation led to a search for convergences of paths from "feature detectors" such as those responding to lines, culminating in "pontifical" or "grandfather" cells that embodied the response to object-forms such as faces and hands. The search was in some instances rewarded in that single neurons might respond *best* to a particular

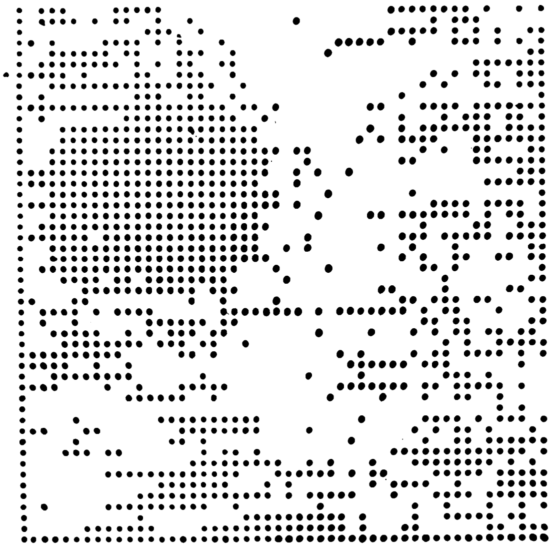

FIG. 1.4. Two dimensional map of points on the retina at which a light spot produces responding in a particular lateral geniculate cell in the brain of a monkey. After Spinelli and Pribram, 1967.

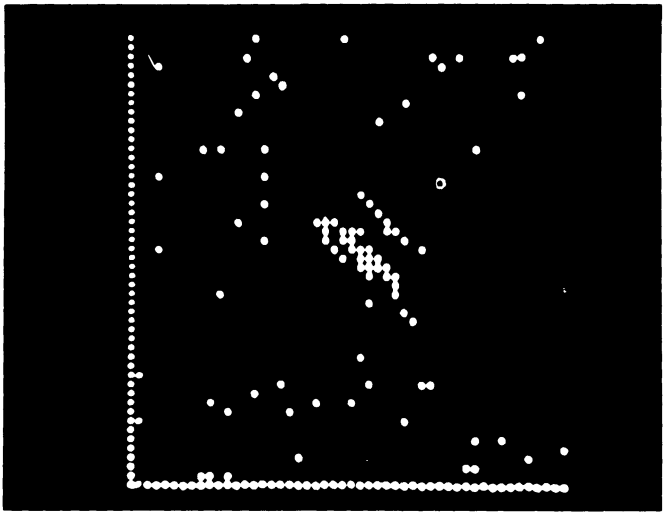

FIG. 1.5. Two dimensional map in the visual field at which a light spot produces responding in a particular striate cortex cell in the brain of a monkey. After Spinelli and Pribram, 1967.

object form such as a hand or face (Gross, 1973). However, response is never restricted to such object-forms. As detailed in Lectures 4 and 5, such "best" responses can also occur in parallel networks in which convergence is but one mode of organization.

About a decade after the discovery of elongated visual receptive fields of cortical neurons, new evidence accrued that called into question the view that figures were composed by convergence of Euclidean features. For instance, in our laboratory at Stanford University we mapped the architecture of cortical dendritic fields by computer and found cortical receptive fields that contained multiple bands of excitatory and inhibitory areas (Spinelli & Barrett, 1969; Spinelli, Pribram & Bridgeman, 1970). In Leningrad similar observations were made by Glezer (Glezer, Ivanoff, & Tscherbach, 1973), who remarked that these cortical neurons responded more like "stripedness" (than line) detectors (Fig. 1.5). The critical report, however, was that of Pollen, Lee, and Taylor (1971), who interpreted similar findings to indicate that the cortical neurons were behaving as Fourier analyzers rather than as line detectors.

At the same time Campbell and Robson (1968), initially on the basis of psychophysical, and subsequently, on the basis of neurophysiological experiments, developed the thesis that vision operates harmonically much as does audition except that the visual system responds (by virtue of a Fourier process) to *spatial* frequencies. The details of these experiments and their intepretation makes up the content of Lectures 2 and 4. Here I want to introduce the critical difference between Euclidean-based geometric and Fourier-based harmonic approaches.

For those using the geometric approach, spots and lines are seen as elementary features that become combined in ever more complex forms as higher levels of the neural mechanism are engaged. When a harmonic analysis is taken as the approach, the elongated receptive field organization of cortical neurons suggests that neurons act as "strings" tuned to a limited bandwidth of frequencies. The ensemble of strings compose resonators or active filters as in musical instruments. A century ago, Helmholtz proposed that sensory receptors are akin to a piano keyboard; that a spatially isomorphic relation is maintained between receptor and cortex as in the relation between keys and strings of a piano, but that each cortical "unit" responds (resonates) to a limited bandwidth of frequencies as do the strings attached to the piano's sounding board. From the operation of the total range of such units, magnificent sounds (in the case of the piano) and sights (by means of the visual system) can become configured (Fig. 1.6).

The geometric and harmonic views differ significantly with respect to the composition of a percept. Irwin Rock (1983) described this difference as follows:

> One confusion here may be with the meaning of "feature." A feature could refer to an identifiable part or unit that must first be extracted or detected, and then along with other features assembled into an overall pattern. Or "feature" could refer to an identifiable emergent characteristic of the form once it is achieved rather than as one of the parts that produces it. (p. 96)

The details of the neurophysiological data as reviewed in Lectures 4 and 5 show that features such as oriented lines, movement and color are best conceived as identifiable emergent characteristics of form because they are already conjoined in the receptive field. Furthermore such features become activated *either by sensory input or by central process to configure a percept.* This evidence, makes the "resonating string metaphor" more reasonable than the feature detector approach.

There are four critical reasons for preferring tuned frequencies to detected features: (a) Neurons in the visual cortex respond to several features of sensory input and there is no evidence that the different features are represented by separate neurons, as would be required if it acted as a detector; (b) the receptive field properties of such neurons can be accounted for by considering them as spatial and temporal differentiations of tuned frequency; (c) tuned frequencies provide a potentially richer panoply of configuration (e.g., texture, paralax), and (d) perceptual research has clearly shown that lines (and therefore line detectors) composing contours are inadequate elements with which to account for the configural properties of vision.

Rock (1983) summarized the evidence and argument as follows:

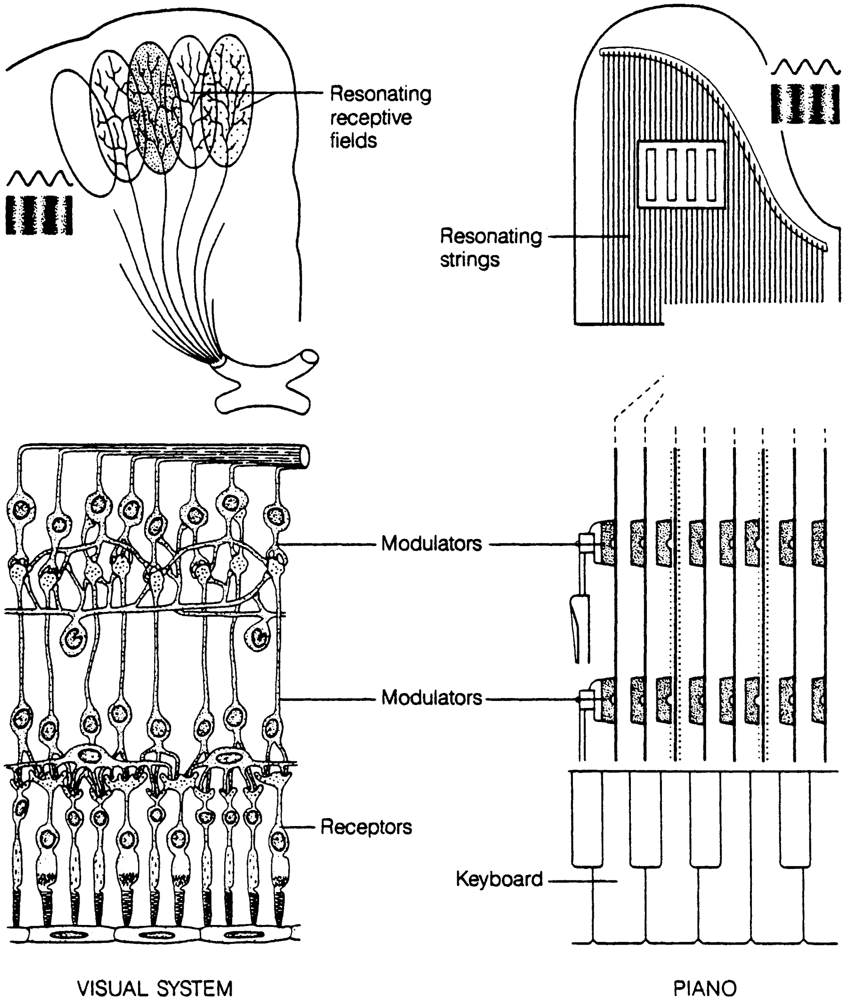

FIG. 1.6. Diagram of essential connectivity of the initial stages of visual sensory processing and its similarity to the connectivity of a metaphorical piano to illustrate the principles of harmonic analysis.

The emphasis on contour detection is entirely misplaced because, as far as form is concerned, a contour simply marks or delineates a location. What matters for form perception is the set of all such locations; and if these can be delineated without contours, contours are not necessary. That is why, in addition to depth, we perceive regions of particular *shapes* in two random dot patterns viewed binocularly despite the absence of any physical contours (Julez 1971). Illusory contours . . . also support this conclusion. (p. 43)

Rock provided the results of innumerable experiments to document his insight that the configural properties of vision are due to a "process of directional integration" (p. 47). The most critical is the demonstration that "the perceived direction of a point with respect to ourselves. . . is a joint function of retinal locus and eye position" (p. 46). The details of the evidence for this approach are presented in lecture 3.

In summary, sensory cortical receptive fields are considered analogous to resonating strings in a piano. The functional relationship among strings (among the receptive fields of the sensory cortex) and with the keyboard (with the sensory receptors) is spatially organized and provides a macrolevel of perceptual processing. The functional relationship among resonant frequencies, characteristic of overlapping functions of the receptive fields of the cortical neurons, provides a microlevel of perceptual processing. It is this cooperative microprocess that allows one to assume that indeed a specific brain process is coordinate with the richness of experience that is perception.

PLASTICITY

Cooperativity, implemented in the dendric microprocess, makes possible parallel distributed processing of considerable flexibility within a single processing layer. Moreover, in multilayered networks *selective* modification can occur provided the *presynaptic* network becomes influenced by iterations of input. Such an arrangement is often referred to as the Hebb rule because Donald Hebb (1949) captured the imagination of the broad scientific community when he called attention to the fact that *selective* modification is dependent on presynaptic effects. The importance of this presynaptic requirement had been familiar to many neuroscientists for a half-century: For example in his *Project for a Scientific Psychology* (1895/1966), Freud ascribed selective learning to the restricted lowering of certain synaptic resistances by the absorption of energy (precathexis) at the presynaptic site due to repeated use. It is *the actual mechanism* by which such selective changes can occur that has taken a century to unravel (see e.g., Stent, 1973; and discussion in Kimble, 1965).

The holonomic brain theory presented in the next lecture is based on a *radical* extension of this rule: A microprocess is conceived in terms of *ensembles* of mutually interacting pre- and postsynaptic events distributed across limited extents of the dendritic network. The limits of reciprocal interaction vary as a function of input (sensory and central) to the network—limits are not restricted to the dendritic tree of a single neuron. In fact, reciprocal interaction among pre- and postsynaptic events often occurs at a distance from one another, that is, in a saltatory fashion. More on this in Lectures 2 and 4.

Perceptual learning is extremely rapid—three to five iterations usually suffice (Kimble, 1967). This type of rapid learning is achieved when several layers of cooperative networks are cascaded—as in cortical layers—so that feedback and feedforward procedures can be implemented. In feedforward computations are fed to all subsequent processing layers in parallel (with possible delays due to longer paths). Feedback implements the results of computation at each layer by back propagation to layers closer to the input source.

These layered networks simulate layered neural configurations such as those characterizing the retina and cerebral cortex. Other neural configurations such as those characteristic of the basal ganglia and brain stem nuclei are better simulated by clusters of interconnected units described in graph theory by "cliques," "hypercubes," and so forth (Fig 1.7). Brain systems are configured by composites of clustered and layered processors related by topologically discrete parallel connections.

Both layered and clustered processors are implementations of dynamical principles more appropriate for modelling the configural aspects of perception than the digital finite-state principles that guided earlier theories concentrating on symbolic processes. The similarity of these current processing theories to neurodynamics and the success such programs are having in simulating the psychological and neurological aspects of perception indicates that the time is ripe for

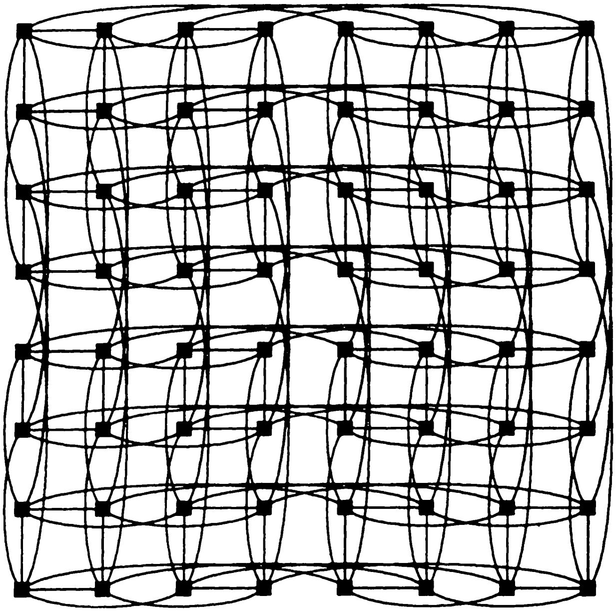

FIG. 1.7. Six dimensional hypercube with 64 nodes, and 6 connections per node. Computer generation by Conrad Schneiker. From: Hameroff, S. R. (1987). *Ultimate Computing.* Amsterdam: Elsevier Science Publishers.

brain theory to be formally realizable whenever possible. However, just as in computer science, the level of description becomes critical in determining the model—that is, the code, the language—in which a particular procedure is to be invoked.

The interesting and often difficult problems are those that specify the transfer functions, the transformations that relate one level, one code, to another: The necessity to deal with these transfer functions is immediately apparent in computer science where one must have available (often at considerable cost) the software that encodes the "transfer functions" connecting machine to machine-language and this to assembler language, assembler to operating system, and so forth. A computational neural theory of perception must specify the relationship between operations of the subneuronal to the neuronal level; those at the neuronal level to those at the neural systems level; and, as well, those at the neural systems level to those at the perceptual level.

Cooperative networks, even when layered, have limitations as well as strengths. Cooperativity, in sensory systems, given iterative inputs provided by movement, is powerful in correlating, in developing perceptual constancies, and is self-organizing. For other kinds of computation, structured constraints must be imposed on the networks. These constraints can come directly by way of sensory input or they can be imposed from within the brain. The centrally imposed top-down constraints are generated by a variety of brain systems that preprocess at the midbrain and thalamic level the input to the primary sensory cortex. These top-down preprocessing procedures, organized by prior experience, are those that constitute the cognitive aspects of perception.

PARALINEARITY

The cooperative stages of sensory processing are described in the theory presented in the next lecture as paralinear computations. Nonlinearities enter only as auxilliaries that sharpen the computational process. The locus of entry of nonlinearities can thus be identified without jeopardizing the advantages that accrue to the overall linearity of the operation of the brain systems involved in configuring percepts.

A beginning in making the distinction between overall linearity and the entry of nonlinearities comes from analyzing the relevant dynamics of neural processing. The input to the brain is in the form of modulations of nerve impulse trains, modulations initiated in receptor activity.

Similarly, the output to muscles and glands is in the form of spatially and temporally patterned trains of nerve impulses. There are, of course many stages of processing intervening between input and output. At each of these processing stations, four types of transformation take place. Walter Freeman (1989) described these stages in the following passages:

> At the first stage pulses coming in to a set of neurons are converted to synaptic currents, [patterns of hyper-and depolarizations] which we call waves. Second, these synaptic currents are operated on by the dendrites of the neurons. This involves filtering and integration over time and space in the wave mode. Third, the wave activity reaching the trigger zones is converted back to the pulse mode. Fourth, it then undergoes transmission, which is translation from one place to another, delay, dispersion in time, etc. The operations of filtering, integration and transmission can be described with linear differential equations. Pulse to wave conversion at synapses is commonly thought to be nonlinear, but in fact in the normal range of cortical operation it is linear. Multiplication by a constant suffices to represent the conversion from a density of action potentials (pulse density) to a density of synaptic current (wave [i.e. polarization amplitude]). But the operation of wave to pulse conversion is nonlinear, and the trigger zone is the crucial site of transformation that determines the neural gain over the four stages. (personal communication)

These passages contain the key elements of the holonomic brain theory presented in the next lecture, in which "the operations of filtering, integration, and transmission can be described with linear differential equations" and "pulse to wave conversion at synapses is commonly thought to be non-linear, but in fact, in the normal range of cortical operation is linear." It is only at the axon hillock where nerve impulses are generated that "wave to pulse conversion is nonlinear." (Fig. 1.8) In the holonomic approach, the configural aspects of perception are coordinate with synaptic and dendritic processing; modelling can therefore take advantage of the practical features of linearity. This leaves to conducted nerve impulse activity the role of imposing nonlinear constraints and of communicating the results of processing at one brain location to another such location. Signal transmission with its attendant gain control (as indicated by Freeman) necessitates the introduction of nonlinearities. But (again, as Freeman noted) pulse to wave conversion at synapses once more linearizes the system. Thus the unconstrained dendritic computational microprocess in perception is essentially linear.

Understanding the neural basis of the imposition of nonlinearities in constraining the linear junctional microprocesses is illustrated by the work of Poggio. Poggio, Torre & Koch (1985) came to the following views:

> [An] analog parallel model of computation is especially interesting from the point of view of the present understanding of the biophysics of neurones, membranes and synapses. Increasing evidence shows that electrotonic potentials play a primary role in many neurones. Mechanisms as diverse as dendrodendritic synapses, gap junctions, neurotransmitters acting over different times and distances, voltage-dependent channels that can be modulated by neuropeptides and interactions between synaptic conductance changes provide neurons with various different circuit elements. Patches of neural membrane are equivalent to resistances, capacitances and phenomenological inductances. Synapses on dendritic spines mimic voltage

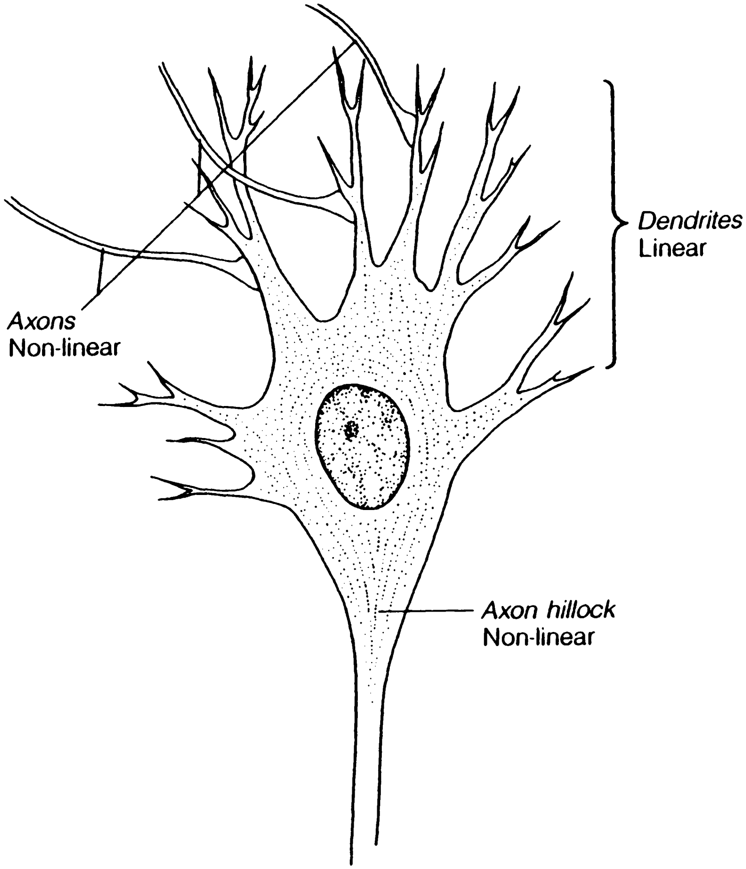

FIG. 1.8. Diagram of an idealized neuron as it is conceived to participate in the processing of signals.

> sources, whereas synapses on thick dendrites or the soma act as current sources. Thus, single neurons or small networks of neurons could implement analog solutions. (p. 317)

When the constraints on processing are asymmetrical, as for instance, when excitatory and inhibitory inputs are spatially or temporally asymmetrical (Poggie, Torre, & Koch, 1985) directional selectivity results. Such asymmetries impose nonlinearities on the basically linear analog microprocess.

The issue of linearity with regard to cortical processing in visual perception has been addressed in a comprehensive review by Shapley and Lennie (1985): "The idea [that within patches of receptive field, linearity is maintained] is an attractive one because it is consistent with the narrow spatial frequency tuning and spread of best frequencies of cortical neurons but is weakened to the extent that the neurons behave non-linearly" (p. 572).

As noted, these nonlinearities are a function of the outputs of neurons that depend on gain control at the axon hillock. The nonlinearities are thus introduced primarily into the perceptual microprocess in the form of overall retinal to cortical mapping that is spatially logarithmic (Schwartz, 1977). However, in addition to the effects on the perceptual macroprocess, "the nature of some of these nonlinearities suggests that they are precisely what make the cells highly tuned spatial frequency filters" (Shapley & Lennie, 1985, p. 575).

To anticipate the theme detailed in Lectures 2 and 4, the configurations (i.e., the internal architecture) of the receptive fields of visual cortical neurons can be described in terms of *spatial* frequency: Recordings of axonal impulse responses of the cortical neuron show that the stimulus that best engages these cortical neurons is a (sine wave) grating (composed of regularly spaced bars of widths equal to those of the spaces), which is drifted across the visual field. The spatial frequency of the gratings that engages the spatial frequency of the receptive field is determined by the widths of the bars making up the grating and the spacings between them. The range of spatial frequencies to which the cortical neuron responds determines the bandwidth of the tuning curve. This bandwidth is approximately an octave (± 1/2 octave) (see review by DeValois & DeValois, 1980).

These experimental results have led to the view that the neural processes involved in spatial vision are kin to those involved in audition. Harmonic analysis is therefore an appropriate tool for developing a computationally realizable theory of the neural processes involved in the configural aspects of perception.

The simplest and most fundamental of the tools of harmonic analysis is the Fourier decomposition, which represents a spatial or temporal pattern by a set of regular oscillations differing in amplitude and frequency. Each regular oscillation is in turn decomposed into sine and cosine components, which differ only in that they are 90° out of phase. The phase of each of the regular oscillations with respect to the others differing in frequency, is encoded by a ratio called the *Fourier coefficient*. Computation of the Fourier representation of *oriented gratings* in terms of their coefficients has more successfully predicted the responses of cortical neurons, than has the display of oriented *single* lines or bars of various widths (DeValois, Albrecht, & Thorell, 1978). At the neural microprocessing level, the holonomic brain theory is thus not only computationally simpler, especially with respect to calculating correlations, than nonlinear theory, but is more accessible to test.

However, each of the sinusoidal Fourier components extends to infinity. Cortical receptive fields are bounded. The limit on the functional receptive field of cortical neurons is produced not only by the anatomical extent of the dendritic field of a single neuron, but also by inhibitory (hyperpolarizing) horizontal networks of dendrites that interpenetrate overlapping excitatory (depolarizing) fields. Lecture 10 deals with the way inhibitory networks modify the functional dendritic field.

These bounded receptive fields provide the data reviewed by Shapley and Lennie (1985), which were obtained using harmonic analysis. They noted that the existence of nonlinearities has caused advocates of the Fourier approach "to propose that the spatial image may be analyzed into spatial Fourier components over small patches of visual field." This "patch" technique of Fourier analysis was pioneered for radioastronomy by Bracewell (1965) and then applied to neurophysiology by Pollen, Lee, & Taylor (1971); Pribram (1971); Robson (1975); and Glezer (1985). For the brain cortex each patch is configured by a simple cortical receptive field.

STATE OF THE ART

Currently, several formalisms have been adopted to construct theories of perception similar in character to the holonomic approach taken in these lectures. These theories differ from the holonomic brain theory in that they do not address the role of each of the various *brain systems* involved in perception. In fact, most of the theories—for example see Ginsberg (1971), Caelli (1984), Watson and Ahumada (1985), Hoffman (1984), Dodwell (1984), Cutting (1985), Cavanagh (1984, 1985) and Palmer (1983)—are based primarily on psychophysical data. Their encoding schemas aim to explain in one model the full range of phenomena involved in pattern recognition by a variety of correlational methods (e.g., those of Anderson, Silverstein, Ritz, & Jones, 1977; Kohonen, 1977), holographic filters (Cavanagh 1975, 1976), or Lie group manifolds (Dodwell & Caelli, 1984; Hoffman, 1984).

Kronauer and Zeevi (1985), have summarized the essentials of the *neural* microprocesses on which the holonomic brain and similar theories must be based:

> The operation in question obviously cannot be a global Fourier transformation or, for that matter, any simple harmonic decomposition scheme, since we are dealing with a space (position) dependent system whose characteristics are inhomogeneous. At best, therefore, we may consider a possible "short distance" spectral decomposition analogous to the time-frequency domain spectrogram so widely used in speech analysis (Flanagan, 1972). (p. 99)

Flanagan (1972) and before him Gabor (1946) showed that in a communication there is a tradeoff between accuracy in the spectral domain and accuracy in the time domain. In fact the unit they found to be most useful to represent and analyze a communication (e.g., speech) was a time-limited sinusoid (repetitive waveform) of specified frequency. It is this unit that forms the basis of the holonomic brain theory as developed in the next lecture.

For vision, the sinusoid is place limited (as well as time limited). As Kronauer and Zeevi (1985), have noted, the tradeoff between space and frequency has consequences:

> Thus, as every engineer well knows, sharpening up the spatial resolution results in a spread of the spatial-frequency characteristics, and vice versa. Does this conclusion, based on pure communication theory considerations, bear any relevance to better understanding of cortical engineering design and signal processing in the visual system? Recent studies indicate that, in fact, cortical neurons in area 17 respond in a way that is localized both in space and in spatial frequency (Maffei & Fiorentini, 1973; Andrews & Pollen, 1979; Tootell, Silverman, & DeValois, 1981; Movshon, Thompson & Tolhurst, 1978), in the sense that a cell's stimulus domain exists in a certain well-defined region of visual space (the so-called receptive field) and is also localized in spatial-frequency to a limited range of luminance-periodicity-modulation. Proceeding from photoreceptors through ganglion- and LGN-cells to cortical simple cells, one finds a progressive loss in localizability of positional information (at the single cell level of operation) and a decrease in spatial frequency bandwidth. (pp. 99–100)

This relationship between space and frequency is fundamental. A convenient way to picture it is to recall the metaphor of a piano (described in a previous section) as developed by Helmholtz (1863) and Ohm (1843) to describe the auditory system. At a macro level of organization, the keys of the keyboard (the receptors) are spatially arranged with respect to one another and this spatial arrangement is maintained in the connectivity between keyboard and the strings of the sounding board. It is at the micro level of individual strings (the receptive fields of cortical cells) that the frequency mode of response occurs: each string resonates at a limited bandwidth of frequency. We are well acquainted with the richness of sensory experience that can be generated by such an arrangement.

Furthermore, Kronauer and Zeevi (1985) indicated that this micro level frequency response is carried out within the functional receptive field, that is, the dendritic microprocess of junctional polarizations.

> The response characteristics of a cortical simple cell can conveniently be described in terms of a receptive field profile (the cell's kernel) that specifies its excitatory and inhibitory substructures. Typically there appear to be two major subclasses of simple-cell receptive field profiles: bipartite ("edge" type) and tripartite. Careful analysis of the receptive fields, reconstructed from spatial-frequency selectivity measurements, indicates additional "ringing" reminiscent of Gabor's elementary function (Andrews and Pollen 1979). Most interesting, however, is the finding that pairs of simple cells that are adjacent in the cortical tissue and have the same preferred orientation are tuned to the same spatial frequency and respond to drifting sine wave gratings 90° out of phase, spatially (Pollen and Ronner 1980). Thus, the

> fact that cortical neurons balance the position/frequency trade-off by possessing both some spatial retinotopic localization and, at the same time, a spatial frequency bandwidth of about one octave with matched sine and cosine (phase quadrature) cell pairs, suggests that important kinds of visual processing are going on in both domains (Zeevi and Daugman 1981).

One of the advantages of processing in both spatial and frequency domains is economical coding. This is due to the efficiency of encoding when uncertainty with regard to frequency and place (in space and time) are minimized. Kronauer and Zeevi (1985) pointed this out in the following passage:

> Some recent theoretical studies have emphasized the principle of economical coding (minimal representation) for the cortex (e.g., Sakitt and Barlow 1982). In view of the high-functional multiplicity found in the cortex, this emphasis seems misplaced. Yet, it is true that, from several view points, the processing is economical. The receptive field patterns of simple cells come very close to minimizing uncertainty in the four-dimensional space comprised of two spatial and two frequency coordinates (Daugman 1980, 1984). Moreover, it seems that no two cells perform the same functions, so there is no wasteful redundancy in the simple sense. (p. 100)

As detailed in the next lecture, this type of economical encoding, is achieved by an *ensemble* of receptive fields. The advantages of such coding are critical: Transformations between frequency spectrum and spacetime are readily accomplished because the transform is invertable. This makes the computing of correlations easy. In addition, the property of projecting images away from the locus of processing (as by a stereo system and by a hologram) and the capacity to process large amounts of information are inherent in holonomic processing. As these properties are also the ones that characterize figural awareness, they make a good point of departure for constructing a theory of brain organization in perception.

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