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Introduction to Karl H. Pribram

Dr. Pribram received his bachelor of science and medical degrees from the University of Chicago. Following a residency at St. Luke's hospital, he became an instructor in surgery at the University of Tennessee. From there he moved on to the Yerkes Primate laboratory as a neurophysiologist while concurrently opening a private practice in neurology and neurosurgery in Florida. In 1948 he moved on to Yale Universtiy where he held appointments in the departments of Psychiatry and Psychology. From 1951 to 1958 he was also director of the Institute for Living in Hartford. Since 1959 he had been at Stanford in the departments of Psychology and Psychiatry and he is Head of the Neuropsychology Laboratories at Stanford. In 1962 he was given a lifetime research award by the National Institutes of Health.

The scope and magnitude of Dr. Pribram's interests and research have been truly remarkable. He has served on the editorial board of journals as diverse as *Human Motivation, Neuroscience Research, Journal of Autism and Developmental Disorders, Journal of Mental Imagery, Cognition and Personality, Journal of Mathematical Biology,* and the *Journal of Human Movement Studies*.

He has published over 150 review and theoretical papers, well over 100 research papers, 13 books and monographs, and numerous book reviews and commentaries.

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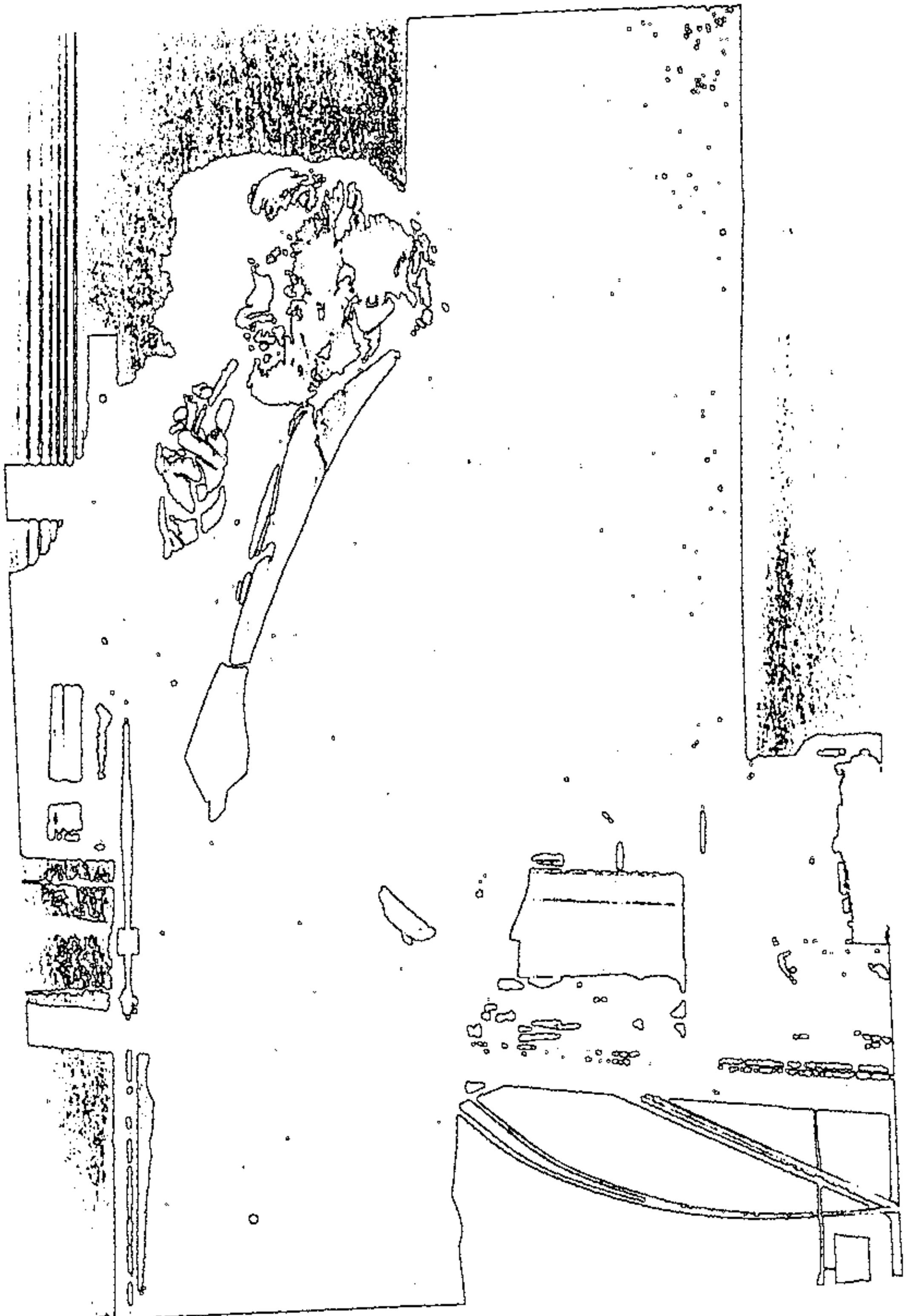

Karl Pribram

His research interests, like his writing, have been diverse and yet there are some central themes that characterize his contributions to science. One of these is the role of cognitive processes in behavior.

In 1960 he was a co-author with George Miller and Eugene Galanter of *Plans and the Structure of Behavior*—a book which critiqued the S-R reflex concept and developed it into an interactionist-feedback model. The book also considered the relationship between thought processes and the functioning of computers—thereby becoming an early contributor to the field of artificial intelligence, and it essentially laid the groundwork for the cognitive revolution that subsequently swept through first human learning research and, more recently, animal learning research.

In 1971 his book *Languages of the Brain* continued the development of the feedback model of behavior, introduced a consideration of the synaptic junction as the locus of neuro-behavioral flexibility (a conjecture now clearly borne out in Eric Kandel's work on habituation in Aplysia), and related the interaction among neural slow potentials that takes place at the synapse to the concepts of holography.

In the popular press Pribram has been described as the Magellan of the Mind and, indeed, in his research he has circumnavigated the cortex from occipital lobe to frontal lobe and back again. He has critiqued the Hubel and Wiesel analysis of visual receptor function—showing that the receptor fields of cortical neurons are not fixed but, instead, may be modified by the nature of the stimulus impinging on them and/or by activity in other parts of the brain—both cortical and subcortical.

He has tackled the 100 year old question of localization of function in the brain and come down squarely on both sides. For example, he has hypothesized that memory storage is distributed—possibly following a holographic model—but that retrieval programs for memory may be localized. That is—memories are *dis*membered during the storage process and *re*membered during the retrieval process.

Karl and his students, and his students' students, have carried on an extensive series of experiments analyzing the function of the amygdala. His experiments have shown that the amygdala is important for the habituation of some, but not all, aspects of the orienting response, and that the amygdala is also important for Pavlovian conditioning. Karl's long research program has also shown that the

4 Brain, Behavioral Operants, Cognitive Operations, and Holonomic Transformations

Karl H. Pribram

INTRODUCTION

First, let me thank you for your hospitality. Not only has Rutgers arranged a small snowstorm as a cheerful setting for a warm welcome: in addition, a prearrival gift made my flight to New Brunswick memorable. On my seat someone had left a New York Times. On the back page of the front section of this honorable newspaper, a full page advertisement had been placed, ostensibly by Omni Magazine. In part, the ad read as follows:

> In a recent issue, OMNI Magazine discussed the problems of perception and memory with Dr. Karl Pribram, the Austrian-born neuropsychologist who developed the first holographic model of the brain. According to Pribram, the brain encodes information on a three dimensional energy field that enfolds time and space, yet allows us to recall or reconstruct specific images from the countless millions stored in a space slightly smaller than a melon.
>
> The Pribram interview is a rich, provocative example of the journalism that has made OMNI the world's leading science magazine.

Provocative, it certainly is. I was puzzled as to what it might have been that I had said that would make someone, anyone, even the current "media hype," attribute to me such a view of "the" brain. Ah, yes. The fields are the receptive fields of neurons. And true, a two dimensional orthogonal (spectral) transform will enfold a three dimensional space/time image. Storage capacity in the spectral domain is indeed prodigious. Of course, this domain is but one of several of the "languages of the brain," but on the whole, someone had read me better than I had initially read them.

The Omni interview and other similar experiences have made me wonder how is it that my theoretical work has engaged so much popular interest, while discoveries made in the laboratory have so often become part of the received wisdom in the neurosciences without popular fanfare or even acknowledgment within psychology. The laboratory research takes up by far the greatest amount of my time and effort, and I therefore welcome this opportunity to write a brief biography of the research program.

The following report outlines the several phases of the research, the major discoveries, the theoretical work that has stemmed from these discoveries, and lists the doctoral and postdoctoral students and colleagues who integrally forwarded the program. But before such descriptions must come the sources which motivated the initiation of the program, previous investigators on whose shoulders we have stood to look beyond the heritage which they left to us.

ROOTS

This story began in Chicago, which at the time of my medical training in neurological surgery was a major center for brain research. At the University of Chicago, where I received my undergraduate and medical degrees, were Heinrich Kluever and Paul Bucy, pioneers in investigations of the functions of the temporal lobe of the brain. I became Bucy's first resident when he moved to the nearby Chicago Memorial Hospital and wrote up our first one hundred brain operations in order to have the residency accredited. Bucy was editing a volume on the precentral motor cortex at the time and I became privy to the controversies and details of explorations of this research, as well as learning the techniques of surgery from a master.

Stephen Polyak was working on the anatomy of the retina and visual system. I was intrigued by the work of Roaf on color afterimages and saw in Polyak's detailing of three sorts of retinal bipolar cells a mechanism for analyzing and further separating the Helmholtzian receptor process while accounting for the effects of color afterimages. I wrote up these suggestions with Polyak's help and submitted the result as a medical student thesis.

Paul Weiss was training Roger Sperry to transplant limbs of Amblystoma. We became well acquainted when Weiss appeared on my medical service during my internship. The friendship has lasted a lifetime and centered on the problem of "resonance": How could it be that a limb induces in the developing nervous system a code that allows the system to "recognize" the limb irrespective of its innervation. Sperry's answer to this question invoked specific chemical codes; mine, suggested in *Languages of the Brain*, devolves on the finding by J. Z. Young of the induction of specific nerve fiber size spectra by each muscle. Probably both chemistry and fiber size are involved.

A. Earl Walker became chief of Neurological Surgery when Paul Bucy left and from Walker I learned the details of thalamic anatomy before joining Bucy. Also during this period Ward Halstead introduced me to the procedures used to study the effects of brain injury in humans.

The University of Chicago was not the only center for neuroscience research in Chicago at the time. Magoun and Lindsley and their collaborators were beginning their research on the mesencephalic reticular formation at Northwestern University. I was to participate in this work in collaboration with Percival Bailey, having received a fellowship to do so, but Bailey changed his plans and went overseas for that year. The proposed collaboration never took place but my interest in the project had been piqued so that I kept abreast of developments as they occurred.

At the University of Illinois Neuropsychiatric Institute, Eric Oldberg had gathered a stellar group that included Percival Bailey, Gerhrdt von Bonin, and Warren McCulloch. After my year with Bucy, I became Oldberg's resident with priviledged access to this group. Bailey took another resident (John Green) and me and sat with us over a six-month period detailing his methods and neuroembryological approach to his pioneering work on the classification of brain tumors.

I occasionally participated in the strychninization experiments of chimpanzee cortex and listened attentively to Bailey, Bonin, and McCulloch discuss the results. Some years later, at Yale University, I was able to put to good use my surgical skills and the knowledge I had acquired from these discussions to complete these chemical stimulation experiments on cat and monkey by explorations of the medial and basal surfaces of the brain which had remained inaccessible to the earlier research.

But perhaps the most exciting part of the research was the exploration of the lateral surface of the human brain for suppressor activity. Though the results obtained were highly controversial, the process of cortical stimulation in which Bucy also participated, the examination of the patient (sometimes left to me) while this stimulation was in progress, and the discussions which ensued were fascinating. I remember well the occasion during one of these procedures when a telegram arrived from Oxford University which stated that Paul Glees had just found connections from the precentral cortex to the caudate nucleus, using his newly developed silver technique. McCulloch suggested that the term "feedback" be applied to explain what was happening and that Glees had found the anatomical basis for such feedback.

These are only some of the highlights of the Chicago period. There are many, many stories of fascinating encounters, but one will suffice. My first public address was made to the Chicago Neurological Society. I presented a case of an oligodendroglioma of the motor cortex which had produced localized seizures of facial sweating. The tumor was successfully removed with no aftereffects and a cessation of the seizures. Two conclusions were reached: Careful resections of cortical tissue which did not deeply invade white matter did not result in any irreversible paralysis; the precentral motor cortex is involved in the regulation of visceroautonomic functions which, at the time, were thought to be autonomous with respect to cortex with hypothalamic mechanisms as the highest level of control.

The other person on the program was Warren McCulloch. I did not understand a single word of what he was talking about and I am afraid most of the others attending the meeting were in similar straits. It took me another thirty years of interaction before I began to appreciate fully what McCulloch had to say, and one of my fondest memories is the week McCulloch spent with us at Stanford discussing his insights and ours just before his death.

Exciting as all of these Chicago experiences were, they did not furnish me with some of the basic tools I needed to accomplish my basic goals, which were: To explore the relationship between brain function and mental processes such as emotion, cognition, and conation. In my search for a hay fever-free location where I might earn my living as a neurosurgeon and at the same time pursue these goals, I heard of the Yerkes Laboratories of Primate Biology near Jacksonville Florida. Fortunately, there was a position open in Jacksonville with J. G. Lyerly, who had devised an improved (superior) approach to frontal lobotomy that was safer than the classical Freeman-Watts procedure and left fewer unwanted side effects. I took my Florida State Board Examinations and began practice.

Lyerly agreed that I might work two half-days per week, plus any free time, for my research at Yerkes. I called Lashley and he responded favorably, stating that he had been looking for a neurosurgeon to assist him in his primate neuropsychological research. Thus began a collaboration which was to prove most influential in shaping the subsequent research program.

Lashley taught me the techniques of experimental psychology, a field of inquiry that I did not know existed. True I had watched Ward Halstead at work in Chicago but had been unimpressed. Nothing that Halstead had done led to any insights into how the brain functioned. Paradoxically, although Lashley was almost solopsistic in his approach and interpretations, he provided many of the insights that led to the discoveries which make up the substance of this report. The discoveries we made while he was still alive, such as the unique relationship of the frontolimbic forebrain to delayed alternation behavior and the sensory specificity of various sectors of the posterior "association" cortex, he tried to ignore. But always, his critical wit sharpened our interpretations and provided the basis for further observation and experiment.

The opportunity to work full time in research and thus make these observations and experiments came when I was asked by John Fulton to join him in the Department of Physiology at Yale University. My association with Yale lasted for a decade, during which time I also directed the research laboratories of the Institute of Living, a mental hospital in nearby Hartford, Connecticut. The facilities at Yale and in Hartford provided ample space for a group of young investigators dedicated to exploring the power of combining the techniques of experimental psychology with those of neurophysiology and experimental neurosurgery. Doctoral students from Yale (e.g., Martha Helson Wilson); Harvard (e.g., Lawrence Weiskrance); McGill (e.g., Mortimer Mishkin); University of California at Berkeley (e.g., William Wilson); and Stanford (e.g., Jerome Schwartzbaum) formed a nucleus of a most productive team, all of whom received their degrees while working on the program.

During this period I spent a month a year at the Yerkes Laboratory, and Kao Liang Chow, an early collaborator, spent a month with me in the north, reestablishing at least in part Yerkes' original vision for his primate research laboratories. This continuing collaboration led to an invitation to succeed Lashley as director of the laboratories, and I filled this post until the president of Yale University sold the laboratories to Emory University in Atlanta.

Also during this period, I began an intimate association with psychologists at Harvard University. I taught summer school there one year; built operant equipment in the Harvard shops and learned a great deal from S. S. Stevens, Gary Boring, and Georg von Bekesy. Once a month, Bert Rosner and I drove up to Harvard (and later MIT) to perform experiments with Walter Rosenblith on monkeys in which we evoked electrical potentials in the cortex by auditory stimulation. Somewhat later, these sessions were extended to explore, with Wolfgang Kohler, the evocation of DC (direct current) shifts under similar conditions.

My interactions with B. F. Skinner were especially memorable and led to a decade of primate operant conditioning experiments which developed into subsequent research in cognitive neuropsychology. Ultimately, I was able to automate the operant equipment by designing a computer-controlled panel dubbed: "Discrimination Apparatus for Discrete Trial Analysis" (DADTA).

At one point in our interaction, Skinner and I came to an impasse over the possible mechanism involved in the chaining of responses. Chaining was disrupted by resections of the far frontal cortex. Skinner suggested that proprioceptive feedback might have been disrupted, but this hypothesis was not supported by my experiments. Furthermore, as I indicated to Skinner, he as a biologist could propose such an hypothesis, but I, as a loyal Skinnerian, had to search elsewhere than the "black box" for an answer to our question. George Miller overheard some of our discussions and pointed out to us that he had available an apparatus that made chaining of responses easy: a computer. Miller explained to me the principles of list programming that he had just learned form Herbert Simon and Alan Newell. The culmination of the collaboration begun by that chance encounter in the halls of Harvard was *Plans and the Structure of*

Behavior, a book influenced also by interactions with Jerome Bruner. The book was written in 1960 at the Center for Advanced Studies in the Behavioral Sciences, adjacent to the campus of Stanford University.

Thanks to Jack Hilgard and Robert Sears of the Psychology Department, and to Tom Gonda in Psychiatry, I was given an appointment at Stanford. During the twenty-five years since my departure from Yale and Harvard, the research therefore has been carried out at Stanford University aided by a lifetime research career award from the United States Department of Health and Human Services.

At Stanford another group of associates, both doctoral and postdoctoral, joined the program. (Altogether, some 50 theses have been completed under its aegis.) Daniel Kimble, Robert Douglas, James Dewson, Muriel Bagshaw, and Leslie Ungerleider were among those who made major contributions. And Nico Spinelli became an integral and almost indispensible collaborator. The results of these, the previous, and subsequent research collaborations can be organized into overlapping phases, each phase representing a problem area and the application of techniques appropriate to that problem area.

Research Phases

Phase I. At the time my research program began, large areas of the primate cortex remained silent to experimental investigation. In humans, damage to these areas resulted in agnosias and aphasia, and in changes in interpersonal emotional interactions. But it was not known whether these changes in competence and behavior were the result of damage to primary sensory-motor system, or whether the changes could occur without such damage. Furthermore, it was not known whether the changes were specific to one or another location within the silent cortex.

By using a battery of behavioral tests and resecting large extents of the silent cortex of monkeys without invading the primary sensory-motor systems, answers to these questions were achieved relatively rapidly. A method was devised that compared (using superimpositions of reconstructions) by summing across the extent of the resections that produced a particular behavioral deficit, and subtracting the sum of the extent of the resections that produced no deficit. This "intercept of sums" technique allowed us to make multiple dissociations among the various deficits produced by the resections and to localize the brain system involved in the behavior represented by each task.

The results were unequivocal. One type of deficit was produced when the far frontal, medial, and basal cortex were resected. Another type of deficit followed resections of the posterior cortical convexity and this type could be further subdivided into sensory specific components, each of which was related to its own portion of the convexal cortex. In no instance was invasion of the adjacent primary sensory-motor systems critical to producing the deficit or even in enhancing it.

Phase II. Having established various specific behavioral indicators for the functions of these areas of the cortex, the next problem was to discover the psychological meaning of the indicators. Much as a Babinsky sign is an indicator of improper functioning of the spinal pyramidal motor system, we now had available signs of malfunction of brain cognitive and related systems.

In order to define the meaning of the behavioral indicators we had to explore the limiting factors for these deficits in a wide range of behavioral tasks. Some of these limits could be established by factorial designs that we used to explore the visual deficit produced by resections of the inferotemporal cortex. Discriminations of color, brightness, size, two- and three-dimensional shapes proved sensitive to the cortical resection. At other times parametric designs had to be invoked, as when we wanted to know the limits of the brightness or size discrimination deficits. But even these experimental procedures often failed to provide sufficiently precise answers. Response operator characteristic curves (ROC) were explored in order to check whether the deficiency produced was a function of changes in detection threshold or in response bias.

The results of this phase of the program yielded a wealth of data. However interpretation was seldom straightforward, in part due to the lack of agreement about the constructs used in experimental psychology. Just how does one compare the results obtained in a fixed interval operant conditioning study with a result obtained in an ROC decisional experiment? How does one compare either of these with results obtained in a delayed alternation situation tested in a Yerkes box or the DADTA machine? Interpretations have been made after much crossvalidation of techniques, often using the same subjects and, of course, comparable resections. But in most cases some conceptual leaps were necessary in making the interpretations and these leaps were guided by findings on human neuropsychological patients.

Phase III. Another line of research, made possible by the initial findings of Phase I, was an attempt at specification of the anatomy and physiological mechanisms of operation of the neural systems of which the critical cortical areas were a part. Chemical and electrical stimulations in anesthetized or problem-solving monkeys were performed. And the effects of such stimulations on electrical recordings of event related potentials (ERP) were assessed while monkeys performed in the DADTA. Also, such effects on the microstructure of receptive fields of single units in the visual system were assayed.

Once again the results of these experiments yielded a good deal of data which are interesting in their own right. However, as in Phase II, interpretation and in some instances controversial interpretation became necessary. One major controversy centers on whether the sensory specificity of the convexal "association" cortex is due to its transcortical *input* via connections from the related primary sensory cortex, or whether the specificity is to be ascribed to an *output* which operates down-stream on the primary sensory systems. We were able to make massive disconnections, some of which appear to be complete, between the primary sensory systems (at both the thalamic and cortical levels) and the inferotemporal cortex involved in visual discriminations. None of these disconnections produced lasting deficits in sensory discriminations and this led me to propose the output hypothesis. The controversy hinges solely on whether the disconnections are in fact total, as it is suggested by input theorists that even a small remnant of connectivity is believed sufficient to mediate an input.

Phase IV. The research program began with the aim to clarify the brain mechanisms involved in cognitive, conative, and emotional processes in humans. The final research phase of the program therefore must address the relevance of the results of the non-human primate research, in which some 1500 monkeys were used, to human neuropsychological findings. Since my early days in the neurosurgical clinic, electrical recordings of event related scalp potentials, computerized tomography, and nuclear magnetic resonance techniques have been developed to aid in the localization of brain pathological conditions. The battery of tests developed by experimental psychologists is also a recent innovation. Several members of the neuropsychological laboratories at Stanford are currently using these tools to provide a basis for comparison of non-human and human neuropsychological data.

Phase V. The laboratory research has yielded many unexpected results. These results have dramatically changed my views from time to time and posed, as critical to further research, problems that I had thought I could ignore. Much of my theoretical work has stemmed from these surprises.

Discoveries

Karl Popper has claimed that science is based on conjecture and refutation, and Karl Lashley was always most comfortable when he operated in this mode. My own research appears to have proceeded in a somewhat more haphazard fashion. Despite the planning represented in the phases described above, the actual research was more truly a search that stemmed from problems and paradoxes (such as unexpectedly finding relatively direct sensory inputs to the motor cortex) rather than from well formulated conjectures or hypotheses.

Theses there were, but only rarely did I derive single testable hypo-theses with experiments designed to confirm or disconfirm. Rather, the rule was that several more or less clearly defined alternatives presented themselves once the thesis, the reason(s) for performing the research, became clear. Experiments were designed to find out which of the alternatives fit the data obtained. Sometimes the data fit none of the alternatives, the thesis itself was found wanting, and new directions had to be taken. Often these new directions stemmed from attempts to systematize the data already obtained and to develop an appropriate frame for sorting and classifying them.

Whatever the merits or deficiencies of this approach, it is shared by many biologists. Claude Bernard, when asked how he proceeded in the laboratory, answered that he simply asked nature some questions. By adopting this perspective, the yield in my program has been substantial and many discoveries were made which may not have been uncovered by a more rigid methodological approach. Some of these are detailed below:

1. Delineation of a mediobasal motor cortex defined the boundaries of the limbic forebrain and established the relationship between limbic cortex and visceroautonomic activity. Based on the earlier work of McCulloch, Bailey, and von Bonin, we established by strychnine neuronography and by electrical stimulation and histological examination, the interrelationship between the amygdaloid complex and the surrounding orbitofrontal, anterior insular, and temporal polar cortex and the relationship of all of these to the limbic forebrain.

The work of Arthur Ward and Robert Livingston had established that visceroautonomic responses were obtained from electrical stimulation of the cingulate gyrus and orbitofrontal cortex. We extended these results to the anterior insula, temporal pole, and amygdala.

Thus the entire anterior portion of the limbic forebrain was shown to constitute a mediobasal motor cortex that regulates peripheral visceroautonomic functions.

2. Establishing the fact that the far frontal cortex is the "association" cortex for the limbic forebrain accounted for the psychosurgical effects of frontal lobotomy. Using the delayed response and delayed alternation techniques we extended the work of Carlysle Jacobsen and Henry Nissen, who had shown that resections of far frontal cortex disrupted performance on these tasks. We found that resections of the various structures composing the limbic forebrain (hippocampus, amygdala, cingulate cortex) and lesions of the head of the caudate nucleus also disrupted performance of delayed alternation (but not of delayed response). We also found that resections of the cortex of the posterior cerebral convexity failed to disrupt performance on these tasks; if anything, monkeys with such resections tended to perform better than their unoperated control subjects.

These findings, and anatomical considerations involving the organization of the projections from the dorsal thalamus to the cortex, indicated that the far frontal cortex can be considered the "association" or higher processing cortex for the limbic forebrain. This relationship between the far frontal cortex and the limbic forebrain helped account to some extent for the changes produced by frontal lobotomy in humans.

3. Controls on visceroautonomic activities by the frontolimbic forebrain were shown to serve as boosters for habituation and conditioning. A great deal of effort went into a determination of the functions of the frontolimbic forebrain. As noted, the anterior por-

tions of this cortex proved to constitute a visceroautonomic motor cortex. The nature of the control over visceroautonomic functions by the amygdala, the "funnel" or critical focus of this motor system, was demonstrated in a series of experiments on habituation of the orienting reaction and of conditioning in fully awake monkeys.

The results of these experiments showed that the visceroautonomic components (galvanic skin conductance, heart and respiratory rates, and adrenocortical responses) of orienting (and conditioning) failed to occur in amydgalectomized monkeys who also failed to habituate the behavioral components of orienting. I concluded that the visceroautonomic components of orienting acted as a "booster" to help register novel events. Without such a booster, familiarization, habituation, could not occur. Similar results were obtained by James McGaugh in his long series of studies on the consolidation of the memory trace.

The experiments using the orienting reaction were extended to monkeys and patients with far frontal lesions with results essentially the same as those obtained with amygdalectomized subjects.

4. The frontolimbic regulation of visceroautonomic activity was shown not to be devoid of sensory guidance: The intensive (protocritic) aspects of pain and temperature sensory inputs were demonstrated to reach the frontolimbic, not the parietal, cortex. The possible sensory input to the frontolimbic forebrain was not ignored. Pain threshold was shown unaffected, but avoidance conditioning was disrupted by all resections which invaded the far frontal or limbic formations including amygdala, hippocampus, and cingulate cortex.

Taste (using bitters) threshold discrimination was shown to be disrupted by resections of the anterior portion of the planum temporalis just forward of the primary auditory input area (and no other cortical resection). And after resections of the temporal pole, monkeys would repeatedly eat meat (hot dogs), something which control monkeys do not do. Thus the anterior portion of the planum temporalis serves as the primary receiving cortex for taste while the temporal polar cortex serves a higher level of gustatory processing.

Temperature discrimination was disrupted by electrical resections and electrical stimulations in the region of the orbitofrontal and anterior insular cortex and the amygdala. No such disruption was seen after resections or electrical stimulations of parietal cortex.

I summarized these findings with a proposal, derived from a distinction made by Henry Head, that the frontolimbic forebrain processes the "protocritic" aspects of sensation while the systems of the cortical convexity process the "epicritic" aspects. Epicritic sensations display local sign (i.e., can be accurately localized in time and space). The protocritic aspects of sensation are devoid of local sign and may reflect the bandwidth of tolerances for an *intensive* dimension of sensations.

5. The sensory-specific aspects of cognitive processes were shown to be dependent on the sensory specificity of restricted regions within the posterior "association" cortex of the cortical convexity: With the exception of taste (and the vestibular sense), the various end stations of the epicritic aspects of sensation in the cortex of the cerebral convexity were well known when this program of research was initiated. At that time it was thought that the expanse of cortex lying between the primary sensory receiving areas served as "associative" function. As noted, the sensory specificity of agnosias found in human patients was thought to result from lesions of the association cortex which invaded the adjacent primary sensory cortex as well.

The multiple dissociation technique demonstrated that, in the monkey, no such invasion of primary sensory cortex was necessary to produce the sensory specific deficits which occur after resections of the "association" cortex. An area specific to the tactile sense, another to hearing, and a third, specific to vision, were located.

A long series of experiments centered on the functions of the inferotemporal cortex, the area shown to be specific to vision. The results of this series showed that, while visual sensory functions such as threshold and detection remained essentially intact, resections produced marked deficits whenever selections among visual imputs were demanded.

Electrical recordings of event related potentials gave similar results. Recordings made from the primary visual cortex were sensitive to changes in numbers and kinds of features which characterized the input. Recordings made from the inferotemporal cortex were sensitive to variables which influenced selection or "choice," especially when this was difficult.

Selection was interpreted to be a cognitive, information process which, when disturbed by a brain lesion in humans, results in an agnosia.

6. Preliminary evidence was provided to show that perceptual constancy is a function of the perisensory systems: Selection among alternatives implies that these alternatives are clearly categorized. Categorizing, in turn, implies object constancy. In one experiment

we showed that object constancy was not related to the functions of the frontolimbic forebrain. In another study, size constancy was disrupted by a combined lesion of the pulvinar of the thalamus and the peristriate cortex from which eye movements are obtained by electrical stimulation. Following such lesions monkeys responded to the size of the retinal image and did not take distance cues into account.

Although these are only first steps, the results of these experiments suggest that object constancy will be found to be a function of the systems of the posterior cerebral convexity, most likely of the perisensory thalamocortical systems, and that the functions of these perisensory systems devolve on their control of motor mechanisms.

7. Reciprocity was demonstrated between the functions of the frontolimbic systems and those of the cortical convexity: A Jacksonian reciprocity was demonstrated to exist between the functions of the frontolimbic formations and those of the cortex of cortical convexity. Resections of the frontolimbic cortex actually speeded learning of sensory discriminations while making the learning of delayed alternation well nigh impossible. Resections of the cortex of the posterior convexity actually speeded learning of delayed alternation while making the learning of difficult sensory discriminations well nigh impossible.

This reciprocity was also demonstrated with electrophysiological techniques. Recovery cycles in the visual system were shortened by electrical stimulations of structures within the frontolimbic forebrain. Receptive fields of neurons in the lateral geniculate nucleus and in the primary visual cortex were made smaller by electrical stimulations of the systems of the posterior convexity and made larger by stimulations of frontolimbic systems.

8. It was shown that actions, defined as the consequences of behavior (in addition to muscles and movements), are represented in the precentral motor cortex. The reciprocity of effects of resections and stimulations of frontolimbic and posterior convexal systems on the functions of the primary sensory receiving areas and the involvement of motor control in the production of object constancy, inspired us to look more closely at some aspects of the functions of the primary motor and sensory systems.

As noted, quite by accident we discovered direct cutaneous and proprioceptive inputs to the precentral motor cortex. We also explored the effects on behavior of extensive resections of this cortex using latch boxes and cinematographic recordings of the behavior of monkeys in a variety of situations. The results of these investigations showed (as had the clinical evidence noted earlier) that all movements remained intact, but that skills in certain learned situations (latch boxes) were impaired: Though the sequencing of behavior was not disrupted, transition time between behavioral elements increased markedly.

I concluded that the precentral cortex exerted control over behavioral "acts" (defined as the consequences of movements) rather than control over specific movements or muscles. Control over acts involved control over movements and muscles, of course, but the nature of the higher level control had in some way to encode the *consequences* of movements rather than specific muscle sequences per se.

9. The possibility that this representation devolved on a spectral analysis of changing loads was tested and neurons in the sensory-motor cortex were shown to be selective of bandwidths of the frequency of a movement. The nature of the encoding process remained opaque to me for almost a decade after completing the initial experiments. Then, a series of events occurred which allowed us to continue the explorations. First, data obtained by Ed Evarts showed that the activity of neurons in the precentral motor cortex was proportional to the load placed on a lever manipulated by a monkey and not, per se, the extension or tension of the muscles used in the manipulation. Second, the results obtained by N. Bernstein in the Soviet Union were translated into English. Bernstein had shown that he could predict the course of a more or less repetitive series of actions by performing a Fourier analysis of the wave forms produced by spots placed over the joints involved in the action.

By this time I had developed the thesis that certain aspects of cortical function could best be understood in terms of orthogonal (linear) transforms of sensory inputs, such as the Fourier. We therefore performed an experiment in which we examined whether neurons in the cat motor cortex were turned to certain bandwidths of frequencies of passive movements of their forelimbs. Here we were testing a specific hypothesis, and the hypothesis was confirmed.

My interpretation of these results is that the motor cortex computes, in the transform domain, a set of values which, when inversely transformed, represent the consequences to be achieved by an act (e.g., load to be lifted).

10. Single neurons in the visual cortex select were shown to select a variety of input features and they were shown to differ in the conjunction of selectivities which characterized them. Thus the

common assumption that single neurons serve as feature detectors or channels needs further exploration. Explorations of unit activity in the primary visual system were based on the work of Kuffler, Hubel and Wiesel, and the many other investigators who took up such investigations. Our concern was to try to classify the many properties of visual receptive fields. For several years we attempted to make a classification of cells (as is the common procedure). But we found that each cortical cell had conjoined selectivity to several feature properties and that different cells displayed different conjunctions. We are currently investigating whether the output of a cell is specific to a specific feature, or whether the cell simply responds that it has been stimulated. If the cell simply responds, then feature encoding would be a function of a spatial configuration of an *ensemble* of neurons and not a particular cell.

Theory

1. The publication of *Plans and the Structure of Behavior* had a major impact on moving psychology from a strictly behavioristic stimulus-response or response-reward stance to a more cognitive approach. In that publication, George Miller, Eugene Galanter, and I called ourselves "subjective behaviorists." I have already noted how I became involved with Miller after reaching an impasse on the problem of the chaining of responses. Clinical considerations, set forth in my contribution to Sigmund Koch's *Psychology as a Science*, were also instrumental in taking more seriously the verbal reports of introspection than was the custom in midcentury. Thus came about the major divergence from Skinner, who abhors the use of subjective terminology.

The thrust of *Plans* was that computers and computer programs can serve as powerful metaphors for understanding cognitive processes and the brain mechanisms involved in them. That thrust has been realized to some extent in the neuroscience community as well as in psychology in that many aspects of complex behavioral functioning are now conceptualized in terms of "information processing," and the initiation of "motor programs."

However, it has also become clear that brain mechanisms are considerably different, even in the fundamentals of their operation, from current serial processing computers. Brain mechanisms rely to a large extent on parallel processing, which suggests that addressing occurs by content rather than by location. Our mails are representative of location addressable systems. Content addressable systems are akin to those in which a broadcast is receivable by a properly tuned instrument, irrespective of location within the broadcast region.

2. These differences were highlighted in *Languages of the Brain*, published a decade after *Plans*. *Languages* continued to explore the power of hierarchically arranged information processing mechanisms but added the mechanisms of image processing which, though they had been integral to the conceptions proposed in *Plans*, were not explored because no appropriate metaphor was available at that time. Image construction depends on parallel processing and thus is better fitted to some aspects of brain anatomy and function than is serial programming.

One of the consequences of considering parallel as well as serial processing was the introduction of a model for feedforward operations. In *Plans* we had made much of hierarchically organized feedback loops. As Roger Brown pointed out in his review of the volume, this left the mental apparatus almost as much at the mercy of input as did the earlier stimulus-response psychologies. In *Languages* this deficiency was remedied by showing that coactivation of two or more feedback loops by a parallel input would produce the kind of feedforward organization basic to voluntary control. This proposal was in consonance with similar suggestions put forward by Helmholtz, Ross Ashby, Roger Sperry, and Hans-Lukas Teuber, but was more specific in its design features than were the earlier suggestions.

3. Of the many languages described in *Languages of the Brain*, the language of the hologram has had the greatest impact—as noted in the introduction. This impact is due to the fact that the optical hologram displays vividly the operations of image processing. Image processing relies on orthogonal transformations such as the Fourier, which because of their linearity are readily invertible. This means that image and transform are reciprocals, i.e., duals of one another and that transformation in either direction is readily achieved.

The transform domain has properties that make it ideal for storage and for computation. Millions of decabits of retrievable information can be encoded in a centimeter cube of holographic memory. IBM uses such storage devices in the machines that read the stripes which identify grocery store items. Correlations are computed by simple convolving (multiplying) one input with the next. This accounts for the value of the fast Fourier transform (FFT) in statistics.

There are other properties of the transform domain which are not so obviously useful but which have had a tremendous theoretical impact. Information becomes distributed in the transform domain so that essentially equivalent images can be reconstructed from any portion of the stored representation. Again, radio or television broadcasting makes a good analogy. At any location within the reach of the broadcast, the coded representations of all of the programs are intermingled. Nonetheless, each program is available through an inverse transformation of the code by an appropriate tuning device. The whole spectrum is enfolded into every portion of space and each part represents the whole: Thus the name, hologram.

Holography was a mathematical invention designed by Dennis Gabor to enhance the resolution of electron microscopy. Optical realizations of the mathematics came only a decade later, and it is necessary to emphasize that other realizations of the mathematics such as those made by computer (as in the IBM example above) are equally valid. To the extent that certain aspects of brain function realize Gabor's mathematics, to that extent they can be thought of as holographic. As there is considerable evidence that one of the properties of receptive fields of cells in the primary visual cortex can be expressed in terms of Gabor functions, there is some merit to pursuing a holographic hypothesis of brain processes with regard to perception and memory.

The enfolding process which characterizes the transform domain provides additional properties which have seized the imagination of scientists and the public. The dimensions which characterize the transform domain are very different from the familiar space-time dimensions which characterize the image domain. Consider for instance the dimensions of a spectral representation of an electroencephalographic record: Its dimensions are frequency and power. Time has been enfolded into the frequency domain.

Causality is a casualty in a domain that enfolds space-time. Thus, ordinary Newtonian-Cartesian-Euclidian mechanics no longer hold until the inverse transformation into the image domain is realized. My interpretation of these attributes of transformation is that the transform domain characterizes potential rather than actual realizations.

The implications of this interpretation are detailed elsewhere. I would not be surprised to read some version in OMNI one of these days. For now, I will finish by noting what a fantastic adventure it has been to explore our world within—an adventure equal to that experienced in expeditions of yore to polar and equatorial territories. And I look forward to continuing emergence of new vistas in the brain and behavioral sciences at this fascinating frontier.

DATA PAPERS

I. Brain Systems Analysis: The selective effect on behavior of brain stimulations and resections.

A. Resections

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II. Experimental Analysis of Behaviors Related to Brain Systems

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III. Psychophysiological Effects Related to Brain Systems

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IV. Electrophysiological Analysis of Brain Systems

A. Evoked potential

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