Afterword

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As a result of the conference, are we any more enlightened as to how brain function influences human values than we were before? In a strange sense, I believe we are. The strangeness arises from the fact that many, if not most, of the speakers did not directly address the relationship between brain and values. At the same time, they brought intuitions to bear that can be tested by making them explicit -- and this has great value in science because it makes possible the asking of precise questions. As I indicated in my introductory statements, there seems to be some implicit understanding that memory and value are closely related; and if so, learning must also be integral to the process of valuation both in setting up the process and running it off. At another pole, values appear to be set by biological factors: drive stimuli and resulting emotional and motivational states as predispositions and dispositions to value one or another perception or action.

The papers by McClelland and by Ahern and Wood bring new dimensions to these issues, dimensions worth pursuing a bit further.

Commentary on Role of Hippocampus in Learning and Memory

From my standpoint, this paper is a seminal contribution to our understanding of the functions of the hippocampal system. In the final chapter of Robert Isaacson's and my four volume compendium on the hippocampal system, I summarized evidence that indicates this system makes possible "recombinant processing". In Isaacson's book on the limbic systems (1982) and in Lecture 9 of mine on perception (Pribram, 1991) we noted that hippocampal function makes innovation possible. What was lacking in these summaries and proposals was a precise model of just how hippocampal processes would accomplish recombination and innovation.

McClelland, in this contribution to Appalachian V, presents such a precise model. Furthermore, his model indicates how hippocampal intervention – which is present whenever a stimulus is novel to the organism (Thatcher & John, 1977) – can lead to dysfunction (catastrophic interference) as well as to creative innovation. McClelland shows how hippocampal input to the cortex can, at other times, lead to interleaved learning. According to McClelland, non-limbic learning is slow and is produced "via interleaved presentation on a representative sample of an entire domain of knowledge." (See Page 535. Also, see Amsel's chapter, Page 505.)

However, Douglas and I (1966) showed that such interleaved learning can also occur in the absence of the hippocampal formation (and thus independently of episodic processing). Could this be due to a difference in brain organization between rodent and primate such as the massive increase

in the area of the frontal cortex? In an earlier report (Pribram, 1958), I had reviewed evidence that animals with more complex nervous systems actually learned more slowly than animals with simpler nervous systems but that the range of what can be learned increases with an increase in brain complexity. McClelland's model shows precisely how an increase in the complexity of the brain can accomplish this enhanced range.

As an addition to the overall model presented by McClelland, there are elaborations of its neurological underpinnings that can fill out the particulars of the "how."

McClelland's current formulation was developed in collaboration with Bruce McNaughton and takes into account the latter's finding of representation in hipppocampal neurons of a path in space. Thus, their model directly matches hippocampal activity with the activity of the cortical convexity (as would be expected of a comparator). On the input side such a model is plausible. However, their model also demands such a comparator process on the output side. This is implausible in view of results obtained by Paul MacLean and myself (Pribram & MacLean, 1953) when mapping cortical connectivity by strychnine neuronography While we were able to readily show multiple inputs to the hippocampal formation, we were totally unable to activate any isocortical region by stimulating the hippocampal cortex. The finding was so striking that MacLean (1990) developed the theme of a schizophysiology of cortical function.

On the other hand outputs are plentiful to the amygdala, to the n. accumbens septi and other subcortical structures via the fornix. Confirmation of the difference between input (encoding) and output (decoding) operations involving the hippocampal formation has recently come from studies in humans using /MRI (Gabrieli, Brewer, Desmond & Glover 1997). Encoding into memory was found to activate the para-hippocampal cortex (including the entorhinal cortex which receives input from the remainder of the isocortex), whereas decoding (retrieval) was found to activate the subiculum which "provides the major subcortical output of the hippocampal region via the fornix" (p. 265).

The subcortical nuclei do not have the laminar structure of cortex and so are poor candidates for the point to point match a computer would ordinarily be conceived to implement. On the other hand, a match could readily be achieved if the comparison would involve a stage during which processing entailed a distributed stage, much as when a holographic memory is used to store and retrieve information (for instance with hololishe). It is the evidence that a distributed store is, in fact, built up in the hippocampal formation during learning that makes this sort of model plausible.

Landfield (1976) and O'Keefe (1986) have developed this sort of model. O'Keefe reviews the evidence and describes the model as follows:

> Attempts to gain an idea of the way in which an environment is represented in the hippocampus strongly suggest the absence of any topographic isomorphism between the map and the environment. Furthermore, it appears that a small cluster of neighboring pyramidal cells would map, albeit crudely, the entire environment. This observation, taken together with the ease that many experimenters have had in finding place cells with arbitrarily located electrodes in the hippocampus, suggests that each environment is represented many times over in the hippocampus, in a manner similar to a holographic plate. In both representation systems the effect of increasing the area of the storage which is activated is to increase the definition of the representation.

A second major similarity between the way in which information can be stored on a holographic plate and the way environments can be represented in the hippocampus is that the same hippocampal cells can participate in the representation of several environments (O'Keefe & Conway, 1978; Kubie & Ranck, 1983). In the Kubie and Ranck study the same place cell was recorded from the hippocampus of female rats in three different environments: All of the 28 non-theta cells had a place field in at least one of the environments, and 12 had a field in all three environments. There was no systematic relationship amongst the fields of the same neurone in the different environments. One can conclude that each hippocampal place cell can enter into the representation of a large number of environments, and conversely, that the representation of any given environment is dependent on the activity of a reasonably large group of place neurones.

The third major similarity between the holographic recording technique and the construction of environmental maps in the hippocampus is the use of interference patterns between sinusoidal waves to determine the pattern of activity in the recording substrate (see Landfield, 1976). In optical holography this is done by splitting a beam of monochromatic light into two, reflecting one beam off the sconce to be encoded and then interacting the two beams at the plane of the substrate. In the hippocampus something similar might be happening. . . . The beams are formed by the activity in the fibers projecting to the hippocampus from the medial septal nucleus (MS) and the nucleus of the diagonal band of Broca (DBB).

Pioneering work by Petsche, Stumpf and their colleagues (Stumpf, 1965) showed that the function of the MS and DB: nuclei was to translate the amount of activity ascending from various brainstem nuclei into a frequency moduled code. Neurons in the MS/DBB complex fire in bursts, with a burst frequency which varies from 4-12 Hz. Increases in the strength of brainstem stimulation produce increases in the frequency of the bursts but not necessarily in the number of spikes within each burst (Petsche, Gogolak and van Zweiten, 1965). It is now widely accepted that this bursting activity in the MS/DBB is responsible for the synchronization of the hippocampal theta rhythm   (O'Keefe, 1986, pp. 82-84).

The November 1995 issue of *Scientific American* shows how such a holographic matching process could work. Of course, in this quotation, the matching process works by way of illuminating crystals, and the neural substitutes for this would be surface distributions of dendritic polarizations in somatosensory cortex (King et. al, 1994; Pribram, 1995):

Given a hologram, either one of the two beams that interfered to create it can be used to reconstruct the other. What this means, in a holographic memory, is that it is possible not only to orient a reference beam into the crystal at a certain angle to select an individual holographic page but also to accomplish the reverse, illuminating a crystal with one of the stored images gives rise to an approximation of the associated reference beam, reproduced as a plane wave emanating from the crystal at the appropriate angle.

A lens can focus this wave to a small spot whose lateral position is determined by the angle and therefore reveals the identity of the input image. If the crystal is illuminated with a

hologram that is not among the stored patterns, multiple reference beams -- and therefore multiple focused spots, are the result. The brightness of each spot is proportional to the degree of similarity between the input image and each of the stored patterns. In other words, the array of spots [weights in a layer of a PDP network] is an encoding of the input image, in terms of its similarity with the stored database of images. (Psaltis & Mok, 1995, p. 76.)

Putting this together with the McNaughton's data showing that the hippocampus represents the path taken by an animal down an alley maze, encoding in the hippocampus may be both holographic-like and patterned in space and time. The hypothesis is that as multiple paths become represented in the hippocampal formation, a transformation into holographic-like surface distribution in the spectral domain is effected. When subsequently a particular path is sought, the buffer operates much as does the holographic memory described above. Initially, actual paths construct the holographic memory and during retrieval, scan paths activate the comparator to access a particularly appropriate actual path. Essentially, the process implements a shift in coordinates from space-time (configurational) to spectral and back to configurational.

The shift of coordinates is suggested to take place by way of scanning, that is, constructing a particular scan path. Computational models such as those proposed by Harth, Unnikrishnan and Pandya (1987) and by Yasue, Jibu and Pribram (Pribram, 1991) have been developed for vision to account for the selection of coordinates as a result of internal scanning. The shift from spectral to the configuration coordinates has been demonstrated in the visual system both at the thalamic and cortical level. Electrical stimulation of temporal or frontal lobe cortex enhances or diminishes the extent of the inhibitory surrounds and flanks of dendritic receptive fields in thalamus and cortex so that the sensory channels can either become multiplexed or fused. As the dendritic fields can be described in terms of a space-time constraint on a sinusoid -- such as the Gabor elementary function, the constraint is embodied in the inhibitory surround of the field. Enhancing the surround enhances processing in configuration coordinates; diminishing the surround enhances the sinusoidal (spectral domain) aspects of processing. Thus, the development of scanpaths operates on the inhibitory process that characterize the fluctuations of the polarizations of the dendritic connection web.

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McClelland Reactions to Pribram's Commentary

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August 1997

I thank Pribram for his kind words about our model of the role of the hippocampus in learning and memory, and agree with several aspects of his commentary. I will comment on two points: (1) the necessity of hippocampal playback for normal cortical learning, and (2) the relationship between hippocampal memory storage and holographic forms of memory. Is hippocampal playback necessary for normal cortical learning?

Pribram mentions data suggesting that in the monkey, the hippocampus is not necessary for normal acquisition of memories in the neocortex, and suggests that this may be a difference between monkey and man. In fact, recent data suggests the same in humans. Vargha-Khadem, (1997), and Mishkin have recently reported three cases of young adults who sustained apparently selective damage to the hippocampus early in life. At least one of these cases shows an above-average IQ, with good performance on various tests that assess adequacy of 'semantic' memory, including vocabulary and encyclopedia knowledge. For example, the patient, who received his education in England, gave a very cogent and accurate answer to the question, 'Who was Martin Luther King?' Yet the patient's episodic memory is grossly deficient, as one would expect from the extensive apparent damage to the hippocampus. Since the hippocampal damage is most likely to have occurred during anoxic periods around the time of his birth, it would seem clear that acquisition of normal semantic memory does not depend on an intact hippocampal system.

This finding is actually completely consistent with my views of the role of the hippocampus, which I fear my writings on the subject have not made totally clear. There is evidence of replay of memories stored in the hippocampus, and the finding of temporally graded retrograde amnesia after a single punctate exposure seems best interpreted as reflecting the neocortical learning that results from the use of this replay mechanism. However, I did not mean to imply that replay of memories stored in the hippocampus is necessary for cortical learning. Day to day exposure to structured information embodied in the events and experiences we have in our interactions with the world are in my view the main source of the experience that drives neocortical learning.

Similarities and Differences Between Hippocampal Memory Storage and Holographic Forms of Memory

Pribram is quite right to note that there are several striking similarities between hippocampal memory and holographic memory. The spatial structure of the world is completely dispersed across the hippocampus, just as it is in a hologram, and small patches of hippocampus do indeed provide degraded representations of entire spatial environments. However, I do not believe the mechanism that gives rise to this is holographic in the sense of relying on interference patterns and linear summation. Instead, as articulated in some detail in a recent paper by McClelland and Goddard (1996), I believe that this is accomplished by a mechanism we call 'sparse, random, conjunctive coding'. Essentially, the idea is this. First, neurons within hippocampal field CA3 recieve projections from a small fraction (perhaps 1-5%) of neurons in entorhinal cortex (EC). While there may be some topographic organization within EC, the fibers leading from EC to field CA3 are quite dispersed, so that a given CA3 neuron can receive direct input from up to 1/2 of the EC. Collareral interactions among CA3 neurons likewise spread very widely, leading to the idealization that each CA3 neuron receives inputs selected completely at random from the full population of EC. Second, neurons in CA3 project to and recieve projections back from a pool of inhibitory interneurons, whose function is to strictly regulate the number of CA3 neurons active at a particular time. The hippocampal theta rhythm modulates the activity of these interneurons, allowing only a very small fraction to fire in the 'trough' of the theta cycle, and a larger fraction to fire at the peak. At the trough, then, the hippocampal representation is extremely sparse (few neurons are active) and the ones that are active are the ones with the strongest total synaptic input from entorhinal cortex. They thus represent a sparse, distributed code, e.g., of the animal's location in space. Because they are distributed approximately uniformly over the hippocampus, the link between external position and position in the

hippocampus is broken. Even though the code is sparse, it is still redundant, in the following sense. There are 300,000 CA3 neurons in the rat, and even if there are 2% active at any given point in the environment, this still comes to 6000 neurons. Each neuron encodes a random subset of the elements that define the particular location in the environment, but each element is represented several times, so that any given element is likely still to be represented if only a fraction of the CA3 is preserved. Tsodyks, Skaggs, McNaughton, and Sejnowski have recently suggested what may happen during the peak of the theta cycle: here, as more and more hippocampal neurons are allowed to become active, the influence of collateral connections among CA3 neurons, rather than bottom-up connections from EC, may become more and more important in determining which CA3 neurons fire. Thus the neurons activated in the later stages of the theta cycle may reflect an associative pattern completion process. During spatial navigation, this process is thought to be responsible for that fact that neurons active in the peak of one theta cycle represent locations in space toward which this animal is moving.

As a more general comment, I have always found Pribram's perspective, emphasizing the distributed nature of memory storage, to be an extremely valuable and indeed largely valid perspective. It seems to me that the brain has found ways of capturing the positive features of this idea. Whether it does so by making explicit use of interference patterns remains a controvertial point, but the more fundamental insight is that representation and processing are indeed highly distributed, and this is especially true within the hippocampus.

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Commentary on the Role of the Frontolimbic System on Episodic Processing

In this scheme of things, valuation is also influenced by more momentary utilitarian considerations provided by desires and the probability that these desires will be fulfilled.

Critical to this aspect of valuation is the case of T.J. presented by Charles Ahern and Frank Wood. Ahern and Wood framed their analysis in the terms used in memory research: the distinction between episodic, skill (procedural), and semantic (reference) types of processing. For reasons that, I hope, are apparent, I equate episodic processing with the current, momentary utilities (desirabilities and probabilities) that influence valuation; and I equate semantic processing with discriminations and preferences.

Given these equations, T.J. is important in that his semantic learning proceeded within normal limits and that his semantic memory is unimpaired, as is his skill in using it. As Zajonc (1966) has claimed on the basis of his studies, episodic processing appears to utilize a brain system independent of procedural and semantic processing.

Furthermore, episodic processing is not a necessary antecedent to skill or semantic (reference) learning or remembering. In these respects T.J. confirms the findings obtained for

decades, with non-human primates. (For review see Pribram 1991, Lectures 7, 8, 9, and especially10). Also, T.J.'s lesions involve the mediobasal structures of the limbic system and the related anterior frontal cortex. However, in monkeys the resections that produced the defects were symmetrical; in T.J. the lesion was primarily, though not exclusively, in the right hemisphere. What is striking about T.J. is how well he can traverse the social scene despite his catastrophically severe deficit in episodic processing. What remains to be investigated is just how his judgements, his values are affected. So far he manages on what he has learned; in the jargon adopted in my papers in this volume he has obtained his preferences from his social environment.

But there is also considerable intactness in T.J.'s emotional processing. Are drive stimuli and their influence on emotions and values influenced by a system separate from that which influences episodic processing? If so, is the drive-emotional system centered on the amygdala and the orbitofrontal cortex (as reviewed by Schore in this volume, while episodic processing involves the hippocampal-dorsal-frontal-cingulate cortex? And if this is so, how do we reconcile the data and models of hippocampal function presented in this conference (and in my discussion thereof) with the fact that semantic learning can proceed without hippocampal intervention? An answer to this last question may be the one given by Vindogradova (1970) (and by Douglas and myself, 1966; 1969) that in learning, an ounce of "emotion" is the equivalent of a ton of repetition. Perhaps the hippocampal models presented here apply to those circumstances when something novel catches our interest -- and not to the rote learning of the alphabet, and other prerequisites to semantic processing.

I have pursued only two of the possible trains of thought brought up during the proceeding of this conference. Of equal interest is the model of visual processing developed by Vogl, Blackwell and Alkon. And what about Sternberg's demonstration of the importance of values in shaping our testing procedures and therefore the formation of their values during the educational process in youths whose far frontal cortex is still developing (Hudspeth and Pribram 1990).

Each of these trains of thought deserves a whole conference of its own. For now, I do feel this conference has added a great deal to our understanding of the role of the brain in shaping our values. But one does have to dig a bit in order to extract the gold.

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Foreword

Ruminations on Sex and Death; Memory and Value

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When Appalachian V was over I felt deep disappointment: More that half the participants had addressed learning and memory -- not, as I had expected, a scientific analysis of how values become organized by the human brain. Over the year that I've been trying to formulate the *Proceedings* for publication, however, I have begun to wonder whether, perhaps, some deeper intuition, probably unconscious, had led these participants to do what they had done.

A clue as to what that intuition might be is given by Bruce MacLennon's introductory presentation. As he states, there is a critical connection between human values and the process of learning and remembering. We value food, shelter, comfort, excitement, challenge, companionship -- and we can find both biological roots and brain mnemic processes for all these evaluations.

At the Second Tucson Conference on Consciousness, the most telling paper in my own view was not presented by a scientist or philosopher -- but by a lawyer. He noted that should the reductionist program (espoused by the Churchlands, Dan Dennet and Francis Crick) succeed, the law would be in serious difficulty. If, indeed, rape and murder were "nothing but" brain processes, where would accountability have gone? My colleagues and I do not have this difficulty: the presentations that made up Appalachian III stated over and over that there is a category error involved in such reductionism. Scale (or level) of organization and the facts of emergence assure that the whole is not only greater than the sum of its parts but is different from such a sum.

Still, there is more to an answer regarding the dilemma of human accountability than the level (social and cultural) at which it operates. How can humans justify wars in the name of spiritual guidance, how do they justify bonus payments of millions of dollars to themselves, while putting their employees out of work? Just what is going on in their brains that allows justification?

One obvious answer is that humans learn and then remember (and act accordingly) what their culture has taught them. Thus, as intuited by the conferees of Appalachian V, learning and remembering are critical components of values -- and I have organized their presentations under the heading "Preferences."

But where do preferences originate? There is an abundance of evidence that the preferences we hold are rooted in collective memories of experiences of death. Without memory, we would not be concerned with dying. The death of intimates would fade and anticipation of our own death would not exist (Edelman's prescient book-title *The Remembered Present* would have been useful in making this point).

But death is biologically linked to another process which was called to our attention recently by the cloning of a sheep: sex. Cloning circumvents death. Sexual reproduction is responsible for death.

In traditional societies and our own mythology and religious practices, this juxtaposition of the sexual and the sacred has often been made explicit. The sacred deals with how we handle death; the sexual, how we circumvent it. The temples of the classical period usually dealt with both. In the Proceedings, I have grouped brain processes aimed at circumventing death under the rubric "Utility."

A. Earl Walker, head of neurosurgery at the University of Chicago when I was there, had made major contributions to our understanding of thalamocortical anatomy. His teaching to us was that if one wanted to know how a particular brain system is organized, first look at its input from (and output to) the periphery. Biological needs are surely important roots of values, and one set of brain systems, the frontolimbic formations, receive their input from -- and control the output to -- the visceral and autonomically regulated peripheral structures.

Autonomic regulation takes two forms, sympathetic and parasympathetic. Essentially, the sympathetic system activates emergency responses (fight and flight reactions) in the circumvention of death. The parasympathetic system regulates longer range circumvention by processes involved in daily maintenance and the maintenance of the species (feeding and sex).

Of interest is the fact that the parasympathetic system has two divisions -- a cranial and a sacral. Thus, when autonomic system involvement shifts from emergency responses to daily maintenance responses, sacral and cranial (brain) regulation takes over.

There is considerable misunderstanding regarding the nature of these maintenance functions. For instance, sexuality and feeding are usually conceived, in our society, as base, simple and mostly a function of our viscera. This is not so. It is the brain that regulates sexuality; gonadal hormones initiate, in embryo, the changes in the brain that are expressed after puberty. Expression of sexuality critically involves the cerebral cortex. A study by Frank Beach, using cats, showed that decortication totally abolished female sexual behavior. A parallel case can be made for the functions of the "olfactory" cortex in making life pleasant for gourmets. (Contrast this with the fact that both classical and operant conditioning survive decortication.)

As developed in my paper in this volume, maintenance is based on a set of processes that can be described in terms of their utility to the organism. Perceived utility leads to cultural preferences which, by way of learning and remembering provide guides to human social transactions. These, more often than not, lead to creative agency. As noted in the final passages of my 1971 book, *Languages of the Brain*:

> Man's brain is so constructed that piece by piece he apprehends the whole through the operations of coding and recoding. Languages, verbal (linguistic) and nonverbal (cultural), are constituted of these pieces. When, because of linguistic and cultural affluence, the means-ends reversal occurs, these languages begin to live lives of their own. Thus complexity is compounded and the original organization can easily be lost sight of. Biological processes have, however, built-in renewal mechanisms. When the linguistic and cultural structures become too cumbersome or conflict with each other, they are often degraded, pruned back to their more essential roots. Clearer vision is then attained of the basic organization which gave rise to the process originally; historical comparison can be made between the primitive and the sophisticated version of the language or culture.

Thus, gradually, wisdom is attained in the regulation of human affairs. In contrast to the cries of woe that are increasingly heard as we approach the new millennium, the biologist immersed in the study of brain process faces social issues hopefully. The power of this peculiar biological organ, the brain, especially in man, is only beginning to be fathomed. True, we must get on with the job before some of the cultural-language structures that have suffered the means-ends reversal overwhelm their creators. But the evidence suggests that remedial language-cultures will quickly be formed by those same sorts of brains that initiated the original. Thus wisdom is recurrently achieved. The biological process does not cease. Men's brains, through Image and Act, will create and communicate continuously, constructing languages – the regulators of human affairs. (384-385)