Modes of Central Processing in Human Learning and Remembering

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Limitations of circuit analysis. In tracing the alpha-gamma linked activities through the segmental loops and some supraspinal circuits acting on the Renshaw and Ia inhibitory interneurons, my aim has been illustrative only. The description is complete enough to show that in the end we are reaching a limit for the sensible use of wiring diagrams in integrative physiology. This is due to the hierarchic nature of the nervous system, on which Hughlings Jackson laid so much emphasis. There is control upon control and each particular mechanism is really well understood only at its own level of analysis. Remembering that Sherrington defined integration as interaction for a purpose, functions must also be attributed to circuitry. This ultimately means understanding of wiring diagrams in a behavioral context.

The difficulties confronting complete behavioral interpretations of the bewildering complexity of interactions in hierarchic systems are virtually insurmountable. Known wiring diagrams generally have to be regarded as constraints or boundary conditions defining possible alternatives. For this reason, our best interpretations of function have consisted in fitting wiring diagrams into broad conceptual generalizations, such as reciprocal innervation, alpha-gamma linkage—with its implications for motoneuron membrane potentials, mechanisms for stabilization of neuronal discharges, feedback operations, arousal, load compensation, ideas on posture, etc. Granit, 1975

Introduction

The aim of this chapter is to relate to human brain processes the reviews of the recent surge of research on problems of learning and memory at the molecular and wiring circuit level which make up the remainder of this volume. As noted by Granit in the above quotation from his analysis of the role of muscle spindles, this endeavor is not an easy one. Still, the situation is not as desperate at it was a quarter of a century ago when Lashley made his famous statement to indicate that what we then knew about brain function precluded learning from occurring at all (Lashley, 1950). The phrase was, of course, made tongue in cheek, but subsequent research (as well as some earlier formulations—e.g., William James, 1950; S. S. Stevens, 1951) have borne out an intuition hidden in Lashley's statement: that the limitations on coping with complex en-

vironments, and therefore the potentialities for overcoming these limitations, arise not so much because of restrictions on the use of the final common path—the efferent control over movement—as Sherrington once suggested (1947), but on limitations in central processing—i.e., in brain function (Broadbent, 1974; Pribram, 1974). Once the problem is clearly framed in this fashion, the prospects for relating the molecular and wiring levels of neurophysiological research to those involving human learning and memory become considerably less bleak.

In this presentation I will rely heavily on the results obtained with a single technique to delineate the sought-after relationship. This technique, experimental psychosurgery—the study of the effects of localized resections of the brain tissue on behavioral performances—focuses on a neural structure and asks what role it displays in causing or overcoming the limitations on central processing manifest in learning and remembering. This is a rather different sort of question than that usually asked in biological approaches to the problem. These ordinarily investigate consolidation, habituation, conditioning or discrimination by inquiring into the molecular or circuit changes produced while the behavior under consideration is in force. In contrast, the psychosurgical question, by its emphasis on processing limitations and potentualities, is akin to that which motivates research on human learning and remembering.

With this parallel in mind let us look at some of the principles of brain organization important to learning and remembering which have been reliably established by psychosurgical experiment.

The Distributed Store

The best known principles that have resulted from psychosurgical research are the ones that Lashley was addressing in his pessimistic statement. One of the most persistent results obtained when restricted resections are made of brain tissue is "nothing." Lashley formulated this result into his laws of (a) mass action—that to be effective a brain lesion must exceed a critical size—and (b) equipotentiality—that spared brain tissue can come to function in lieu of that which has been resected.

A great deal of misunderstanding of the nature of brain organization has resulted from the enunciation of the principle when formulated in this fashion. Psychologists especially were prone to accept the idea that all parts of the brain functioned alike (and therefore that the study of the detailed anatomical arrangements of brain organization had become superfluous). Neurophysiologists and neuroanatomists, on the other hand, intimately acquainted with the exquisitely precise wiring of the brain, looked askance at the type of behavioral analysis which was so gross as to miss the obvious distinctions between brain parts.

The research results of the past twenty-five years can, as we shall see, put these misconceptions to rest. The brain has been shown to be made up of systems which manifest different functions. However, within any system and even to some extent between systems, the laws of mass action and equipotentiality hold. Electrical recording of brain potentials evoked by sensory events has demonstrated that the basis for the laws is

the distribution of input over a wide extent of tissue (John, 1967; Pribram, Spinelli & Kamback, 1967; Spinelli, Starr & Barrett, 1968; Bachy-Rita, 1972; Morrell, 1972; Pribram, Nuwer & Baron, 1974). The conclusion has been reached, therefore, that the lack of effect of restricted resections of brain tissue is due to the encoding of input which has become fairly widely distributed within any particular neural system.

The mechanism of distribution and the nature of the encoding process are areas of current research activity which relate the molecular and circuit level of inquiry to the behavioral. I have elsewhere (Pribram, Nuwer & Baron, 1974) detailed the various possibilities and the probability that distribution depends on the interactions among hyper- and de-polarizing potential changes at synaptic and dendritic locations, interactions which then result in conformational changes in local membrane proteins (Pribram, 1971). The result of such an encoding process would be a distributed store with holographic-like properties that make possible the construction of reconstruction of the configuration of the input from any restricted part of the store.

A second property of a holographic-like distributed store relevant to the circuit level of inquiry is its facility for organizing associative memory. Whenever two inputs occur together during storage, the subsequent occurrence of either alone will evoke a "ghost image" of the other. This associative property of the holographic memory mechanism is an important alternative to the step by step forging of neuronal connections as a function of repetition and practice. As we shall see there is a considerable amount of evidence that both types of associative processes occur—one is a fairly rapid "imprinting" of input, the other is more extended in time and critically depends on repetition.

But in order to fully appreciate the evidence it is first necessary to review the data that highlight the diversity of brain systems involved in learning and memory. Only against this background do the distinctions and commonalities among processes become fully evident.

Sensory Specificity in Central Processing

The diversity of cognitive processes is manifest in the first instance in their sensory specificity. When resections of primate "association" cortex are made, the expectation that some general associative or learning capacity would become impaired is not borne out. Learning deficits do result, but these are limited to one or another sensory mode—which mode is affected depends on the locus of the lesion within the extent of "association" cortex (Pribram, 1960). This experimental result reflects clinical experience with man where "agaosias" due to brain injury are, as a rule, restricted to one or another sensory mode. Even in the intact person it is difficult to demonstrate cognitive processes that are not sensory mode specific (Wallach & Averbach, 1955). Most thinking is pursued either in terms of incipient sounds (auditory), images (visual), feels (somatosensory) or tastes (gustatory and olfactory).

The sensory specificity of cognitive processes does not preclude their operating on more wholistically organized mechanisms. The distributed

storage is a good candidate for providing the matrix of such operations. Thus a paradox exists—the association cortex operates within a wholistic matrix, but the operations are sensory mode limited. The paradox is resolved by evidence that the sensory specificity is due to the discrete *output* from localized portions of the association cortex to one or another sensory projection system (Blum, Chow & Pribram, 1950; Pribram, H. & Barry, 1956; Pribram & Bagshaw, 1953; Dewson, Pribram & Lynch, 1969; Pribram, 1969). Cognitive processes are thus found to be akin to motor or command functions (see, e.g., Mountcastle, Lynch, Georgopoulos, Sakata & Akuma, 1975 for a detailed analysis of responses to desired objects in mediate extrapersonal space). In fact the critical output pathway from the association cortex is to the basal ganglia, structures that have classically been considered to be motor in function (see below).

Motor Functions as Central Control Processes

These data fit with others that have revised our view of the operation of the motor systems of the brain. The classical view held that motor control was exercised directly on muscle to shorten it or to increase its tone. Over the past 25 years it has become evident that an even larger share of the control issues to the muscle spindles, receptors that are connected in parallel with muscle fibers and thus monitor their contractions. Central regulatory mechanisms depend on signals from the spindle to adjust the system as necessary. Control is exercised by modulating the monitor through feedback loops, such as the setting of a thermostat can be changed by resetting the control dial (see, e.g., reviews in Miller, Galanter and Pribram, 1960; Pribram, 1960; Granit, 1970; Pribram, 1971; Granit, 1975). Thus the mechanism of motor control is akin to that of homeostasis rather than that of a piano keyboard. Motor systems in the brain to a large extent send signals to receptors, not effectors.

Although not as varied as the sensory mechanisms, a considerable diversity of organization also characterizes the motor control operations of the brain. Two major types of operation are identified in the clinic: one is mainly concerned with postural readiness, the other with the execution of skills.

When diseases strike the basal ganglia, patients show postural disturbances and more or less continuous involuntary movements such as tremors. The type of disorder depends on which of the basal ganglia is affected. Faulty feedback due to the disease is held responsible for the disorders (Bucy, 1949). The disturbances have recently been at least partially overcome by the administration of DOPA (Dioxy phenyalaline) which suggests that the tremors are due to the depletion of this catechol amine which is ordinarily found in especially high concentrations in the basal ganglia (for review see Ungerstedt, 1974). When overdoses of DOPA are administered cognitive disturbances appear—these and those that accompany the postural disturbances could readily result from the control by the basal ganglia over *sensory* functions noted above. More of this in a moment.

The second major type of motor control centers on the cerebellum. When the cerebellar hemispheres are injured, the patient suffers a loss of control of skill—his movements become as awkward as when he initially undertook the activity. The development of a skill entails the smooth coordination of various muscle groups and the elimination of extraneous contractions. Precise timing is of the utmost importance and the cerebellum is most likely a very powerful computer that can calculate "in fast time"—i.e., before a movement must occur—what its outcome will be (Ruch, 1951; Eccles, Ito and Szentagotha, 1967; Pribram, 1971).

The difficulties produced by cerebellar lesions in the execution of skilled acts become especially noticeable when patients intend, i.e., will, their movements. Voluntary control becomes manifest when a signal regulates two or more mechanisms in parallel. By contrast to a feedback loop which is "closed", the parallel processing that defines voluntary control forms an open or helical loop and is called a feed forward (Teuber, 1960; MacKay, 1966; Pribram, 1971; McFarland, 1971). The arrangement of the cerebellar output provides just such a multiple disposition of signals—to the periphery, to the cortex and to the nuclei of the upper brain stem which connect to the basal ganglia (Eccles, Ito & Szentagotha, 1967).

Cerebellar control over muscular contraction is accomplished, much as other central controls, largely through the regulation of receptors. The question has not as yet been investigated as to whether cerebellar output can regulate sensory as well as motor receptors. However the senses are well represented in the cerebellar cortex through input fibers. This representation may well be the immediate origin of signals that simultaneously move a sense organ (e.g., an eye movement) and change the setting of the brain's receiving mechanism for that sense, sufficient to compensate for the movement.

These considerations added to the finding that the basal ganglia are involved in regulating sensory functions make it necessary to view the motor mechanisms of the brain not just as movers of muscles but as central control processes that operate on a variety of other neural mechanisms and even on the senses. Thus what an organism senses is to some considerable extent what he is set to sense, i.e., what he is competent to sense and what he attends. Perceptual competence and attention are therefore akin to motor skills.

Perception as Central Process

We are thus forced to the conclusion that what is usually called a motor skill is a somatomotor skill involving the somatosensory system and that what we ordinarily refer to as perception is a visuomotor, auditory motor or other special sensory motor skill. This view is supported by evidence (Malis, Pribram & Kruger, 1953) of a relatively direct input to the precentral somatomotor cortex from somatic receptors (skin and muscle). Also, in the visual mechanism at least, visuomotor systems abutt the areas receiving retinal input (as is the case in the somatosensorymotor cortex), and these systems have recently been shown to be im-

portant to the perception of constancy: (specifically size constancy; ablation of this cortex produces a monkey who attends retinal image size while ignoring distance cues—Ungerleider, Ganz & Pribram, in press).

A caution is in order here. The view that perception involves a sensory-motor skill does not mean that perception *is* a central motor response essentially devoid of any sensory component—the position taken by Sperry (1952) and Festinger, Burnham, Ono, & Bamber (1967). Rather, neurology and psychophysics (e.g., Gibson, 1966) as well as everyday experience indicates that perceptual skills whether somatic, visual, auditory or other (e.g., gustatory-olfactory) are *sensory* motor performances of a special sort: perceptual acts that encompass reliably repeatable, i.e., invariant, environment-organism relationships. The motor component of these acts is not so much a "response" to input as it is a control (often a readiness) over the sensory input mechanisms.

In humans a further complexity arises. Specialization occurs in the contribution made by each hemisphere of the brain. Auditory-verbal processes dominate the adult left hemisphere (in most right handed persons) and visual spatial processes play the major role in the right (see reviews in Dimond & Beaumont, 1974). The differences between auditory and visual learning and remembering noted above thus become dramatized as differences in hemispheric function—differences between left brain and right brain skills.

The Central Processing of Skills

The mechanism for learning sensory-motor skills has been studied and is well described by the observations of ethologists (see the review by Bateson, 1964) and those engaged in experiments on perceptual learning (e.g., Gibson, 1953). As Bateson points out, the laws of imprinting and those of perceptual learning are not altogether different. And, on careful examination, the laws of simple instrumental or operant conditioning clearly converge on the same processes from the vantage of a response oriented psychology (see for instance Premack, 1965). In each instance an innately determined environment-organism relationship is modified by experience in which consequent occurrences shape and differentiate the innately determined process. Shaping as well as imprinting consists of relatively gross initial modification of the environment-organism relationship which is accomplished rather rapidly (e.g., the imprinting of following a moving object rather than random investigatory sensing; the pressing of a lever rather than random investigatory movement). This initial change is followed by slowly progressive differentiation of the relationship (differentiating the imprinted object so that first any similar and then only it per se elicits the response; pressing the lever only when an S^D is present).

The variables important to shaping appear to be "stimulus novelty" and "response density." The role of stimulus novelty (and therefore of stimulus familiarity or repetitiveness) has been clearly documented for imprinting by Hess (1959) and Bateson (1964). The related concept of response rate or repetition density has been invoked by Premack (1965)

to explain under what conditions any specific innate behavior can serve a reinforcing function to another. E. Roy John has shown (1967) that initially during the shaping process a great number of brain sites (especially in the core of the brain) show electrical activity. As discrimination (perceptual) learning proceeds, the loci involved become markedly restricted. Just what goes on in these more restricted locations is currently under study by James Olds (Olds, Disterhoft, Segal, Kornblith, & Hirsh, 1972). No clear picture of relationship among loci has as yet emerged; perhaps, as we shall see shortly, no simple time dependent cause effect process is involved.

These studies and the more common behavioral analyses suggest that the differences between the processes of learning and memory in different modalities are attributable to differences in their differentiating mechanisms and that commonalities are to be found in those processes responsible for initial imprinting and shaping. This conclusion supports the intuition of those who are concentrating their investigations of neural mechanisms on problems such as habituation to novelty, simple conditioning, and consolidation of the memory trace.

Central Processing in Orienting and its Habituation

In analyzing the mechanisms involved in the simplest form of neural modification resulting from experience, the approach of asking about the contributions of specific brain structures to the limitations and potentialities in central processing has proved rewarding. Decrementing of neural responses occurs in interneurons of all sensory systems when they are subjected to repetitive stimulation (see reviews in Horn and Hinde, 1970). Any change in stimulus elicits more continuous responses in another more medially placed neural system and these two systems converge to produce the typical behavior of habituation and dishabituation (Groves and Thompson, 1970). The medial cells which for a time track or monitor the change in stimulus are located in that part of the central nervous system in which viscero-autonomic neurons originate. Thompson's unit analyses were carried out in the spinal cord but similar dishabituating "arousal and monitoring" behavioral effects are obtained when the core structures of the brain such as the mesencephalic reticular formation and the hypothalamic region are stimulated electrically (see review by Pribram and McGuinness, 1975). Furthermore, the visceroautonomic responses that ordinarily occur during orienting and dishabituation are abolished by resections of certain forebrain structures: the amygdala (Bagshaw, Kimble and Pribram, 1965) and frontal cortex (Kimble, Bagshaw and Pribram, 1965; Luria, Pribram and Homskaya, 1964). There thus appears to be an intimate relationship between the arousal aspect of orienting and dishabituation and the visceroautonomic nervous system.

Another peculiarity was manifest by these resections. While visceroautonomic reactivity to novelty was abolished, behavioral orienting remained intact. Not so, however, with regard to behavioral habituation which was abolished along with the visceroautonomic orienting

hypothalamic

responses. Thus behavioral habituation to novelty—the appreciation of familiarity—seems to depend on the occurrence of visceroautonomic reaction to novelty.

This is not to say that learning and remembering cannot occur in the absence of habituation. The evidence is clear that discrimination learning, the making of selective differential responses to cues, is unimpaired by the brain resections that interfere with habituation (see, e.g., Douglas and Pribram, 1969). Such resections do, however, severely impair the learning and retention of the ability to perform adequately in tasks such as discrimination reversal, delayed alternation and, in some instances (i.e., resection of frontal cortex), delayed response (Pribram, 1973).

The analysis of the neural mechanisms involved in the orienting reaction to novelty and its habituation thus leads to the same points as that obtained from the analysis of the neural mechanisms involved in the development (learning and remembering) of sensory motor skills: two separate mechanisms can be identified. In the case of skill a rapid imprinting-shaping process can be separated from one that is more extended over time and trials and leads to an invariant organism-environment relationship. The imprinting-shaping process appears to be akin to orienting and its habituation, and the brain structures directly involved have little to do with learning and remembering invariances. Instead, defects in orienting and its habituation and the learning and remembering of regularly varying performances such as reversals, alternations and delay tasks are produced by resections of the identical brain structures.

These data lead to the inescapable conclusion that two rather different brain-behavior systems, or rather sets of systems, operate during learning and remembering. One, as we have seen, leads to the processing of invariants. The other is more concerned in processing recurrent variation. In this set of systems, for learning (i.e., habituation) to occur, changes must be of sufficient regularity to be computable. When recurrence results in a residue of the computation, the residue provides the context in which further experience can be processed, and any subsequent recurrence is treated as "familiar", thus precluding orienting. Visceroautonomic reactivity appears to be integral to such computations (Pribram, 1971).

Two Modes of Central Processing in Man

A well designed series of experiments has been performed that aimed at relating diverse sets of data on the limitations of central processing. Usually these data are considered in experiments on selective attention, sensory search, and memory scanning in studies of human learning and remembering. The results provide additional insight into the difference between the two sets of systems we have been delineating and the psychological processes which they control (Schneider, 1975). The experiments did not involve manipulation of brain structures; however, in contrast to most studies on cognitive behavior on man which use verbal or pseudoverbal material, these experimental procedures resembled those that characterized the non-human primate psychosurgical research that

gave rise to the distinction between the two types of learning and memory processes (see below and review by Pribram, 1969). The human work centers on a display framing a variable number and types of patterns— e.g., numerals, letters or geometric forms. A variable number of such frames can be presented to a subject after which a single presentation is made containing one or more of the patterns (numbers, letter or geometrical forms) that have previously appeared—or alternatively, patterns that have not appeared. The specific experiments consisted of embedding the to-be-remembered patterns in frames containing similar types ("same-distractors") or different types of patterns ("different-distractors"). Thus the numerals 7 and 2 might be embedded in frames ⟍ and ⟋ in the same distractor condition, while they would appear in frames ⟍ and ⟋ in the different distractor condition. Frame size (i.e., number of patterns per frame) and number of frames in the to be remembered (memory) set could be varied at will on each episode (trial sequence).

Using this technique, clearcut differences between the same and different distractor were obtained in the effects of varying frame size and size of the memory set on the number of correct responses and on response latency. To simplify a large number of results in a variety of conditions: in the different-distractor condition, response appeared to be automatic in that latency was short and varied little with episode (frame and memory set size). However, many errors were made originally when frame amd memory set size were large and these droppped out only gradually with practice. By contrast, when same-distractors were used latency of response varied (linearly) according to episode (frame and memory set size) indicating that processing demanded active search specific to the episode. Practice had little effect—however, subjects could eliminate or attenuate the influence of same-distractors when properly instructed or when they themselves adopted an appropriate response strategy (e.g., exhaustive vs self-terminating, i.e., speedy, scanning). In the same-distractor, episode sensitive, condition, the position of the distractor proved to be an important variable: when self-terminating scans were adopted they often eliminated certain positions from scan thus leading to error; when scanning was exhaustive, the positions of the distractors had a sizeable influence on reaction time. No such position effects were obtained in the different-distractor conditions in which processing was automatic.

As noted, these experiments are similar to many that have been performed on non-human primates. In the animal experiments, however, brain resections were carried out so that the two modes of processing were related to specific brain systems. The results show the posterior convexity of the brain to be involved in the automatic type of processing which in earlier reviews (Pribram and Melges, 1969) was called "participatory", and the frontolimbic forebrain in the episodic type (previously called preparatory).

Episodic and Automatic Central Processing

Terminology always poses difficult problems. In this instance "episodic" and "automatic" were chosen to describe the two central processes because they best connote the body of evidence that is covered. The term "episodic" is Tulving's (1972; Tulving and Gold, 1968) and is based on his data that indicate that a memory process specific to incidents or episodes can be distinguished from that which organizes the long term memory store. This specificity to situation is what Chomsky (1963), Quillian (1967) and Pribram (1971) have called context specificity and context sensitivity to distinguish it from the context-free processes that handle invariant relationships.

Shriffin and Schneider call the context dependent, episodic memory processes "controlled" because memory search is found to be self paced in their same-distractor situations. Their term "automatic" refers to the context free processing of invariants which proceeds according to the properties of the situation rather than those imposed by the organism. It is adopted here because it emphasizes the automatic nature of the process for which the term "search", which Shriffin and Schneider use, is really inappropriate (see Pribram, 1971, Chapter 17).

Kinshela (personal communication) has also emphasized the automatic nature of the processing of invariants. He has developed and tested a mathematical model which shows that the selection of invariants proceeds automatically from considerations of the amount of "noise" and the structural redundancy in the situation. Garner (1962) has specified the tradeoff between external redundancy (how many features or dimensions of a situation specify a difference) and the internal redundancy (how much differentiation has the organism already achieved). Kinshela's model does not distinguish between external and internal redundancy but Wilson (1968) and Pribram and McGuinness (1975) have formulated a model of channel competence based on an information theoretic approach to psychosurgical data which takes this relationship into account.

The issue concerns the theme of this chapter: the way in which the limitations and potentialities of central processing can be understood. Much of the work in human cognitive experimental psychology and especially that addressed to attention, deals with the problem in terms of limitations on channel capacity. The psychosurgical data reviewed in the first section show, however, that there is actually a fantastic excess of channel capacity in the brain—lesions hardly affect capacity even when they involve 80-90% of the channel.

Thus, the limits on processing must stem from some other property of the channel than its capacity. This property has been shown (Pribram & Tubbs, 1967) to be the structure of the redundancy of the process. An analogy helps to point out the difference between a capacity and a competency concept: limits on capacity can be conceived to be similar to an exoskeleton, whereas processing limitations due to an inadequate structure of redundancy are more akin to an endoskeleton. Endoskeleta have the advantage that they can be flexibly "restructured" when the situation demands. Restructuring becomes a cognitive skill (Pribram, 1971).

Thus, rather than depending on limitations of capacity, central processing appears to partake of a skill—a competency. A strict definition of channel competence is given in information theoretic terms by the statement that competence is the reciprocal of equivocation where equivocation is the sum of noise and redundancy (Pribram & McGuinness, 1975). This definition of competency is identical to the mathematical derivation used by Kinshela.

To summarize, human experimental approaches to cognitive processing and those that have come from the study of the effects of selective brain resections on cognitive behavior have demonstrated the existence of two distinct central processing mechanisms. One deals with specific episodes, is therefore context (i.e., situation) dependent and necessitates a considerable amount of centrally controlled computing of the regularities (recurring variables) that describe the situation. The other processes invariances in the relationships between the organism and the situation and thus processing proceeds relatively automatically with repetition.

Particular Brain Mechanisms Involved in Central Processing

We have therefore once again, and by still another set of experimental data, arrived at the distinction between two clearly different types or modes of processing important to learning and remembering. One process is demonstrated to be involved in shaping, in orienting and its habituation, and in active control over specific episodes in experiments on sensory search, attention and memory. This process is drastically interferred with by lesions in the frontolimbic part of the forebrain. The second process is demonstrated to be involved in practice and in the attainment of sensory-motor skills and is shown by experiments on sensory search, attention and memory to be automatic. This process is drastically impaired by resections of the posterior convexity of the cerebral cortex.

Much more can be stated about the relationship between brain and these two behavioral processes. As noted earlier, the automatic process is sensory specific and may be different in the way it is structured in different sensory modes. Such differences have as yet not been systematically investigated. However, semantic processing has been shown to be a simultaneous parallel process involving the long term memory store (see reviews by Neisser, 1967; Pribram, 1971; Schneider, 1975). It was also noted earlier that the studies of Roy John (1967) and James Olds (Olds, Disterhoft, Segal, Kornblith and Hirsh, 1972) have failed to yield any clear cut sequential, i.e., time dependent cause effect order in the appearance of critical electrical events during such semantic processing. Rather many such events occur simultaneously in a variety of structures and behavioral response appears to result from a correlation among these events (see also Pribram, Day and Johnston, 1977).

A good deal is also known about the relationship between brain systems and episodic processing. Different systems of the frontolimbic forebrain have different functions in the overall determination of episodic control. As noted, resections of frontal cortex and amygdala

result in impaired viscaroautonomic responses during orienting and a subsequent failure of behavioral habituation to occur. Orienting and habituation are not per se controlled processes—in fact the orienting reaction is often referred to as the orienting reflex. However, orienting does serve as a signal that interrupts ongoing brain-behavior activities— i.e., it signals novelty, a distractor. If the distracting event is repeated, habituation results unless it is overridden by some other mechanism. According to the data presented here two types of override appear to occur. One type sorts events into differential categories and by practice develops differential sensory motor skills to cope with the differences. The other overcomes habituation by "effort"—i.e., by coordinating the tendency to return to prior semantic processing with the tendency to continue to orient.

Again, considerably more can be stated regarding the neural structures involved in making such coordinations. Semantic processing has been shown to involve the connections from the cortex of the posterior convexity to the basal ganglia of the forebrain, systems on which sensory motor readiness depends (Pribram, in press). As already reviewed, the tendency to orient is a function of a fronto-limbic forebrain (and hypothalamic) system. The functions of the readiness and orienting systems are coordinated by a third, the hippocampal system. Evidence for such coordination and the effort involved has been reviewed in detail elsewhere (Pribram, 1971; Pribram and McGuinness, 1975; Pribram and Isaacson, 1976; Pribram, in press).

Overcoming the Limits on Central Processing

A further suggestion has been tendered in the form of a model (Pribram and Isaacson, 1976). The functions of the hippocampal system are conceived to be similar to those of the cerebellum (histological parallels abound) in that both are critical to the development of feed-forward, open-loop (helical) brain and behavior processes (see Pribram, 1971; McFarland, 1971). In the case of the cerebellum this is suggested to be accomplished by computing, in fast time (as opposed to real time), a correlation between feedback controlled spinal and brain stem sensorymotor reflexes on the one hand and similarly feedback controlled basal ganglia readinesses. In the case of the hippocampal system, as we have seen, the coordination occurs (also in fast time) between feedback controlled fronto-amygdala-hypothalamic orienting reflexes and the basla ganglia readiness mechanism. Feedforward is conceived to result when two sequentially operating feedbacks can serve to bias the other (Pribram, 1971; Pribram and Gill, 1976). Feedforward is proposed to account for the success of biofeedback procedures that introduce a second external feedback which becomes coordinated with the internal, thus providing as it were a "prosthesis" that enhances the ordinary limitations of the effort mechanism.

These limitations have been dealt with experimentally as limitations of short term memory or alternately of attention span. The purpose of the studies on humans briefly reviewed earlier (Schneider, 1975) was to

show that the results of experiments on sensory search, on attention, and on memory scan could be accounted for by a single theoretical formulation. The success of the endeavor suggests that we can conceptualize the limitations on central processing in a unitary fashion and the neurological data noted above support the formulation (see also Pribram, 1974).

A practical consequence emerges from this analysis. Central processing limitations exist ubiquously, whether because of inadequate encoding of earlier experience, brain injury or inadequate heredity (which all of us sense to some extent in the highly complex society only a combination of brains could have constructed). Thus sensorymotor prostheses based on the episodic-automatic distinction delineated for brain function can become useful engineering and educational instruments for therapy and for growth.

In conclusion, experimental psychosurgical studies of the integrative physiology of the brain, when coupled with neurophysiological data and results of human cognitive work on learning and remembering, are providing broad but specific generalizations applicable to man. This essay has delineated some of these: the distributed store, sensory specificity in central processing, motor functions as central controls over input, and the distinction between episodic and automatic processing. The yield is rich and shows practical as well as theoretical promise.

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