

1969  
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Reprinted from: THE FUTURE OF THE BRAIN SCIENCES  
(Plenum Press, 1969)

## THE PHYSIOLOGY OF REMEMBERING

Karl H. Pribram

To those of us working at the brain-behavior interface, and I am tempted to say to the scientific community as a whole, the overriding issue is the one posed by Descartes at the beginning of the Age of Reason. Are mind and body to be conceived separately and thus studied by irreconcilably independent methods, or, can we come to understand and overcome the implied dualism of the Nature of Man? This issue is not an ethereal one--it is of practical importance in the everyday course of man's existence. We have seen that all the pills in the world and the life-saving devices of medicine go for naught if the minds of men do not keep pace with the technical developments they can devise.

But my prediction is an optimistic one: By the end of the twentieth century a fresh wind will have swept away the remaining cobwebs that continue today to divide the creative community.

Humanists and scientists will soon recognize that despite the now obvious differences, their

methods as well as their aims display remarkable similarities. The technique of the journalist in making notes on the human scene is not altogether different from that of the ethologist observing the animal community, or of the pharmacologist charting the effects of a drug on the nervous system or on behavior. The re-enactment performed by the novelist is not that foreign in approach to the re-enactment of the computer scientist simulating behavioral processes or for that matter, to the in vitro re-enactment of life processes by the biochemist. Observation, analysis, reconstruction, test to meet an esthetic<sup>2</sup> criterion--these are the procedures used by creative men whether they be humanists or scientists because this is the way their brains work.

It is therefore to an understanding of man's brain--the organ that regulates human affairs--that we must look for this new view of man. And the brain sciences at the present rate of progress are not going to disappoint us. Already enough is known which was not known only a quarter of a century ago to mark clearly the outlines of the new view.

Let me take as my focus the study of memory as so many others have done at this conference. Undoubtedly one of the prime functions of brain is to allow us to re-experience and act on past and therefore future events. Yet only two decades ago the foremost research scientist in the brain-behavior field was able to state that what we then knew about the brain made it inconceivable that either animals or man could learn at all.

The winds of change began to blow less than ten years ago. I predicted then that the 1960's would be a decade of decision for the study of memory (22). And so it has turned out--old techniques have been revived, refined and applied with new

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<sup>2</sup>The esthetic criteria for "pure" science are truth, evidence and elegance; those for the "purer" arts are coherence, plausibility and impact. So differences there are, of course, but the human endeavor is not always pure nor need it be.

vigor; new methods, especially those of information processing have been developed and focussed on the problem. Behavioral scientists have made especial progress in the analysis of verbal memory which has led to a beginning in an understanding of the processes of recognition and recall (11, 17). Biological scientists have, for the most part, addressed themselves, and successfully, to the issue of storage. Thus a major area of investigating memory has devolved on showing that biochemical and histological changes can come about in brain tissue as a function of experience; on showing how long such changes last; and, by imaginative use of the phenomenon of retrograde amnesia, how rapidly or slowly storage occurs (16)

But I want now to turn to another equally fascinating area, one explored in my own research--the question of what sorts of organizations of memory processes must exist in the brain to allow remembering to take place.

I use the word remembering advisedly because it gives a clue to what I consider to be the central issue in this area of research: literally, remembering or recollecting refers to the assembling of dismembered mnemonic events. I propose, therefore, first to give the evidence for believing that mnemonic events are distributed in the brain and then to describe experiments which tell us something about the way in which memory becomes usefully organized.

#### A Neural "Image"--The Spatial Distribution of Input Information

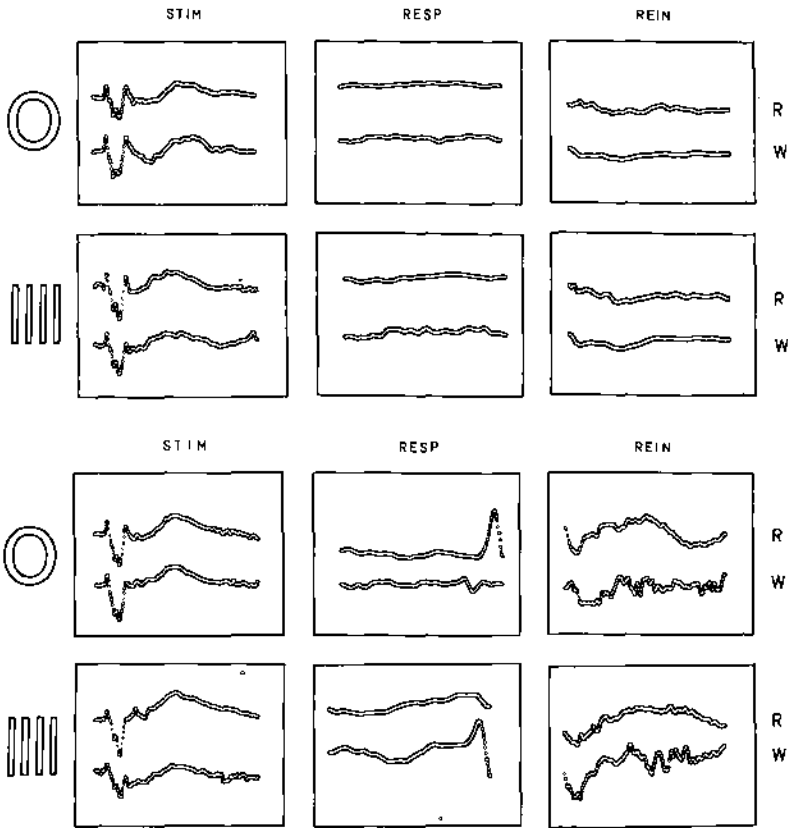
A recurrent puzzle in the study of brain has been the fact that a large portion of the input systems can be destroyed without impairing the organism's ability to make responses to highly organized patterned aspects of its environment. This observation is made daily in the neurological clinic and in the laboratory has been demonstrated in a variety of ways. Thus Lashley removed 80-90% of the striate cortex of rats without impairing

their ability to discriminate patterns (14). Galambos has cut up to 98% of the optic tracts of cats and these animals could still perform skillfully on tests necessitating the differentiation of highly similar figures (18). Not only removals but a variety of other methods for disturbing the presumed organization of the input systems have been tried to no avail: Sperry surgically cross-hatched a sensory receiving area and even placed mica strips into the brain troughs produced in order to electrically insulate small squares of tissue from one another (28). Lashley, Chow and Semmes tried to short-circuit the electrical activity of the brain by placing strips of gold foil over the receiving areas (15). And I have produced multiple punctate foci of epileptiform discharge within a receiving area of the cortex by injecting minute amounts of aluminum hydroxide cream (13). Such multiple foci, although they markedly retarded the learning of a pattern discrimination, do not interfere with its execution once it has been learned (whether learning occurred before or after the multiple lesions are made).

These experiments have been interpreted to show that each sensory system functions with a good deal of reserve. Since it seems to make little

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Fig. 1. Averaged recordings of electrical activity obtained from the occipital cortex of monkeys performing a differential discrimination: circle as opposed to vertical stripes. A standard 500 msec of activity is represented in each trace; the amplitude represented is variable, however, and depends on how many signals were averaged in order to make the record; for example, many more signals were obtained when the monkey made a correct response than when he made an error during criterion performance. The records under STIM are the wave forms evoked by a display lasting 1 msec; the records under RESP were generated just prior to the response;



the records under REIN were generated after the response and during the period when reinforcing events occurred. The upper six panels were made from records obtained while the monkey was performing at chance; the lower six panels were made from records obtained after the monkey attained an 85 percent criterion (200 consecutive trials). The records in line with R were made when the monkey performed correctly; those in line with W were made when the monkey was wrong. The waves generated just prior to response (the intention waves) are similar whenever the monkey is about to press the right half of the panel, regardless of whether this is for the circle or vertical stripes, and regardless of whether this response proves to be correct or wrong.

difference to performance which part of the system is destroyed, the suggestion has been offered that this reserve is distributed in the system--that the stored information necessary to making the discrimination is paralleled, reduplicated over many locations. This interpretation suggests that the epileptic foci produced by aluminum hydroxide cream implantations interfere in some fashion with this reduplication of information storage.

The correctness of this view has now been put to direct test. Over the past few years Spinelli and I have shown that, in fact, electrical activity recorded from widely distributed points in the visual cortex of monkeys shows differential patterns to different stimuli and further that other widely distributed points within the system show evidence of storage of response linked information (26). Let me describe the experiment more fully.

Records were made of the electrical activity occurring in the monkey's brain while he was solving this problem. From the wave form of these records we could distinguish whether the monkey saw the circle or the vertical stripes; whether he made the correct response or an error; and whether he intended to press the right or the left half of the panel once he knew the problem. All of these differential electrical responses occurred in the visual cortex (that part of the brain which also receives the visual input) though different electrodes recorded different events. Apparently experience and current input converge in the input system (Figure 1).

Thus there is now, in addition to indirect, some direct evidence that signals become distributed within the input systems.<sup>3</sup> Further, this evidence

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<sup>3</sup>The data presented describe the spatial distribution of input events. There is good reason to believe that these events become temporally distributed as well. Evidence to this effect is also beginning to accumulate (1).

shows that even within the input systems these signals reflect not only the occurrence of sensory events but also provide response linked information: the intention to press one or another panel and the outcome of this action.

What this amounts to is the production of a neural representation initiated by the patterns which excite the receptor--i.e. a neural "image" triggered by an external world. This internal representation is, however, not a direct replica, or as the cognitive psychologists are wont to call it, an "iconic image".

Even the initiating events are expressions of relationships which obtain between the effects of excitation at one receptor point with that of its neighbors. These relationships can be described mathematically as convolutions. Thus, for instance, the shape of the visual receptive field of a retinal ganglion cell represents the convolution of a derivative of the shape of the retinal image produced at that point (27). Mathematical expressions of the type involved in these transformations are called holographic because they are used to make holograms, photographs of the interference patterns produced when coherent light is split to form a reference and a beam reflected from the object to be imaged. By analogy, the neural image is likely to be holographic in nature.

The question remains as to how interference effects can be produced in the brain. Synaptic events consequent on the arrival of nerve impulses form wave fronts (9). Such arrival patterns can interact with others and with wave forms produced by the spontaneous potential changes which occur in neural tissue. Immediate cross correlations result and these can be the occasion for the generation of new spatial and temporal patterns of nerve impulses. The assumption made here is that the totality of this process can be conceived as a neural "hologram", an "image" which is perceived.

Much work needs to be done to establish the

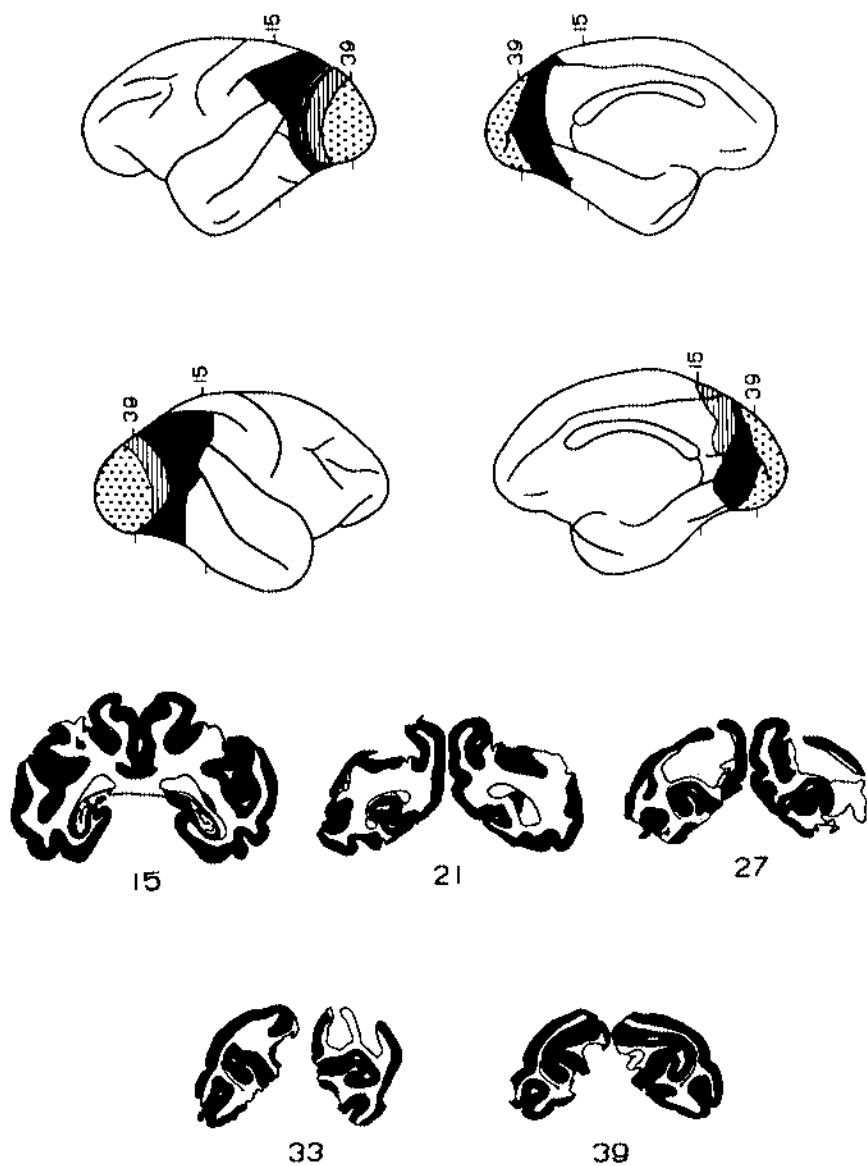


Fig. 2. Disconnection of striate and infratemporal cortex by extensive prestriate ablation.



limits over which this view holds. Do the mathematical expressions which interpret the shape of visual receptive fields at the ganglion cell layer of the retina give equally useful interpretations at more central stations in the visual system? What sort of neural reference mechanism corresponds to the coherent source in the hologram--is it anatomical or is there a physiological spatial or temporal rhythm of neural firing which serves this function? How is the effect of the holographic cross correlation stored? By a tuning of cell-assemblies or by a change in protein conformation, by both or some as-yet-undisclosed possibility? These questions can be posed in the laboratory with techniques available today. Were there no other reason, this alone would make the model of a neural holographic process an exciting one to pursue.

#### The Primate Sensory Specific Intrinsic Cortex

This evidence for distribution of mnemonic patterns demands of remembering some sort of organizing process. Experimental data have accumulated which make it likely that this process involves the functions of the so-called association cortex of primates. These regions of the brain are not to be confused with the polysensory association cortex which immediately surrounds the projection areas which has been studied so extensively by electrophysiologists in cats. Rather the primate areas in question are located within the parieto-temporal preoccipital convexity, somewhat remote from the projection terminals. Further, they are sensory specific. Sensory specificity was established by making lesions of various sizes in various locations and testing the ability to learn and to retain discriminations in various modalities (20, 23).

These studies showed the parieto-occipital area to be concerned in somesthetic choices (19, 33); the anterior temporal cortex to have something to do with taste (2, 24); the middle temporal region to be involved in auditory discrimina-

tions (8, 32); and the inferior temporal convolution important to vision (3, 6). By now these findings have been well established by a series of experiments involving over 950 monkeys.

The initial problem posed by these results can be stated as follows: Why can't, e.g. inferotemporally lesioned monkeys remember a + vs - or a 0 vs 1111 after surgery, when they do 90% or better before? This problem becomes compounded in the light of anatomical and physiological evidence that e.g. the inferotemporal cortex is afferently connected with the visual system only indirectly-- and that its function is not dependent on this input from the primary visual system.

For instance, removals of prestriate cortex which totally circumsect the primary visual cortex leave monkeys still able to perform visual discriminations at the 85% level when tested for the first time postoperatively (Figure 2).

What errors are made are within a field deficit produced by invasion of optic radiations as shown by subsequent histological analysis. Further, there is no effect on discrimination from cross-hatching the inferior temporal convolution, whereas undercutting this cortex produces a marked effect (25).

#### How the Brain Controls Its Input

To explain findings such as these I suggested some years ago the possibility that the inferotemporal cortex works through efferents to control--organize--the input within the primary visual system. This possibility was entertained on the basis of neurobehavioral evidence (21) which showed that this cortex functioned to allow a rich sampling of the visual world to occur and these data have since been supplemented by further experiment (4,5).

Obtaining direct physiological evidence that this efferent control actually takes place has occupied my colleagues and me for the past years.

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Fig. 3. Effects of stimulation of the posterior "association" cortex of a cat on a visual receptive field recorded from a neural unit in the optic tract. (These records are made by moving a spot with an X-Y plotter controlled by a small general purpose computer--PDP-8--which also records the number of impulses emitted by the unit at every location of the spot. The record shown is a section parallel to and 2 SD above the background firing level of the unit. Note the dramatic change in the configuration of the receptive field, especially after stimulation of the posterior "association" cortex--IT, inferotemporal.)

The following results have been obtained:

1. Changes in shape of and size of visual receptive fields of units in optic nerve can be produced by electrical stimulation of the infero-temporal cortex. Thus there is evidence that an effect can be registered as far peripheral as the retina (Figure 3).

2. Other evidence of the existence of efferent control as far peripheral as the retina has been obtained (29, 30, 31).

3. Changes are produced by electrical stimulation of the inferotemporal cortex in recovery functions of visually evoked responses. (Figures 4, 5).

Finally, the pathways over which this efferent control is exerted are being delineated. One outflow is to the superior colliculus. Another, much to our surprise, is a sizeable one to the putamen, one of the basal ganglia. Less dramatic are connections to the anterior commissure; to the n. medialis dorsalis and pulvinar of the thalamus; to the pons; and to other parts of the temporal lobe.

#### Receptor Control by Central Motor Structures

The meaning for behavior of these results can be best illustrated by the effect of infero-temporal lesions on the recording of stimulus, intention and reinforcement waves recorded from the visual cortex, as described in the first experiment discussed.

I fully expected that an inferior temporal lesion would selectively affect one of these wave forms only, leaving the others unchanged. Thus, we would have been able to say whether stimulus differentiation or some response-linked process were primarily involved. This did not happen. Instead, those electrodes from which we had obtained the best differential recordings now show-

ed no such differences and other electrodes which had been relatively unimpressive showed some reliable differences. However, these differences were now mostly response-linked in a peculiar fashion which we have not as yet been able to decipher clearly. It seemed as if the whole "frame of reference" within which the brain activity had been working prior to the lesion was now shifted--and, in fact, shifting from time-to-time. Behaviorally, the monkeys appeared as surprised as we by the effects of the surgery: they went into the task situation fully confident of their ability, only to find that they made errors. This resulted in spurts of performance, hesitations, and much trial and error to test out what had been changed in the situation. It seemed as if they were completely baffled for a while--not realizing, of course, as we did, that it was the insides of their heads, their brains, we had altered and not the situation.

The inferior temporal visual "association" cortex (and as already noted, parallel findings are available in the auditory system) thus seems to work via structures to which motor functions have usually been attributed. But recently, it has become evident that even these very motor functions are largely controlled via efferents to their receptors--the gamma fibers to the muscle spindles. By changing the bias on the spindle, movement is induced. So perhaps it is not too surprising if structures such as the corpora quadrigemina (colliculi) and the basal ganglia should be shown to work via changes they effect in biasing input.

In summary, I have presented evidence that information becomes distributed in the sensory projection systems and that the functions of the so-called posterior association areas of the primate are to organize input so as to make it memorable. This organizing process does not appear to occur within these "association" areas per se, however. Rather, their effect is exercised downstream via structures heretofore labelled as mo-

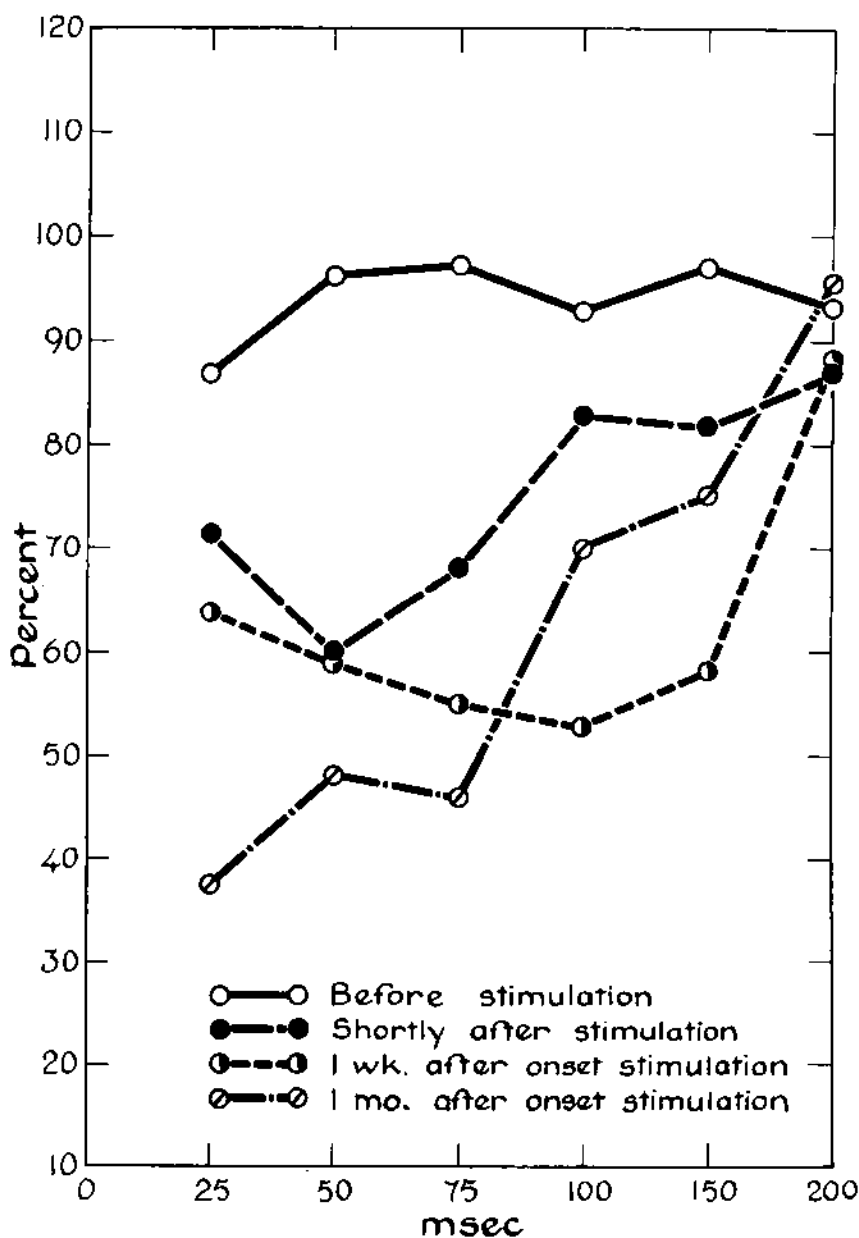


Fig. 4. A plot of the recovery functions obtained in one monkey before and during chronic stimulation of the inferotemporal (IT) cortex.

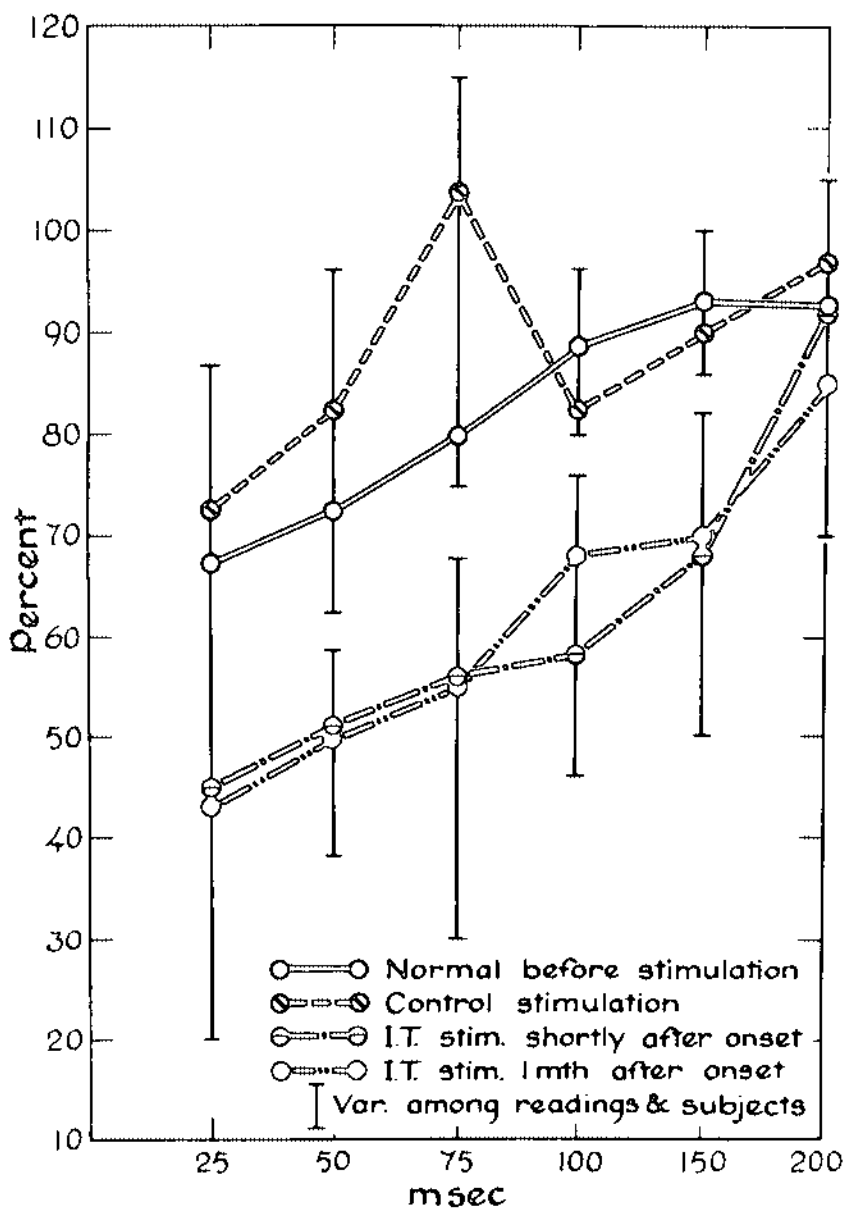


Fig. 5. A plot of the recovery functions obtained in 5 monkeys before and during chronic cortical stimulation.

tor in function. In view of the fact that such control over movement is now recognized to be largely due to regulation of muscle receptors, it is perhaps not altogether unlikely that other receptor mechanisms such as the auditory and visual are also controlled via these "motor" pathways.

### CONCLUSIONS

This unforeseen result is, of course, compatible with the behavioral evidence for the importance of motor function in perception and recognition such as that of Ivo Kohler (12) and of Richard Held (10).

Thus the beginnings have been made--at least in specifying the structures involved in the organization of memory functions in the brain. Next we need to find out how these structures produce the psychological processes we call remembering. What is already clear, and this is important, is that changes in patterns of organization--coding--are as important to the process of effective remembering as is storage per se. Let me illustrate this with a homely example:

First, what is a code? Not so long ago my laboratory came into the proud possession of a computer. Very quickly we learned the fun of communicating with this mechanical mentor. Our first encounter involved twelve rather mysterious switches which had to be set in a sequence of patterns, each pattern to be deposited in the computer memory before resetting the switches. Twenty such instructions or patterns constituted what is called the "bootstrap" program. After this had been entered we could talk to the computer--and it to us--via an attached teletype.

Bootstrapping is not necessarily an occasional occurrence. Whenever a fairly serious mistake is made--and mistakes were made often at the beginning--the computer's memory is disrupted and we must start anew by bootstrapping.



Imagine setting a dozen switches twenty times and repeating the process from the beginning every time an error is committed.

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U U D D U U U D U D U D
U U U U U U U U U D D D
U U U U D U D U D U U U
U U D D U U U U U U U U
U U D D U U U D U U D D
D D U D D D U D D U U U
U D U D D U D U U D U D
U D U D U U U U U U D U
D U D D U U U U U U U U
D U U U U U U U D D U U

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And so on.

Imagine our annoyance when the bootstrap didn't work because perhaps on setting the 19th instruction an error was made in setting the eighth switch. Obviously, this was no way to proceed.

Computer programmers had early faced this problem and solved it simply. Conceptually, the twelve switches were divided into four triads and each combination of up down within each triad given an Arabic numeral. Thus

D D D became 0

D D U became 1

D U D became 2

D U U became 3

U D D became 4

U D U became 5

U U D became 6

U U U became 7

Conceptually, switching the first toggle on the right becomes a one, the next left becomes a 2, the next after this a 4 (and the next an 8 if more than a triad of switches had been necessary, i.e. if for instance our computer had come with sixteen switches we should have conceptually divided the array into quads). Thus the bootstrapping program now consisted of a sequence of twenty patterns of four Arabic numerals:

e.g. 3 7 2 2

0 0 1 4

3 4 5 6

2 2 1 5

1 0 3 7

etc.

and we were surprised at how quickly those who bootstrapped repeatedly, actually came to know the program by heart. Certainly fewer errors were made in depositing the necessary configurations--the entire process was speeded and became, in most cases, rapidly routine and habitual.

Once the computer is bootstrapped it can be talked to in simple alphabetical terms: e.g. JMP for jump, CLA for clear the accumulator, TAD for add, etc. But each of these mnemonic symbols merely stands for a configuration of switches. In fact, in the computer handbook the arrangement for each mnemonic is given in Arabic notation: e.g. CLA = 7200. This in turn, is easily trans-

lated into U U U D U D D D D D D D D D should we be forced to set the switches by hand because the teletype has gone out of commission.

Programming thus is found to be in the first instance the art of devising codes, codes that facilitate learning, remembering and reasoning. The logic of a computer is primarily a code, a set of signals or signs which allows ready manipulation. The power of a program lies in the fact that it is a useful code. If you doubt this, try next month to check your bank statement against your record of expenditures and do it all using Roman rather than Arabic numerals. Can you imagine working out our national budget in the Roman system?

Coding and recoding are thus found to be essential operations of the brain. Recoding maintains some sort of representational identity<sup>4</sup> among event structures much as such identity obtains between the sequences of openings and closings of switches in a computer and the programs which provide these openings and closings. Codes are languages, however, and various languages have greater or lesser powers and efficiency of control. The evidence I have presented suggests that one of the principal functions of the brain is to construct languages although these languages have, by contrast with those used in computer science, built into them a good deal of ambiguity. From this ambiguity, of course, stem the opportunities for construction of creative novelties. If indeed it turns out that such languages are at least in part hierarchically related as there is good reason to suspect, we would be a long way toward understanding in depth the mind-brain issue. For it is through action that these brain codes become externalized representations, e.g. as culture. Thus, it is turning out

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<sup>4</sup>And hereby hangs the crucial problem: just how isomorphic is this identity and by what means is it achieved when isomorphism does not hold?

to be our understanding of coding, the language of the brain, through which unity is affected in the nature of man.

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