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THE PHYSIOLOGY OF REMEMBERING

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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 novel-
ist is not that foreign in approach to the re-enact-
ment of the computer scientist simulating behavioral
processes or for that matter, to the in vitro re-en-
actment of life processes by the biochemist. Obser-
vation, analysis, reconstruction, test to meet an
esthetic[2] criterion--these are the procedures used
by creative men whether they be humanists or scien-
tists 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. Un-
doubtedly one of the prime functions of brain is to
allow us to re-experience and act on past and there-
fore 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 mem-
ory (22). And so it has turned out--old techniques
have been revived, refined and applied with new

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[2]The esthetic criteria for "pure" science are truth,
evidence and elegance; those for the "purer" arts
are coherence, plausibility and impact. So differ-
ences 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 mnemic events. I propose, therefore, first to give the evidence for believing that mnemic 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). Gal-
ambos 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 or-
der to electrically insulate small squares of tis-
sue 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 inter-
fere with its execution once it has been learned
(whether learning occurred before or after the mul-
tiple 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

Fig. 1. Averaged recordings of electrical activity
obtained from the occipital cortex of monkeys per-
forming a differential discrimination: circle as
opposed to vertical stripes. A standard 500 msec
of activity is represented in each trace; the ampli-
tude 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 perform-
ance. The records under STIM are the wave forms
evoked by a display lasting 1 msec; the records un-
der RESP were generated just prior to the response;
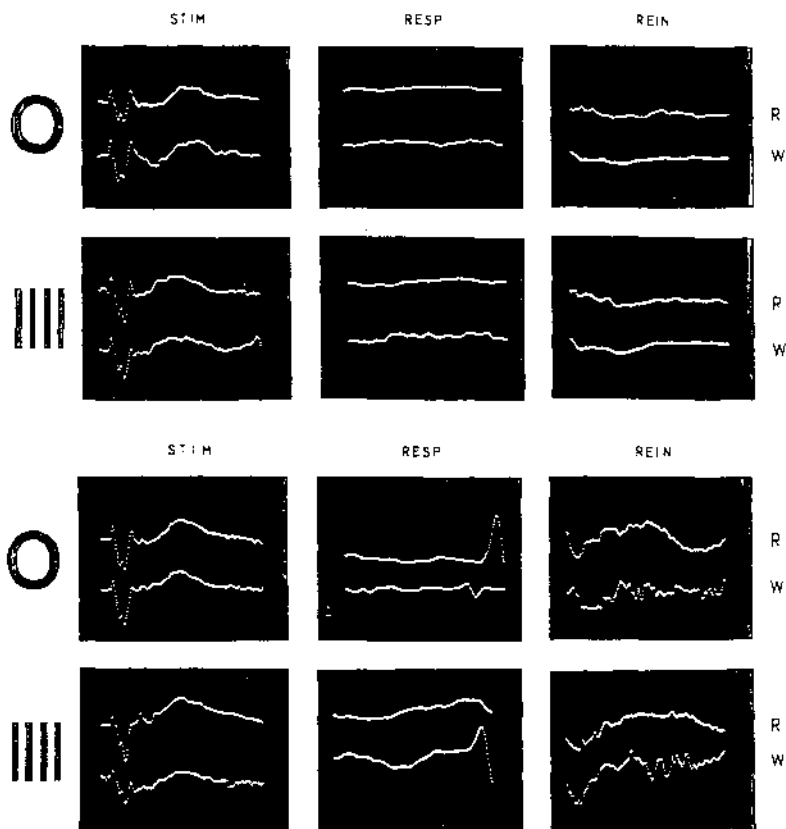
the records under REIN were generated after the re-
sponse and during the period when reinforcing events
occurred.   The upper six panels were made from re-
cords obtained while the monkey was performing at
chance; the lower six panels were made from records
obtained after the monkey attained an 85 percent
criterion (200 consecutive trials).   The records in
line with R were made when the monkey performed cor-
rectly; those in line with W were made when the mon-
key 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 dis-
crimination 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 pat-
terns 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 solv-
ing this problem. From the wave form of these re-
cords 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 dif-
ferential electrical responses occurred in the vis-
ual cortex (that part of the brain which also re-
ceives the visual input) though different elec-
trodes recorded different events. Apparently ex-
perience 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.[3] Further, this evidence

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[3]The data presented describe the spatial distribu-
tion of input events. There is good reason to
believe that these events become temporally dis-
tributed as well. Evidence to this effect is also
beginning to accumulate (1).

shows that even within the input systems these sig-
nals reflect not only the occurrence of sensory
events but also provide response linked informa-
tion: 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 re-
presentation 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 re-
inal ganglion cell represents the convolution of a
derivative of the shape of the retinal image pro-
duced at that point (27). Mathematical express-
ions 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 gen-
eration 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.

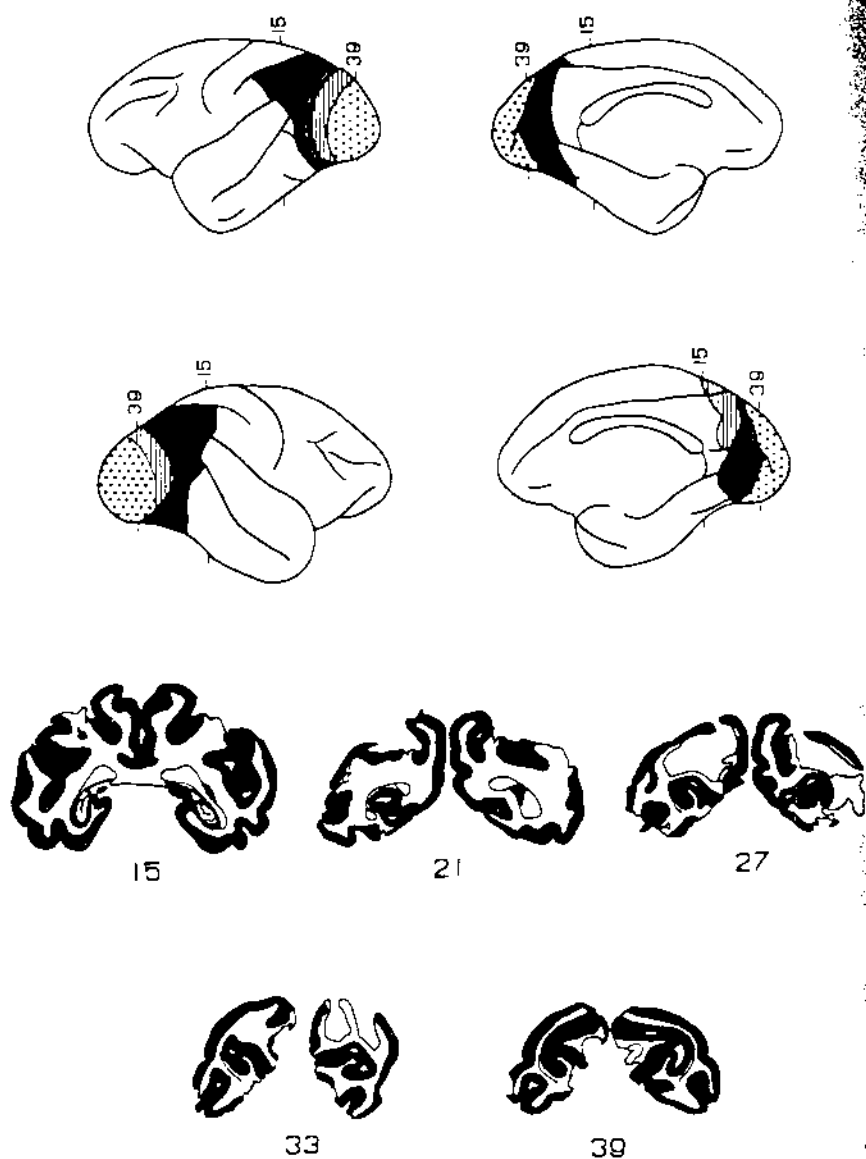Much work needs to be done to establish the

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

limits over which this view holds. Do the mathe-
matical expressions which interpret the shape of
visual receptive fields at the ganglion cell lay-
er of the retina give equally useful interpreta-
tions at more central stations in the visual sys-
tem? What sort of neural reference mechanism
corresponds to the coherent source in the holo-
gram--is it anatomical or is there a physiologi-
cal 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 pro-
tein conformation, by both or some as-yet-undis-
closed 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 ex-
citing one to pursue.

The Primate Sensory Specific Intrinsic Cortex

This evidence for distribution of mnemic pat-
terns demands of remembering some sort of organiz-
ing 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 estab-
lished by making lesions of various sizes in vari-
ous 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 some-
thing to do with taste (2, 24); the middle tempo-
ral region to be involved in auditory discrimina-

tions (8, 32); and the inferior temporal convolu-
tion 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. infero-
temporally lesioned monkeys remember a + vs - or a
0 vs 1111 after surgery, when they do 90% or bet-
ter 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 in-
put from the primary visual system.

For instance, removals of prestriate cortex
which totally circumsect the primary visual cor-
tex 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 defi-
cit produced by invasion of optic radiations as
shown by subsequent histological analysis. Fur-
ther, 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 inferotem-
poral cortex works through efferents to control--
organize--the input within the primary visual sys-
tem. This possibility was entertained on the ba-
sis 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 oc-
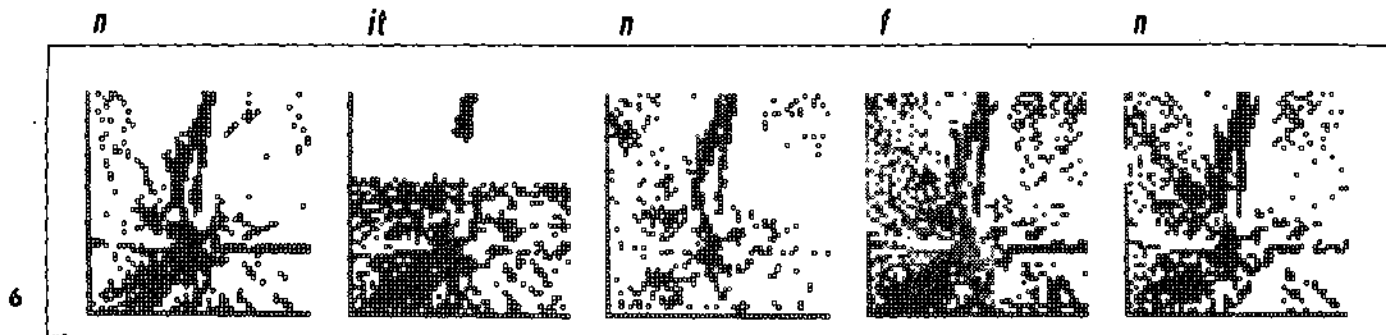cupied my colleagues and me for the past years.

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 com-
puter--PDP-8--which also records the number of impul-
ses 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 recep-
tive field, especially after stimulation of the poster-
ior "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 ef-
ferent control as far peripheral as the retina
has been obtained (29, 30, 31).

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

Finally, the pathways over which this effer-
ent 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 commisure; 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 ex-
periment 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 ob-
tained the best differential recordings now show-

ed no such differences and other electrodes which
had been relatively unimpressive showed some re-
liable differences. However, these differences
were now mostly response-linked in a peculiar
fashion which we have not as yet been able to de-
cipher 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. Be-
haviorally, the monkeys appeared as surprised as
we by the effects of the surgery: they went into
the task situation fully confident of their abili-
ty, only to find that they made errors. This re-
sulted 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 realiz-
ing, of course, as we did, that it was the in-
sides 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 qua-
drigemina (colliculi) and the basal ganglia should
be shown to work via changes they effect in bias-
ing 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 pri-
mate are to organize input so as to make it mem-
orable. This organizing process does not appear
to occur within these "association" areas per se,
however. Rather, their effect is exercised down-
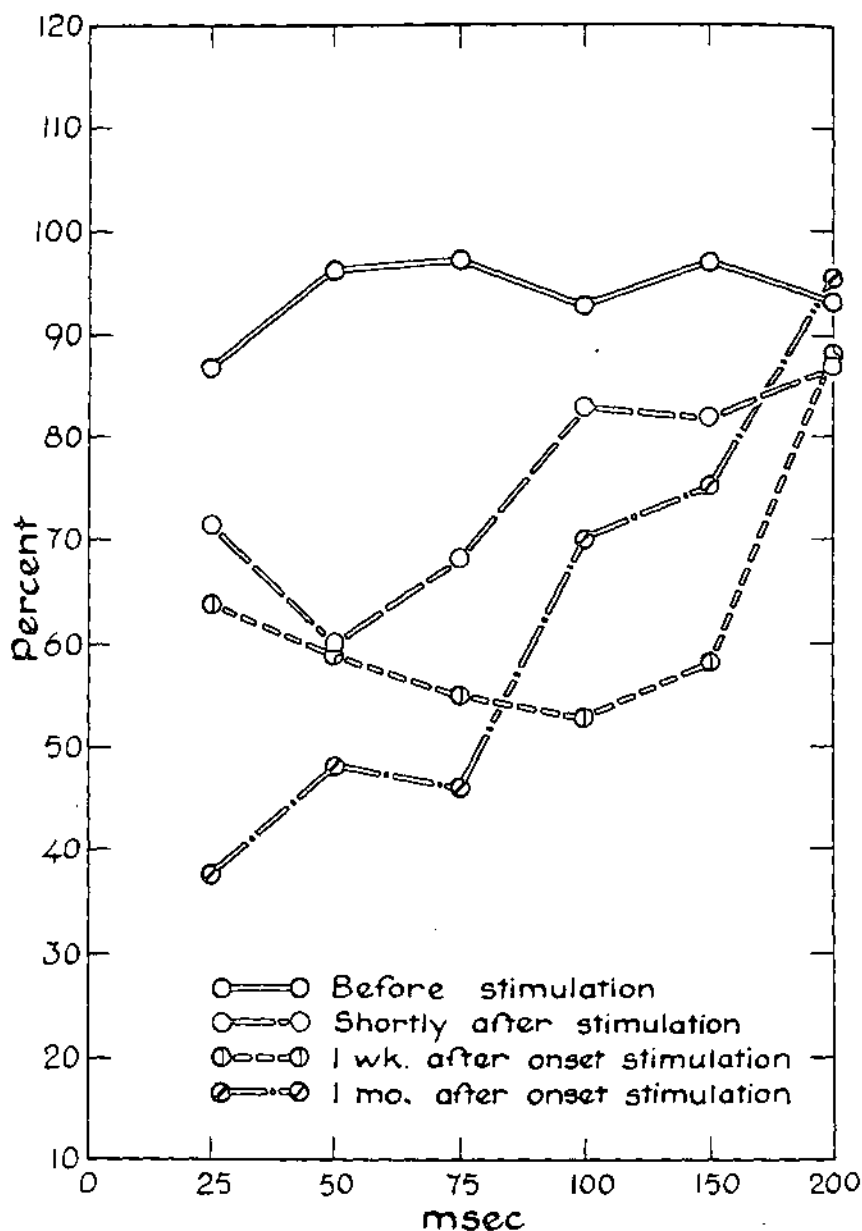stream via structures heretofore labelled as mo-

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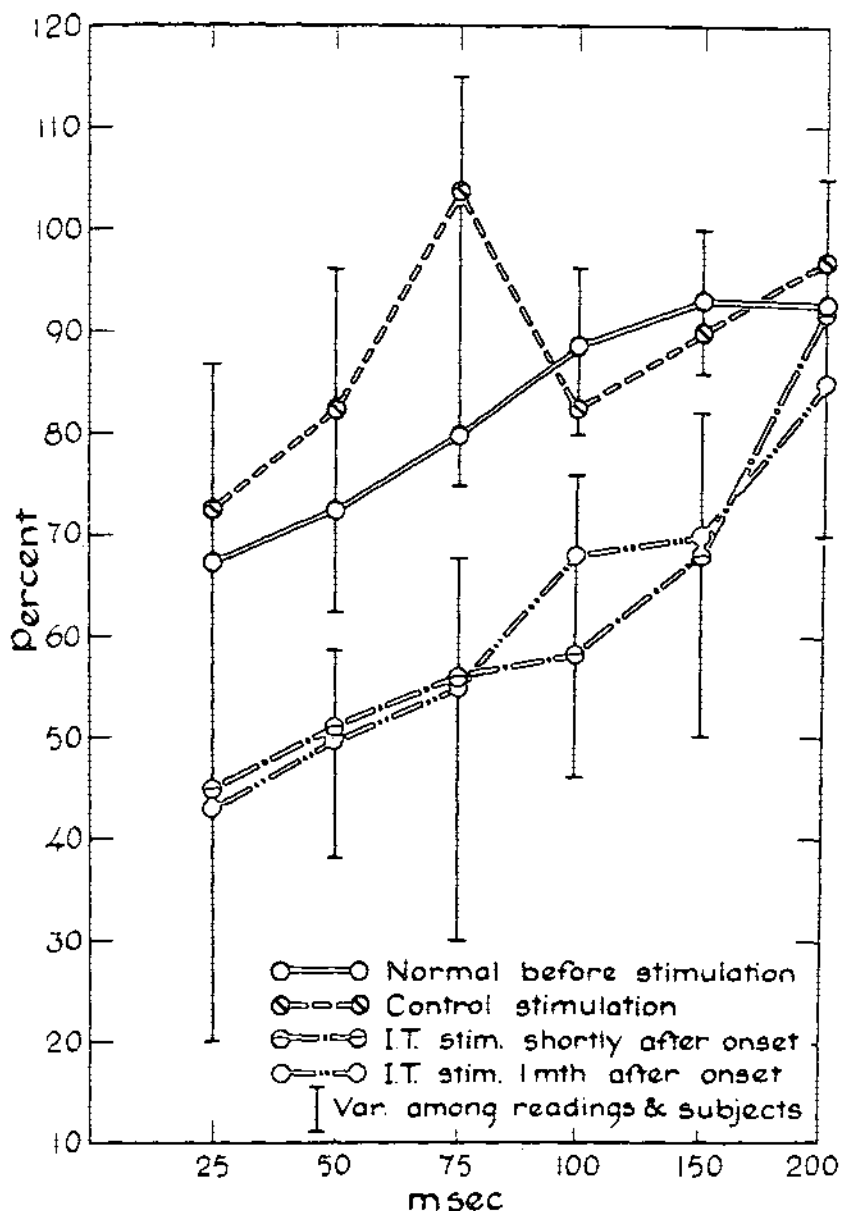   of the inferotemporal (IT) cortex.

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 begin-
ning 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 pro-
ceed.

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
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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 di-
vided the array into quads). Thus the bootstrap-
ping program now consisted of a sequence of twen-
ty patterns of four Arabic numerals:

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e.g.  3 7 2 2

      0 0 1 4

      3 4 5 6

      2 2 1 5

      1 0 3 7
```

<div align="center">etc.</div>

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 configura-
tions--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 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 mani-
pulation. 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 es
sential operations of the brain. Recoding main-
tains some sort of representational identity[4]
among event structures much as such identity ob-
tains between the sequences of openings and clos-
ings 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 lan-
guages have, by contrast with those used in com-
puter science, built into them a good deal of am-
biguity. From this ambiguity, of course, stem
the opportunities for construction of creative
novelties. If indeed it turns out that such lan-
guages are at least in part hierarchically relat-
ed 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 representa-
tions, e.g. as culture. Thus, it is turning out

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[4]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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