DISSOCIATION OF TWO BEHAVIORAL FUNCTIONS IN THE MONKEY AFTER EARLY HIPPOCAMPAL ABLATIONS

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INTRODUCTION

Bilateral excisions of medial temporal lobe structures (uncinate-amygdaloid region, hippocampus, hippocampal gyrus) in patients suffering from long-standing psychotic, or epileptic, symptoms resulted in a well-known severe anterograde amnesia (Scoville, 1954; Scoville and Milner, 1957). Subsequent clinical evidence pointed to the hippocampus as the critical structure in the memory loss (Penfield and Milner, 1958; Milner and Teuber, 1968; Milner, Corkin and Teuber, 1968).

Follow-up examinations of one of Dr. Scoville's patients (H.M.), operated upon in 1953, with permanent and severe anterograde amnesia, confirmed that the salient deficit remains in the transmodal establishment of new memories after delays as short as two minutes (Prisko, 1963; Sidman, Stoddard and Mohr, 1968). However, in spite of his global amnesia, patient H.M. performs normally on tests of motor and perceptual skills though he cannot remember having encountered the tasks before (Milner, 1962). More recently, he has been able to master a complex visual puzzle (the Tower of Hanoi) within a normal range of trials and to retain it with savings one year later (Cohen, Eichenbaum, DeAcado and Corkin, 1985). Instances of preserved learning co-existing with amnesia have been repeatedly noted in patients with brain damage other than that of medial temporal lobe structures (Warrington and Weiskrantz, 1968; Lhermitte and Signoret, 1972; Cermak and Butters, 1972; Brooks and Baddeley, 1976; Weiskrantz and Warrington, 1979; Cohen and Squire, 1980). The finding that the hippocampus is not essential for all learning is paralleled by extensive evidence obtained with rats (for reviews, see Hirsh, 1974; O'Keefe and Nadel, 1978; Olton, Becker and Handelman, 1979).

Though, in the clinic, the critical structure for memory was presumed to be the hippocampus, in all cases of amnesia there was either bilateral excision of both hippocampus and amygdaloid complex, as in patient H.M., or bilateral excision of hippocampus with unilateral excision of amygdala. No comparable memory loss was found after bilateral ablations limited to the uncinate-amygdaloid region (Scoville and Milner, 1957). However, in the absence of cases with selective damage to the hippocampus, its role in memory remained to be established.

To assess the behavioral functions of the hippocampus and to obtain
tests. When appropriate, age x lesion interactions were examined with
the use of two-way analyses of variance, followed by tests of simple main
effects and by a posteriori between-group comparisons using the Newman-
Keuls test (Kirk, 1968). Since, in most cases, the number of trials to
learning criterion paralleled the number of errors, statistical comparisons
were based on the number of errors. It should be noted that statistical
analyses were carried out for all groups of infants and juveniles, in-
cluding those with fornix sections in both age groups. However, results
reported here concern only groups of normal, control and hippocampectomized
monkeys. All levels of confidence were 2-tailed.

Results - Spatial reversals

On the first post-operative tests, groups of hippocampectomized in-
fants and juveniles were significantly impaired (p's<.032-.016). The def-
cit persisted longer in infant, than it did in juvenile, monkeys: on the
second round of tests, one year after surgery, infant hippocampectomized
monkeys, unlike hippocampectomized juveniles, were still significantly
impaired. Two years following surgery, significant impairment was no
longer found.

- Object reversals

Since adult monkeys with hippocampal ablations obtain normal scores
on this task, we did not expect, nor did we find, any post-operative
abnormalities in the hippocampal group of infants or juveniles.

- Successive retentions - 24-hr and 1-hr intervals

In contrast with the performance of adult operated monkeys, no sig-
nificant differences were found between normal and operated groups in
the two age groups in either of the two conditions. This finding did not
contribute, as yet, to the understanding of the nature of preserved cap-
acities after hippocampectomy. Or so it seemed, as long as the spared
performance on the successive retentions task was viewed in isolation.
However, as mentioned in the Introduction, assessment of chronic effects
of early hippocampectomy was to provide another example of spared learning
capacity. Taken together, the two instances became easier to interpret
in the context of a co-existing memory deficit, uncovered shortly after-
wards. The differential effects of early hippocampal damage on associative
learning, as contrasted with recognition memory, are described below.

Associative learning spared, recognition and association memory
not spared after early resections of hippocampus.

- Concurrent object discrimination task

Though infants and juveniles with hippocampal ablations were not imp-
aired, as a group, on the successive retentions task, individual monkeys had
obtained elevated learning scores. Thus, the sparing of the capacity that
mediates retention, and re-learning, of simple object discriminations was
not clear-cut. Accordingly, the concurrent object discrimination task,
known to be sensitive to the effects of hippocampal ablations in adult
monkeys was chosen to serve as an unfamiliar test of associative learning
(see Introduction, for descriptions of the task). At the time when it
was administered, monkeys that had been operated upon in infancy were
approximately 4 to 5 yrs of age, and those that had been operated on as
2 yr old juveniles, were approximately 7 yrs of age.

The results were clear-cut: Only older, but not younger hippocamp-
ectomized monkeys were impaired on this task. Two-way analysis of variance

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