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Short communication

RESPONSE TO STIMULUS CHANGE FOLLOWING OBSERVATION OR EXPLORATION BY THE RAT: A CONFIRMATION OF DIFFERENTIAL EFFECTS OF HIPPOCAMPAL DAMAGES

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Abstract. The experiment attempted to confirm the previous finding that hippocampal lesions in rats affected the information acquired by distant observation of the brightness difference of the T-maze arms, but left the information intact when it was gained by maze exploration. An alteration was introduced in the latter procedure allowing a complete elimination of olfactory stimuli, which might be utilized as nonmemorial cues. Despite this alteration the results were virtually the same as previously. Following maze exploration the hippocampally lesioned rats tended to enter the arm that had been subsequently changed in brightness, similarly to control rats. However, unlike the controls, they responded on the chance level after distant observation. This finding is not compatible with Olton's hypothesis postulating the involvement of the hippocampus in the working memory, or with the O'Keefe–Nadel theory of processing spatial information by the hippocampus.

In our previous study (4) we investigated in rats the effect of hippocampal lesions on the memory involved in a response to stimulus change. The experiment was conducted in an enclosed T-maze under two different conditions of stimuli exposure. In the "passive" test the rat could inspect the white-black maze arms, but was prevented from entering by transparent partitions. In the "active" test the rat was permitted to explore the entire T-maze. In both tests, on a sub-

sequent free choice trial, the color of one arm was changed, so that both arms were either white or black. The majority of sham operated controls entered the arm that had been changed between trials in both tests. Rats with lesions of the anterodorsal or the posteroventral hippocampal region made random choices in the passive test, while in the active test the same groups showed a significant preponderance of choices of the visually changed arm. Since the detection of stimulus change and the identification of the place in which this change occurred required an intact spatial memory, our findings challenged the hypotheses postulating involvement of the hippocampus in working memory (6) or in processing spatial information (5).

However, there is a difference between the passive and the active test that deserves particular attention. Since rats explored the entire maze in the active test, the arms were scent marked by the rat's passage. After the color of one arm had been changed for the arm of the opposite color, the rat faced the arm he has already explored and the other arm that was novel. In spite of careful cleaning and wiping of the arms, a complete elimination of scent marks might not be guaranteed, thus the highly developed sense of smell could help the rat to find the unentered arm of the maze. If the hippocampal rats were guided by their scent marks, their normal performance in the active test would not be surprising. This possibility was absent in the passive test, where the rats were prevented from entering the arms during the presentation of the stimuli.

In the present study we attempt to attain the olfactory symmetry in the active test by changing the set of black and white arms used during the exploration for a new set of black-black or white-white arms, not contacted before by the given rat. Under such condition the rats could not utilize scent marks, i.e., the nonmemorial cues or the memory of the specific smell of the arm explored in trial 1 (the taxon cues, according to the terminology introduced by O'Keefe and Nadel — 5).

In the previous experiment both tests were performed on the same subjects, and the passive test preceded the active one, so the experience gained in the first test might improve the performance of the hippocampal rats in the second i.e., the active test. Therefore it seemed necessary to check the effect of a different order of tests. Finally, considering the value of our findings for the current hypotheses of hippocampal functions, the replication of previous results might be important.

The experiment was conducted on 54 naive male rats of Wistar strain, about 3 mo old. Rats were randomly assigned into one of the three groups, 18 subjects in each: anterodorsal hippocampal (DH), posteroventral hippocampal (VH) and sham operated control group (C).

Brain lesions were performed under semiaseptic conditions by stereotaxic coagulation using the same parameters as in the previous experiment (for details of surgery and histology see 2). The examples of typical lesions are presented in Fig 1. The placement and the extent of DH and VH lesions closely resemble those performed in the previous experiment. Following surgery, the rats were given three weeks for recovery. During this time they were handled in order to substitute the experiences, which were given to previous groups (emotionality testing and open field behavior — 2,3) and made the conditions of the present experiment comparable to those of the previous one.

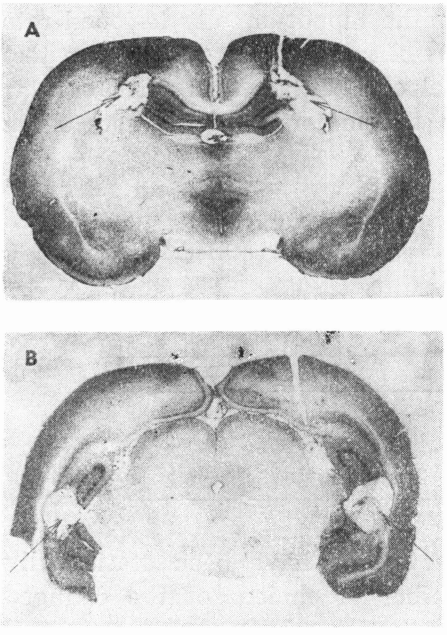

Fig. 1. Histological cross sections of typical lesions of rats from the anterodorsal (*A*) and the posteroventral (*B*) hippocampal group. The arrows indicate the placement of lesion.

Both tests, active and passive, were performed in an enclosed T-maze and consisted of two trials, exposure trial and choice trial, separated by a 1 min break. In the exposure trial of the active test the rat was allowed 3 min exploration of the maze arms, one with a black insert, the other with a white insert. The rat was then taken out of the maze and during the break time both inserts were replaced by two other inserts of the same color, i.e., either black or white. In the choice trial the rat was reintroduced to the maze and faced with a choice between two visually alike arms.

In contrast to the active test, in the exposure trial of the passive

test, the rat was allowed only to observe the maze arms, but was prevented from entering them by transparent partitions separating the arms from the choice-point of the maze. After 15 min exposure, the rat was removed from the maze and reintroduced 1 min later for the choice trial. The partitions were removed, so the rat was free to enter either arm.

In both tests the choice trial was terminated as soon as the animal entered one of the arms. The first entry, defined as four legs being in one arm was recorded. The active test was followed by the passive test with one week interval. Only a single session was held in each test.

As seen in Table I, in the active test the choices of the visually changed arm were preponderant among the hippocampally lesioned rats (DH or VH) as well as among the control rats (C). In the passive test rats with both hippocampal lesions selected either arm with similar frequency, while in the control group the majority of the rats chose

TABLE I

The number of rats choosing the visually changed and the unchanged maze arm

Tests / Operation	Active test		Passive test	
	changed	unchanged	changed	unchanged
DH	15	3	10	8
VH	16	2	10	8
C	16	2	16	2

the visually changed arm. These observations have been statistically confirmed. The differences in the number of choices of the changed arm between each hippocampal group (DH or VH) and the control group were significant in the passive test ($Ps = 0.03$, Fisher exact probability test), while in the active test these differences were non-significant. Thus, the hippocampal lesions affected the response to stimulus change examined in the passive test, but had no effect in the active test.

The results of the present experiment are closely similar to our previous data (4). A complete elimination of scent marks and of eventual specific smell of the arms explored in trial 1 of the active test did not affect the rats' preference for the visually changed arm. Therefore, the response to change tendency displayed by hippocampal rats could not be attributed to taxon or nonmemorial cues. The order of test

presentation also did not contribute to the level of performance. Thus, it might be concluded that the hippocampal rats were guided by the memory traces, adequate enough for the detection of the place of change in the active test.

The reason why the same subjects responded on the chance level in the passive test is open to several interpretations and we have discussed them in detail in the previous paper (4). According to our view-point, the dissociation between the performance of the hippocampal rats in the passive test and that in the active test suggests different memory types with different characteristics. The memory acquired in the passive test requires an intact hippocampus, while for that gained in the active test the function of the hippocampus is not indispensable. Since the responses to change in the active test rely on the spatial information and this information is useful for one trial of the experiment (the exposure of stimuli and the subsequent free choice may be viewed as a single trial) the lack of hippocampal effect is not compatible with the hypotheses postulating the involvement of the hippocampus in the working memory (6) or in the neural representation of space (5). It should be noted that in contrast to other findings (1), the effects of the anterodorsal and posteroventral hippocampal lesions on the passive test and the active test were alike.

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