

Short-Term Odor Memory: Effects of Posterior Transection of the Lateral Olfactory Tract in the Rat

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THANOS, P. K., B. M. SLOTNICK. *Short-Term Odor Memory: Effects of Posterior Transection of the Lateral Olfactory Tract in the Rat*. *PHYSIOL BEHAV* 61(6) 903–906, 1997.—Rats were trained on a series of novel 2-odor discrimination problems before and after combined unilateral bulbectomy and posterior transection of the contralateral lateral olfactory tract. In postoperative tests, experimental rats performed as well as controls when a short intertrial interval (30 seconds) was used but, in contrast to controls, failed to learn a 2-odor discrimination when the intertrial interval was 10 minutes. When tested on a reversal task, controls showed memory for original learning by making many errors while experimental rats quickly acquired the task. The results suggest that lateral olfactory tract afferents to posterior olfactory cortex may play a significant role in short-term memory for odors. © 1997 Elsevier Science Inc.

Odor memory Lateral olfactory tract Entorhinal cortex Hippocampus

INTRODUCTION

BECAUSE rats readily learn both simple odor detection and discrimination tasks and more complex problems including learning sets (4,8,12,13,15,16,17), paired associated learning (1) and delayed matching- and non-matching-to-sample (5,9), the rodent olfactory system provides a useful model for a neurobiological analysis of cognitive functions (14). Rats also display excellent short-term memory for odors. Thus, Lovelace and Slotnick (3) found that intertrial interval delays for up to 30 min had little effect in how rapidly novel discrimination problems were learned.

The anatomical pathways mediating these learning and memory functions are not known. Slotnick and Risser (18) failed to find deficits in long-term memory for preoperatively learned odor discriminations in rats with posterior transection of the lateral olfactory tract (LOT) or with lesions of the mediodorsal thalamic nucleus. However, interruption of both of these pathways produced marked deficits in retention and, thus, the storage or recall of long-term odor memory may involve both the olfactory thalamocortical system and olfactory projections to the limbic system (amygdala and entorhinal cortex).

With regard to short-term odor memory, Staubli, Ivy and Lynch (23) found that rats with lesions of the entorhinal cortex performed well on an olfactory discrimination task when a short intertrial interval (ITI) was used but poorly when the ITI was 3–10 min. When tested on an olfactory discrimination reversal task, experimental rats made fewer errors than controls presumably because they had little or no memory for the initial discrimination task. In a subsequent study, Staubli, Fraser, Kessler and Lynch

(22) reported that rats with entorhinal lesions showed good retention of preoperatively learned odor tasks but poor retention when tested on those acquired postoperatively. Because the entorhinal cortex provides a major source of afferents to the hippocampus, a structure that has been widely implicated in mediation of short-term memory, Staubli et al. (22,23) suggested that olfactory deafferentation of the hippocampus by entorhinal lesions produces rapid forgetting of newly acquired olfactory information. In support of this conclusion Otto and Eichenbaum (9) reported that rats with perirhinal and entorhinal cortical lesions were impaired on a delayed nonmatching-to-sample task when the delay was 30–60 s but not when a short delay (3 s) was used.

While the results of Staubli et al. (22,23) and Otto and Eichenbaum (9) are in agreement with many studies implicating the hippocampus in memory function (e.g., 21), recent reports suggest that it is damage to rhinal cortical regions (including the perirhinal, entorhinal and parahippocampal cortices) that is responsible for memory loss observed from large hippocampal lesions (7,24,25). These regions have reciprocal connections with neocortical areas subserving all sensory modalities (6) and they or components of them may be the structures critical for mediating short-term memory. Because lesions in the Staubli et al. (22,23) and Otto and Eichenbaum (9) studies damaged these rhinal cortical areas, it is uncertain whether the effects obtained reflect a general disruption of short-term memory function or one specific to olfaction. To examine this question the present experiment used a modification of the Staubli et al. (23) procedures to assess short-term memory function in rats with lesions that

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deafferent posterior olfactory cortical areas (including the entorhinal cortex) from olfactory input but otherwise leave these cortical areas intact.

METHODS

Subjects

Ten adult male Sprague Dawley rats (300–350 g) were housed individually in plastic cages in a temperature and humidity controlled vivarium maintained on a normal 12/12 h light-dark cycle. Food was provided ad lib. Animals were allowed a total of 10 ml of water each day, except for 3 d after surgery when supplementary water was given.

Apparatus and Preoperative Tests. The odor generator, runway and training procedures used in this study were identical to that described in detail by Lovelace and Slotnick (3). Briefly, rats were trained to traverse an alleyway and sample odors presented in 2 adjacent odor sampling tubes. One odor was designated as S+ and the other as S-. On each trial the S+ odor was present in the left or right odor sampling tube and the S- odor was present in the other sampling tube. Responses on a water delivery tube within each sampling tube were detected using a high impedance circuit (2). The position of each odor on each trial was predetermined using a quasi-random order with the restriction that one odor was not presented to the same sampling tube for more than 3 consecutive trials and that it was presented to each tube an equal number of times in a block of 30 trials. For each session, the sequence began at a randomly determined place in the trial series. After initial training, a non-correction procedure was used in all trials. A criterion response (3 licks) at the water delivery tube within the sampling tube containing the S+ stimulus was reinforced with water (.1 ml) and scored as a correct response (hit). Responding within the sampling tube containing the S- odor was not reinforced. A criterion response terminated the trial and the rat was removed to a clean cage for the duration of the intertrial interval.

Rats were trained on a series of eight 2-odor discrimination tasks. Two novel odors were randomly selected from a large stock of perfumes and food flavorings for each problem (Table 1). Thirty-one trials were given on each task and each session was separated by 24–48 h. The first trial of each session was considered an information trial; the outcome of that trial was noted but was not used in determining accuracy. For problems 1–6 and 8, the ITI was 30 s. For problem 7 the ITI was 10 min.

Postoperative tests. Beginning 14 d after surgery, training was continued using the same procedures. Novel odors were used in each task (Table 1) and the ITI for postoperative problems 1–6 and 8 was 30 s. The ITI for problem 7 was 10 min.

Twenty-four h after completing postoperative problem 8 all rats were trained on another novel 2-odor discrimination and, 1 h later, were tested on a reversal of that problem. A 30 s ITI was used in these tests. In the initial task, banana odor served as S+ and coconut odor served as S-. In the reversal task coconut served as S+ and banana served as S-. All rats were given 10 trials on the initial task and trained to a criterion of 5 consecutive correct responses on the reversal task.

For all tests, odor concentration was set at a level that produced a clearly discriminable odor stimulus for a human observer. After each problem was run, the system was washed with 95% ethanol and air dried. Between preoperative problems 4 and 5 a no-odor session was used to examine the possibility that residual odor cues might be present in the apparatus and support discriminative responding. Each rat performed at chance in this test.

Surgical Procedures. Rats were anesthetized with a mixture of 100 mg/kg Ketamine and 20 mg/kg Xylazine) and clamped

TABLE 1
ODOR PAIRS USED IN EACH PROBLEM

Problem	ITI	S+ Odor	S- Odor
Preoperative Tasks			
1	30s	Magnolia	Butterscotch
2	30s	Cherry	Clove
3	30s	Anise	Rose
4	30s	Almond	Peppermint
5	30s	Carnation	Club After Shave
6	30s	Gardenia	Honeysuckle
7	10m	Oeillet	Fougere
8	30s	Lily	Jasmine
Postoperative Tasks			
1	30s	Tuberose	Sweet Pea
2	30s	Lilac	Orange
3	30s	Lavender	Trefoline
4	30s	Citron	Mayrose
5	30s	Chypre	Eucalyptus
6	30s	Mimosa	Root Beer
7	10m	Pine	Narcissus
8	30s	Carnation	Cepacol
Reversal Task			
Initial	30s	Banana	Coconut
Reversal	30s	Coconut	Banana

into a stereotaxic machine. The left olfactory bulb was removed by aspiration under microscopic control using a fine glass pipette. In 5 rats, the right lateral olfactory tract was exposed on the anterolateral convexity of the hemisphere and transected using a #11 scalpel blade at or just rostral to the frontal level of the bregma skull suture. Five rats served as surgical controls. Three of these rats received only the unilateral bulbectomy (unilateral bulbectomy control). The other two received the same surgical procedures as experimental rats except that the knife cut in the right hemisphere was made just dorsal to the LOT. One unilateral bulbectomy control and 2 experimental rats became ill after surgery and were dropped from the study.

Histology. Upon conclusion of the behavioral tests, all animals were deeply anesthetized with chloral hydrate and perfused through the heart with saline followed by 10% formalin. The brains were removed and stored in a mixture of 20% sucrose and 10% formalin for several days before being sectioned at 50 microns on a freezing microtome. Every third section through the lesioned areas was mounted on glass slides and stained with cresyl violet. The stained sections were examined microscopically and the position and extent of the lesions was plotted on drawings from the Paxinos & Watson (11) atlas of the rat brain.

The percent correct responses in trials 2–31 of each 2-odor discrimination problem and the number of errors to a criterion of 5 consecutive correct responses on the reversal task was calculated for each rat. Between and within group comparisons were made using the Mann-Whitney U-tests and the Wilcoxon Matched-Pairs test respectively. An alpha level of .05 was used in all comparisons.

RESULTS

The left olfactory bulb was completely removed in all animals. The right LOT was completely transected at or just rostral

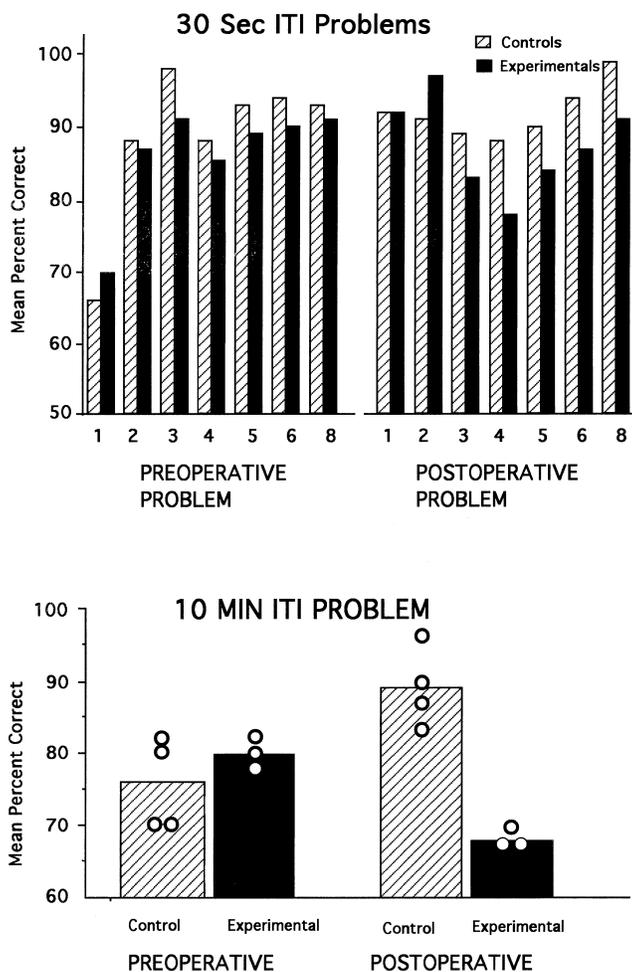


FIG. 1. Top, mean percent correct responding in trials 2–31 for each of the 7 preoperative and 7 postoperative short ITI odor discrimination problems for the 4 control and 3 experimental rats. Bottom, mean percent correct responding on the preoperative and the postoperative 10 min ITI tests for control and experimental rats. Open circles indicate the scores of individual rats.

to the level of the crossing of the anterior commissure in each of the 3 experimental rats. The knife cut extended dorsally into the dorsal bank of the rhinal fissure and ventrally into the piriform cortex and through the LOT but spared the olfactory tubercle. The lesions were similar to those illustrated by Slotnick and Schoonover (20) except that the LOT was transected at a more posterior level than in that study. The knife cuts in the two LOT control rats were largely lateral and dorsal to the LOT but did extend just below the rhinal fissure to interrupt the most dorsal aspect of the tract. The scores of the 2 unilateral bullectomy controls and the 2 LOT controls were essentially identical on all tasks and, thus, these animals were combined into a single control group.

Preoperatively, the groups did not differ in performance as measured by percent correct responding in 30 trials in each of the 30-s ITI tests. In the postoperative short ITI tests, experimental rats performed somewhat more poorly than controls (Figure 1A) but differences between groups were not significant and, on each of these short ITI problems, all rats achieved criterion performance of 5 consecutive correct responses.

Performance on the preoperative 10 min ITI tests was somewhat but not significantly poorer than that on the short ITI tests. The performance of control rats improved significantly ($p < .05$) on the postoperative 10 min ITI test and each made 5 or fewer errors. However, experimental rats performed more poorly than controls on this test ($p < .05$) and none reached criterion in the 30 trial session (Fig 1B).

The 2 groups did not differ in acquisition of the initial banana vs. coconut problem but, on the reversal task, the controls made more errors than in original learning (.3 vs. 16 errors; $p < .05$) while the 3 experimental rats performed about as well as in original learning (1 vs. 3 errors) and rapidly acquired the task (Figure 2).

DISCUSSION

The present results indicate that rats with unilateral olfactory bullectomy plus posterior transection of the contralateral LOT have a deficit in olfactory memory. Experimental rats performed about as well as controls when a short ITI was used but, unlike controls, failed to learn a novel odor discrimination task when the ITI was 10 min. Further, their enhanced performance on the reversal task suggests that they did not remember the significance of the odors used in initial training. The high levels of accuracy on the short ITI problems of rats with a unilateral bullectomy and contralateral transection of the LOT is in agreement with prior reports that rats with this combination of lesions perform well on simple odor detection and discrimination tasks (19,20).

The effects of posterior rhinal cortical lesions produced in prior studies of olfactory learning may be complex and affect

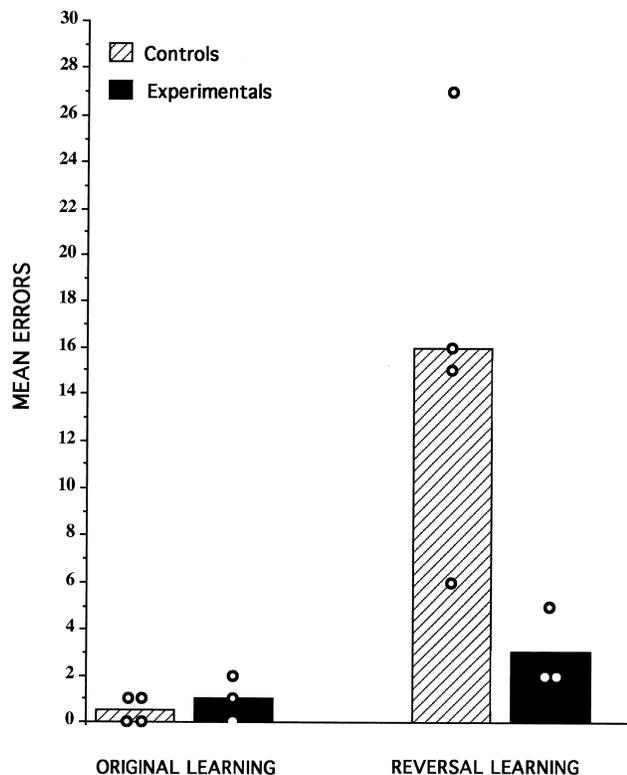


FIG. 2. Mean errors to criterion on the banana vs. coconut discrimination task and for the reversal task. Open circles indicate the scores of individual rats.

processes other than encoding stimulus-reinforcer associations. Thus Otto, Eichenbaum, Schottler, Staubli and Lynch (10) found that entorhinal cortical lesions facilitated performance in some odor discrimination tasks and Bunsey and Eichenbaum (1) found that similar lesions disrupted the ability of rats to learn some sequences of odor stimuli. In these cases, as in the studies on short-term odor learning, it is unclear whether the lesion-induced changes in behavior are specific to processing of odor signals or

to a more global disruption of learning. This problem was avoided in the present study because posterior transection of the LOT served to deafferent perirhinal, entorhinal and parahippocampal cortices from olfactory input without damaging these cortical structures. As our results closely replicated those of Staubli et al. (23), it is likely that the deficit in short-term odor memory obtained in the present study was specific to olfactory deafferentation of posterior rhinal cortex.

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