An age related position reversal impairment in the rat

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Seventeen-day-old and 38-day-old rats were compared on position habit reversal. Ss were drawn from the same litters and assigned randomly to either the 17-day-old or the 38-day-old test condition. The 17-day-old and the 38-day-old groups were matched on position habit acquisition. The 17-day-old group was significantly poorer on position habit reversal ($p < .01$). Spontaneous alternation levels in the two groups were also compared. Both groups exhibited chance levels of alternation ($\bar{X} = 57\%$). The litter mothers ($N = 4$) alternated significantly above chance ($\bar{X} = 83\%$), but were similar to their 38-day-old offspring on position habit reversal. The poor reversal performance of the 17-day-old group is consistent with the hypothesis that hippocampal integrity in the rat develops at approximately 30 days of age.

Douglas et al (1973) have hypothesized that behavior which is dependent upon hippocampal integrity develops at about 1 month of age in the rat. This hypothesis is derived from the neuroanatomical investigations of Altman and his coworkers (Altman & Das, 1965; Altman, 1966) which demonstrate a sixfold postnatal increase in dentate granule cells. The rate of increase in granule cells is most dramatic beginning at about 2 weeks of age and declines substantially over the subsequent 2-week period. Recently, Bayer et al (1973) have reported that the number of granule cells in the dentate gyrus does not differ significantly between 30-day-old and 90-day-old rats.

Since the granule cell layers are rapidly developing in infants prior to 4 weeks of age, it seems reasonable to assume that the hippocampus is not then functioning in an adult manner. Infant behavior should, to some degree, parallel that seen in hippocampectomized adult Ss. It is possible, of course, that some normal functions of the pyramidal cells are ongoing at this time, as Douglas et al (1973) have suggested. Nonetheless, behavioral studies of rats irradiated during the period of rapid granule cell development do suggest that cell loss in these layers affects behavior in the same way as hippocampal lesions (Bayer et al, 1973).

More importantly for the ontogenetic hypothesis, studies of behavior prior to 30 days of age in the rat, during the accelerated development of the granule cell layers, have demonstrated parallels between the performance of normal infant Ss and hippocampally damaged adults.

Douglas et al (1973), in a longitudinal study of spontaneous alternation, demonstrated that the great majority of young rats did not reach an alternation criterion of 15/20 successes until approximately 28 days of age. Riccio and co-workers have repeatedly demonstrated passive avoidance impairments in rats prior to 30 days of age (Riccio et al, 1968; Riccio & Schulenberg, 1969; Schulenberg, Riccio, & Stikes, 1971;

Riccio & Marazzo, 1972), while the work of Ernst (1972) has suggested that such a deficit may no longer be apparent at 35 days of age. Both the absence of spontaneous alternation and impaired passive avoidance are characteristic deficits subsequent to hippocampal lesions in adult rats (Douglas, 1967).

Unlike rats with hippocampal damage, however, rats prior to 4 weeks are described as extinguishing responses more rapidly than older rats both in active (Riccio & Marazzo, 1972) and in passive (Schulenberg et al, 1971) avoidance paradigms. They are also described as impaired in the retention but not the acquisition of simple tasks (Campbell & Spear, 1972). It has been suggested that the extinction deficit is related to this repeatedly demonstrated deficit in retention (Altman et al, 1973). Poor retention and rapid extinction are not features of the hippocampal syndrome in adult infrahumans.

There must, of course, be many differences between adult and infant rats other than the presence or absence of hippocampal integrity. If, however, the lesion parallel is valid, some explanations tentatively suggested to explain the behavior of damaged adults might be ruled out. For instance, if the rapidly extinguishing infant shows a reversal impairment, one would seek an explanation of reversal impairment other than slowed extinction.

The present study is concerned with position habit reversal, behavior classically affected by hippocampal damage (Douglas, 1967) and not yet investigated in the developmental paradigm. Hippocampally damaged adults are not typically impaired in the acquisition of a position habit (Kimble & Kimble, 1965; Niki, 1966), unless they are trained against a well-established position preference (Samuels, 1972). They are, however, invariably impaired on position reversal using either shock (Thompson & Langer, 1963) or appetitive reward as motivators (Kimble & Kimble, 1965; Niki, 1966; Samuels, 1972).

In the present experiment, the split litter technique was used to compare reversal acquisition in rats 17 days of age with reversal acquisition in littermates at 38 days of age.

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Table 1
Spontaneous Alternation: Number of Ss in the 15- to 16-Day-Old and 36- to 37-Day-Old Groups in Each Alternation Category

		15- to 16- Day-Old Ss (N = 18)	36- to 37- Day-Old Ss (N = 17)
Number	0	2	1
of Alter-	1	5	6
nations	2	7	7
	3	4	3

METHOD

Subjects

The litters of four pregnant Sprague-Dawley albino females obtained from Canadian Breeding Laboratories (Montreal, Quebec) served as Ss. The four adult females also served as Ss following the testing of their offspring. Each litter was split evenly between a 17-day-old and a 38-day-old reversal test condition. Three of the litters contained 10 pups each. The fourth litter contained only 5 pups, and the extra pup was assigned to the 17-day-old condition. There were a total of 18 pups run in the 17-day-old condition and 17 pups run in the 38-day-old condition. The litters were each housed in a 8 x 18 x 14 in. plastic nest box throughout the experiment and supplied with food and water ad lib. The mother rat remained in the box. Pups were removed to individual cages during testing and then returned to the nest box. Ss were earmarked for identification 3 days prior to testing.

Apparatus

A wooden T-maze constructed of ½ in. plywood served as the testing apparatus. The start arm of the maze was 5 in. wide and 12 in. long, with 6.5-in.-high walls. The choice arms were 10.5 in. long but otherwise identical to the start arm. The start arm was painted gray, the choice arms, white. The top of the maze was enclosed with 3/8-in. Plexiglas panels. Sliding doors separated each choice arm from the start alley. The maze floor was composed of 1/8-in.-diam brass rods with ½-in. separation center to center. The grids were wired to a Lehigh Valley shock control unit, No. 511-10, modified to permit independent shock delivery to the grids in each arm of the maze. The maze was placed on a table in a 6 x 8 ft room illuminated overhead by fluorescent room lights.

Procedure

The experiment was begun on the 15th postnatal day for the infant rat group and on the 36th postnatal day for the older rat group. Three pups from one litter in the infant group did not have their eyes open on the 15th day and were not run until Day 16. The four adult mothers were tested 4 weeks after the 36-day-old group was run. On the first day of the experiment, each rat was given two trials in the T-maze to evaluate spontaneous alternation. On each trial, the S was placed in the start arm and, after 3 sec, both choice arm doors were opened. When the S's whole body had entered the choice arm, the S was detained in the choice arm for 30 sec.

On the second day of the experiment, two additional spontaneous alternation tests were given, one in the morning and one in the afternoon. There was a minimum of 4 h between the two tests. Following the spontaneous alternation test in the afternoon, position habit training was initiated. Ss were placed in the start arm of the maze, with the doors to the choice arms removed. The S was given 5 sec to enter one of the choice arms. If the S did not enter a choice arm within 5 sec, he was given a 1-sec 1-mA shock in the start arm. If he entered the incorrect

choice arm he was also given the 1-sec 1-mA shock. A correction procedure was followed. Shocks were repeated at 1-2-sec intervals until the S entered the safe arm. Each S was detained in the safe arm for 30 sec and then removed. It was not necessary that the S avoid shock in the start arm for a successful trial, only that his initial choice be the correct arm.

Ss were first trained to choose the right arm of the maze. Each S was run for 20 trials or until he achieved a criterion of five successive correct choices. Ss failing to reach criterion in the afternoon session were run an additional 20 trials to the following morning. All Ss were run on each trial, and there was a variable intertrial interval which was never less than 2 min.

On the third day of the experiment, Day 17 for the infant group and Day 38 for the older group, Ss were given position reversal training. Procedures were identical to those described for training the right position habit except that the left choice arm, not the right, was safe. Ss were weighed on the day following reversal training.

RESULTS

Spontaneous Alternation

There were no differences between the 15-16-day-old rats and the 36-37-day-old rats on the spontaneous alternation tests. Both groups had mean alternation scores of 57%. This suggests that individuals in both groups were failing to alternate. However, four rats in the infant group and three rats in the older group alternated on all of the tests, and another seven rats in both groups alternated on two of the three tests. The number of Ss in each alternation success category is shown in Table 1. The four adult female Ss, by contrast, had a mean alternation score of 83%, a level typical of adult Ss.

Position Acquisition and Reversal

The 37-day-old rats reached criterion on the original position habit in an average of 6.2 trials. The range of trials to criterion in the 37-day-old group was 5-10. No rat in the older group made more than two errors prior to criterion. Mean errors for this group was .94. See Table 2.

Fourteen Ss in the 16-day-old age group also acquired the position habit in 10 or fewer trials. The mean trials to criterion for these 14 Ss was 7.1. This was not significantly different from the acquisition rate of the older group. One S made three errors prior to criterion; the others made two or fewer errors, as in the older group (mean errors = 1.2). The remaining 4 infant Ss were outside the acquisition range of the older group, taking from 13 to 31 trials to reach criterion on the position habit. These Ss were not included in the analysis of trials to criterion on acquisition or position reversal. The four adult females also acquired the position habit with no more than two errors to criterion ($\bar{X}$ errors = .75).

Criterion on the position reversal was reached significantly sooner by the 38-day-old rats ($t = 3.194$, $df = 29$, $p < .01$). The infant rats which had acquired the

position habit at the same rate as their older littermates took 11.6 trials to criterion on the average, while the older rats reached criterion in 8.2 trials. See Table 2. Errors to criterion were also significantly different ($t = 2.894$, $df = 29$, $p < .01$). The infant mean was 5.1 as compared to the older group mean of 2.9. See Table 2. The four infant rats, excluded from the analysis because they inordinately perseverated left responses during right habit acquisition, acquired the left habit rapidly (mean trials to criterion = 6.3). Both the infant and older Ss were significantly slower on reversal than on acquisition of the position habit (t for the 38-day group = 3.546, $df = 32$, $p < .01$; t for the 17-day-group = 4.857, $df = 26$, $p < .01$). Reversal scores of the adult females were similar to those of the 38-day-old Ss. Mean trials to criterion for the females was 8.5.

The first trial choices of Ss on the reversal problem provided an estimate of 24-h retention. All Ss in the 38-day-old group chose the previously correct side on the first reversal trial. Eight of the 18 Ss in the infant group failed to choose the previously correct side.

Successful avoidance trials during criterion performance were also examined. During position acquisition, the older group received start-arm shock on an average of three of the five criterion trials. The infant group was slightly more successful, receiving shocks on an average of 2.1 trials. During criterion reversal trials, however, the two groups were identical in avoidance performance, each receiving shocks on an average of 1.7 trials.

Weights

Seventeen-day-old pups from the 10-pup litters ranged from 30.2 to 38.6 g in weight. Pups from a given litter were, however, within 3 g of each other. The 17-day-old pups from the 5-pup litter ranged from 42 to 45.7 g in weight. There appeared to be no relationship between the variability in weight and variability on the reversal problem in this group. The 3 17-day-old pups that made three or fewer errors on reversal averaged 36.7 g in weight, while the 11 pups making four or more errors prior to successful reversal averaged 36.1 g in weight. The 3 pups from the small litter averaged five errors to reversal criterion as compared with an average of 5.2 errors among the large-litter Ss.

In the 38-day-old group, sex differences in weight were apparent. Males averaged 163.3 g and females averaged 131.9 g. The largest female and the largest male were the two rats from the five-pup litter. Differences in reversal performance were again not attributable to weight variation. The three 38-day-old rats that made four or more errors to reversal criterion were within one standard deviation of the mean weight for their sex.

DISCUSSION

The reversal results of the present study support the hypothesis that the behavior of infant rats during the

Table 2
Position Acquisition and Reversal: Mean and Median Trials to Criterion and Errors for 17- to 18-Day-Old and 37- to 38-Day-Old Rats

Acquisition				Reversal			
Trials to Criterion		Errors		Trials to Criterion		Errors	
Mdn	M	Mdn	M	Mdn	M	Mdn	M
17- to 18-Day-Old Ss							
7	7.1	1	1.2	10.5	11.6	5	5.1
37- to 38-Day-Old Ss							
6	6.2	1	.94	7	8.2	2	2.9

period of rapid increase in granule cell numbers resembles that of adult hippocampectomized rats. The alternation data are at variance with that hypothesis, but the tests may not have been sufficiently sensitive.

Rats at 38 days of age acquired a position reversal habit with significantly fewer errors than littermates at 17 days of age. This occurred even though both groups were similar in acquiring the original position habit. Moreover, only in the infant group did some individuals exhibit prolonged position preferences during acquisition. These preferences were not apparent during the spontaneous alternation tests of the same Ss.

The chance levels of spontaneous alternation displayed in both groups (57%) were similar to those reported by Kirkby (1967) for 20-day-old and 40-day-old albino rats. The mean levels in Kirkby's study were 53% and 65%, respectively. Douglas et al (1973) had predicted different proportions of successful alternators at those two ages, but this was not found in the present study. It should be emphasized that the present test was less extensive than that used by Douglas et al, who ran to a 15/20 criterion. In addition, Ss in the Douglas et al experiment were hooded rats rather than albinos.

With respect to the relationship between alternation deficits and reversal impairment, it is interesting that the three Ss who exhibited 100% alternation in the infant group and who were included in the reversal analysis all made seven or more errors on the reversal problem, as compared with a median error score of two in the older group. Since there is considerable interest in a monolithic theory of hippocampal function, it would be valuable to pursue the temporal relationship between alternation performance and the position reversal impairment.

The occurrence of the reversal deficit in the infant group was particularly striking in view of the reports that they extinguish more rapidly than older animals on other shock-motivated tasks. In this experiment as well, the infant Ss showed poorer 24-h retention of the original habit, as evidenced by first trial choices on the reversal problem. The reversal impairment, then, is not likely to be explained by the hypothesis that infant Ss are deficient in response inhibition. In reversal tasks, it is not necessary that Ss inhibit responding per se, but that

they inhibit particular choices. Infant Ss should be readier to abandon the just acquired choice in view of the poor retention and rapid extinction characteristics attributed to them.

There is recent evidence even in hippocampectomized adult rats that the impairment may not be linked to an inability to extinguish a previously acquired habit. This has been testable only in nonspatial reversal problems where response errors other than the previously correct response are possible. In such problems, it has invariably been the case that prolonged position habits, not failure to extinguish the previously rewarded response, are primarily responsible for the deficit (Silveira & Kimble, 1968; Webster & Voneida, 1964; Teitelbaum, 1964). The present results suggest that even their position reversal deficits may not be a function of slow extinction.

A final parallel between the infant results and the reports of hippocampal lesion effects is the overlap in performance between the infant and older groups. Three of the infant group took fewer than nine trials to criterion on the reversal problem, while three members of the older group took nine or more trials to criterion. Isaacson and Kimble (1972) have recently called attention to the statistical nature of hippocampal deficits, particularly on discrimination tasks. Current theories of hippocampal function will have to address themselves to this range of variability in individual S performance.

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