Early Learning Failure Impairs Adult Learning in Rats

T. Manrique
A. Molero
A. Cándido
Department of Experimental Psychology and Physiology of Behavior
University of Granada
Campus Cartuja, Granada 18071, Spain
E-mail: tmanriqz@ugr.es
E-mail: amolero@ugr.es
E-mail: candido@ugr.es

Milagros Gallo
Department of Experimental Psychology and Physiology of Behavior; Institute of Neurosciences F. Oloriz
University of Granada
Granada, Spain
E-mail: mgallo@ugr.es

ABSTRACT: Early life experiences may affect adult learning ability. In two experiments we tested the effect of early learning failure on adult performance in Wistar rats. In the first experiment 17-day-old rats (PN17), but not 25-day-old rats (PN25), trained in a hidden platform water maze task showed deficits in tone-shock avoidance learning when they were 3-months-old. The second experiment, which included random-platform and non-platform control groups, confirmed the effect of early (PN18) spatial learning failure on adult avoidance learning. However, post-weaning training (PN25) without platform also tended to induce adult learning deficits as long as the adult task difficulty was increased. The older non-platform group did not differ from the impaired group which received early training in a fixed hidden platform task. The results are discussed in terms of the relevance of early learning outcome and developmental stage on adult general learning deficits which may be related to the learned helplessness phenomenon and developmental neural plasticity. © 2005 Wiley Periodicals, Inc. Dev Psychobiol 46: 340–349, 2005.

Keywords: preweaning; spatial learning; avoidance learning; rat; water maze; learned helplessness

Exposure to uncontrollable aversive events may impair later learning ability in rats. It has been suggested that the animal learns to be helpless, suffering motivational, cognitive, and emotional changes that lead to passivity and impaired learning (Overmier & Seligman, 1967; Maier & Seligman, 1976). The conventional procedure to induce learned helplessness involves exposure to inescapable shocks and later testing in an avoidance task (see for example Drugan, Basile, Ha, Healy, & Ferland, 1997; Vollmayr & Henn, 2001). However, the learned helplessness phenomenon has been reported using different tasks (see Maier & Seligman, 1976; Overmier, 2002 for review). A critical factor seems to be uncontrollability, either experiencing inescapable aversive events or unsolvable discrimination problems (Hiroto & Seligman, 1975).

It can be proposed that uncontrollability may be induced either by applying an unsolvable task or by imposing excessive learning demands at an early stage of developmental maturation. It is well known that early experiences with uncontrollable stressful events may have long lasting effects on adult performance. On one hand, it has been reported that inescapable shocks received as a weanling profoundly impair adult escape behavior (Hannum, Rosellini, & Seligman, 1976) and undermine the ability of adults rats confronted with shocks to reject tumors (Seligman & Visintainer, 1985). On the other hand, positive effects of early handling which can be considered a mildly stressful stimulation, have been described in a variety of avoidance tasks (Chapillon, Patin, Roy, Vincent, & Caston, 2002; Gschanes, Eggenreich, Windisch, & Crailsheim, 1995; Nuñez et al., 1995; Tejedor-Real, Costela, & Gubert-Rahola, 1998). Thus, it seems interesting to test the potential effect on adult learning ability of training infant rats in a task that they are not able to solve due to developmental immaturity.

Learning to locate a hidden platform in the Morris water maze has several advantages for this purpose (Morris, 1981). First, this learning ability appears late during development. Significant acquisition deficits have been reported in preweaning rats younger than 20 days of age. These deficits range from a complete failure to express spatial learning (Rudy & Paylor, 1988; Rudy, Staedler-Morris, & Albert, 1987; Schenk, 1985) to
inferior performance relative to adults (Carman & Mactutus, 2001; Kraemer & Randall, 1995) depending on the procedure requirements. Thus, applying the conventional spatial learning task to 17–19 day old rats results in a learning failure due to incomplete brain maturation. Second, the task involves learning to avoid a mild stressor. Finally, it does not require food deprivation in contrast to spatial tasks in other mazes, avoiding constraints to control motivation in lactating rats.

The present study was designed to test whether early failure in spatial learning may induce a long-lasting effect on an independent aversive learning task. Adult performance on a tone-shock avoidance task by rats that were trained in a spatial task at an early age was tested. Thus, if there is a general effect of early training outcome on adult learning it should appear in a task which involves not only different aversive stimuli (water vs. shock avoidance) but also different sensory (visual vs. auditory) and motor (swimming vs. jumping) requirements.

EXPERIMENT 1

A pilot experiment was designed to compare adult performance in the acquisition of a tone-shock avoidance response in three groups of rats. Two groups were previously trained in a hidden platform water maze task, one of these groups after weaning (postnatal day 25), and the other before weaning (postnatal day 17), i.e., at an age reported as too early to solve this task. A third group received no early training.

METHODS

Subjects

Subjects were 11 male and 12 female Wistar rats bred at the University of Granada. All the rats used belonged to three litters. The female pregnant rats were checked daily for new births being the first postnatal day (PN0) the morning in which the new litters were first observed. Three days after birth each litter was culled with their dams in standard clear polyethylene hanging cages. The female pregnant rats were checked daily for new births being applied for minimizing fatigue, as proposed by Kraemer and Randall (1995). However, as it has been shown that reducing the task requirements may allow spatial learning in preweanlings (Carman & Mactutus, 2001; Carman, Booze, & Mactutus, 2002),

APPARATUS

For the early training, the water maze was located in a 4 × 5 m room containing a great amount of extra-maze cues (electrophysiological instruments, posters, lights, video-camera, etc.) visible to the swimming animal. The pool consisted of a 200 cm diameter and 30 cm deep circular plastic tank with a removable 11 cm diameter circular platform. The temperature of the water was maintained at 24–26°C. The water level was 22 cm and the platform was placed 1 cm below the water surface. In order to ensure that the platform was invisible the water surface was covered by small pieces of white polyethylene. The pool was divided conceptually into four quadrants, and the platform was placed approximately 35 cm from the pool border in the center of each quadrant depending on the behavioral conditions.

The experimental apparatus used for the adult training consisted of a modified rat operant conditioning chamber (LETICA LI-200) made of four walls: two opposing walls (31 × 28 cm) were made of clear polyethylene; the other walls (31 × 23.5 cm) were opaque polyethylene and modular aluminum plates, respectively. The floor was formed by a grid of 19 stainless steel rods 4 mm in diameter and were positioned 2 cm center-to-center; these were connected in series to a LETICA LI 2700 shock-source module designed to produce continuous scrambled current of 1 mA. Five photo-electric cells were mounted 25 cm above the grid at 5 cm intervals, beginning 5 cm from the aluminum wall. Corresponding lights (5 mm in diameter) were mounted in the opposite wall. Lights and cells formed an electrical circuit connected to a response recorder. A vertical jump interrupted the circuit and it was recorded as a response (Cándido, Catena, & Maldonado, 1984; Cándido, Maldonado, & Vila, 1991; Cándido, González, & de Brugada, 2004). A buzzer, producing 80 dB SPL at 24 V, was used as the warning signal.

Avoidance and escape latencies were measured by a LETICA L1 130/100 digital chronometer, accurate to 0.1 s. The temporal sequence of the events was controlled by the LI 2700 module connected to a computer.

Procedure

Morris water maze task. A spaced learning procedure was applied for minimizing fatigue, as proposed by Kraemer and Randall (1995). However, as it has been shown that reducing the task requirements may allow spatial learning in preweanlings (Carman & Mactutus, 2001; Carman, Booze, & Mactutus, 2002),
a large circular pool was used in order to increase the difficulty of the task. Each subject received 10 blocks of training, applied in two daily sessions, morning and afternoon, during 5 consecutive days. The two daily blocks were separated by a 5 hr interval. Each block consisted of four trials. There was an inter-trial interval of 5 min. Each trial began by placing the subject into the water facing the pool wall at one of the four compass conditions (east, west, north, or south). Each subject was released once from each of the four compass points during a block of four trials. The order varied randomly. The animal was allowed to swim freely for 60 s or until it climbed onto the hidden platform. If it did not find the platform, after 60 s it was placed on the platform by the experimenter and remained there for 15 s. During the inter-trial intervals the subjects were group-housed in a cage lined with an electric heating pad behind a large column which hid the swimming pool. During the inter-block intervals, the preweaning rats were returned to their home cage with the dam in the vivarium. The postweaning group was housed with the rest of the litter. Latencies to reach the platform were recorded.

Avoidance task. Before the onset of the adult training experience, at the age of 3 months, the animals were housed in individual cages. The subjects were randomly assigned to morning or afternoon session and counter-balanced by sex and group. The learning procedure followed was that described in detail by Cándido, Maldonado, and Vila (1988).

The daily session consisted of 60 trials. Each rat was placed into the chamber and was allowed 5 min to explore it before the trial began. Each trial consisted of a warning signal followed 5 s later by a 1 mA electric shock. Both continued for 30 s or until the rat showed an escape response breaking the photocell beam by jumping. An avoidance response was one that occurred within 5 s of the warning signal onset. Training lasted until the rat reached the acquisition criterion of 10 consecutive avoidance responses (CARs) or until a maximum of 240 trials (four sessions). Those animals that failed to escape the shock in five consecutive trials were eliminated and training did not continue. The number of trials required to reach 3, 5, and 10 CARs were used as the dependent variables.

RESULTS

Morris Water Maze

Figure 1 shows the mean latencies to reach the platform of the groups trained in the Morris water maze. A 2 × 2 × 10 (age × sex × blocks of trials) analysis of variance (ANOVA), the within subject factor being the latency to reach the platform in the last trial of each block, showed significant main effects of age ($F_{(1, 12)} = 22.96; p < .01$), blocks of trials ($F_{(9, 108)} = 8.22; p < .01$), and the interaction age × blocks of trials ($F_{(9, 108)} = 3.27; p < .01$). Analyses of the interaction revealed shorter latencies to reach the platform of the older group (PN25) compared to the younger group (PN17) in trial 8 ($F_{(4, 14)} = 5.05; p < .05$) and trial 10 ($F_{(1, 14)} = 8.18; p < .01$). Repeated measures ANOVA analyses indicated spatial learning both in the younger ($F_{(9, 63)} = 3.30; p < .01$) and in the older group ($F_{(9, 63)} = 5.81; p < .01$). However, Newman–Keuls post-hoc analyses showed faster learning in the older group, the latencies to reach the platform for blocks 8 ($p < .05$), 9 and 10 ($p < .01$) being significantly shorter than those of the first blocks of trials. However, the younger group showed reduced latencies only in block 9 ($p < .01$), and only in comparison with the first block in the case of block 10 ($p < .05$).

Avoidance Task

Figure 2 shows the number of trials required by each group for reaching 3, 5, and 10 consecutive conditioned avoidance responses (CARs). None of the subjects had to be excluded due to absence of avoidance responses. A 2 × 3 (sex × group) analysis of variance (ANOVA) showed only a significant effect of group using CARs 5 as the learning criterion ($F_{(2, 18)} = 4.02; p < .05$). Newman–Keuls post-hoc comparisons showed that the group trained in the spatial task at PN17 required a significantly higher number of trials to reach the learning criterion than both the non-trained control group and the group trained at PN25 ($p < .05$). Similar tendencies appeared using CARs 3 and 10 as learning criteria, but the differences did not reach a significant level. There were no other significant effects.

DISCUSSION

The results of the early training in the water maze task revealed that the younger group was impaired in finding the hidden platform location compared to the older group. These results are congruent with previous data showing a late development of spatial learning in rats (Carman & Mactutus, 2001; Kraemer & Randall, 1995; Rudy & Paylor, 1988; Rudy et al., 1987). Our procedure was designed in order to minimize fatigue, including a spaced
distribution of trials as proposed by Kraemer and Randall (1995). This fact may have favored learning in the younger group, as can be seen in the last two trials. Spatial learning at this age has been reported employing a procedure adapted to the pups requirements, such as a reduced size of the pool (Carman & Mactutus, 2001; Carman et al., 2002). However, using the present behavioral procedure the differences in latencies to locate the platform between both age groups were evident. Seventeen-day-old pups are less proficient than 25-day-old in learning to find the platform.

The results of the adult avoidance training showed that the group trained in the spatial task at the age of 17 days needed a higher number of trials for acquiring an avoidance response than both the control non-trained group and the group trained at the age of 25 days. Although the tendency appeared using different learning criteria, the fact that the differences were significant only using a CARs 5 criterion may reflect floor and ceiling effects when the task is too easy (CARs 3) or too difficult (CARs 10).

Thus, the results point to a deleterious effect on adult learning ability of having been trained in a different task before reaching the developmental stage required for solving it. No effect of being efficiently trained at a later developmental stage was evident compared to the control group that did not receive early training.

EXPERIMENT 2

The results of Experiment 1 showed that those rats which failed to solve a spatial task due to developmental immaturity exhibited as adults acquisition deficits in a different avoidance task. Experiment 2 was designed to replicate this finding. In addition, control groups were added in order to exclude alternative interpretations. On one hand, in spite of the fact that we used the procedure of Kraemer and Randall (1995) in order to minimize the contribution of fatigue, due to the large size of the pool, the possibility of increased fatigue in the younger group in relation to the older cannot be excluded. Having been subjected to fatigue producing exercise during infancy may then be responsible for the adult learning impairment. On the other hand, irrespective of developmental stage, the learning impairment found in adults may be due to those rats having been trained in an unsolvable task. In order to examine whether the adult learning impairment was due to inability to learn a solvable task or whether similar results could be found after training the animals in an unsolvable task at a later developmental stage, or after being subjected to exercise, random platform and non-platform yoked control groups were added. One animal of each control condition (random and the non-plat) was yoked to each animal of the experimental group. These were matched for the starting point and swimming time. Moreover, in order to test retention in the early spatial task, a probe trial without platform was added. Additionally, the immobility time in this probe trial was recorded as a measure of “behavioral despair,” a construct related to learned helplessness. If learning failure was due to premature developmental stage, the preweaning group trained in the spatial task would show learning deficits in the adult task. However, if training age is not a factor, those groups performing either an unsolvable task or exercise should be impaired.

METHOD

Subjects

Eighty-three Wistar rats (44 males and 39 females) obtained from nine litters were housed as described in Experiment 1. The subjects were randomly assigned to four sex counter-balanced behavioral groups labeled as follows: Experimental
analysis of variance (ANOVA) showed significant main effects of age \((F_{(1, 52)} = 79.32; p < .01)\), block of trials \((F_{(7, 364)} = 56.61; p < .01)\), and the interaction age \(\times\) block of trials \((F_{(7, 364)} = 13.8; p < .01)\). The analysis of interaction age \(\times\) block revealed a significant decrease of the latencies to reach the platform along the blocks both in PN18 group \((F_{(7, 203)} = 28.55; p < .01)\) and in PN25 \((F_{(7, 233)} = 47.44; p < .01)\). Post-hoc Newman–Keuls comparisons of the younger group showed no significant differences between blocks 1 and 5 but they differed on blocks 6, 7, and 8 \((p < .01)\). The latencies to reach the platform decreased progressively between blocks 6 and 7 \((p < .05)\) and blocks 7 and 8 \((p > .01)\). In contrast with the PN18 group, the older group (PN25) showed progressive and faster decline of the latencies to reach the platform between blocks 1 and 2 \((p < .05), 2 and 3 \((p < .01), 3 and 4 \((p < .05), 4 and 5 \((p < .01), 6 and 7 \((p < .05)\) but no significant differences between 7 and 8 showing a potential floor effect. The rest of differences between blocks of trials were significant \((p < .01)\). The younger group showed longer latencies than the older group in blocks 2–8 \((p < .01)\).

**Procedure**

All subjects received an early training procedure similar to that used in Experiment 1, except for the three following differences. First, training consisted of only eight blocks of trials, the number being reduced in order to delay preweaning training onset, in this way allowing a greater sensory maturation. Second, random and non-platform control groups were added. Animals from the random group remained in the platform for 15 s after each trial, whether or not they had found the platform by themselves. Third, a retention test without platform was added. This probe trial took place following the last block of trials (block 8). On the probe trial the subject was allowed to swim freely for 60 s after being released from a fixed starting location. The video recordings of the probe trials were used to measure search time in the target quadrant and immobility time. Three seconds was set as the minimum criterion for each immobility period. The adult avoidance task was performed as described in Experiment 1.

**RESULTS**

**Morris Water Maze**

**Acquisition.** Figure 3a shows the main latencies to reach the platform of the two experimental groups. The rest of the groups are not represented because they were yoked. A \(2 \times 2 \times 3 \times 8\ (\text{sex} \times \text{age} \times \text{group} \times \text{block of trials})\) analysis of variance (ANOVA) showed significant main effects of age \((F_{(1, 52)} = 79.32; p < .01)\), block of trials \((F_{(7, 364)} = 56.61; p < .01)\), and the interaction age \(\times\) block of trials \((F_{(7, 364)} = 13.8; p < .01)\). The analysis of interaction age \(\times\) block revealed a significant decrease of the latencies to reach the platform along the blocks both in PN18 group \((F_{(7, 203)} = 28.55; p < .01)\) and in PN25 \((F_{(7, 233)} = 47.44; p < .01)\). Post-hoc Newman–Keuls comparisons of the younger group showed no significant differences between blocks 1 and 5 but they differed on blocks 6, 7, and 8 \((p < .01)\). The latencies to reach the platform decreased progressively between blocks 6 and 7 \((p < .05)\) and blocks 7 and 8 \((p > .01)\). In contrast with the PN18 group, the older group (PN25) showed progressive and faster decline of the latencies to reach the platform between blocks 1 and 2 \((p < .05), 2 and 3 \((p < .01), 3 and 4 \((p < .05), 4 and 5 \((p < .01), 6 and 7 \((p < .05)\) but no significant differences between 7 and 8 showing a potential floor effect. The rest of differences between blocks of trials were significant \((p < .01)\). The younger group showed longer latencies than the older group in blocks 2–8 \((p < .01)\).

**Probe trial.** Figure 3b shows the main search time in target quadrant for all the groups. A \(2 \times 2 \times 3\ (\text{sex} \times \text{age} \times \text{group})\) ANOVA of the time spent in the quadrant that had previously contained the platform during the probe trial showed a significant main effect of group \((F_{(2, 52)} = 22.43; p < .01)\) and the interaction between age \(\times\) group \((F_{(2, 52)} = 7.14; p < .01)\). There were no other significant effects. The analysis of interaction age \(\times\) group revealed that PN25 experimental group spent significantly more time searching the platform than the younger experimental group \((F_{(1, 22)} = 10.26; p < .01)\). PN18 non-platform group also spent significantly more time in the platform quadrant than PN25 non-platform group.
(F(1, 18) = 5.19; p < .04). There were no significant differences between random groups (F(1, 18) = 0.61; p < .44). For those conditioned at 25 days of age there was a significant effect of group (F(2, 31) = 38.44; p < .01). Post-hoc Newman–Keuls comparisons showed that experimental, random and non-plat groups differed significantly (p < .01). No effect of group was seen in the younger groups. Besides, post-hoc Newman–Keuls comparisons showed that PN25 experimental group remained searching for the platform in the target quadrant longer than the rest of the groups (p < .01).

Table 1 presents the mean immobility time of each group during the probe trial. The 2 x 2 x 3 (sex x age x group) ANOVA revealed a significant main effects of age (F(1, 52) = 5.66; p < .05), group (F(1, 52) = 7.10; p < .01), and the interaction of age x group (F(2, 52) = 8.56; p < .01). The analysis of interaction age x group showed that the younger experimental group was significantly different from the PN25 experimental group (F(1, 22) = 5.40; p < .05), which remained swimming during the whole test. There were no significant differences between random groups (F(1, 18) = 1; p < .33). The older non-platform group remained immobile longer than the younger non-platform group (F(1, 18) = 5.20; p < .03). An ANOVA of the younger groups revealed no significant group effect (F(1, 27) = 1.48; p < .25). An ANOVA of PN25 groups yield a significant effect (F(3, 31) = 6.68; p < .01). Post-hoc comparisons showed that the non-platform group spent almost 30% of the probe trial immobile, behaving significantly different from the rest of the groups (p < .01). Besides, post-hoc Newman–Keuls comparisons showed that this group differed significantly from the rest of the groups regardless the age.

Avoidance Task

Figure 4 presents the main number of trials required by each group to reach the 3 (a), 5 (b), and 10 (c) consecutive conditioned avoidance responses criteria (CARs) in Experiment 2. There were significant differences between both ages in the experimental group (F(1, 22) = 15.94; p < .01) but not in the rest of the groups. For those conditioned at 18 days, there was a significant effect of group (F(3, 36) = 6.81; p < .01). Post-hoc Newman–Keuls comparisons revealed that the younger experimental group performed significantly worse than the rest of the groups (p < .01). There were no other significant effects.

The analysis of CARs 5 showed only a significant effect of the interaction age x group (F(3, 75) = 5.42; p < .01). Again, there were significant differences between both ages in the experimental group (F(1, 22) = 23.07; p < .01) but not in the rest of the groups. For those conditioned at 18 days, there was a significant effect of group (F(3, 36) = 4.81; p < .01). Post-hoc Newman–Keuls analyses revealed that the younger experimental group performed significantly worse than the rest of the groups (p < .01). The group effect did not reach significance in

### Table 1. Immobility Time (s) of the Different Groups During the Probe Trial of the Morris Water Maze in Experiment 2

<table>
<thead>
<tr>
<th></th>
<th>PN18 (Mean ± SEM)</th>
<th>PN25 (Mean ± SEM)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Experimental</td>
<td>3.5 ± 1.71</td>
<td>0 ± 0</td>
</tr>
<tr>
<td>Random</td>
<td>0.97 ± 0.92</td>
<td>0 ± 0</td>
</tr>
<tr>
<td>Non-platform</td>
<td>0.75 ± 0.71</td>
<td>29.9 ± 12.11</td>
</tr>
</tbody>
</table>

FIGURE 4 Mean (±SEM) number of trials needed by each group to reach the 3 (a), 5 (b), and 10 (c) consecutive conditioned avoidance responses criteria (CARs) in Experiment 2.
PN25 group ($F_{(3, 39)} = 2.73; p < .06$). Again, post-hoc Newman–Keuls comparisons revealed that the younger experimental group performed significantly worse than the rest of the groups ($p < .01$). There were no other significant differences.

Thus, both in CARs 3 and 5 the younger experimental group needed significantly more trials to reach the learning criteria than the rest of the groups.

The analysis of variance (ANOVA) of CARs 10 revealed again only a significant effect of the interaction age × group ($F_{(3, 73)} = 6.53; p < .01$). There were significant differences between PN18 and PN25 experimental groups ($F_{(1, 22)} = 16.79; p < .01$), but not between the random ($F_{(1, 17)} = 0.21; p < .65$), non-plat ($F_{(1, 18)} = 2.52; p < .13$), and control ($F_{(1, 18)} = 0.01; p < .9$) groups. For the young group there were a significant group effect ($F_{(3, 36)} = 5.47; p < .01$). As in the case of the previous learning criteria, the experimental group performed significantly worse than the rest of the groups ($p < .01$). The group effect did not reach significance in PN25 group ($F_{(3, 39)} = 2.45; p < .08$). Post-hoc Newman–Keuls analyses showed significant differences between the Exp PN18 and the rest of groups ($p < .03$) except the PN25 non-plat group ($p < .28$). This later group showed also marginal differences with the PN25 experimental group ($p < .08$).

**DISCUSSION**

These results confirm the main findings of Experiment 1 concerning the deleterious effect of early learning failure on the acquisition of a different avoidance response during adulthood, but also contribute new data.

The latencies to reach the platform during acquisition as well as the search times in the target quadrant during the probe trial showed spatial learning deficits in the younger (PN18) experimental group compared to the older experimental group (PN25). Although the younger group latencies to reach the platform declined during the last acquisition trials, during the probe trial these animals showed significantly lower search time in the target quadrant than the older group. No evidence of a search pattern targeting a specific quadrant was found in either random or non-platform groups. The typical search pattern shown by the random groups included exploration and crossings throughout the four quadrants and no age differences were evident. However, the search pattern of the non-plat groups during the probe trial seemed to differ between the age groups. The younger PN18 group seemed to exhibit a pattern similar to the random groups, with active swimming and crossings of the four quadrants. However, the older PN25 group showed reduced exploration and long periods of floating without swimming. The immobility time results during the probe trial in Morris water maze showed that the PN25 group, trained without platform, remained immobile significantly longer than the rest of the groups. Thus, the absence of the escape platform during training seemed to lead to different outcomes depending on the age of the pups. Passivity in the older group could be interpreted as learned helplessness because the situation was inescapable. Immobility may be an adaptive response if the animal learned to wait until the end of the trial to be taken away (Glazer & Weiss, 1976). Accordingly, the older group trained without platform tended to perform worse in the adult avoidance task when the difficulty was increased. This did not seem to be the case in the younger group trained without platform which showed immobility times similar to the rest of the groups and no deficits in the adult avoidance task. However, the differences between both groups did not reach significance.

Taken together, these results show that training the animals in a solvable task before the maturational requirements are met may have a higher impact on later adult learning than exposing them to an inescapable mildly stressful situation.

**GENERAL DISCUSSION**

The main finding reported in the present experiments is that learning difficulties at an early age, due to deficits in solving a spatial task, may induce long-lasting deleterious effects on learning a different avoidance task in adult rats. Adult rats trained to locate a hidden platform in a water maze at the age of 17 (Experiment 1) or 18 (Experiment 2) days required a higher number of trials to reach the learning criteria in a shock avoidance task than those rats receiving a similar training at the age of 25 days, regardless the difficulty of the task. In both experiments the younger group of trained rats showed spatial learning deficits, i.e., longer latencies to locate the platform and reduced search time in the target quadrant during the probe trial, compared to the older group. However, in both experiments the latencies to reach the platform of the younger groups decreased during the last acquisition trials. This fact could be interpreted as emergent new learning abilities, although they were not yet evident in the probe trial of Experiment 2. These results are in agreement with previous studies reporting a late ontogeny of some types of spatial learning. Rudy et al. (1987, 1988) reported a maturational deficit in rats younger than 20 days in the spatial abilities required for learning the relationship between the hidden platform and distal cues, although they were able to learn the platform location using proximal cues. Additionally, the results confirm other reports (Carman & Mactutus, 2001; Kraemer & Randall, 1995).
showing an inferior performance in pups younger than 20 days compared to older rats, even when a spaced trials learning procedure was used, which facilitate learning by reducing fatigue. Moreover, in the present experiments the spatial learning deficit was facilitated by the large size of the pool.

Using different learning criteria adult learning deficits of the young experimental group in the shock avoidance task were evident. These deficits cannot be attributed to unspecific effects arising from the exposure of the pups to aversive events or handling, nor to exercise or fatigue. It is therefore conceivable that in younger rats evidencing emergent albeit inefficient learning abilities, the perceived difficulty in learning a solvable task may be a critical factor in explaining adult learning deficits. This explanation is supported by the greater impairment in those groups trained at an early age in Experiment 2 compared to Experiment 1. It can be seen that the PN18 experimental group in Experiment 2 required a higher number of trials in reaching the avoidance learning criteria than the PN17 group in Experiment 1. However, in the early learning task the PN18 group of Experiment 2 performed better than the PN17 group in the previous experiment, showing evidence of emerging learning abilities. It is thus suggested that in Experiment 1 the animals would not have had as much chance to perceive the spatial task as solvable as the animals in Experiment 2. The magnitude of the deficit observed in the adult tone-avoidance task can therefore be related to the perceived learning failure rather than to the objective outcome of the early spatial task. Previous results showing that experiencing unsolvable discrimination problems may lead to learned helplessness and later learning deficits (Hiroto & Seligman, 1975) lend support to this proposal.

Such an interpretation would imply that the younger rats discriminate between the solvable fixed platform spatial task and the unsolvable random platform and non-platform tasks. Both fixed and random platform conditions involved placing the animal on the platform after each trial if they had not found it before. It can be expected that the younger animals are able to identify the platform location based on proximal cues. They may therefore perceive the fixed platform condition as a solvable task in spite of the fact that they are unable to solve it because this task requires complex processing of distal cues. However, the animals may perceive the random condition as an unsolvable task due to the changing location of the platform. Thus, although the outcome is similar in both conditions, i.e., failure in reaching the platform, the cognitive appraisal of the situations may be different. It has been proposed that experiencing situations in which the demands are perceived to outweigh the resources may be an important source of stress (Kemeny, 2003). The deleterious effect of early training in the fixed location platform task on adult learning may therefore be due to an excessive level of demand, leading to learned helplessness.

An interpretation in terms of learned helplessness may also account for the tendency to adult avoidance learning deficits evidenced in the group trained in the non-platform condition at 25 days of age. This tendency approached significant levels when task difficulty was increased using CARS 5 and 10 criteria. Moreover, the older random group performance in the adult avoidance task did not differ from the impaired younger group, which received early training in the fixed located platform task. The reduced activity or immobility seen in most rats belonging to the older random group during the probe trial suggest that such reduced responding may be related to learned immobility produced by the contingency between staying immobile and waiting to be taken away. Similar reinforcement mechanisms of immobility have been reported by Glazer and Weiss (1976) for inescapable shocks. A conservative explanation central to the learned helplessness phenomenon is the assumption that prior action-outcome noncontingency experience produces interference with subsequent learning, subsequent action-outcome relationships being judged as non-contingent or as less strongly related than they are (Reed, Frasquillo, Colkin, Liemann, & Colbert, 2001). Additionally, according to Maier and Seligman (1976), prior experience with action-outcome noncontingency will also produce motivational deficits and short-term emotional disturbances. Such a motivational deficit would prevent the initiation of responding, which may be the case in the PN25 group trained without platform. However, both the active swimming pattern and the absence of adult learning deficits in the non-platform younger group indicates that this condition may have been perceived differently by rats of different maturational stages.

It could be proposed that the younger pups do not experience swimming in the absence of platform as a stressful avoidance unsolvable task, but rather as exercise, which may be reinforcing in itself at this developmental stage. In fact, developing mice aged 14–21 days are able to acquire preferences for a place paired with administration of D-amphetamine at doses that induce lower increases in locomotor activity than at postweaning ages (Cirulli & Laviola, 2000). Moreover, physical activity has been reported to be naturally reinforcing for children if multiple, short exercise bouts are used, as it is the case in the present experiments (Epstein, Kilanowski, Consalvi, & Paluch, 1999).

There is an alternative epigenetic explanation of the results which would rely on specific changes in the brain learning systems. It is well known that early stimulation during sensitive developmental periods may modify the organization of the neuronal circuitry thus leading to permanent changes that influence adult behavior (Kolb,
The results of the younger experimental group performance in the spatial task showed that training took place during a critical developmental period in which learning abilities were emerging. Shaping of the specific brain circuits relevant for this task could therefore have been influenced by the perceived early learning failure. However, the fact that the adult deficits were found in an independent learning task points to a more general deleterious effect on brain plastic mechanisms. This would imply that early training in a learning task, before the specific brain circuits involved are able to solve it, may modify the synaptic organization compromising plastic changes in a variety of learning systems.

Whatever the relevant mechanism may be, the adult learning deficits shown by the early trained animals are more pronounced than those exhibited by the animals trained in the random condition at a later age. The group trained at an early developmental stage in the fixed location platform showed significant deficits in the adult tone avoidance task at different levels of difficulty. However, the deficits of those rats trained in the non-platform condition at 25 days of age approached significance only when the difficulty of the task was increased. This is consistent with previous findings reporting a higher beneficial effect of combined tactile-visual stimulation in the first postnatal week compared to the fourth on adult passive avoidance (Gschanes, Eggenreich, Windisch, & Crailsheim, 1998). Although infantile amnesia is a fairly pervasive phenomenon (Spear & Riccio, 1994) and retention of spatial navigation tasks does not exceed several days in preweaning rats (Carman & Mactutus, 2001; Carman et al., 2002; Kraemer & Randall, 1995), in the present study early learning training effects were evident 73 days later. This shows that there are long-lasting effects of early stimulation on either emotion and/or learning related brain systems organization and that these effects are independent of memory recall.

Although more research will be needed to explain the mechanisms and processes involved, it may be concluded that early training in a spatial task, before achieving the maturational stage required to solve it, may have long lasting effects on adult learning. These effects do not necessarily arise from early stressful events. The present findings thus point to the role of early learning experiences and infant history of success and failure in shaping adult learning abilities in general.

NOTES

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