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Behavioural Brain Research 133 (2002) 117–124

BEHAVIOURAL BRAIN RESEARCH

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Research report

Effects of predictable and unpredictable intermittent noise on spatial learning in rats

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Received 17 July 2001; received in revised form 4 December 2001; accepted 4 December 2001

Abstract

The effects of predictable (periodic) and unpredictable (aperiodic) intermittent noise of moderate intensity (68 dB) on the learning of a complex T-maze by genetically defined rats were investigated. In Experiment 1, three groups ($n = 8$) of rats learned a multiple T-maze, one group under control conditions, one group with predictable intermittent noise and one group with unpredictable intermittent noise. Results showed a profound effect of noise on learning and behavioural scores. Noise-exposed animals made less errors, finished their trials sooner and explored less. There was no difference between predictable and unpredictable noise. Further tests, during which formerly noise-exposed groups learned a new route under control conditions (Experiment 2) or the former controls learned a new route with noise (Experiment 3), suggest that the effects of noise on learning were caused by an effect of noise on memory formation and/or retrieval, rather than by long-term shifts in behavioural strategies. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Noise; Intermittent; Predictability; Spatial learning; Rat; Attention

1. Introduction

Recent development of sophisticated genetic rodent models of learning and behaviour has led to renewed interest in non-genetic factors that might interfere with experimentally controlled genetic determinants of behaviour [38]. For example, in a study with identical experimental protocols, Crabbe et al. [7] found considerable differences in several behavioural parameters across different laboratories when testing the same strains of mice. The present study investigates aspects of the acoustic environment. Background noise represents an important, though often poorly controlled, factor in laboratory settings. Noise of moderate intensity is produced by air conditioning devices and experimental equipment or is provided as a 'masking' noise.

In studies on spontaneous behaviour of laboratory rodents, systematic control of background noise began with a study by Broadhurst [4], who found a different influence of low (78 dB) and high (94 dB) intensity noise on open-field behaviour of rats. Subsequently, the use of predefined background noise became a standard procedure in many open-field studies [5,15,16,24,28,36]. By contrast, there are very few studies on the possible effects of noise on learning. An early report was given by Morey [22], who found higher swimming speed in rats in a water maze when the sound of an auto horn was added during trials. Bhattacharya et al. [2] reported enhanced maze learning in mice exposed to loud noise (109 dB (A)) before trials. Two studies in chickens with intermittent noise found better visual discrimination learning with moderate (83 dB) compared to higher intensity (101–123 dB) noise [12] and better learning with periodic intermittent than with aperiodic intermittent noise [18]. Thus, aside from the intensity of noise, the predictability of noise might be crucial in determining the effects of noise on behaviour and learning.

The present study is part of a systematic research on the effects of environmental factors on spontaneous behaviour and learning in genetically defined laboratory rodents. A recent study revealed a profound influence of continuous white noise-like background noise of moderate intensity (70 dB) on maze learning in rats (prior submission). With acute noise exposure, rats made less

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PII: S0166-4328(01)00466-1

errors and took less time to complete their trials. The present study specifically addresses the question whether the effects of noise differ when the background noise is predictable (periodic) or unpredictable (aperiodic). Whereas studies in chickens [18] suggested better performance with predictable noise, studies in humans did not provide a clear-cut picture. O'Malley and Poplawsky [23] found improving effects of aperiodic intermittent noise, whereas Carter and Beh [6] reported impairing effects. Improving and impairing effects might depend on the frequency of the intermittent noise [3] or the type of task [31]. As one important effect of noise in humans might by masking of inner speech [25], the mechanisms leading to noise-induced changes during spatial learning in rodents could be fairly different. Therefore, the present study should give a first estimate whether the predictability of background noise might be a relevant factor in studies on spatial learning in laboratory rodents.

In Experiment 1, three groups of rats were compared; a control group without noise (≤ 35 dB), a group with periodic intermittent noise (PN) and a group (UN) with aperiodic intermittent noise (both 68 dB). Experiments 2 and 3 were designed to evaluate the extent to which the influence of noise reflected an immediate influence of acute noise or a long-term change in behavioural strategies. In Experiment 2, the group having received aperiodic intermittent noise in Experiment 1 learned under control conditions (UN-C), such that one group with additional noise (PN) and two groups without noise, but different experimental histories (Control, UN-C), were compared. In Experiment 3, the control group from Experiment 1 and 2 learned under the influence of predictable noise (C-PN), so that two noise-exposed groups (PN, C-PN) with different experimental histories could be compared.

2. Method

2.1. Animals

Subjects were 24 female rats of the DA inbred strain (ZVZ/Harlan-Winkelmann, Borchen, Germany), aged 6 months and weighing 171 ± 8 g. DA rats have normally pigmented eyes [14]. They were housed individually on a 12:12 h light:dark cycle in standard laboratory cages ($37 \times 21 \times 15$ (l $\times$ w $\times$ h) cm) and received ad lib food and water. Rats were handled before maze learning started. The handling procedure consisted of taking each rat individually from its cage and keeping it on the hands for 5 min. This was repeated for 5 days.

2.2. Maze and acoustic environment

The mazes used in the three experiments were complex elevated multiple T-mazes, as described in Ref. [26]. For each experiment, a new maze route was used. In Experiment 1, the maze had 12 choice points and the length of the direct route to the goal was 8 m. The maze used in Experiment 2 had 18 choice points and the route length was 12.4 m. The maze in Experiment 3 had 12 choice points and the route from start to goal measured 8 m. At the start position of the maze, there was a circular plastic box that confined the rats until a trial started and at the end of the route there was a goal box similar to the rats' home cage. At the goal, rolled oats were provided as a food reward. The maze was placed in a sound-protected room with background noise level of ≤ 35 dB. During noise treatment, computer-generated broadband noise of 68 dB with a frequency maximum from 70 to 3000 Hz was delivered through speakers suspended above the maze at a height of 190 cm. Predictable (PN) and unpredictable (UN) intermittent noise were identical except for the sequencing of noise bursts. In the PN condition, short periods of noise (67 ms) were separated by intervals of 1 s. In the UN condition, the lengths of the noise bursts were the same, but the intervals varied randomly between 67 and 1933 ms with a mean duration of 1 s. Thus, mean total duration of noise exposure was the same in the PN and the UN condition.

2.3. Procedure

Rats were taken individually from their home cages and placed at the start position of the maze in the plastic cylinder. Lifting the confining cylinder by means of a string mechanism started a trial. After reaching the goal box, subjects were allowed to feed for 20 s. During noise trials, the noise generator was turned on 5 s before a trial was started and turned off 5 s after rats had reached the goal box. The rats' behaviour was monitored through an observation window. The number of errors, the time animals took to finish a trial, the amount of exploration and the rate of freezing were recorded. During freezing—a behaviour indicating fear—a rat remains motionless, cowering flat on the ground or with his back humped. An error was defined as any entry with the whole body (tail not included) into a cul-de-sac. Measures of exploration were the frequency of rearing, sniffing, turning and head-dipping. These behaviors were recorded separately. For the sake of clarity, they will be reported as a combined exploration score. This is justified since all exploration measures responded in the same way to the experimental conditions. For example, in Experiment 1, each of the four measures differed significantly between controls and each of the noise-exposed groups, while there was no difference between the noise-exposed groups. Similarly, in Experiment 2, all exploration scores differed significantly from controls in the first trial block and none differed during late trials.

2.4. Statistics

For statistic analysis of errors, times spent on the maze and exploratory behaviour scores from five trials were combined and ANOVAs with noise as independent factor and trial blocks as a repeated measure were carried out. For further analysis of significant main effects of noise, Fisher's LSD was used, for comparison of differences between noise treatment in single blocks of trials after finding a significant noise × trial block interaction, Tukey's HSD test was applied. In addition, simple factorial ANOVAs were run to test for the noise effect on the first single trial of each experiment. Freezing scores, which were not normally distributed, were analyzed using a Kruskal–Wallis ANOVA (Experiment 1 and 2) or a Mann–Whitney *U*-test (Experiment 3).

3. Results

3.1. Experiment 1

The main results of Experiment 1 are depicted in Fig. 1. Intermittent noise had a profound effect on errors (Fig. 1a), the time taken for running through the maze (Fig. 1b) and exploratory behaviour (Fig. 1c). The strength of this effect was equal with PN or UN. There was a significant reduction in the number of errors over blocks of trials ($F_{6,126} = 271.59$, $P < 0.0001$), a significant effect of noise ($F_{2,21} = 22.88$, $P < 0.0001$) and a significant interaction ($F_{12,126} = 2.26$, $P < 0.05$). Planned comparisons between noise treatments showed a significant difference between controls and the PN ($P < 0.0001$) and UN ($P < 0.0001$) group, but not between the noise treatment groups ($P > 0.7$). Further exploration of the noise × trial block interaction showed a significant difference in the first trial block between controls and the PN ($P < 0.005$) as well as the UN treatment ($P < 0.0005$), whereas there was no such difference in the last trial block (all $P > 0.15$). In the first trial, there was no difference in the number of errors between treatments ($F_{2,21} = 0.28$, $P > 0.75$).

The time spent on the maze decreased over trial blocks ($F_{6,126} = 124.64$, $P < 0.0001$). There was a significant effect of noise treatment ($F_{2,21} = 24.27$, $P < 0.0001$), but no interaction trial block × noise ($F_{12,126} = 1.76$, $P > 0.05$). Comparisons between noise treatments revealed a difference between controls and the PN ($P < 0.0001$), as well as the UN ($P < 0.0001$) treatment, but no difference between noise groups ($P > 0.8$). There was no difference between treatments in the first trial ($F_{2,21} = 0.59$, $P > 0.5$).

Exploratory behaviour changed over blocks of trials ($F_{6,126} = 450.80$, $P < 0.0001$). There was a difference between treatments ($F_{2,21} = 41.18$, $P < 0.0001$). This

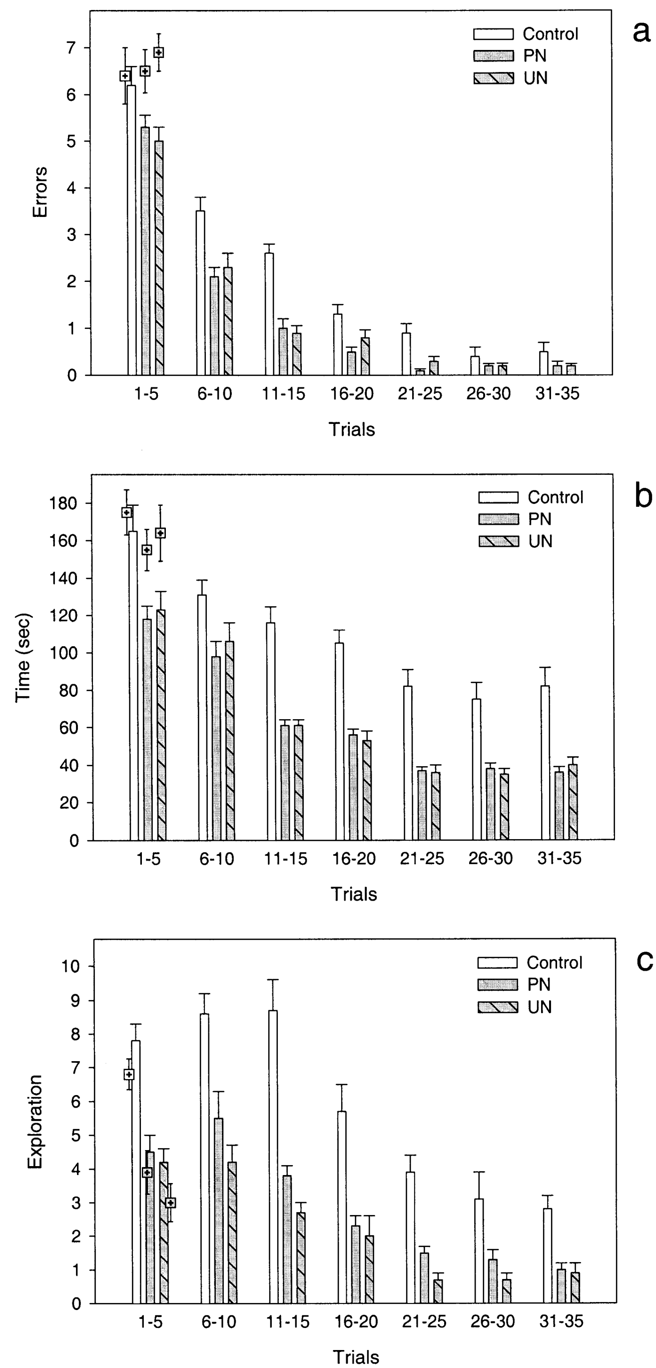

Fig. 1. Errors (a: top); time spent on the maze (b: middle); and exploration (c: bottom) in Experiment 1. Means ± S.E.M. Bars are based on individual means for five trials; square dots refer to the first trial. Control: control group ($n = 8$) without noise (≤ 35 dB); PN: group ($n = 8$) with predictable periodic intermittent noise (68 dB); UN: group ($n = 8$) with unpredictable aperiodic intermittent noise (68 dB). For further details of acoustic stimulation, see text.

difference was significant between the control group and the noise-exposed groups (both $P < 0.0001$), but not between the noise groups ($P > 0.1$). In addition, there was a trial block × noise interaction ($F_{12,126} = 40.52$, $P < 0.0001$). In controls, exploratory behaviour increased during the first three blocks, before it started to decrease. In the noise-exposed groups, reduction of exploratory behaviour began earlier. A difference between treatments was already present in the first trial ($F_{2,21} = 12.35$, $P < 0.0005$). Both the PN group ($P < 0.005$) and the UN group ($P < 0.0005$) differed from the control group, whereas the difference between the noise groups was not significant ($P > 0.25$).

Freezing behaviour occurred rarely and differences between the groups were not significant (Kruskal–Wallis test: $\chi^2 = 4.00$, df = 2, $P > 0.1$).

3.2. Experiment 2

The findings of Experiment 2 are summarized in Fig. 2. The number of errors (Fig. 2a) decreased over blocks of trials ($F_{4,84} = 414.65$, $P < 0.0001$). There was a significant effect of noise ($F_{2,21} = 11.18$, $P < 0.0005$) and a significant noise × trial block interaction ($F_{4,84} = 2.51$, $P < 0.05$). The PN group differed from controls ($P < 0.0005$) and the UN-C group ($P < 0.005$), while there was no difference between controls and UN-C rats ($P > 0.3$). Further exploration of the noise × trial block interaction showed that the PN group differed from the control and the UN-C group in the first and second block of five trials (all: $P < 0.001$), while there was no difference between controls and the UN-C group (both: $P > 0.95$). In the third to fifth block of five trials, differences between groups were not significant. In the first trial, no group differences were present ($F_{2,21} = 0.09$, $P > 0.9$).

The time spent on the maze (Fig. 2b) decreased over blocks of trials ($F_{4,84} = 130.12$, $P < 0.0001$). There was a significant effect of noise treatment ($F_{2,21} = 22.20$, $P < 0.0001$), but no interaction ($F_{4,84} = 0.68$, $P > 0.7$). Controls differed from the UN-C ($P < 0.05$) and the PN ($P < 0.0001$) group and the difference between the UN-C and the PN group was also significant ($P < 0.0005$). There was no difference between treatment groups in the first trial ($F_{2,21} = 0.09$, $P > 0.9$).

The rate of exploratory behaviour (Fig. 2c) changed over blocks of trials ($F_{4,84} = 5.27$, $P < 0.001$). There was a significant effect of noise treatment ($F_{2,21} = 14.12$, $P < 0.0005$) and a significant noise × trial block interaction ($F_{4,84} = 3.76$, $P < 0.001$). Control rats explored more than PN ($P < 0.0001$) and UN-C rats ($P < 0.02$) and UN-C rats explored more than PN rats ($P < 0.02$). Further exploration of the trial block × noise interaction showed that the difference between controls and PN rats was significant over the whole experiment (all: $P < 0.005$), whereas the difference between controls and UN-C rats was significant during the first ($P < 0.0005$), but not the second ($P = 0.08$) or later trial blocks (all: $P > 0.7$). During the first trial, the UN-C group differed from the control group ($P < 0.01$), but not from the PN

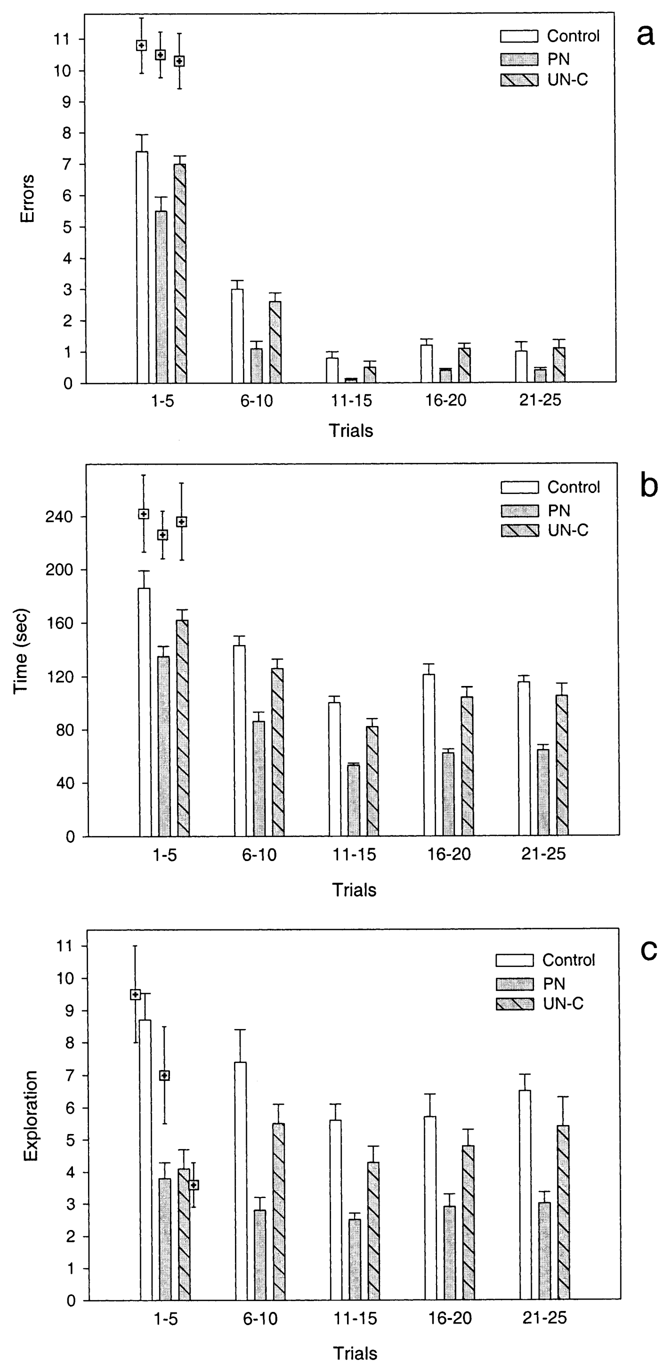

Fig. 2. Errors (a: top); time spent on the maze (b: middle); and exploration (c: bottom) in Experiment 2. Means ± S.E.M. Bars are based on individual means for five trials; square dots refer to the first trial. Control: control group ($n = 8$) without noise (≤ 35 dB); PN: group ($n = 8$) with predictable periodic intermittent noise (68 dB); UN-C: group ($n = 8$) which had experienced unpredictable aperiodic intermittent noise (68 dB) in Experiment 1 and learned the maze under control conditions in Experiment 2.

group ($P > 0.05$). The difference between controls and PN rats was also not significant ($P > 0.2$).

Freezing behaviour occurred rarely and differences between the groups were not significant (Kruskal–Wallis test: $\chi^2 = 0.34$, df $= 2$, $P > 0.8$).

3.3. Experiment 3

Results from Experiment 3 are given in Fig. 3. The number of errors (Fig. 3a) decreased over blocks of trials ($F_{3,42} = 160.73$, $P < 0.0001$), but there was no difference between groups ($F_{1,14} = 0.57$, $P > 0.4$) and no interaction ($F_{3,42} = 0.08$, $P > 0.95$). Also, in the first trial, the difference in errors was not significant ($F_{1,14} = 0.86$, $P > 0.3$).

Similarly, the time (Fig. 3b) spent on the maze decreased ($F_{3,42} = 64.22$, $P < 0.0001$). In addition, there was a difference between groups ($F_{1,14} = 7.77$, $P < 0.02$), but no interaction ($F_{3,42} = 1.18$, $P > 0.3$). Rats that had been noise exposed in Experiment 1 and 2 finished their trials slightly sooner. There was no difference between the groups in the first trial ($F_{1,14} = 0.37$, $P > 0.5$).

Exploratory behaviour also changed over blocks of trials ($F_{3,42} = 8.39$, $P < 0.0002$), but there was no difference between groups ($F_{1,14} = 0.53$, $P > 0.4$), no interaction ($F_{3,42} = 1.91$, $P > 0.1$) and no difference in the first trial ($F_{1,14} = 0.66$, $P > 0.4$).

Freezing behaviour occurred rarely, but was overall more frequent in C-PN rats (U-test: $Z = -2.22$, df $= 1$, $P < 0.05$).

4. Discussion

The results demonstrated a profound effect of intermittent noise of moderate intensity on the number of errors, the time taken until reaching the goal and the extent of exploratory behaviour. Overall, the effects of predictable and unpredictable noise were similar. With regard to parameters that commonly are considered valid measures of spatial learning in maze experiments, intermittent noise had an improving effect on performance. This finding raises several questions, particularly, (1) why noise improved rather than impaired performance; (2) why the effects of predictable and unpredictable noise were similar; (3) how noise affected performance; and (4) what might be the physiological basis of noise effects.

Results reveal a different time course of response to noise between the different parameters. A first interesting aspect is a clear differentiation between the effect on error scores and the effect on exploratory behaviour. This allows for distinguishing errors related to spatial memory for the route from possible errors due to other factors (for detail see Section 4.1). A second interesting effect is that the effects on exploratory behaviour were asymmetric, in that the onset was immediate, while the return to control-like behaviour after cessation of acoustic treatment occurred with a considerable delay.

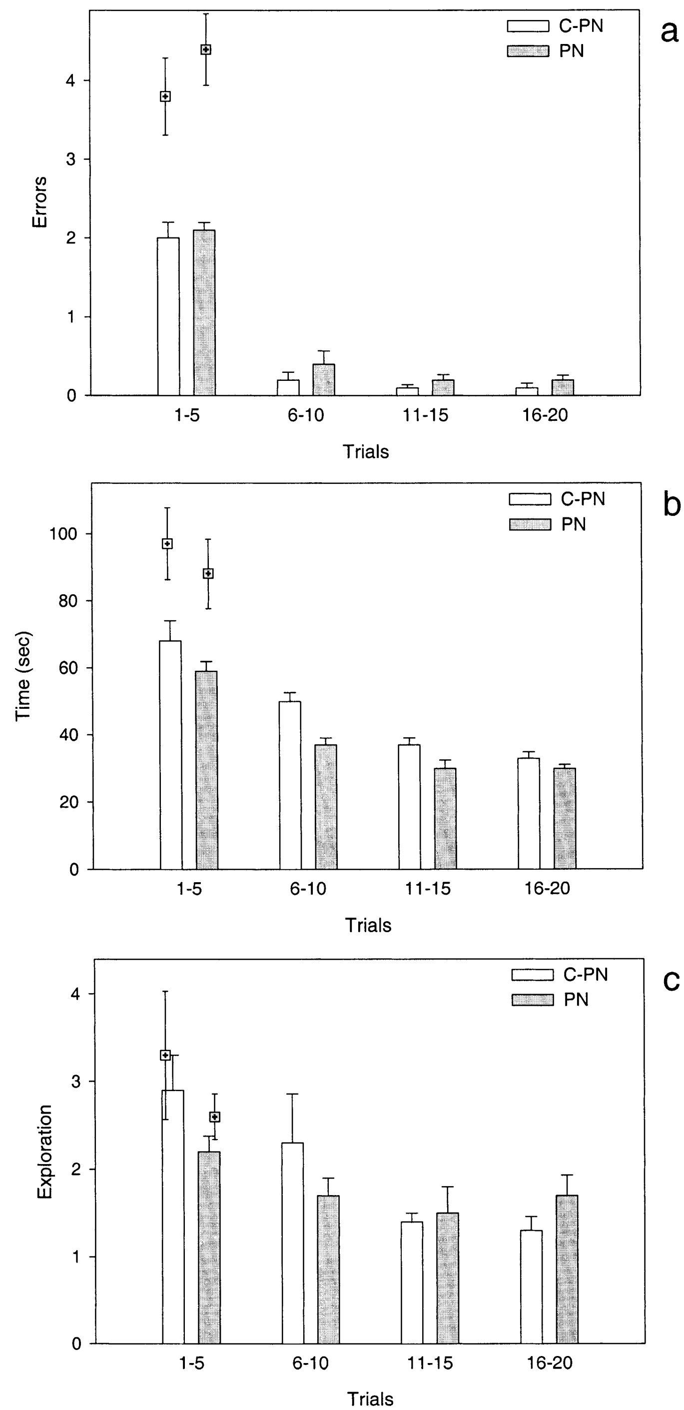

Fig. 3. Errors (a: top); time spent on the maze (b: middle); and exploration (c: bottom) in Experiment 3. Means ± S.E.M. Bars are based on individual means for five trials; square dots refer to the first trial. C-PN: control group ($n = 8$) without noise (≤ 35 dB) during Experiments 1 and 2, which learned the maze under PN conditions in Experiment 3; PN: group ($n = 8$) with predictable periodic intermittent noise (68 dB).

This becomes particularly clear in Experiment 2. This lag-effect might raise the question whether the design, which was intended to compare experimental histories, could have had disadvantageous effects in that the group noise-exposed during all experiments (PN) might have developed a reduced effect due to habituation. Results of Experiment 3, where the control group from Experiment 1 and 2 was compared to the PN group from these experiments under the same acoustic treatment (PN), suggest that this was not the case. The error scores of both groups were closely similar. Regarding the time spent on the maze and exploratory behaviour, the former controls (C-PN) took some trials to perform at the same level as the PN group. Similar to the behaviour of the UN-C group in Experiment 2, this hints at a long-lasting component in the noise effects. This finding is of general interest because it suggests that not only differences in acute noise exposure, but also different individual histories of acoustic experience can affect learning experiments.

4.1. Improved learning

Errors scores represent the most important parameter in experiments on spatial learning and memory. The time until a subject reaches the goal is also often taken into consideration. The latter measure is, however, liable to biases caused by motivational and other factors, which do not reflect true learning [20]. In the present study, comparison of error scores with times until reaching the goal and frequency of distinct exploratory behaviors suggests that differences in error scores reflect true learning rather than confounding factors [37]. In principle, it is conceivable that rats in a maze show behaviour that is not due to insufficient knowledge of the maze route, but nevertheless has to be judged as an error by the experimenter. For example, a rat might be interested in exploring the whole maze including alleys he has memorized as cul-de-sacs. In this study, a comparison of error scores with exploratory behaviour indicated that differences in exploratory behaviour did not confound error scores because otherwise there should have been a clear difference in error scores between the experimental groups on the first trial of an experiment. In all experiments, there was no difference in error scores in the first trial, before any route learning could have occurred. By contrast, there was a clear effect on exploratory behaviour in the first trial of Experiment 1, with less exploration than in controls in both noise-exposed groups (PN, UN). In Experiment 2, the group that had been noise-exposed in Experiment 1 and was run under control conditions (UN-C) in Experiment 2, started with reduced exploratory behaviour. Only over a number of trials, the rate of exploratory behaviour approached the level of the control group. Again, despite this profound difference from the control group in exploratory behaviour in the first trial, there was no difference in errors and the number of errors in the UN-C group was close to the control group all over Experiment 2. Thus, different experimental histories profoundly affected exploratory behaviour, but not the number of errors. Also, the noise treatment group in Experiment 2 (PN) did not differ from the other groups (Control, UN-C) in the number of errors in the first trial. As soon as learning could play a role, error scores between treatment groups began to differ. Overall, results show a clear improvement of learning under noise exposure, although they do not permit the deciding to what extent the difference in learning was dependent on better acquisition or better retrieval or a combination of these.

4.2. Predictable versus unpredictable noise

Effects of predictable and unpredictable noise were fairly similar. Regarding studies on differential effects of intermittent noise in humans [6,23], one reason might be that noise during spatial learning in rats cannot interfere with processes analogous to human inner speech [25]. A conclusive answer to this possibility would require testing the effects of predictable and unpredictable intermittent noise on route learning in humans. The facilitating effects of periodic versus aperiodic intermittent noise on discrimination learning in chickens [18], however, suggest that the presence or absence of inner speech is not the only factor. At least two other factors could be important. Firstly, there might be a difference between tasks that require a subject to recall a fixed route and tasks that require flexible use of different and spatially distinct cues. For instance, Marczynski and Urbanic [21] found impairing effects of single noise bursts on rats' spatial working memory in a radial maze. Secondly, there might be two modes of perceiving intermittent noise. In humans, perception of periodic noise can switch from the percept of a rasping stream of noise to the percept of distinct elements [17]. Therefore, it is possible that despite their different temporal structure, the rats perceived both types of noise as a continuous stream. This would be consistent with the fact that periodic and aperiodic intermittent noise had about the same effect as well as with the finding of a similar effect of continuous (prior submission) and intermittent noise (this study). A study on locomotor activity in rats of about the same age as in the present study also found similar effects of continuous and intermittent noise [8]. Thus, the main effects of noise in the present study might have been due to modulation of arousal by a perceptually continuous stream of background noise.

4.3. Psychological mechanisms

Experiments on the effects of enhanced arousal on psychological variables were mainly carried out with humans [11]. A main effect of moderately increased arousal might be a more selective use of cues [9,10] and a facilitating effect of noise on long-term memory formation. The fact that the influence on behaviour and learning follows a similar inverted U-shaped function [8,12,13] suggests that the effects of noise-induced arousal in humans and animals have a similar basis.

4.4. Physiological mechanisms

Acoustic stimulation can be expected to exert a complex effect on physiological activity in several brain regions. Nevertheless, there are some physiological effects, such as the modulation by noise of major transmitter systems, which can be assumed to be central to the effects observed. A number of studies on spatial learning suggest a crucial role of cholinergic systems in maze learning. If given the anticholinergic, scopolamine rats could find the goal in a simple maze in a cued but not in a spatial version [33]. Also, in a 14-U multiple T-maze, scopolamine strongly impaired learning [34]. Noise of moderate intensity, as used in the present study, increased choline uptake in several brain regions [19] including the prefrontal cortex and the hippocampus. Therefore, the facilitating effects of noise might have been due to increased cholinergic activity. It should be mentioned, however, that intensity and duration of noise exposure might be critical. Whereas Lai [19] found an activating effect of noise of 70 dB that is approximately the level used in the present study, with noise of 100 dB, cholinergic activity was reduced. Similarly, Thiel at al. [35] found impaired learning and prevention of cholinergic activation by noise during escape learning. In their study, subjects were exposed to noise for 2 h before experimental sessions. Similar to noise of high intensity, this also might have led to exhaustion of cholinergic systems.

A second important factor might be activation of noradrenergic systems. Central noradrenergic systems spreading from the locus coeruleus are crucially involved with selective and flexible control of attention [29]. Acoustic stimulation immediately increases the activity of these central noradrenergic systems [1,30]. In humans with impaired attention due to the antinoradrenergic clonidine, attention could be improved again by noise [32].

In terms of psychological and physiological mechanisms, it might be of interest how noise effects on memory might be distinguished from emotional effects. Of course, it cannot be excluded that the noise effects also have an emotional component. But it should be kept in mind that emotional factors and long-term memory formation are closely related in terms of some of the factors involved. For example, glucocorticoids, which are widely used as an indicator of emotionality in laboratory animals, are crucially involved with long-term memory formation [27].

All in all, results showed comparable effects of predictable and unpredictable noise of moderate intensity on maze learning in rats. In terms of classical maze learning parameters, performance was profoundly improved. A detailed analysis of error scores and other behavioural measures suggests that an effect on memory formation and/or retrieval is likely. The physiological mechanisms involved require further study, but an immediate effect on neurotransmitter systems mediating attention and spatial learning is likely.

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