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Research report

Inertial stimuli generated by arena rotation are important for acquisition of the active place avoidance task

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The active place avoidance task is used for testing cognitive abilities in rats. A rat, placed on a rotating circular arena, should avoid an unmarked sector defined with respect to stable extra-arena cues. We hypothesized that the inertial stimuli generated by the arena rotation may contribute to the performance in the task. These stimuli provide permanent information to the rat concerning changes in its position with respect to the extra-arena cues, it means to the reference frame in which the to-be-avoided sector is defined. To test the hypothesis, we trained one group of rats on a stable arena while extra-arena cues rotated around the arena. This eliminated the inertial stimuli generated by the arena rotation while preserving other aspects of the task. Six out of seven rats from this group did not learn this modified task. The remaining rat learned it equally well as rats from a control group learned the standard active place avoidance task. After six days of training, we changed the tasks between the groups. The control rats solved the modified task as well as the standard task. We conclude that the inertial stimuli generated by the arena rotation are important for acquisition of the active place avoidance task but not for performance once the task has been mastered. We suggest that rats must perceive the distal extra-arena cues as stable in order to associate the position of the to-be-avoided sector with these cues.

1. Introduction

The ability to orient in space is essential for the survival of animals. During navigation, animals process various types of information including accelerations and decelerations. Accelerations and decelerations are sensed by the vestibular system, proprioceptors and skin mechanoceptors. They are processed in the brain and provide information about the changes of an organism's position and angular orientation in the environment. It has been shown that animals can navigate when only these inputs are available [5,6,9,15–17,21,31,32]. For example, golden hamsters are able to return to a starting position after being passively transported to some other place in darkness [6]. Damage to the vestibular system results in deficits in spatial learning and memory [24].

In a non-inertial environment a subject can perceive accelerations and decelerations. An example of a non-inertial environment is a rotating arena. The rotation produces centrifugal acceleration which is directly proportional to the force acting on an animal's vestibular system, skin mechanoceptors and proprioceptors. Stimuli invoked by such an inertial force is referred to as "inertial stimuli". An inertial environment in which no such forces exist is referred to as a "stable environment".

A rotating arena dissociates orientation cues into "arena cues" and "extra-arena cues". A subject on a rotating arena can represent its position with respect to the reference frame defined either by the arena cues or by the extra-arena cues. It has been shown that rats are capable of representing positions with respect to both reference frames simultaneously [8].

The active place avoidance task [3] is a well established behavioral task in neuroscience research, e.g. [2,4,14,27,33]. It is performed on a slowly rotating arena (1 rpm) in which a rat should avoid a 60° wide unmarked sector defined by extra-arena cues. Rats learn the active place avoidance task quickly. They reach a stable level of performance after four 20-min long training sessions [27]. Wesierska et al. [33] and Kubik and Fenton [14] showed that two cognitive processes are important for solving the task – segregation of stimuli into coherent subsets (arena frame and extra-arena frame) and navigation with respect to one of the subsets (extra-arena frame). The task is hippocampus-dependent [2], however, unlike the Morris water maze task, it is sensitive to unilateral lesion during training [4].

Since the active place avoidance task is performed on a rotating arena, the inertial stimuli are constantly present. They provide information to a subject that its position is changing with respect

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to the stable extra-arena world by which the to-be-avoided sector is defined. For this reason they may contribute to performance in the task. We expected that the contribution of the inertial stimuli generated by the arena rotation would be rather mild because they are relatively weak due to the slow rotation of the arena (1 rpm) and because the extra-arena visual cues provide all the necessary information for solving the task. However, a pilot experiment indicated that the contribution is essential. To confirm this finding, we performed the experiment presented in this paper. One group of rats was trained in the standard active place avoidance task described above whereas another group was trained in a modified version. The difference between the tasks was that in the standard task the arena rotated while the surrounding world was stable whereas in the modified task the arena was stable while the surrounding world together with the to-be-avoided sector rotated around the arena. By rotating the world around the stable arena we eliminated the inertial stimuli generated by the arena rotation while keeping the other aspects of the task unchanged including the necessity to actively locomote in order to avoid the to-be-avoided sector. Therefore, it was possible to directly test the role of the inertial stimuli generated by arena rotation on acquisition of the task. The two groups of rats were trained for six days (Phase 1). The duration of the training was sufficient for the rats trained in the standard task to reach a stable level of performance [27]. After six days the tasks between the groups were switched and training continued (Phase 2). The purpose of Phase 2 was to test whether the rats which mastered the standard task in Phase 1 were able to solve the modified task.

2. Material and methods

2.1. Subjects

The subjects ($n = 14$) were male adult Long-Evans rats obtained from the breeding colony of the Institute of Physiology, Czech Academy of Sciences. They were three months old at the beginning of the experiment and weighed between 250 g and 300 g. They were housed in groups of two to three per cage in a temperature-controlled animal room (21 °C) with a 12/12 h light/dark cycle. Food and water were freely available. The rats were housed in the animal room for 10 days before the experiment started. The experimental procedures were carried out during the light period of the cycle. They were in accordance with the Institutional and NIH guidelines and the directive of the European Communities Council (86/609/EEC).

2.2. Apparatus

The apparatus consisted of a circular arena (diameter = 79 cm) surrounded by an annular belt (inner diameter = 80 cm, outer diameter = 130 cm) (Fig. 1A). The arena and the belt could be rotated independently of each other by two electromotors located below the arena and the belt.

The arena wall (height = 40 cm) was transparent. The belt wall (height = 100 cm) was a black curtain with a black annular board at the top (inner diameter = 65 cm, outer diameter 130 cm) (Fig. 1A). The belt, the black curtain and the black annular board formed an enclosed space around the arena. A subject on the arena could see only a part of the ceiling of the experimental room directly above the arena through the opening in the annular board.

Three salient cues were attached to the black curtain. A white card (width = 42 cm, height = 55 cm) was on the west side, 34 cm above the arena. Another white card of the same size was on the northeast side, 38 cm above the arena. A lamp was located on the east side, 80 cm above the arena. The lamp was the only source of light in the experimental room. It illuminated the enclosed space around the arena.

There was a camera located above the arena. The camera was connected to a computer-based tracking system (iTrack, Bio-Signal Group, USA) located in an adjacent room. Since either the arena or the belt rotated during experiments, a subject's position on the arena could be represented with respect to the reference frame defined either by the arena or by the belt. The computer-based tracking system recorded both positions with a 40 ms sampling rate by tracking two infrared light emitting diodes. One diode was attached to the subject on the arena, while the other was attached either to the arena or to the belt. Tracking the second diode made it possible to calculate the position of a subject with respect to the rotating reference frame.

The computer-based tracking system also controlled a device for delivering an electrical current. When activated, a subject felt an aversive stimulus on its paws.

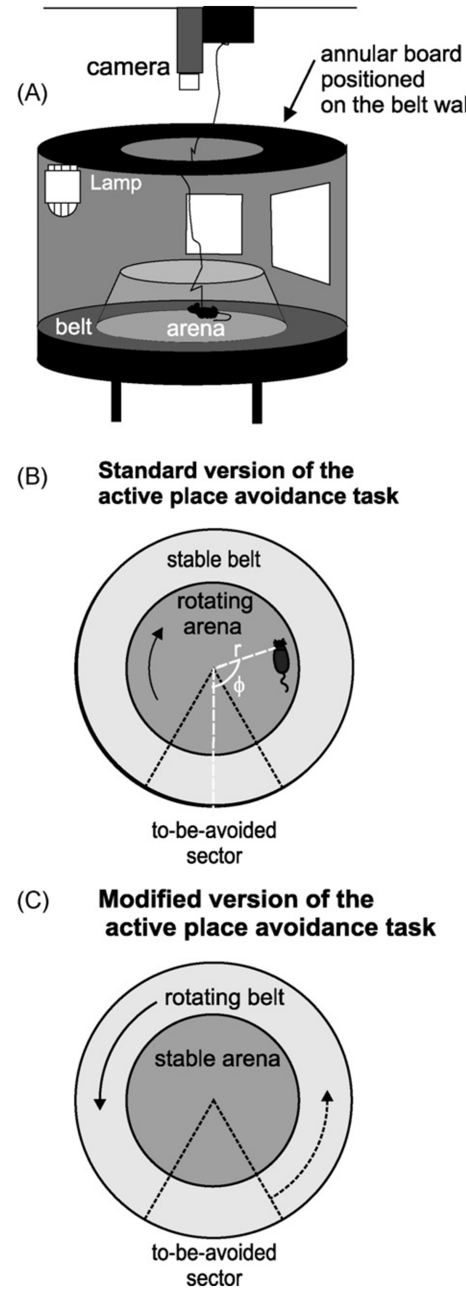

Fig. 1. (A) Behavioral apparatus. (B) Schematic illustration of the standard active place avoidance task. A rat on the rotating arena should avoid a 60° to-be-avoided sector defined with respect to the stable belt. (C) Schematic illustration of the modified active place avoidance task. A rat on the stable arena should avoid a 60° to-be-avoided sector defined with respect to the rotating belt.

2.3. Initial manipulation with the animals

Each animal was handled by the experimenter for 2- to 3-min over three consecutive days prior to experiment onset.

After the last handling day, in order to the connect the rats with the device for delivering electric current, a hypodermic needle was used to pierce the rats' skin on the neck. The sharp end of the needle was bent into a closed loop in order to prevent the needle from slipping out of the skin. The procedure was carried out in awake rats as they tolerated this procedure well.

2.4. Behavioral training

The rats were habituated to the arena in 5- to 8-min sessions carried out over two consecutive days. The arena and the belt were stable during the habituation sessions. The animals could freely explore the arena as no aversive stimuli were presented.