



Spatial learning and memory differs between single and cohabitated guinea pigs

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ABSTRACT

In socially-living animals, social enrichment enhances spatial learning and memory while separation from conspecifics can severely impair these abilities. In the present work, guinea pigs were kept in isolation or cohabitated in heterosexual pairs and then subjected to a labyrinth task. Latency-time to bait, error-rate, amount of movement and pre- and post-experimental cortisol (CORT) were registered. During a 5d-acquisition phase, single animals ($N=19$) showed a more efficient encoding of spatial information, with significantly decreased latency-time and error-rate over the time course. In contrast, cohabitated animals ($N=19$) did not show a significant improvement. Three days after acquisition, memory was tested in a retention test, under the same conditions. With regard to behavioral performance, there was no significant difference between cohabitated and single animals. Pre-experimental CORT was significantly higher in cohabitated animals when compared to single ones. Post-experimentally, CORT increased significantly in singles but not in cohabitated animals when compared to pre-experimental values. Thus, both groups did not differ from each other at that point. Social condition seemed to be an important modulator, in that learning and memory were more impaired in paired animals than in single ones. The failure of cohabitated animals to encode spatial memory more quickly may have been caused by a more chronically up-regulated HPA-axis. The post-experimental CORT increase of singles may be due to more efficient handling of short-term stress exposure.

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1. Introduction

Spatial memory is the ability of an individual to recognize, store and retrieve knowledge about spatial features of its environment [1]. It is a domain that seems to be particularly susceptible to the negative effects of stress exposure. Spatial information is predominantly processed in the hippocampus [2]. This brain structure is highly sensitive to steroid hormones, showing considerable malleability both during development and adulthood. The hippocampus has been proposed as a major site for negative feedback control of the HPA (hypothalamic-pituitary-adrenal)-axis [3,4]. Chronic stress can cause dendritic retraction and atrophy in the hippocampus [5,6] and thus may impede spatial learning and memory [7–9]. Acute stress may impair spatial abilities as well. However, its actions are less dependable, as conflicting results have been reported [10–13]. McEwen and Gould [14] proposed that hippocampal damage is positively correlated with the length and power of a stressor. Thus, spatial ability may be affected permanently when stress is severe and sufficiently long-lasting, but reversibly so when the stressor is applied less intensely and for a shorter period.

An experimental paradigm that has received considerable attention in studies concerning stress and spatial ability is the social environment [15]. Female and male rats raised in a socially enriched environment performed better on a spatial memory task than rats reared in isolation [16]. Long-term environmental-enrichment reduced the spatial memory decline in aging mice [17]. In male rats raised either socially or isolated from weaning, social enrichment enhanced the speed at which subjects acquired spatial knowledge [18].

Considering this background, the aim of the present work was to determine whether the socio-sexual environment influences spatial learning and memory in guinea pigs (*Cavia aperea f. porcellus*). The species was chosen because of the various advantages this rodent model possesses. Endocrinology and behavior have been documented systematically [19–21]. Furthermore, guinea pigs – while polygynous – form mutual, long-lasting bonds between males and females [22,23]. These relationships are largely controlled by female choice [24–26]. Significant changes in the neuroendocrine makeup of cohabitated or pair-bonded animals have been found [27,28]. Similarly, isolation stress can lead to substantial behavioral and endocrine deficits [22], while the presence of a preferred partner can act as a social buffer [29].

Relatively few studies have been done on spatial learning in guinea pigs, perhaps due to the species' – often-biased – reputation of overall

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timidity and fear of open spaces when compared, for instance, with rats. This is aggravated by the fact that guinea pigs often respond to various stressors with prolonged immobility [27,30,31]. Nonetheless, some studies have successfully employed a Morris water task (MWT) as a device for the assessment of spatial learning [32,33]. The MWT is made up of a round pool filled with opaque water. An escape platform is submerged a few centimeters under the water surface, representing the goal the animal has to reach [34]. However, swimming does constitute a considerable stressor in guinea pigs [35]. When prolonged it may jeopardize pairbonding via activation of the HPA-axis and blur possible differences between cohabitated and single animals. Thus, we deemed it necessary to develop a specially designed labyrinth for testing spatial ability in guinea pigs, using elements of both Y-type and radial arm maze. For the present study, animals were kept either in isolation or in heterosexual pairs and had then to perform a learning and memory task. To get an additional picture of tonic stress load and its potential effects on spatial ability, cortisol (CORT) – the major glucocorticoid in guinea pigs [36] – was examined. Taking into account the aforementioned studies, we hypothesized that cohabitated animals would perform better than single ones.

2. Methods

2.1. Animals

Domestic guinea pigs (females: $N=20$; males: $N=20$) from a heterogeneous, multi-colored stock were used in the experiment. Subjects did not differ substantially with regard to their age ($18\text{ months} \pm 6$) and body mass ($810\text{ g} \pm 139$). All were intact, socially skilled and sexually experienced in that they grew up from birth until adolescence in a high-number heterosexual environment [22], with frequent regular handling. Females were neither pregnant nor lactating before the experiment. Estrous cycle was controlled as far as care was taken not to use animals during their vaginal estrus.

Initially kept in isosexual groups in two environmentally enriched enclosures ($4 \times 4\text{ m}$ each, with shelters, viewing platforms, etc.), guinea pigs were transferred to acclimatization cages ($90 \times 48 \times 40\text{ cm}$) 14 days prior to the experiment and housed in pairs ($N=10$) or as singles (females: $N=10$; males: $N=10$). Cage floors were covered with standard woodchip bedding material. Subjects were maintained on a light–dark cycle of 12L:12D (lights on at 0700 h) and constant temperature conditions ($23\text{ }^\circ\text{C} \pm 2$). Food was provided daily at 1300 h and consisted of a mixture of guinea pig pellets (Altromin 3022, Altromin, Lage, Germany) and cereals, supplemented with fruit, vegetables and hay. Water was available *ad libitum*. Experiments were carried out in accordance with the European Communities Council Directive 86/609/EEC and complied with the current laws of animal protection decreed by the Austrian Federal Ministry of Education, Science and Culture.

2.2. Experimental design

For logistic reasons, work was carried out in five runs from July to September in 2007 and 2008. The experiment consisted of four consecutive parts. After 14 days of acclimatization, a blood sample was taken at 1000 h. Twenty-four hours later, the acquisition phase started. The labyrinth used was in effect a hybrid of a Y- and radial-arm-maze, with four arms projecting at equal angles from a central enclosure, each splitting in a Y-shape at their ends (Fig. 1). Total number of choices was thus eight. The maze followed a design by Millesi et al. [37]. It was constructed of laminated fiberboard and erected on a floor made of the same material and color (beige). Previous pilot studies of ours had optimized its design and size, taking into account the general behavior and environmental preferences of domestic guinea pigs. Arms had a width of 15 cm. Height of the maze was 40 cm. It covered an area of $2.4 \times 2.4\text{ m}$ and was located in a room

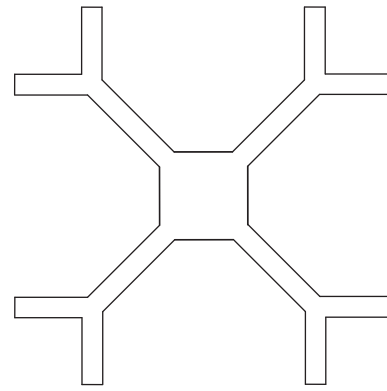


Fig. 1. Labyrinth: total area covered 5.76 m^2 .

subjected to the same environmental conditions as the animal facility. An even illumination was strived for, with light intensity at the bottom of the labyrinth ranging from 300 to 350 lx.

Subjects started directly with training, without habituation. This acquisition phase consisted of five consecutive training days. One arm of the labyrinth was assigned at random to be baited (with a single piece of cucumber), and this arm remained consistent throughout the experiment for each subject. The guinea pigs could not see the bait until they had reached the distal end of the arm. Animals performed within a time window of 1000 to 1200 h, with one trial per animal per day. Subjects were placed unfed and singly in the center, with their head pointing to a direction opposite of the baited maze arm. A trial lasted 10 min, i.e., subjects had to stay in the maze for the full period, even if they already had found the bait earlier. Animals were then put back in their acclimatization cages. To minimize potential intra-maze cues further, the labyrinth was thoroughly cleaned with a 5% acetic acid solution, tap water and paper towels after each trial. New bait was provided as well for the following run.

Seventy-two hours after day 5 of the acquisition phase, animals again had to perform in the labyrinth. During this retention test, conditions were identical to those of the acquisition phase. After bleeding, the experiment effectively ended, and subjects were returned to their isosexual groups.

2.3. Behavioral measures

Performance in the labyrinth was recorded with a camera mounted above and quantified with the Observer VideoPro software (Noldus, Wageningen, The Netherlands). The following parameters were measured: (1) Latency to bait, i.e., the period from release into the maze until retrieval of the bait. If the task was not accomplished within the allotted period, the full 10 min were adopted. (2) Error-rate, i.e., the errors made during each trial until the bait was claimed. A wrong arm entry was scored when the guinea pig's head and forelegs passed into a non-baited arm. (3) Adjusted percentage of movement, i.e., the amount of time in percent the animal spent moving until it reached the bait, movement being defined as a position change of \geq one body length. Guinea pigs react to strong stressors with immobility [27]. The quantity of movement shown may then reflect the acute behavioral reaction to a specific event and serve as a momentary measure of the guinea pigs' emotional state.

2.4. Blood sampling and hormone analysis

Blood samples (approx. $300\text{ }\mu\text{l}$) were taken without anesthetizing subjects by puncturing marginal ear veins [38]. The procedure generally lasted less than 3 min per animal, a period in which a possible HPA-reaction would not come to bear yet [23]. After centrifugation, plasma was stored at $-20\text{ }^\circ\text{C}$ until further analysis.

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