Physiology & Behavior 151 (2015) 238–245

Contents lists available at ScienceDirect

Physiology & Behavior

journal homepage: www.elsevier.com/locate/phb

The effects of extrinsic stress on somatic markers and behavior are dependent on animal housing conditions

Damien Huzard [a,b], Dave G. Mumby [b], Carmen Sandi [a], Guillaume L. Poirier [a,1], Michael A. van der Kooij [a,*,1]

[a] Laboratory of Behavioral Genetics, Brain Mind Institute, School of Life Sciences, École Polytechnique Fédérale de Lausanne (EPFL), Lausanne 1015, Switzerland
[b] Center for Studies in Behavioral Neurobiology, Department of Psychology, Concordia University, Montréal, Québec, Canada

HIGHLIGHTS

- A socially-enriched environment (SEE) prevents stress-induced anxiety.
- Rats in a SEE make less mistakes in an operant task.
- A SEE changes somatic markers suggestive of stress.
- In SEEs, stressed rats display less aggressive behaviors.

ARTICLE INFO

Article history:
Received 7 April 2015
Received in revised form 11 July 2015
Accepted 14 July 2015
Available online 26 July 2015

Keywords:
Anxiety
Environmental enrichment
Resilience
Social behavior
Stress

ABSTRACT

Properties of the environment play an important role in animal wellbeing and may modulate the effects of external threats. Whereas stressors can affect emotion and impair cognition, environmental enrichment may prevent the occurrence of such negative sequelae. Animals exposed to semi-natural group-housing experience a complex environment; whereas environmental enrichment might protect against stressors, a socially-enriched environment(SEE) could entail aggressive inter-male encounters with additive stress effects. In the present study, we investigated the effects of exposure to external stressors, footshocks and forced swimming, on adrenal gland and body weights as well as on behavior in rats housed under SEE or standard, non-enriched environment (NEE), conditions. We found that SEEs reduced the anxiogenic effects of stress. Moreover, SEEs improved the performance in an operant task and prevented the increase in impulsive behavior produced by external stressors on NEE animals. Whereas these findings are indicative of stress-buffering effects of SEEs, adrenal gland weights were increased while total body weights were decreased in SEE rats, suggesting that SEEs may simultaneously exacerbate physiological measurements of stress. Finally, in the SEE, total aggressive behaviors and body wounds were paradoxically reduced in animals that received external stressors in comparison to non-stressed controls. The consequences of the external stressors applied here are not uniform, varying according to the housing condition and the outcome considered.

1. Introduction

The environment can impact quality of life, modulating behaviors and social interactions and ultimately even playing a role in psychopathologies [1–5]. While a breadth of literature on the impact of the social and physical environment on physiology and behavior of individuals, communities, and societies exists [6–9], our understanding of the impact of interactions between the social environment and the individual in determining physiological and behavioral outcomes remains incomplete.

Animal experimentation has started to address this issue through the application of diverse forms of environmental enrichment procedures [10–12]. A common approach consists of physical environmental enrichment, involving increased size and/or complexity of the cage, thereby enhancing sensory inputs and often enabling a diversified interaction with the environment. In some instances, the environmental enrichment involves a social component, allowing interactions between various individuals. Interestingly, some studies suggest that the combination of complex inanimate stimulation and social stimulation is required in order to obtain optimal effects of enriched environments as compared to housing conditions enriched in either physical or social aspects alone [8,10–13].

* Corresponding author at: Johannes Gutenberg University Medical Centre, Department of Psychiatry and Psychotherapy & Focus Program Translational Neurosciences, Mainz, Germany.
E-mail address: m.vanderkooij@uni-mainz.de (M.A. van der Kooij).
[1] Shared last authorship.

http://dx.doi.org/10.1016/j.physbeh.2015.07.018
0031-9384/

For that matter, semi-natural environments have been developed to recreate ecological but controllable laboratory setups [14,15]. They typically include socially-enriched environments (SEEs), combining both environmental and social enrichments. Previous studies have shown that a SEE has many effects on the brain and behavior, including increased neural plasticity [16,17], enhanced hippocampal neurogenesis [10,11,18,19], improved learning and memory [8,10,12,19–21] and decreased anxiety-like behavior [22]. In contrast, exposure to sustained stressors can lead to hippocampal atrophy, increased anxiety and impaired learning and memory [23–26].

Given that environmental enrichment and stress can affect the brain and behavior in opposite ways, one might predict that SEEs would negate the detrimental effects of stress on the brain and behavior. Indeed, whereas maternal separation-stress enhanced the corticosterone response and increased anxiety-like behaviors in adulthood [27], a SEE was found to reverse these effects [28]. Moreover, animals housed in SEEs exhibited resiliency to social defeat, as illustrated by decreased anxiety in the light–dark box and less immobility time in the forced swim test [29]. The effects of chronic stress on hippocampal morphology (dendritic hypotrophy) and function (spatial learning deficits in the radial arm maze) were attenuated in rats housed in SEEs during adulthood [30]. On the other hand, physiological parameters, such as plasma corticosterone, indicate that some forms of social housing (e.g. in the visible burrow system, VBS) induce stress, owing to the agonistic interactions between males competing for the females in the colony [31]. The stressful nature of VBS-housing is demonstrated by a reduction in body weight, enlarged adrenal glands and increased basal levels of plasma corticosterone [32,33].

We hypothesized that SEEs would have additive effects on somatic markers (adrenal gland weight and body weight) suggestive of stress exposure, owing to the possible occurrence of intermale aggressive encounters. Here we questioned whether this somatic stress-inducing environmental manipulation is accompanied by corresponding perturbations in, social, cognitive, and anxiety-like behaviors.

2. Methods

2.1. Animals

Long–Evans males (n = 48) and females (n = 18) were used in this experiment. Males and females were housed in a 12 h reversed day–night cycle (lights off at 8 am) with food and water available ad libitum and with controlled temperature (20–22 °C) and humidity (56–58%). Experimental procedures were approved by the Animal Research Ethics Committee of Concordia University, and followed the guidelines of the Canadian Council on Animal Care (CCAC).

2.2. Housing conditions and experimental groups

Males arrived at postnatal day 21 (P21) from the local breeder (Charles-River, Saint-Constant, Quebec, Canada) in groups of four. After 1 day, males were pair-housed in standard Plexiglas cages (l × w × h: 45 × 20 × 25 cm). In order to habituate them to the experimental manipulations, animals were handled 5 days/week in the 3 weeks preceding the experiment. Handling consisted of either holding the rat for 1 min in the housing room, tail marking (Liquid Tip, Sanford®) or weighing. At P53, rats were randomly assigned to their housing condition: non-enriched environment (NEE, n = 12) or social enriched environment (SEE, n = 36). SEE males were weight-matched (<8% difference between any male in a group) and introduced to their behavioral setup (starting time: day 1) in groups of four. Males were fur-marked allowing identification during social interactions. NEE rats were socially isolated in standard cages and submitted to the same schedule as SEE rats, except that fur-marking was absent. Additionally, from the outset, NEE and SEE rats were split into subgroups and kept under either control (ctrl) or external stress conditions: NEE-ctrl (n = 6), NEE-stress (n = 6), SEE-ctrl (4 SEE cages, n = 16) and SEE-stress (5 SEE cages, n = 20).

2.2.1. Females and hormonal injections for estrus induction

Two females were added to each SEE in order to provide further social enrichment which has been previously shown to increase competition and agonistic behaviors between males [34]. In order to avoid pregnancy and yet maintain a natural estrous cycle, ovariectomized females (6–8 months old at the start of experimentation; kindly provided by Professor J. Pfaus, Concordia University) were made sexually receptive every 4 days (including days 1 and 5) by inducing estrus with a standard protocol: subcutaneous injection of estrogen (estradiol benzoate: 10 μg in 0.1 ml of sesame oil) and progesterone (500 μg in 0.1 ml of sesame oil), respectively administered 48 h and 4 h before heat induction [35]. Females were introduced into the SEE cages a few minutes after the males on day 1 and were present throughout the remainder of the experiment. On the periods when rats were handled, males were kept singly housed and females were pair-housed in standard cages in the housing room of NEE rats (adjacent to the SEE room).

2.2.2. Socially-enriched environments (SEEs)

The SEE setup (Fig. 1) consisted of a large cage (l × w × h: 144 × 62 × 90 cm) with 3 sides of wire mesh and 1 long side made of transparent Plexiglas to permit viewing and video-recording. SEEs were divided into three floors, and rats were free to move across them using vertical paths on the sides of the cage. The top floor was covered with woodchip bedding (Sani-chips, Harlan®) and equipped with a food dispenser and a water bottle. The middle floor was separated into two distinct, similar-sized compartments separated by a wall with a 15-cm swinging doorway at the bottom. The left chamber floor was covered with gravel and the right chamber with woodchip bedding. One metallic shelter was present in each chamber. The bottom floor was covered with corncob bedding (Harlan®). A food dispenser and a water bottle were placed on this floor, along with a 50-cm long T-shaped PVC pipe (20 cm diameter). In all floors several cardboard pieces and some pieces of wood were placed as chewing material and regularly renewed. During behavioral testing for anxiety or cognition, cleaning and weighing, SEE rats were individually placed in standard cages in another housing room.

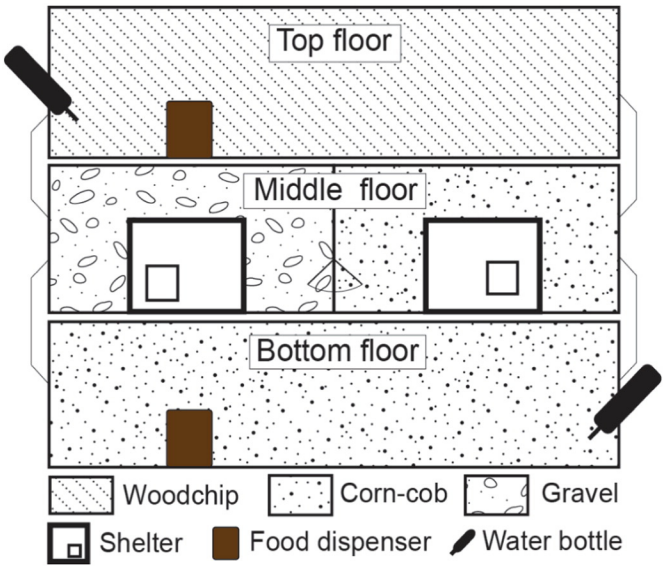

Fig. 1. Schematic diagram of the enriched environment. Adapted from http://www-psychology.concordia.ca/fac/mumby/research_topics_enrichment.html.