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Stress inhibits psychomotor performance differently in simple and complex open field environments

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ABSTRACT

Stress affects psychomotor profiles and exploratory behavior in response to environmental features. Here we investigated psychomotor and exploratory patterns induced by stress in a simple open-field arena and a complex, multi-featured environment. Groups of rats underwent seven days of restraint stress or no-stress conditions and were individually tested in three versions of the ziggurat task (ZT) that varied according to environmental complexity. The hyperactivity of the hypothalamic–pituitary–adrenal (HPA) axis due to stress procedure was evaluated by the pre- and post-stress levels of circulating corticosterone (CORT). Horizontal activity, exploration, and motivation were measured by the number of fields entered, the time spent in the central fields, path length and speed, and stop duration. In addition, vertical exploratory behavior was measured by the times rats climbed onto ziggurats. Stress-induced psychomotor changes were indicated by reduced path length and path speed and increased duration of stops only within the complex arena of the ZT. Rats in stress groups also showed a significant decline in the vertical movements as measured by the number of climbing onto ziggurats. No stress-induced changes were revealed by the simple open-field arena. The exploratory patterns of stressed animals suggest psychomotor inhibition and reduced novelty-seeking behaviors in an environment-dependent manner. Thus, multi-featured arenas that require complex behavioral strategies are ideally suited to reveal the inhibitory effects of stress on psychomotor capabilities in rodents.

Introduction

Stress is characterized by a complex cascade of physiological and behavioral alterations (Bekris et al., 2005; de Kloet et al., 1999; Mason et al., 1961; Metz, 2007; Selye, 1936). The psychological consequences of stressful experiences have been also reported in both human subjects (Ilgen and Hutchison, 2005; Ohman et al., 2007; Preston et al., 2007; Rosnick et al., 2007; Taylor et al., 2007; van Wingen et al., 2012) and animals (Belda et al., 2004; Devilbiss et al., 2012; Kippin et al., 2008; Koenig et al., 2005; Palchykova et al., 2006; Seif et al., 2004; Ver Hoeve et al., 2013). These effects are generally associated with high emotionality characterized by some subjective experience of strong feelings, anxiety and fear, and physiological changes (Avital and Richter-Levin, 2005; Avital et al., 2001; Kalynchuk et al., 2004).

In laboratory investigations, open-field activity provides the primary indicator of stress-induced elevated emotionality in rodents, such as rats (Hall, 1934). As a commonly used and validated task for evaluating emotionality, the open field mostly involves a short period of exposure of an animal to a simple, novel environment (Broadhurst, 1969; Eilam et al., 2011; Gentsch et al., 1981; Heiderstadt et al., 2000; Ramos and Mormède, 1998; Roth and Katz, 1979). The fundamental hypothesis underlying the application of the open-field task is that when a rat is placed in a novel environment, it can show an emotional response in exploratory behavior reflected by some locomotor changes (Archer, 1973; Suarez and Gallup, 1981; Walsh and Cummins, 1976). This particular emotional situation refers to an internal disturbance related to a perceived threat (Arakawa, 2007; Walsh and Cummins, 1976). For a stressed rat, however, these emotional disruptions can be exaggerated and behaviorally measured by different parameters such as ambulation or locomotion, the latency to ambulate, total distance traveled, freezing or hypoactive state (e.g. stop duration), the time spent in central areas, vocalization, rearing and grooming frequency, defecation and urination (Jadavji et al., 2011; Laurence et al., 2012; Metz and Schwab, 2004; Wilson et al., 2013). Furthermore, elevated amounts of time spent in

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the center of an open field are regarded as an indicator of reduced anxiety-like behaviors and elevated risk taking (Ageta et al., 2008).

Despite the potential value of the open-field task to reveal stress-induced behavioral alterations in animals, controversy remains regarding the degree to which stress alters behavior and determines the direction of post-stress changes. This may originate, in some part, from variables such as recording procedures, the level of illumination, the color and size of the open field, the animals' strain and sex, age, and the type and intensity of a stressor (Bowman et al., 2006; Castanon and Mormède, 1994; Faraday, 2002; Mercier et al., 2003; Ordyan and Pivina, 2004; Ossenkopp et al., 1994; Sternberg et al., 1992; Trullas and Skolnick, 1993; Walsh and Cummins, 1976; Wilson et al., 2013). Moreover, variability may arise from the type of environment in which the animal is tested for stress-induced novelty-seeking behavior and risk taking (Nemati et al., 2013). The hypothesis of an environment-dependent stress response focuses on structural features of a particular environment that determine the patterns and frequency of movement. Thus, environmental features may serve as interventions or stress facilitators to modulate the stress response and associated exploratory patterns. Therefore, the testing environment should be considered an experimental variable in studies of locomotor/exploratory behavior (Clark et al., 2006).

One would assume that, compared to a simple (or featureless) arena, a complex (or multi-featured) environment provides rats with a distinct opportunity to show specific locomotor manifestations following stress. Compared to a simple open-field arena, a complex environment may encourage vertical in addition to horizontal exploration. Furthermore, it may more strongly motivate the use of complex motor patterns when discovering the environment or, conversely, to reveal locomotor inhibition during exploration than a traditional open field. The stress-induced locomotor inhibition in a complex environment may therefore represent a measure of risk-assessment behavior.

The present study used a complex open-field task, the ziggurat task (ZT; Faraji et al., 2008; Faraji et al., 2011b), to assess the effects of acute and chronic restraint stress on exploratory patterns in rats. We show that the experience of stress leads to characteristic changes in novelty-seeking and exploratory behaviors suggesting that a complex open field is an ideal task for the comprehensive assessment of stress-induced psychomotor profiles.

Material and methods

Subjects

Thirty-nine adult male Long–Evans rats, weighing 320–390 g were used. The animals were housed in pairs under a 12:12 h light/dark cycle and temperature set at 22°–23 °C. All testing was performed during the light phase of the cycle at the same time of day. The animals received water ad libitum. The experiment was approved by the local animal welfare committee of Avicenna Institute of Neuroscience (AIN).

Experimental design

Fig. 1 illustrates the time course of experimental manipulations. Animals were divided into six experimental groups: Control 1–3 ($n = 6$ for each group) and Stress 1–3 ($n = 7$ for each group). Groups 1, 2, and 3 of each control and stress conditions were tested in (1) simple open field without ziggurat; (2) central ziggurat, and (3) standard ZT with sixteen ziggurats (Figs. 2A–C). All experimental interventions including blood sampling, restraint stress and behavioral testing were performed with a one-day interval for each group. In order to assess the pre-stress (baseline) levels of circulating corticosterone (CORT), all groups were subjected to blood sampling one day prior to beginning the stress or no-stress conditions, respectively. Rats in stress groups experienced restraint in a separate room. All six groups were again subjected to blood sampling a day before the last day of the experiment. Five to ten minutes after stress on the last day of stress, rats in stress and control groups were placed individually in the ZT environment and allowed to explore the ZT for 15 min.

Blood samples and restraint stress

Blood samples

Rats were placed in a restraint tube and blood samples were obtained by tail notch with a scalpel blade (Craig et al., 2008). Blood was collected within the first 1–2 min of being placed in the tube. Blood samples (0.3–0.6 ml) were placed in heparinized tubes and transferred to centrifuge tubes. Plasma was obtained by centrifugation at 8000 rpm for 8 min. The plasma samples were stored at −20 °C until further analysis.

Restraint stress

Animals in stress groups were maintained in a transparent Plexiglas tube (8 cm inner diameter) of adjustable length (Metz et al., 2005), 3 h/day between 8:00 am to 1:30 pm for 8 consecutive days. Restraint stress in the present experiment was chosen because it produces significant morphological changes (Garrett and Wellman, 2009), lasting behavioral effects (Jadavji and Metz, 2008; Miracle et al., 2006) as well as significant increase in plasma CORT (Cook and Wellman, 2004). The tubes maintained the animals in a standing position without compression of the body. In order to prevent potential habituation, the animals in the tubes were also manually vibrated for 5–10 s every 30 min.

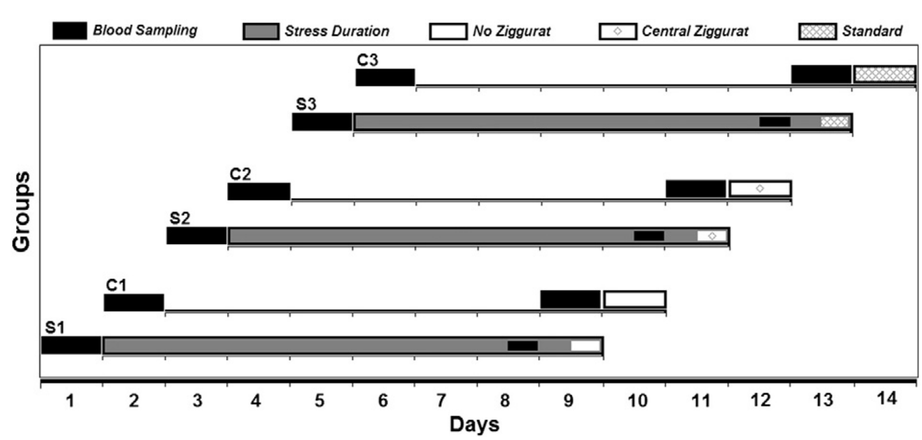

Fig. 1. Schematic illustration of the experimental design. S, Stress; C, Control.