

PHYSICAL EXERCISE DURING PREGNANCY IMPROVES OBJECT RECOGNITION MEMORY IN ADULT OFFSPRING

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Abstract—Exercising during pregnancy has been shown to improve spatial learning and short-term memory, as well as increase brain-derived neurotrophic factor mRNA levels and hippocampal cell survival in juvenile offspring. However, it remains unknown if these effects endure into adulthood. In addition, few studies have considered how maternal exercise can impact cognitive functions that do not rely on the hippocampus. To address these issues, the present study tested the effects of maternal exercise during pregnancy on object recognition memory, which relies on the perirhinal cortex (PER), in adult offspring. Pregnant rats were given access to a running wheel throughout gestation and the adult male offspring were subsequently tested in an object recognition memory task at three different time points, each spaced 2-weeks apart, beginning at 60 days of age. At each time point, offspring from exercising mothers were able to successfully discriminate between novel and familiar objects in that they spent more time exploring the novel object than the familiar object. The offspring of non-exercising mothers were not able to successfully discriminate between objects and spent an equal amount of time with both objects. A subset of rats was euthanized 1 h after the final object recognition test to assess c-FOS expression in the PER. The offspring of exercising mothers had more c-FOS expression in the PER than the offspring of non-exercising mothers. By comparison, c-FOS levels in the adjacent auditory cortex did not differ between groups. These results indicate that maternal exercise during pregnancy can improve object recognition memory in adult male offspring and increase c-FOS expression in the PER; suggesting that exercise during the gestational period may enhance brain function of the offspring. © 2013 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: perirhinal cortex, wheel running, maternal, cognition, learning.

INTRODUCTION

Substantial research has established that exercise can improve both mental health and cognitive function. In

laboratory animals, most research on the cognitive enhancing effects of exercise has primarily focused on how exercise improves spatial learning (Vaynman et al., 2004; Albeck et al., 2006). The improvements in spatial learning likely occur as a result of exercise-induced changes in the hippocampus, such as increased neurogenesis (van Praag et al., 1999), enhanced long-term potentiation (van Praag et al., 1999; Farmer et al., 2004; O'Callaghan et al., 2007), and increased expression of neurotrophic factors (Trejo et al., 2001; Fabel et al., 2003; Vaynman et al., 2004; Adlard et al., 2005; Berchtold et al., 2005; Griffin et al., 2009). Specifically, brain-derived neurotrophic factor (BDNF) has been established as the putative substrate that underlies many of the exercise-related improvements in hippocampal function (Dishman et al., 2006). For example, an exercise-induced increase in hippocampal BDNF levels has been shown to be necessary for improvements in spatial learning in the Morris water maze following exercise (Vaynman et al., 2004).

More recent studies have shown that physical exercise can also improve non-spatial forms of learning and memory that rely on structures other than the hippocampus. For instance, exercise has been found to improve associative learning (Van Hooymissen et al., 2004; Burghardt et al., 2006; Eisenstein and Holmes, 2007) as well as object recognition memory (O'Callaghan et al., 2007; Fahey et al., 2008; Griffin et al., 2009; Hopkins and Bucci, 2010; Hopkins et al., 2011). Object recognition is a non-spatial form of memory that depends on the perirhinal cortex (PER; Dere et al., 2007) and is based on the spontaneous tendency of rodents to spend more time exploring a novel object than a familiar one. Compared to sedentary rats, those that had access to a running wheel exhibited enhanced object recognition memory, an effect that could not be attributed simply to changes in general exploratory behavior (Hopkins and Bucci, 2010; Hopkins et al., 2011). Moreover, enhanced object recognition memory was associated with increases in BDNF expression in PER but not in the hippocampus of rats that exercised (Hopkins and Bucci, 2010).

Although the effects of exercise on the adult brain have been well documented, less is known about the effects of exercise on the developing brain. Brain development starts in utero and continues until at least the end of the adolescent period (Rice and Barone, 2000). Throughout this developmental process the brain can readily be affected by internal and external factors. Notably, exercise has been found to have more robust

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Abbreviations: Au1, auditory cortex; BDNF, brain-derived neurotrophic factor; IB, immunobuffer; PBS, phosphate-buffered saline; PER, perirhinal cortex; PND, postnatal day.

and long-lasting effects on both the brain and behavior when rats exercise as juveniles rather than as adults. For example, rats that exercised during adolescence had greater increases in cell proliferation (Kim et al., 2004), BDNF expression (Adlard et al., 2005; Hopkins et al., 2011), and object recognition memory (Hopkins et al., 2011) than adult exercisers. In addition, in the rats that exercised as adolescents, the exercise-induced improvements in behavior lasted long after exercise stopped, while in adults the effects did not persist (Hopkins et al., 2011).

Similarly, a growing number of studies have reported that regular physical exercise during pregnancy can enhance cognition and behavior in the offspring. Exercise by pregnant rats has been found to improve spatial learning (Parnpiansil et al., 2003; Akhavan et al., 2008; Dayi et al., 2012) and short-term memory (Lee et al., 2006; Kim et al., 2007) in juvenile offspring, as well as increases BDNF mRNA levels and hippocampal cell survival (Lee et al., 2006). In addition, regular aerobic exercise during pregnancy decreases anxiety-like behavior in offspring (Aksu et al., 2012). However, little work has been done to determine how long the effects of maternal exercise during pregnancy endure in the offspring. Indeed, most studies that have examined the effects of maternal exercise on offspring have tested pups soon after birth or during adolescence, thus it remains unknown if these effects endure into adulthood. In addition, few studies have focused on how maternal exercise can impact cognitive functions that do not rely on the hippocampus. To address these issues, the present study tested the effects of maternal exercise during pregnancy on object recognition memory in adult offspring. Pregnant rats were given access to a running wheel throughout gestation and the adult male offspring were subsequently tested in an object recognition memory task at three different time points, spaced 2-weeks apart. In addition, c-FOS expression was measured in the PER of the offspring after the final recognition memory test to determine if there were differences in neuronal activity related to recognition memory.

EXPERIMENTAL PROCEDURES

Subjects

Male ($N = 2$) and female ($N = 5$) Long Evans rats weighing approximately 250–300 g were obtained from the Harlan Laboratories, Inc. (Indianapolis, IN, USA) and allowed to mate (two females and one male per cage) during a 72-h period. After the 72-h period, female rats were assigned to either exercise ($N = 2$) or sedentary conditions ($N = 3$). Rats were checked for birth daily and the day pups were first observed was designated postnatal day 0 (PND 0). Rats were weaned at PND 21 and group housed according to sex. Eleven (EX group) and ten (NX group) male offspring were used in this study. Rats had free access to food (Purina standard rat chow: Nestle Purina, St. Louis, MO, USA) and water and were maintained on a 14:10 light–dark cycle throughout the study. Behavioral

testing took place at approximately 1 pm. All procedures were conducted in accordance with the Association for Assessment and Accreditation of Laboratory Animal Care Guidelines and the Dartmouth College Institutional Animal Care and Use Committee.

Physical exercise regimen

Pregnant rats in the exercise group had 24 h access to a stainless steel running wheel (34.5 cm diameter, 1.3 mm rods placed 0.9 cm apart; Philips Respironics, Bend, OR, USA) inside the home cage throughout pregnancy. Wheel rotations were monitored by an automatic counter mounted on the side of the apparatus. The counters recorded every 1/2 turn of the running wheel and nightly running distance was calculated by dividing the count by 2 and multiplying by 1.08 to convert to meters. The running wheel was removed from the cage once the pups were born.

Novel object recognition

Object recognition memory was assessed in a plastic tub (30 × 34 cm with 38 cm high walls) that was monitored by a video camera and located in a dimly lit room. One set of test objects was made of plastic building blocks (Learning Resources Inc., Vernon Hills, IL, USA) constructed into distinct configurations with approximately the same dimensions. One of the objects was purple and roughly similar in shape to a dumbbell and the other was green and shaped like a cross. The second set of objects was made of glass and one object resembled a small red cup and the other a blue ashtray. The third set of objects included a red magnet and a large bolt, which were both approximately 6 cm long. The first set of objects that rats were exposed to was always the plastic objects, the second set was always the glass objects, and the third set was always the magnet/bolt.

Behavioral testing began when the male offspring were approximately 60 days old. Rats were tested in a novel object recognition paradigm that was designed to minimize spatial learning and hippocampal involvement (Bevins and Besheer, 2006; Dere et al., 2007). Indeed, rats exhibit impaired performance in this task following lesions of the PER (Bussey et al., 1999; Forwood et al., 2005; Aggleton et al., 2007; Mumby et al., 2007; Warburton and Brown, 2010) but not after hippocampal lesions (Brown and Aggleton, 2001; Winters et al., 2008; Warburton and Brown, 2010; Kealy and Commins, 2011). Moreover, the difficult training procedure (i.e., long sample-test interval and short sample session) was intentionally chosen so that a categorical distinction could be made between exercising and non-exercising groups (Hopkins and Bucci, 2010). On day 1 (habituation session) each rat was exposed to the tub individually for 10 min to habituate to the testing environment. On day 2 (sample session), rats were placed in the tub and given 5 min to explore two identical sample objects. Twenty-four hours later (test session), rats were again placed in the tub with one familiar and one novel object (counter-balanced across subjects) and given 2 min to

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