

Short communication

Voluntary exercise facilitates pair-bonding in male prairie voles

William M. Kenkel^{a,b,*}, C. Sue Carter^{a,b}^a Department of Psychology, Northeastern University, Boston, MA 02115, United States^b The Kinsey Institute, and Department of Biology, Indiana University, Bloomington, IN 47405, United States

HIGHLIGHTS

- Male prairie voles were given access to running wheel equipped cages.
- Exercised males gained more weight, had less subcutaneous fat, and larger testes.
- Exercised males formed partner preferences faster than control males.

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ABSTRACT

The neuropeptides oxytocin and vasopressin have been implicated in exercise, as well as monogamy and parental behavior. In this study, we compared behavioral and neuroendocrine effects of access to an exercise wheel vs. the sedentary state typical in lab animal housing. Male prairie voles (*Microtus ochrogaster*) were studied because of their extensive repertoire of social behaviors including pair bond formation and biparental care, which are influenced by oxytocin and vasopressin. Subjects in one group had access to a running wheel in their cage (wheel), and voluntarily ran approximately 1.5 km/day for six weeks; these animals were compared to males in standard housing conditions ($n = 10/\text{group}$). Males allowed to exercise formed partner preferences significantly faster than controls and exhibited fewer oxytocin neurons, as measured by immunohistochemistry in the bed nucleus of the stria terminalis. We observed no differences in terms of anxiety-related behavior, or alloparental responsiveness. Males with a running wheel equipped cage gained more total body weight, and by the end of the six weeks were found to have less subcutaneous fat and larger testes as a percentage of bodyweight. The changes to gonadal regulation and pair-bonding behavior associated with voluntary exercise are discussed in terms of their possible relevance to the natural history of this species.

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1. Introduction

Regular voluntary exercise is one of the best-established mechanisms for increasing wellness and behavioral plasticity [1]. Social bonds and other positive relationships also are protective, especially in the face of stressful experiences [2]. The neuropeptides oxytocin (OT) and arginine vasopressin (AVP) have been shown to have a central role in social bonding [3], and parental behavior [4], as well as adaptation to various stressors [5]. OT in particular has been shown to be one of the mechanisms by which social support infers stress resilience [6,7]. Likewise, voluntary exercise produces anxiolytic effects [1,8] and also leads to the up-regulation of OT systems [9,10].

OT plays important roles in the autonomic changes that follow access to voluntary exercise. In exercise trained animals, OT acts in the nucleus tractus solitarius (NTS) to restrain exercise-induced tachycardia [11]. Furthermore, exercise training in rats leads to increased levels of OT in the NTS [9]. OT increases parasympathetic cardiac tone to slow the heart by acting on the dorsal–vagal complex (including the NTS and the dorsal motor nucleus of the vagus (DMX)) [12].

Social behaviors, including alloparental care [4,13] and pair-bond formation [3] also are regulated by the simultaneous actions of both OT and AVP. In male prairie voles, the expression of alloparental care also involves a sustained increase in heart rate, similar to an acute bout of exercise [14–16]. Exercise increases the expression and release of these neuropeptides, and social support is likewise anxiolytic. In this context, we examined the hypothesis that male voles allowed to voluntarily exercise would be more likely to express alloparental care, form pair-bonds and explore a

* Corresponding author at: The Kinsey Institute, and Department of Biology, Indiana University, Bloomington, IN 47405, United States.

E-mail address: wm.kenkel@gmail.com (W.M. Kenkel).

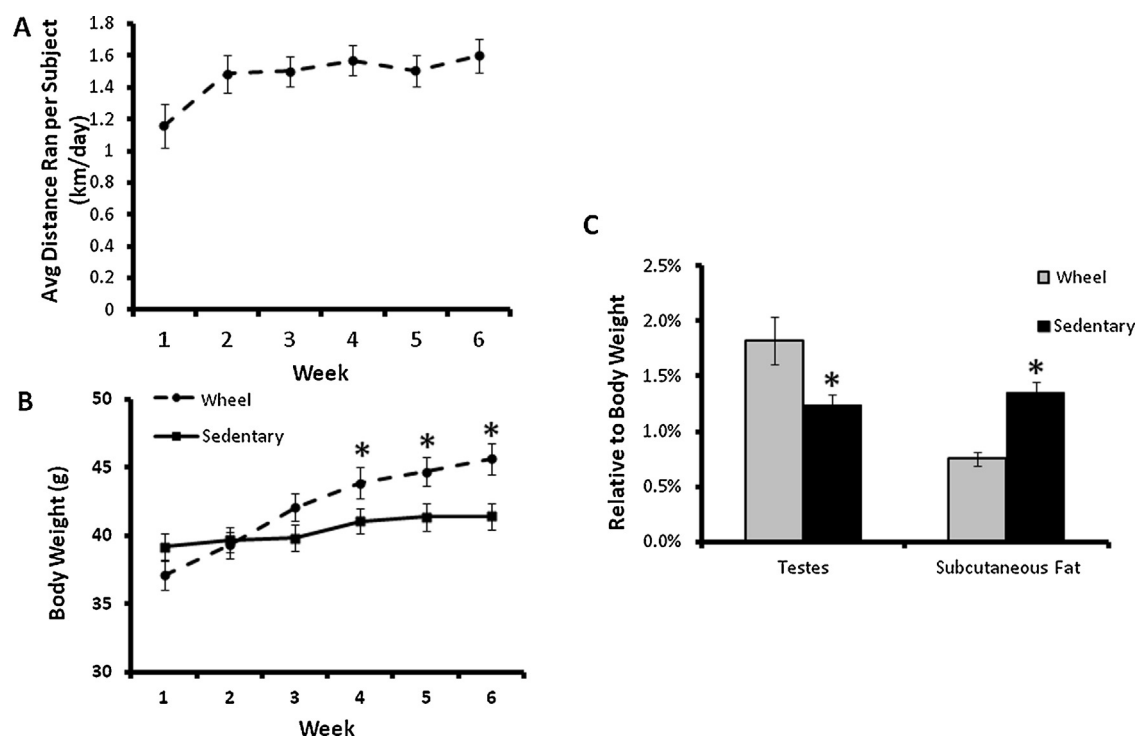


Fig. 1. (A) Average distance run per day per animal over the course of 6 weeks in the exercise treatment. (B) Average body weight over the course of 6 weeks in each treatment, weight increased over time in the exercise treatment only ($n = 10/\text{group}$, $p < 0.05$). (C) Testes and subcutaneous fat weight as a percentage of body weight. Testes were significantly larger in the exercise treatments and subcutaneous fat was significantly smaller ($p < 0.05$ for all comparisons). * indicates significant difference between sedentary and exercise conditions.

novel open-field (used to index anxiety). At the conclusion of the study, we examined the effects of exercise on fat deposition, and testes weight, as well as the central abundance of cells and fibers immunoreactive to OT and AVP.

2. Methods

2.1. Subjects

Male F2 or F3 descendants of wild prairie voles caught near Champaign, Illinois were used in these experiments at 60–90 days of age. Subjects were maintained on a 14/10 h light/dark cycle in a temperature and humidity controlled vivarium. Food (Purina rabbit chow) and water were available ad libitum. All test subjects were sexually naive and had never been exposed to pups. All procedures were conducted in accordance with the National Institutes of Health Guide for the Care and Use of Laboratory Animals and were approved by the University of Illinois at Chicago Institutional Animal Care and Use Committee.

2.2. Experimental design

Male prairie vole subjects were randomly assigned to either of two conditions for 6 weeks: placed with their sibling in a standard mouse cage ($18 \times 28 \times 20$ cm) equipped with a running wheel (wheel, $n = 10$), or left with their same-sex sibling in a similar cage without a running wheel (sedentary, $n = 10$). Animals of each condition were weighed once every week. In the exercise treatment, distance ran was calculated via the equipment's tally of wheel rotations which were recorded every day and halved to account for the two animals in each cage. Pair housing was used to avoid the effects of social isolation, to which voles are particularly sensitive [17].

Following 6 weeks in these housing conditions, animals were subjected to three behavioral tests in order of presumed increasing

salience. Experiments began during the lights-on period between 10:00 and 11:00 am. Subjects were exposed to an open field test (OFT), then returned to their home cage for 24 h, then tested in an alloparental test, returned to their home cage for 24 h, and finally cohabitated with a novel female for 30 min, followed immediately by a partner preference test (PPT) designed to assess the tendency to prefer a familiar female vs. one that is otherwise similar but unfamiliar. Behavior was later analyzed by two trained, experimentally-blind observers using Noldus Observer (Noldus Information Technology, The Netherlands).

2.3. Open field test

The open field consisted of a clear plexiglas testing arena 42×42 cm square, with walls 30 cm high, under indirect lighting at typical colony levels. Testing in the arena lasted for 10 min, during which time behavior was video recorded. Observers recorded the amount of time spent in the center quarter of the arena, time spent autogrooming and the amount of total locomotor activity. Time spent in the center of the arena is often used as an index of both state and trait anxiety [18].

2.4. Alloparental test

Testing of alloparental responses to an unfamiliar 1–3 day old pup was conducted based on previously published procedures [4]. Testing occurred in a novel cage in which a male was immediately presented with a pup and behavior recorded for 20 min. In the rare instances of an adult male expressing aggression toward the pup, the test was aborted and the pup either returned to its home cage or euthanized. Observers recorded the latency to approach the pup and durations of: carrying the pup, licking/grooming the pup, huddling over the pup and total time in contact with the pup.

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