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# Autonomic, behavioral and neuroendocrine correlates of paternal behavior in male prairie voles

Q1 William M. Kenkel <sup>\*</sup>, Gessa Suboc, C. Sue Carter <sup>1</sup>

Q2 Brain and Body Center, Dept. of Psychiatry, University of Illinois at Chicago, Chicago, IL 60612, United States

## HIGHLIGHTS

- We measured the effects of fatherhood in prairie voles compared to Virgin males.
- Fathers had lower resting heart rate and lost body weight and body fat.
- Fathers had greater oxytocin innervation in autonomic brainstem regions.
- Fathers displayed less anxiety-related behavior.

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## ABSTRACT

Socially monogamous prairie voles (*Microtus ochrogaster*) are biparental and alloparental. In the present study, we compared behavioral, cardiovascular and neuroendocrine parameters in male prairie voles with experience caring for pups (Fathers), versus reproductively inexperienced Virgin males. Father and Virgins showed generally similar responses to unrelated pups. However, in the Fathers studied prior to and during pup exposure, heart rate was lower and respiratory sinus arrhythmia tended to be higher than that in Virgins. Fathers also displayed comparatively lower levels of anxiety-related behaviors in an open field test. In Fathers, compared to Virgin males, we also found higher levels of oxytocin-immunoreactivity in the paraventricular hypothalamus and two brainstem regions involved in the autonomic regulation of the heart – the nucleus ambiguus and nucleus tractus solitarius. However, Fathers had less oxytocin in the bed nucleus of the stria terminalis. Vasopressin did not differ significantly in these regions. Fathers also weighed less and had less subcutaneous fat and larger testes as a percentage of bodyweight. In conjunction with earlier findings in this species, the present study supports the hypothesis that oxytocin may be involved in the adaptation to fatherhood. These findings also support the hypothesis that males, with or without prior pup experience, may show simultaneous patterns of behavioral nurturance and autonomic states compatible with mobilization and vigilance.

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## 1. Introduction

The biological basis of mammalian maternal behavior has been traditionally linked to the hormones of birth, including the hypothalamic neuropeptide, oxytocin (OT) [1–3]. In contrast, in the absence of birth-related events, the neurobiology of paternal behavior has been more difficult to identify. Studies in several species have implicated OT, as well as the related neuropeptide, arginine vasopressin (AVP), in male caretaking [4–7]. For example, in human males plasma OT levels increase during the transition to fatherhood [8,9] and Fathers'

behavioral and physiological readiness to engage with their infant is enhanced by the actions of OT [4,5].

Studies in socially monogamous, biparental voles have been especially useful in identifying the possible role of OT and AVP in male caregiving behavior in males [10,11]. In prairie voles, sexually naïve males exposed to unfamiliar pups also show an increase in peripheral OT, as well as evidence of increased central OT and AVP neuronal activity [12]. In the biparental mandarin vole, paternal behavior in Fathers is accompanied by an increase in OT expression in the paraventricular (PVN) and supraoptic (SON) nuclei of the hypothalamus [13].

Based on these findings, we hypothesized that experience as a biological Father, involving, among other things, chronic pup exposure, would be associated with an up-regulation of the central OT and AVP systems. These hormonal changes might also accompany changes in the behavior and physiology of the male including anxiety-like behaviors and the reactivity of the autonomic nervous system. We have previously

<sup>\*</sup> Corresponding author at: Dept. of Psychology, Northeastern University, 360 Huntington Ave., 125 NI, Boston, MA 02115, United States. Tel.: +1 607 342 0721.

E-mail address: [w.kenkel@neu.edu](mailto:w.kenkel@neu.edu) (W.M. Kenkel).

<sup>1</sup> Current address: Department of Psychiatry, University of North Carolina, Chapel Hill 27599, United States.

observed that in reproductively naïve male prairie voles, the cardiovascular response to a pup includes a sustained increase in heart rate [14]. Both OT and AVP project to brainstem autonomic regions and regulate cardiovascular activity [15,16]. Our lab has also previously described a role for chronic OT in the capacity of parasympathetic tone to slow heart rate in voles [17]. However, autonomic responses in males with experience as Fathers have not previously been studied, and we could not exclude the possibility that in naïve males the increase in heart rate was simply a response to the novelty of a pup. Furthermore, the finding of increased heart rate in males was in contrast to a general pattern of reductions in autonomic and emotional reactivity reported in maternal females of a number of species, including humans [18] and rats, which has been attributed in part to hormones of birth and lactation including OT [19,20]. Therefore, we sought here to describe the cardiovascular response to a pup in male voles with fathering experience.

Fathering behavior in prairie voles also has been associated with reductions in body weight [21], suggesting that adaptations to prolonged exposure to pups, or other aspects of paternal behavior, might affect metabolism. Data from other species indicate that OT plays a role in the regulation of appetite, and other metabolic and autonomic functions [15,16,22].

In the present experiments, conducted in male prairie voles, we examine some of the behavioral, neuroendocrine, physiological and autonomic adaptations to paternal behavior. This was done by comparing behavioral and autonomic responses to an unfamiliar pup in males with experience as Fathers versus Virgin males. Radiotelemetry was used to record heart rate, including a measure of respiratory sinus arrhythmia (RSA) and a more general index of heart rate variability (SDNN), in freely behaving animals. RSA indexes parasympathetic activity, while SDNN indexes the combined outputs of sympathetic and parasympathetic innervation of the heart (see below).

We hypothesized that, in comparison to Virgins, experienced Fathers would show lower levels of heart rate and higher RSA and possibly SDNN. As an independent index of anxiety-related behavior, we also examined the hypothesis that Fathers would be more exploratory in an open field test (OFT) [23]. Finally, we also examined the hypothesis that Fathers, in comparison to Virgin males, would show higher levels of OT- and AVP-immunoreactivity in brain regions previously implicated in brain regions involved in the regulation of social behavior, stress reactivity and the autonomic nervous system. Brain regions that contain OT and AVP-ergic cell bodies that we examined consisted of: the PVN, SON, bed nucleus of the stria terminalis (BNST) and medial pre-optic area (MPOA). OT and AVP projections were quantified by the intensity of fiber density in regions that regulate the autonomic nervous system, including: the dorsal motor nucleus of the vagus (DMX), nucleus ambiguus (NA) and nucleus tractus solitarius (NTS).

## 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 turned on at 06:30 AM in a temperature and humidity controlled vivarium. Food (Purina rabbit chow) and water were available ad libitum. Prairie vole offspring remained in their natal group with their parents in large polycarbonate cages (24 × 46 × 15 cm) containing cotton nesting material. Offspring were weaned at 21 days of age, prior to the arrival of the next litter to prevent premature exposure to pups, and then pair-housed with a same-sex sibling in smaller cages (17.5 × 28 × 12 cm) in a single-sex colony room until testing. Thus, all test subjects were sexually naïve and prior to this experiment 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. Experiments began during the lights-on period between 10:00 and 11:00 AM.

### 2.2. Experimental design

In Experiment 1, male vole subjects were randomly assigned to one of two conditions for 6 weeks: raising pups with an age-matched female (Fathers,  $n = 10$ ), or left in a standard cage with their same-sex sibling (Virgin,  $n = 10$ ). In the Father condition, males were previously paired with an age-matched female 3 weeks prior to the study period to ensure that pups were present for the 6 weeks of comparison. This time frame was selected so as to permit the subjects to raise 2 litters. Males were weighed once every week and at the conclusion of 6 weeks were tested in an OFT and alloparental test before being sacrificed for immunohistochemical tissue processing. Animals were returned to their home case for 24 to 48 h between the OFT and alloparental test and between the alloparental test and sacrifice. Fathers and Virgins were age-matched at the time of testing.

Upon observing robust differences between Fathers and Virgin males at 6 weeks (Experiment 1), a second cohort of males (Experiment 2,  $n = 8$ ) was established to examine autonomic changes resulting from fatherhood. Originally, males from Experiment 2 were to be sampled throughout a similar 6 weeks of paternal experience. However, we observed differences at the first time point (10 days after the birth of first litter) and the experiment was discontinued as signal quality in the radiotelemetric transmitters had begun to decay in some males.

In Experiment 2, males were implanted with radiotelemetric transmitters that permit the recording of heart rate, heart rate variability, locomotor activity and temperature. Following recovery from surgery, heart rate was recorded at baseline in the home cage, with their siblings. After obtaining a 10–15 min baseline, males were tested for alloparental behavior. The day after alloparental testing, males randomly assigned to the Father conditions were paired with an adult female and allowed to mate and raise a litter of pups. Fathers remained with their mates and pups until the pups were 10 days old, at which point the females and pups were removed. At this time, Fathers and Virgin males underwent an alloparental test. In each alloparental test stimulus pups were 1–3 days old and unrelated to the subjects.

### 2.3. Open field test

The open field consisted of a clear Plexiglas testing arena of 160 42 × 42 cm square, with walls 30 cm high. Animals were transferred 161 into the open field and placed into a standardized corner of the arena. 162 Lighting in the room was maintained at typical colony levels for the 163 light cycle. Testing in the arena lasted for 10 min, during which time 164 behavior was video recorded. Behavior was later analyzed by two 165 trained, experimentally-blind observers using Noldus Observer (Noldus 166 Information Technology, The Netherlands). Observers recorded the 167 amount of time spent in the center quarter of the arena, time spent 168 autogrooming and the amount of total locomotor activity indexed by 169 the number of lines crossed. Time spent in the center of an arena has 170 been described as a measure of both state and trait anxiety in a variety 171 of rodent species [23]. Inter-rater reliability was approximately 98% 172 across the measured behaviors. 173

### 2.4. Alloparental test

Testing of alloparental responses towards an unfamiliar 1–3 day old 175 pup was conducted based on previously published procedures [12]. 176 Testing occurred in a novel cage in which a male was immediately 177 presented with a pup and behavior recorded for 20 min during video 178 recording. In the rare instances of an adult male expressing aggression 179 towards the pup, the test was aborted and the pup was either returned 180 to its home cage or euthanized. Behavior was later analyzed by two 181 trained, experimentally-blind observers using Noldus Observer (Noldus 182

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