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Research report

Cardioacceleration in alloparents in response to stimuli from prairie vole pups: The significance of thermoregulation

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HIGHLIGHTS

- Both male and female prairie voles show cardioacceleration while caring for pups.
- Pup-induced cardioacceleration depended on the pup's age.
- Pup vocalizations decreased with pup age and temperature.
- Pup-induced cardioacceleration is blocked by increasing temperature.

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ABSTRACT

Autonomic responses, including changes in heart rate and respiratory sinus arrhythmia (RSA) can provide indications of emotional reactivity to social stimuli in mammals. We have previously reported that male prairie voles (*Microtus ochrogaster*) spontaneously care for unfamiliar infants, showing a robust and sustained increase in heart rate in the presence of a pup, thus providing an opportunity to examine the physiology of care-giving in reproductively naïve animals. However, the purpose of such heart rate increases has not been explained by previous efforts. In the present study, we first compared male and female prairie vole cardiac responses in the presence of a pup and found no evidence of sex differences in heart rate or RSA. Using male prairie voles, we then examined the characteristics of pups that were capable of eliciting physiological responses, including age of the pup and pup odors. As prairie vole pups increased in age they vocalized less and there was an associated decline in alloparental cardioacceleration. Exposure to pup-related odors induced cardioacceleration in adult males, and this effect also diminished with increasing pup age. Finally, we were able to block the cardioacceleratory effect when the testing environment was warmed to a temperature of 36 °C [vs ambient room temperature (approximately 22 °C)]. These findings suggest that pup-induced cardioacceleration is a robust phenomenon across alloparental prairie voles of both sexes, and depends on multi-modal processing of different stimuli from the pups. Young pups require care-giving behavior, which appears to drive cardioacceleration in the alloparents. This study also supports the usefulness of autonomic measures in the evaluation of social experiences.

1. Introduction

Caretaking behavior in response to infants shown by non-reproductive animals, also known as alloparenting, is a prominent characteristic of many socially monogamous species [1,2]. Alloparenting plays an especially important role in successful reproduction in communal species [3], including humans [4]. The analysis of alloparental behavior has also provided a useful model for discovering the autonomic and neuroendocrine factors capable of influencing the physiology of social behavior, more broadly defined [5–7]. However, the features of an infant that can elicit social approach and allocare have not been well-identified. In previous research, behavioral and endocrine measures during interactions with young animals have been used to assess the features of infants that elicit alloparenting [6]; however, both have limitations. For example, behavioral measures can be difficult to interpret, since animals may show approach to an infant followed by an attack. In small mammals, blood sampling used for most endocrine measures is invasive and often only a single sample is

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possible, restricting repeated sampling, and temporal resolution. Measures of autonomic responses, such as heart rate, have the advantage of continuous, non-invasive measurement of physiological state during social engagement. Via radiotelemetry, autonomic measures can be studied in the context of specific behaviors and can be taken repeatedly with minimal disturbance to the subject. In addition, knowledge of the neural control of heart rate provides new insights into the neurobiology of sociality [8].

Prairie voles are a socially monogamous species that has proven a particularly useful model for the analysis of the neurobiology of alloparenting. As in humans, the autonomic regulation of heart rate in prairie voles involves both sympathetic and parasympathetic processes, and prairie voles (like humans) have high levels of vagal activity, indexed by respiratory sinus arrhythmia (RSA) [9]. RSA represents the contribution of the vagal parasympathetic tone in dampening heart rate, and is widely interpreted as an index of emotion, sociability, and adaptability to stress [10,11]. In the presence of a pup, alloparental male prairie voles show a rapid and robust cardioacceleration, but do not show parasympathetic withdrawal which is typically associated with increases in heart rate [5,7]. Given the seemingly innocuous nature of a helpless pup and gregarious nature of the alloparent, such a response was largely unexpected. This cardioacceleratory response was also novel on account of the behavioral calmness and immobility that accompany alloparental care as well as the decrease observed in circulating glucocorticoid levels [6]. Typically, the activity of the hypothalamic-pituitary-adrenal axis, which releases glucocorticoids, and the activity of the sympathetic nervous system, which regulates heart rate, are positively correlated [12]. It remains to be investigated whether other rodent species show similar cardioacceleratory responses while providing care for pups.

In prairie voles, pup-induced cardioacceleration is not a result of increased locomotor activity [5]; in fact, alloparental prairie voles are relatively less mobile while a pup is present, showing instead a still, arched-back posture over the pups. What is more, the cardioacceleratory response did not habituate to prolonged nor repeated exposure to infants. Additional experiments revealed that pup-induced cardioacceleration was also observed in male vole fathers even after 10 days of paternal experience [7]. These experiments suggested that full expression of pup-induced cardioacceleration depends on physical proximity to the pup and heightened sympathetic drive to the heart [5].

Temperature regulation using the body heat of the offspring has been suggested as a regulatory factor for parenting behavior [13], and possibly could be relevant to the reaction of prairie voles to infants. Likewise, infants from altricial rodent species may require caregiver warmth for their own thermoregulation [14,15]. However, studies of both prairie vole fathers as well as reproductively naïve prairie vole males did not reveal a change in core body temperature in the caregiver during acute bouts of alloparental care [5,7]. Alternatively, specific characteristics of the pup might induce increased vigilance and/or social engagement in the alloparent. Originally, the cardioacceleratory response was interpreted as supporting the notion that an optimal range of autonomic activation (in this case activation of the sympathetic nervous system) was critical for positively engaging with the pup. Since approximately 20% of male prairie voles are non-parental (some even attack the pup), we hypothesized that these responses might represent hypo- and hyper-arousal respectively.

The purpose of the present study, conducted in reproductively naïve adult prairie voles with indwelling transmitters, was to measure autonomic function in response to direct exposure to pups or stimuli from pups to explore the purpose of pup-induced cardioacceleration. In Experiment 1, pup-induced cardioacceleration was compared in females and males. Females and males did not differ; therefore, the remaining experiments were aimed at identifying pup-related stimuli capable of inducing cardioacceleration in males. In Experiments 2 and 3, the effects of the age of the pup on alloparental behavior and cardioacceleration (Experiment 2), as well as pups' rates of isolation-induced ultrasonic vocalization (Experiment 3) were tested. In Experiment 4, the effect of odors obtained from pups at increasing ages was examined. Finally, we sought to re-evaluate the role of temperature and thermoregulation by examining cardioacceleration in an environment of increased ambient temperature (Experiment 5).

2. Methods

2.1. Subjects

Descendants of wild prairie voles (F4 generation) captured near Champaign, Illinois were used in these experiments. Subjects of 60–90 days of age were maintained on a 14/10 h light/dark cycle 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 ($24 \times 46 \times 15$ cm) containing cotton nesting material. Offspring were weaned at 20 days of age, prior to the arrival of the next litter to prevent premature exposure to pups, and then were pair-housed with a same-sex sibling in smaller cages ($17.5 \times 28 \times 12$ cm) in a single-sex colony room until testing. Except in Experiment 1 (see below), all test subject cohorts were made up of sexually naïve males that had never been exposed to pups, other than their own littermates, at the beginning of testing. Stimulus pups were drawn from the colony and used for testing immediately following removal from their natal nest.

Experiments 1 and 2 were conducted at the University of Illinois at Chicago and replicated upon moving our laboratory to Northeastern University. Experiments 3, 4, and 5, were conducted at Northeastern University. 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 and Northeastern University Institutional Animal Care and Use Committees. Experiments began during the lights-on period between 10:00 and 11:00 AM. Throughout all the experiments in which cardiovascular responses were recorded, it is likely that disturbing the home cage and removing the sibling contributed to tachycardia. However, we have previously compared the magnitude of this response to that following the introduction of a novel pup [5], which is marked by its magnitude and persistence.

2.2. Experimental design

Experiment 1: To test for sex differences in the cardiovascular response to pups, naive male and female prairie voles were implanted with radiotelemetry devices and allowed to recover with their siblings (see methods below). Beginning two weeks after surgery, male and female subjects ($n = 8$ for each sex) were tested for behavioral and cardiovascular responses to a pup. As in our previous investigations [5,7], baseline data were collected over the hour prior to testing, from which 5 min of data were collected while animals were stationary; data were selected as temporally close to stimulus presentation as possible. Immediately prior to testing, the non-implanted sibling cage-mate was removed, and a 1–3-day-old pup from an unrelated breeder pair was introduced into the subjects' cage. Stimulus pups remained in the subject's cage for 20 min while behavioral and cardiovascular data were recorded.

Experiment 2: Since the age of the pup is likely to contribute to the alloparent's behavioral and cardiovascular responses, we next varied the stimulus pups' age, using male vole subjects. Beginning two days after surgery, a separate cohort of male subjects ($n = 8$)