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Post-weaning living with parents during juvenile period alters locomotor activity, social and parental behaviors in mandarin voles

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ABSTRACT

Neonatal parental care plays an important role in the development of offspring behavior, but little is known about the effect of post-weaning contact between offspring and parents on locomotory, social and parental behavior. Here, we explore this concept using socially monogamous mandarin voles (*Microtus mandarinus*). Voles were assigned to live with parents and siblings from the same litter until 45 d (natural dispersal time in the field) or to live with siblings from the same litter after weaning at 21 d (normally weaned time, the control). At 70 d of age, behaviors were recorded in open field and social interaction tests, and parental care toward their own offspring was measured. Results show that voles that live with parents post-weaning engaged in less locomotory activity and rearing behavior in the open field test, less sniffing of novel individuals and displayed more parental care, compared to voles that did not continue to live with their parents. These findings demonstrate that parent–offspring interaction post-weaning alters locomotory activity, social behavior and parental behavior of offspring at adulthood.

1. Introduction

The early social environment can affect the physiological and behavioral development of humans and other mammals, of which, parental care is the most important social factor (Meaney, 2001; Champagne and Curley, 2005; Branchi, 2009). For example, reduced maternal care or parent-pup interaction during the neonatal period suppresses or impairs parental behavior in offspring (Gonzalez et al., 2001; Lovic et al., 2001; Kikusui et al., 2005; Jia et al., 2011). Similarly, neonatal paternal deprivation can increase anxiety and reduce sociality and levels of parental behavior in adult mandarin voles (*Microtus mandarinus*) (Jia et al., 2009, 2011). Compared to biparental-reared prairie voles (*Microtus ochrogaster*), single mother-reared females exhibit remarkably low spontaneous alloparental behavior and both males and females show delayed onset of partner preference formation (Ahern and Young, 2009). The majority of studies in this field have focused on parental effects during the pre-weaning period, and whether parental presence during the post-weaning period affects offspring remains poorly understood.

Weaning is the age when a young mammal switches from its mother's milk to solid food. After weaning, mothers tend to sharply reduce the time and effort devoted to offspring (Martin, 1984) and offspring become nutritionally and behaviorally independent (Kikusui et al., 2009). However, offspring in some mammal species often continue to stay with their parents following weaning, although their parents do attempt to drive them away. For example, rhesus monkey (*Macaca mulatta*) mothers may actively reject offspring during weaning, and offspring play an increasingly prominent role in initiating contact with their mother as they grow (Hinde, 1977). Parent–offspring interaction may continue for a significant time after weaning; however, the effect of this on offspring is not well understood.

The frequency and diversity of social contact with sibling and conspecifics during juvenile development can induce shifts in adult behavioral phenotypes. Rodents may be especially sensitive to manipulations in their social environment during this juvenile period (Ruscio et al., 2007). For example, deprivation of both maternal and littermate contact through early weaning enhances anxiety and aggression over a long period of time (Nakamura et al., 2003; Kikusui et al., 2004; Kanari et al., 2005), and results in decreased play-fighting behavior (Shimozuru et al., 2007). Late weaning can significantly increase the growth rate of lambs and pigs (Callesen et al., 2007; Knights et al., 2012) and in some species, juveniles also provide alloparental care for younger siblings. This experience is associated with more anxiety-like and less exploratory behavior, and elevated parental behavior and reproductive success in prairie voles (Stone et al., 2010; Greenberg et al., 2012). However, providing alloparental care in mandarin voles increases locomotory activity, social investigation and maternal care in adulthood (Wu et al., 2013). Only one study has investigated the effect of post-weaning interaction between mothers and pups on adult

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explorative and social behavior in rats and some sex-specific effects were found (Ferdman et al., 2007). Although several research groups have examined the effect of post-weaning social isolation on emotional behavior, social behaviors and some neuroendocine systems (Bibancos et al., 2007; Ruscio et al., 2007; Pan et al., 2009; Curley et al., 2011), they have been unable to elucidate whether the effects were led by the absence of parents or social deprivation. Little is known about the effect of post-weaning parent–offspring interaction on anxiety and specific social behavior in highly social species; less is known about the effect on offspring parental behavior from post-weaning contact with parents.

The mandarin vole is a socially monogamous rodent widely distributed across China (Tai et al., 2001; Tai and Wang, 2001). During the breeding season, burrow systems are occupied by family groups comprised of parents and offspring from different litters. Male–female pairs provide biparental care to offspring (Smorkatcheva, 1999; Tai et al., 2001). Mandarin vole offspring are generally weaned at 21 d of age (Jia et al., 2009) and some disperse, leaving the natal nest and establishing autonomy (Kikusui and Mori, 2009). However, the majority of juveniles remain in their natal nest for 45–50 d, and some as long as 70 d (Smorkatcheva, 1999). In the lab, mandarin vole families have higher levels of social interaction via biparental, alloparental, and affiliative behavior and stable pair-bonds (Jia et al., 2009; Song et al., 2010; Yu et al., 2012). Fathers show more amicable behavior toward younger adolescents and more agonistic behavior toward older adolescents, and levels of amicable and agonistic behavior vary linearly with offspring age (Wang and Tai, 2012). This species is therefore an interesting model for exploring the effect of parent–offspring contact following weaning.

Early social experience is dominated by family encounters, and typically regarded as positive experiences that can help individuals prepare for societal interaction (Lareau, 2003). Parental care is the most important early experience and can affect anxiety-like, social and parental behavior in offspring. If receiving parental care is always beneficial, even after weaning, we predicted that mandarin voles that have post-weaning parental interaction should show lower levels of anxiety and high levels of affiliative and parental behavior.

2. Methods

2.1. Materials

Mandarin voles were laboratory-reared F2 generation animals (30–34 g) that originated from a wild population in Henan, China. Animals were maintained on a 14:10 light:dark cycle (lights on at 20:00 h) at 25 ± 3 °C, and allowed free access to food (carrots and rabbit chow) and water in polycarbonate cages (44 cm × 22 cm × 16 cm) containing cotton for nesting material. All procedures were in accordance with the Guide for the Care and Use of Laboratory Animals of China and were reviewed by the Institutional Animal Care and Use Committee at Shaanxi Normal University.

2.2. Experimental design

Twenty pairs of laboratory-bred male and female mandarin voles were used as breeding pairs for the production of subjects. Female mandarin voles gestate for 21 d. After the delivery of the first litter, most females underwent a postpartum estrus and copulated with their mates. Generally, mandarin voles gave birth to the second litter within 1 week of weaning the first litter. However, some breeding pairs did not produce a second litter until the first litter was at postnatal day 45 and animals from the first litter were assigned to the treatment group. In this group (hereby DAY45), offspring were not removed from the parental cage at 21 d of age, and instead allowed to remain with their parents until 45 d of age. They were then removed and housed in same-sex sibling pairs until testing. In the control (hereby DAY21), offspring were housed together with their parents until 21 d of age (weaning age per standard laboratory procedures), then removed and housed in same-sex sibling pairs until testing at 70 d of age. In this study, only litters containing three or more pups were used to generate our experimental groups. If the parents produced a second litter during postnatal days 21–45 of the first litter, the offspring were excluded from this study.

2.3. Open field test

When subjects (10 females and 10 males per group) were 70 d old, locomotory activity and anxiety-like behavior were assessed in an open field chamber made of white glacial polyvinyl chloride (50 cm × 50 cm × 25 cm). The arena was divided into 16 quadrants (four central and 12 peripheral) (Fiore and Ratti, 2007) and illuminated with one lamp 1.5 m above. Light intensity was approximately 200 lux in the center of arena. Tested voles were placed individually into the center of the open field and left to explore for 5 min. The following were scored using a digital video camera: time spent in the central and peripheral area; number of transitions between quadrants; frequency of rearing (raising on hind legs sniffing the air or the wall of the box); and the duration of self-grooming, walking (moving in the cage), inactivity (sitting quietly) and sniffing (nose very near to the bottom of the box). Total transitions were considered an indicator of locomotor activity. Rearing and the percentage of time spent in the central area are widely interpreted as 'explorative' and indicative of reduced anxiety (Weiss et al., 2001; Lomanowska et al., 2006). The box was cleaned and deodorized with 70% alcohol solution after each test to remove any olfactory cues.

2.4. Social interaction test

Following the open field test, subjects at 75 d of age were observed during a social interaction test. Tested animals had a similar body weight as stimulus animals. Stimulus animals were sexually naive individuals of the same sex and unfamiliar with the subject. In order to identify individual animals, the stimulus animal was marked by cutting a bundle of hair on the back. Prior to testing, the stimuli and focal animals were placed on the opposite side of the observed cage and acclimated for 15 min, but were initially separated by a clapboard in the middle of the cage. Once the clapboard was removed the test commenced and we recorded the total duration and frequency of the following behaviors using a video camera for 10 min: attacking (active fighting between two voles such as wrestling, biting or chasing), contact interaction (physical contact with mutual responses and orientation toward the other animal), sniffing partners, staring (vigilantly staring at the stimulus), submission (lying down and showing their belly to the stimulus), retreating (trying to escape and keeping away from the stimulus), self-grooming (cleaning fur or scratching) and other nonsocial behavior. Precautions were taken to prevent injury and minimize stress on animals. During a pretest, stimulus voles were selected from voles that seldom attacked another animal. The test cage was relatively large enough for both animals to retreat easily and exclude each other. Any fight lasting more than 10 s was interrupted by tapping the side of the cage. If a bout of attacking behavior lasted more than 20 s and the animal did not respond to our tapping, we terminated the encounter and separated the individuals before any injury. Serious injuries (e.g. bites that drew blood) were not observed during these brief social interactions. All animals were healthy and showed normal locomotor activity