



Social recognition in paired, but not single, male prairie voles



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ARTICLE INFO

Article history:

Received 6 November 2014

Initial acceptance 6 January 2015

Final acceptance 10 June 2015

Available online xxx

MS. number: A14-00898R

Keywords:

cognitive ecology

monogamy

pair bond

prairie vole

social recognition

Social recognition is an integral component of behaviour that underlies many much larger behavioural suites. For example, monogamous pair bonding is relatively meaningless if an individual cannot recall with whom the bond was with. The prairie vole, *Microtus ochrogaster*, is a socially monogamous rodent, well known for its long-term pair bonds between males and females. Although previous work has shown that bonded males reliably spend more time with their pair-mate over an unfamiliar female, recent work has demonstrated that single male prairie voles do not discriminate between females. This discrepancy raises the important question: do paired males distinguish between nonmate females? We asked whether pair bonding alters the expression of social recognition in male voles by comparing social recognition of single and pair-bonded males using the habituation/dishabituation paradigm. We found that pair-bonded, but not single male prairie voles showed social recognition of (nonmate) females, suggesting a shift in cognitive behaviour after pair bond formation. This difference was not due to differences in motivation to engage in social exchanges, as males attempted to contact unfamiliar females at similar levels. Based on these data, we speculate that the stage of life (single or bonded) influences the relevance of attending to social information of same- and opposite-sex conspecifics.

The Association for the Study of Animal Behaviour. Published by Elsevier Ltd.

Social recognition is a fundamental cognitive ability that contributes to most aspects of behavioural biology. Social recognition can be thought of as the ability to process and subsequently make use of social information, enabling animals to discriminate among conspecifics and socially interact based on past experiences. Without this ability an animal would be unable to differentiate between kin and potential mates, neighbours and intruders, dominant and submissive conspecifics, healthy or diseased individuals, or their own versus another's offspring (Carter & Keverne, 2002; Choleris, Kavaliers, & Pfaff, 2004; Colgan, 1983; Kavaliers, Choleris, Agmo, & Pfaff, 2004). The role of social recognition in these behaviours has obvious significant implications for fitness.

A pair bond between two individuals forms the foundation for a monogamous relationship. Such a bond requires much more than simply positive affiliative behaviour directed towards the pair-mate. The need to identify and discriminate a mate from other conspecifics is crucial if an animal is going to establish a bond that lasts longer than a single encounter. Therefore, although it may not

often be discussed in this way, social recognition is a necessary component of monogamous relationships.

Social recognition has been studied in a number of species. However, much of the attention has focused on traditional laboratory rodents, like mice (*Mus musculus*) and rats (*Rattus norvegicus*), and indeed significant progress towards understanding the mechanisms that underlie social recognition and some of the contexts in which social recognition emerges has been gained (Bielsky, Hu, Szegda, Westphal, & Young, 2004; Choleris et al., 2003; Ferguson, Aldag, Insel, & Young, 2001; Ferguson, Young & Insel, 2002; Kogan, Frankland, & Silva, 2000). For example, several studies have implicated the neuromodulators oxytocin and vasopressin (and their respective receptors OTR and V1aR) in the lateral septum as necessary for social recognition (Bielsky, Hu, Ren, Terwilliger, & Young, 2005; Everts & Koolhaas, 1999; Ferguson et al., 2002). Unfortunately, these species do not form monogamous pair bonds.

Prairie voles, *Microtus ochrogaster*, are particularly useful in studies of social behaviour because they are socially monogamous (Carter, 1998; Carter, DeVries, & Getz, 1995; Getz, McGuire, Pizzuto, Hofmann, & Frase, 1993; McGuire, Getz, Bemis, & Oli, 2013; Ophir, Phelps, Sorin, & Wolff, 2008; Solomon & Crist, 2008). Although some males and females in the population are known to engage in extrapair mating (Ophir, Phelps, et al., 2008; Solomon, Keane, Knoch, & Hogan, 2004; Wolff, Mech, Dunlap, & Hodges, 2002),

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most prairie voles nest in pairs and share in offspring care (Getz & Carter, 1996; Wolff et al., 2002). Furthermore, much has been learned in the past 20 years regarding their neurobiology and social behaviour (Carter, 1998; Carter et al., 1995; Ophir, Wolff, & Phelps, 2008; Resendez & Aragona, 2013; Solomon et al., 2009; Young & Wang, 2004; Young, Young, & Hammock, 2005), and recently they have been studied for their social investigation and recognition (Ophir, Zheng, Eans, & Phelps, 2009; Zheng, Foley, Rehman, & Ophir, 2013). For example, Zheng, Foley, et al. (2013) showed that social recognition in male voles differs across social contexts. Of particular note, was that single male prairie voles showed social recognition of other males, but not of females. Zheng, Foley, et al. (2013) proposed that this difference in behaviour might relate to an emphasis on the relevance of knowing male identity (perhaps to establish and defend a territory) over female identity (initiating courtship leading to a bond may be equally good for any available female at this stage of life). Furthermore, it is plausible that a male's skill at defending his home range (which might rely on discriminating between neighbouring and competing males) has the power to impact his desirability to females, thereby increasing the potential importance of establishing territories for single males.

This interesting result raises a larger question: if social recognition is indeed necessary for social monogamy, do male prairie voles discriminate between females at all? Social recognition of female conspecifics should be particularly relevant to male prairie voles that have pair bonded. Indeed, pair-bonded males show a characteristic 'partner preference' for their mate over other females (Williams, Catania, & Carter, 1992) and selective aggression towards strangers, but not mates (Young, Liu, & Wang, 2008; Young & Wang, 2004), strongly suggesting that males are able to at least discriminate between their partner and other females. However, it is unclear whether males are able to distinguish among nonmate females or if bonding induces a change in the expression of social recognition among nonmate females. In this study, we ask whether pair bonding alters the expression of female social recognition among male prairie voles. Specifically, we test the hypothesis that pair-bonded males will demonstrate social recognition. To test this hypothesis, we compared the ability of single and pair-bonded males to discriminate between unfamiliar females using the habituation/dishabituation paradigm.

METHODS

Animals

All animals used in this study were from the F2 generation within a breeding colony derived from wild stock originally trapped in Champagne-Urbana, Illinois, U.S.A. At weaning (21 days), offspring were separated into same-sex litters and housed in polycarbonate cages (29 × 18 × 13 cm) lined with Sani-chip bedding and provided nesting material. No animals in this experiment were raised in isolation. Water and rodent chow (Rodent Chow 5000, Harlan Teklad, Madison, WI, U.S.A.) were provided ad libitum and animals were maintained on a 14:10 h light:dark cycle (lights on at 0600 hours) with ambient temperature maintained at 20 ± 2 °C. This study was approved by the Institutional Animal Care and Use Committee of Oklahoma State University (AS 09-6). All animals included in this study were sexually naïve adults (≥ 60 days of age) and unrelated to other animals to which they were exposed during the experiment.

Behavioural Testing

Twenty-eight adult sexually naïve males were eartagged and randomly divided into two experimental groups: pair bonded and

single. All testing occurred between 0700 and 1600 hours and was semirandomized such that each day an equal number of pair-bonded and single males were tested but the order of testing was randomized.

Pairing and partner preference tests

Before establishing a pair bond between animals assigned to the pair-bonded group, we induced sexual receptivity in the females by exposing them for 48 h to soiled bedding and nesting material from an unfamiliar male that was unrelated to the female and the focal male (Carter, Getz, Gavish, McDermott, & Arnold, 1980; Dluzen, Ramirez, Carter, & Getz, 1981; Richmond & Stehn, 1976). Next, we co-housed males assigned to this group with females for 24 h to establish a pair bond (Williams et al., 1992; Winslow, Hastings, Carter, Harbaugh, & Insel, 1993). Notably, Williams et al. (1992) demonstrated that 24 h of cohabitation, even without mating, is sufficient to establish a pair bond. We confirmed that a pair bond had been established using a partner preference test (Williams et al., 1992) immediately after the period of cohabitation. Males were placed in a three-chamber apparatus (60 × 50 × 40 cm) consisting of a neutral chamber (20 × 50 × 40 cm), and two smaller adjacent chambers (each 30 × 25 × 40 cm) (see Ophir & DelBarco-Trillo, 2007). The female with whom a 'paired' male had just been housed was tethered in one of the adjacent chambers and a novel female was tethered in the other. Prior to their involvement in this test, novel females were also induced to be sexually receptive as described above. This design allows the male to move and interact freely with each female, while limiting the interactions between females. Tethering, which involves using a plastic zip-tie as a collar connected to a light-weight chain attached to the apparatus, does not inhibit animals from normal activities (e.g. moving, eating or mating; Ophir, Phelps, Sorin, & Wolff, 2007; Wolff & Dunlap, 2002). After 3 h, males were returned to their home cages with their original pair-mate. We quantified time spent in side-by-side contact with each female to determine which female subject males preferred. A pair bond was defined as when a male spent at least twice as much time in contact with the paired female over the stimulus female (Carter et al., 1995; Carter & Getz, 1993; Insel & Hulihan, 1995; Insel, Preston, & Winslow, 1995; Williams et al., 1992).

Focal males assigned to the single group remained in their home cages with a single male sibling during the pair-bonding period. To ensure that pair bonding alone would account for behavioural differences, single males also underwent a choice test akin to the partner preference tests. Single males were presented the same pairs of females that served as stimuli for a male assigned to the pair-bonded group. Female pairs were reused only once to test a male serving in the single group and a male serving in the paired group. We counterbalanced the order of which male (single or paired) was first across the experiment.

Partner preference tests were recorded using a Sony HDR-XR200V camcorder (Sony, New York, NY, U.S.A.) placed approximately 1 m above the apparatus. Videos were scored using Observer XT software (Noldus Information Technology, Leesburg, VA, U.S.A.). To use videos in Observer XT, the .mov files the recorder produced were converted into .mpg files using Quicktime X (Apple Inc, Cupertino, CA, U.S.A.). Video observers were blind to the mating status of the male (paired or single).

Partner preference test analyses

We analysed partner preferences in two ways. First, we used ANOVA to compare the time that single and paired males spent with each female. Comparing the data in this way allowed us to determine whether bonded males demonstrated a preference for partners and whether they were indeed bonded. It also allowed us

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