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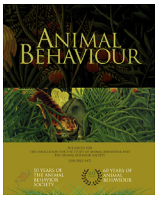

Social recognition is context dependent in single male prairie voles

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Single males might benefit from knowing the identity of neighbouring males when establishing and defending boundaries. Similarly, males should discriminate between individual females if this leads to more reproductive opportunities. Contextual social cues may alter the value of learning identity. Knowing the identity of competitors that intrude into an animal's territory may be more salient than knowing the identity of individuals on whose territory an animal is trespassing. Hence, social and environmental context could affect social recognition in many ways. Here we test social recognition of socially monogamous single male prairie voles, *Microtus ochrogaster*. In experiment 1 we tested recognition of male or female conspecifics and found that males discriminated between different males but not between different females. In experiment 2 we asked whether recognition of males is influenced when males are tested in their own cage (familiar), in a clean cage (neutral) or in the home cage of another male (unfamiliar). Although focal males discriminated between male conspecifics in all three contexts, individual variation in recognition was lower when males were tested in their home cage (in the presence of familiar social cues) compared to when the context lacked social cues (neutral). Experiment 1 indicates that selective pressures may have operated to enhance male territorial behaviour and indiscriminate mate selection. Experiment 2 suggests that the presence of a conspecific cue heightens social recognition and that home-field advantages might extend to social cognition. Taken together, our results indicate social recognition depends on the social and possibly territorial context.

Social recognition can be broadly defined as the ability of an individual to distinguish one conspecific from another (Ferguson et al. 2002). This includes identification of an individual's specific social status, sex, or any other possible aspect of the phenotype. A more refined definition of this behaviour is how an individual integrates previous knowledge of another conspecific and changes their behaviour in a biased manner (Choleris et al. 2009). In either case, the importance of this behaviour should not be underappreciated given its implications as a fundamental building block for more complex behavioural phenotypes such as aggression or social bonding.

Social recognition has been studied across many taxa (Gheusi et al. 1994; Tate et al. 2006; Bierbach et al. 2011; Jarcho et al. 2011; Sheehan & Tibbetts 2011; Bos & d'Ettorre 2012), but perhaps no animals have contributed to a deep understanding of social recognition more than rodents (Bielsky et al. 2005; Choleris et al. 2009; Albers 2012; Bychowski & Auger 2012; Wacker & Ludwig 2012). The paradigms developed in rodents that test social recognition are robust (Halpin 1974; Johnston 1993; Ferguson et al. 2002), often yielding reliable and predictable outcomes under controlled conditions (Macbeth et al. 2009a). Indeed, rodent models have greatly advanced our understanding of the mechanisms of social recognition and memory, and suggest that the neural mechanisms that govern social recognition are highly conserved (Ferguson et al. 2002; Choleris et al. 2009).

It should come as no surprise that animals frequently use social recognition in daily life. For instance, the dear enemy effect (Fisher 1954; Temeles 1994) implicitly assumes and relies upon an animal's ability to recognize and discriminate between conspecifics. Similarly, mate choice may rely on the ability to distinguish between potential partners, whether this functions as a means to avoid inbreeding with kin or to choose mates in good body condition (Kavaliers & Colwell 1995; Kavaliers et al. 2004; Mateo 2004; Zala et al. 2004). Unfortunately, seldom do studies designed to test social recognition in the laboratory consider the behavioural ecology of the study species (but see: Hurst et al. 1994; Ferkin & Johnston 1995; Kavaliers & Colwell 1995; Solomon & Rumbaugh 1997; Zala et al. 2004). Indeed, many studies explicitly designed to test social recognition ignore the social context or how it relates to this crucial cognitive ability. This is surprising because one of the prime motivations to understand social recognition is to gain a better

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appreciation for how this cognitive behaviour subserves other, more complex, social behaviours; this goal can only be achieved if an animal's natural history is taken into consideration.

Behaviours associated with a monogamous mating system represent one such area in which the role of social recognition is important in understanding a larger behavioural phenotype, and the biological relevance provides an important contextual backdrop. Several hypotheses attempting to explain the evolution of monogamy have been proposed, and the most prominent of these have highlighted the influence of male territorial behaviour used to defend ecological resources or mates from competing males (Orians 1969; Emlen & Oring 1977; Clutton-Brock & Vincent 1991; Wolff & Macdonald 2004). In the most general sense, monogamy can be characterized by selective affiliation with a mate, biparental care of offspring, and selective aggression involving territory and mate defence (Kleiman 1977; Clutton-Brock & Vincent 1991). Clearly, all three of these component behaviours require social recognition, but the sex and social context of the learning event is likely to produce differences in motivation and hold different biological valences for the individual. Nevertheless, it is unknown what role social recognition plays in each of these component behaviours.

Most laboratory studies that are designed to test social recognition have used mice or rats. When these studies have focused on male social recognition, stimulus animals will either be ovariectomized females (to control for effects of sexual receptivity) or juvenile males (to control for effects of male–male aggression). Although these methods have been effective at enabling researchers to assess the capacity for social recognition, they also have limited the ability to assess social recognition under social contexts that may carry particular biological relevance for this cognitive behaviour. With this in mind, prairie voles, *Microtus ochrogaster*, are a particularly well-suited species to investigate the influence of social recognition. Unlike rats and mice, female prairie vole oestrus is induced by exposure to males or pheromones in their urine (Richmond & Stehn 1976; Carter et al. 1980; Dluzen et al. 1981). Thus, male motivation to investigate females for which sexual receptivity has not been induced should be comparable to that of rats and mice that are exposed to ovariectomized females without the need to perform surgery on stimulus females. Although field studies have indicated that territorial aggression probably results in exclusion of competitor males from established home ranges (Getz & Hofmann 1986; McGuire et al. 1990; Getz et al. 1997; Jacquot & Solomon 2004), prairie vole aggression in the laboratory is relatively low in males that are not pair bonded (Pitkow et al. 2001; Young & Wang 2004; Gobrogge et al. 2009). Thus, the likelihood of male–male aggression interfering with measures of social recognition when using single adult males as stimulus animals is low.

Furthermore, due to their socially monogamous mating system (Gavish et al. 1981; Carter & Getz 1993; Getz et al. 1993; Ophir et al. 2008), prairie voles offer an excellent opportunity to study social recognition in ways that relate to biologically meaningful contexts. Although the social organization of prairie voles is complex, all males begin life as nonreproductive unpaired individuals. At sexual maturity, males may choose to remain at the nest (as part of communal breeding units), or leave the nest (Getz & McGuire 1993; Getz et al. 1993). Males that leave the nest will form male–female breeding units, join other communal breeding units, or remain single and 'wander' (Solomon & Jacquot 2002; McGuire & Getz 2010; McGuire et al. 2013). Wanderers characteristically traverse large areas that they do not defend and are thought to mate opportunistically (Getz et al. 1993; Solomon & Jacquot 2002; Ophir et al. 2008). While some wanderers continue with this reproductive tactic until death, others will become 'residents' (McGuire & Getz 2010), a monogamous tactic in which males establish and defend territories, form pair bonds and exclude conspecifics, presumably to defend offspring and mate guard (Getz et al. 1993). Although residency is the most common tactic among prairie voles (estimated to account for 54–75% of the population: Getz et al. 1993; Solomon & Jacquot 2002; Ophir et al. 2008), a significant proportion of males will be sexually mature and single at some point in their lives. Indeed, about two-thirds of wanderers are former residents (from either male–female breeding units or communal breeding units) and transition to/from residency appears to be common (Solomon & Jacquot 2002; McGuire & Getz 2010; McGuire et al. 2013).

EXPERIMENT 1: DOES SOCIAL RECOGNITION VARY WITH SOCIAL CONTEXT?

The cognitive demands necessary to succeed during the single 'wandering' phase of life may differ based on the context in which an animal finds itself. For instance, natural selection may favour single males that are able to remember the location and identity of females in space and time as a means to maximizing reproductive opportunities (Gaulin & FitzGerald 1989; Jones et al. 2003; Ferkin et al. 2008; Ferkin 2011). Presumably, tracking female receptivity may lead to such benefits. Alternatively, the costs associated with learning female identity may provide little added benefit to reproduction, in which case it may not be worth the effort needed to discriminate between females. Thus, a lack of female recognition, which would lead to treating all females the same, may be equally or more beneficial to single males trying to maximize reproductive opportunities.

Recognition of other males may be important for single males if the value of establishing territories is high. For example, given that territorial residency is the most common reproductive tactic among prairie voles (Getz et al. 1993; Solomon & Jacquot 2002; Ophir et al. 2008), and transitions from single wanderer to paired resident are common, it seems plausible that single males would benefit by learning the identity of conspecifics with whom they will compete for territory. Alternatively, because single males are nonterritorial, encountering any male may present a threat to their reproductive success or survival regardless of their identity; in which case, recognition of other males may provide little value.

Our aim in this study was to assess the capacity for social recognition in single male prairie voles. We assumed that social recognition performance in different contexts would reflect the relevance and salience of social identity for single males. For example, the ability to discriminate between males should connote the importance of intermale aggression, whereas the ability to discriminate between females should suggest the reproductive value of female identity to males is relatively high. Here we test the general hypothesis that social recognition varies as a function of social context.

Methods

Subjects

All prairie voles in this experiment were F2 or F3 descendants from a breeding colony generously donated by Dr Tom Curtis (Oklahoma State University, Tulsa), and originally trapped from wild-caught voles from Champaign County, Illinois, U.S.A. We outbred these voles with wild prairie voles collected in Champaign County. New litters were weaned at 21 days old and housed in same-sex groups in polycarbonate cages (29 × 18 × 13 cm). We kept a 14:10 h light:dark cycle throughout the experiment (lights on at 0600 hours) and provided Rodent Chow 5000 (Harlan Teklad, Madison, WI, U.S.A.) and water ad libitum. Males and females were