



Mechanistic substrates of a life history transition in male prairie voles: Developmental plasticity in affiliation and aggression corresponds to nonapeptide neuronal function

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ABSTRACT

Although prairie vole (*Microtus ochrogaster*) social behavior is well-characterized in adults, surprisingly little is known about the development of social behavior in voles. Further, the overwhelming majority of studies in prairie voles examine social behavior in a reproductive context. Here, we examine developmental plasticity in affiliation and aggression and their underlying neural correlates. Using sexually naive males, we characterized interactions with an age-matched, novel, same-sex conspecific in four different age groups that span pre-weaning to adulthood. We found that prosocial behavior decreased and aggression increased as males matured. Additionally, pre-weaning males were more prosocial than nonsocial, whereas post-weaning males were more nonsocial than prosocial. We also examined nonapeptide neural activity in response to a novel conspecific in brain regions important for promoting sociality and aggression using the immediate early gene cFos. Assessment of developmental changes in neural activity showed that vasopressin neurons in the medial bed nucleus of the stria terminalis exhibit functional plasticity, providing a potential functional mechanism that contributes to this change in sociality as prairie voles mature. This behavioral shift corresponds to the transition from a period of allopatric cohabitation with siblings to a period of time when voles disperse and presumably attempt to establish and defend territories. Taken together our data provide a putative mechanism by which brain and behavior prepare for the opportunity to pairbond (characterized by selective affiliation with a partner and aggression toward unfamiliar conspecifics) by undergoing changes away from general affiliation and toward selective aggression, accounting for this important life history event.

1. Introduction

Phenotypic differences in social behavior, and relevant underlying mechanisms, are most commonly examined on an evolutionary timescale using comparative neuroanatomical studies. Such research has defined distinct neural profiles that underlie differences in closely related species that exhibit monogamous or promiscuous mating phenotypes (Wang, 1995; Young, 1999), highly social or highly territorial phenotypes (Goodson et al., 2012; Wang et al., 2013), and uniparental or biparental phenotypes (Roland and O'Connell, 2015; Bales and Saltzman, 2016). However, variation in social behavior also occurs between or within individuals of the same species. Behavioral phenotypic plasticity can take many forms, including behavioral shifts across the lifespan within individuals.

Life history events are very likely to correspond to important changes in cognition and behavior. For instance, sexually naive adult

prairie voles (*Microtus ochrogaster*) are commonly considered to be highly social and display non-selective affiliative behavior toward novel conspecifics (relative to other vole species; Shapiro and Dewsbury, 1990). Interestingly, however, during or just after formation of a pairbond, prairie voles exhibit selective aggression toward unfamiliar conspecifics, and develop selective affiliation toward their familiar partner (Young et al., 2011; Blocker and Ophir, 2016). This shift in behavior is a striking example of a non-seasonal shift in sociality that relates to pairbonding, a poignant moment in the life history of a prairie vole. Similarly, single male prairie voles discriminate between other males but not females at a time when male identity is presumably highly relevant to them (Zheng et al., 2013). However, after males form pairbonds, a time when the identity of other females is likely to be more meaningful, they show clear evidence of social discrimination for unfamiliar females (Blocker and Ophir, 2015).

Development is another often-overlooked timescale on which

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individuals may exhibit social behavioral plasticity. Although the social needs of an animal vary from birth to adulthood, very few studies have examined developmental shifts in sociality. For example, high amounts of prosocial behavior and low levels of aggression might be most beneficial at young ages when an animal is vulnerable and dependent on parents, siblings, and/or communal members for survival (Shapiro and Insel, 1990; Curley et al., 2009). However, when an organism reaches sexual maturity, the same suite of behaviors might become detrimental, and instead aggression could produce greater fitness enhancing outcomes (i.e., to successfully compete for and obtain territories, mates, and food resources; Nelson et al., 2013). Thus, the valence of social interactions and the subsequent behavioral response is likely to shift as an animal matures in a manner that corresponds with shifts in behavioral priorities associated with greater fitness (Silk, 2007). The social needs and priorities of an animal change throughout development, emphasizing the need for mechanisms enabling behavioral plasticity to appropriately respond to environments they commonly experience or should be biologically prepared to experience (Snell-Rood, 2013).

Prairie voles are an excellent species for examining shifts in social behavior throughout development. In the wild, prairie vole pups are reared in groups comprised of either 1) single-female units with offspring, 2) a male-female breeding pair with multiple generations of offspring, or 3) breeding communal groups comprised of a male-female pair, multiple generations of offspring, and unrelated adults that often serve as alloparents (Getz et al., 1993; McGuire and Lowell, 1995). Around the time of reproductive maturation (roughly postnatal day [PND] 45), juveniles disperse (McGuire et al., 1993). At dispersal, a minority of prairie voles will remain single (or ‘wander’), whereas a majority of them will adopt a socially monogamous mating tactic known as ‘residency’, in which they establish independent territories, form pairbonds and mate, and ultimately rear offspring biparentally (Getz et al., 1993; McGuire et al., 1993; Solomon and Jacquot, 2002; Ophir et al., 2008b; McGuire and Getz, 2010).

Prairie vole social behavior has been studied extensively in relation to pairbonding (Young and Wang, 2004; Young et al., 2011; Lieberwirth and Wang, 2016). In contrast, nonsexual affiliation in prairie voles has been surprisingly understudied — particularly at ages prior to adulthood. Preliminary (unpublished) findings from our lab suggest that a shift toward a less social phenotype might occur in sexually naïve males before pairbond formation. In the present study, we assessed whether a developmental shift from a more social phenotype to an increasingly less social and more territorial phenotype exists in the prairie vole outside the context of reproduction. Intuitively, it would be more advantageous for an individual to exhibit greater prosocial behavior and less aggression prior to dispersal given that juveniles benefit from parental care and familial cooperation for survival (Solomon and French, 1997). Similarly, it might be beneficial for prairie voles to become less gregarious as they mature (around the age of sexual maturation and dispersal) in anticipation of shifting toward mating tactics that are closely associated with territoriality and selective affiliation (i.e., residency).

The nonapeptides, vasopressin (VP) and oxytocin (OT), are well known for modulating pairbonding, sexual behavior, nonsexual affiliation, parental care, stress response, and aggression (Young, 2009; Goodson and Thompson, 2010; Neumann et al., 2010). VP and OT are evolutionary conserved peptides produced in distinct neuronal population throughout the basal forebrain and midbrain (Farina-Lipari and Valentino, 1993; Farina Lipari et al., 1995). These distinct cell groups exhibit some overlapping, yet also different, contributions to behavior (Kelly and Goodson, 2014). Among the many VP and OT cell groups, two accessory cell groups are of particular interest for the current study: the VP cell groups of the medial bed nucleus of the stria terminalis (BSTm) and the anterior hypothalamus (AH). VP neurons in the BSTm directly promote gregariousness (a preference for larger groups) and suppress aggression in male finches (Kelly and Goodson, 2013). Furthermore, BSTm VP neurons are responsive to positive social stimuli in

songbirds (Goodson et al., 2009), and to copulation, but not aggressive or agonistic interactions, in male mice and chickens (Ho et al., 2010; Xie et al., 2011). Conversely, the VP cell group of the AH has been implicated in promoting aggression. For instance, studies examining VP release or VP receptors in the AH suggest a primary role for AH VP in flank marking and overt aggression (Albers, 2012). Although not a direct assessment of AH VP neurons, selective aggression displayed by pairbonded male prairie voles is closely associated with higher densities of VP receptors and increased levels of VP release within the AH (Gobrogge et al., 2009). Nevertheless, surprisingly few studies have directly examined AH VP neuronal function (Kelly and Goodson, 2014).

Here, we sought to investigate developmental changes in nonsexual affiliative and aggressive behavior in male prairie voles. We examined male interactions with age-matched, novel males at different stages of development ranging from pre-weaning to reproductively mature adulthood (Carter and Getz, 1985; Solomon, 1991; Mateo et al., 1994). Because the BSTm VP and AH VP cell groups play an important role in prosocial and aggressive behaviors, respectively, we also examined immediate early gene (IEG) activity within these cell groups to evaluate nonapeptide neuronal functional changes associated with changes in nonsexual affiliative and aggressive behavior. Our main hypothesis was that males should demonstrate a shift away from a social phenotype toward a more territorial phenotype as they mature, with the main shift likely to occur around sexual maturity and the age of dispersal (i.e., PND45). We also hypothesized that BSTm VP neurons would become less responsive, and that AH VP neurons would become more responsive, to interactions with a novel, same-sex conspecific as prairie vole males reach adulthood. Although we had no a priori predictions about how or if BSTm OT neurons would respond to exposure to a same-sex conspecific over development, we chose to characterize this cell group because OT and VP frequently influence common behaviors and there is an extreme lack of functional data on BSTm OT neurons.

2. Materials and methods

2.1. Animals

Prairie voles used in this study were obtained from our breeding colony, from breeding pairs that were offspring of wild caught animals we captured in Champagne County, Illinois, USA. All animals were housed in standard polycarbonate rodent cages (29 × 18 × 13 cm) lined with Sani-chip bedding and provided nesting material. Animals were kept on a 14L:10D cycle, and were provided with rodent chow (Laboratory Rodent Diet 5001, LabDiet, St. Louis, MO, USA) and water ad libitum. Ambient temperature was maintained at 20 ± 2 °C. All procedures were approved by the Institutional Animal Care and Use Committee of Cornell University (2013-0102).

2.2. Experimental design

Our study aimed to assess changes in social behavior, and the underlying neural mechanisms, throughout development of the prairie vole. We tested male prairie voles at four ages to capture ages representative of distinct developmental milestones: PND15 (pre-weaning, dependent on parents for survival), PND30 (post-weaning, independent), PND45 (end of sexual maturation; beginning of dispersal), and PND60 (adulthood; reproductively viable) (Carter and Getz, 1985; Solomon, 1991; Mateo et al., 1994). PND15 subject (and stimulus) animals were housed with their parents and siblings, whereas PND30, PND45, and PND60 subject (and stimulus) animals were housed with a same-sex sibling. Sample sizes for each age group were: PND15 n = 10, PND30 n = 10, PND45 n = 10, and PND60 n = 11.

We characterized nonsexual social behavior in sexually naïve males at each age mentioned above. All tests were video recorded with a camera positioned above the cage for subsequent behavioral scoring (see Section 2.3). Stimulus animals received a zip-tie collar the day

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