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Research Report

Dopamine and monogamy

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ARTICLE INFO

Article history:
Accepted 27 July 2006
Available online 1 September 2006

Keywords:
Microtus
Vole
Reward
Mesolimbic
Nucleus accumbens
Addiction

ABSTRACT

Social attachments play a central role in human society. In fact, such attachments are so important that deficits in the ability to form meaningful social bonds are associated with a variety of psychological disorders. Although mother–infant bonding has been studied for many years, we only recently have begun to examine the processes that underlie social bonds between adults. Over the past decade, central dopamine has become a focus of such research, especially its role in pair bonding between mates in species that display monogamous life strategies. Neuroanatomical and pharmacological studies in rodents have firmly established central dopamine systems, especially the mesocorticolimbic dopamine circuitry, in the formation, expression, and maintenance of monogamous pair bonds. As this research has progressed, it has become apparent that there is considerable overlap between the processes that underlie pair bonding and those that mediate responses to abused substances. This suggests that social bonding and substance abuse each may affect the other. Herein we review the current state of knowledge of central dopamine involvement in pair bond formation, expression, and maintenance. We first describe the neuroanatomical substrate within which dopamine exerts its effects on social bonding. We then describe dopamine receptor subtype-specific influences on pair bonding and how dopamine receptor activation may interact with activation of other neurochemical systems. Finally, we describe possible interactions between social bonding and substance abuse.

1. Introduction

Affiliative behavior is a fundamental part of the natural history for many animal species, including humans, and has been shown to have adaptive significance. Schooling by fish, flocking by birds, and other types of group living may serve to reduce predation (Hass and Valenzuela, 2002; Seghers, 1974). At the individual level, young baboons are more likely to survive if the mother has established strong social ties (Silk et al., 2003). As an extreme example, intimate contact between mother and infant can alter the rate of autonomic maturation (Feldman and Eidelman, 2003).

In some cases, natural selection may favor the formation of bonds between specific individuals. For example, there is evidence that remaining with the same partner enhances lifetime reproductive success in California mice (*Peromyscus californicus*) (Ribble, 1992). Such selective pressures may lead to the evolution of a monogamous mating strategy (Kleiman, 1977), manifested by strong affiliative bonds between members of a breeding pair. Monogamous pair bonds are relatively

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doi:10.1016/j.brainres.2006.07.126

rare among mammalian species (Kleiman, 1977) and appear to have evolved independently several times (Komers and Brotherton, 1997). Only about 3% of mammalian species display such bonds, and even fewer appear to exhibit obligate monogamy (Kleiman, 1977). A number of theories have been proposed regarding the evolution of monogamy (Kleiman, 1977; Orians, 1969; Wittenberger and Tilson, 1980), however, it is unlikely that any single theory accounts for all instances of monogamy. This conclusion is supported by the observation that monogamy is not a unitary process, but rather can have species-specific manifestations (Dewsbury, 1987).

Pair bonding is part of a spectrum of individual-specific affiliative behaviors, all of which appear to share common traits such as approach and avoidance behaviors, social recognition, the formation of conditioned preferences, and motivation (Depue and Collins, 1999; Insel and Fernald, 2004; Young, 2002; Young et al., 2001). Thus, pair bonds between mates (including romantic bonds between humans), mother–infant bonds, and friendships likely all derive from the same basic mechanism (Bartels and Zeki, 2004; Depue and Morrone-Strupinsky, 2005; Fraley and Shaver, 2000; Insel, 1997; Pedersen, 2004). Although it is impossible to know exactly the evolutionary sequence that produced the neural mechanisms underlying affiliative behaviors, knowledge of current functions of neurochemical systems permits speculation as to the evolution of attachment processes.

Biogenic amine involvement in the central processes important for pair bonding appears to be phylogenetically very old (Nestler, 2002) and may predate the divergence of chordate and invertebrate taxa (Huber, 2005). These processes may originally have mediated the formation of associations between behavior and positive outcome. For example, forming an association between a particularly nutritious food source and the cues that facilitate locating that food source would likely have adaptive value. In mammals, such associations appear to be mediated via activation of central dopamine pathways (reviewed by Ikemoto and Panksepp, 1999), but in fact, monoamine systems appear to mediate the formation of conditioned preferences in taxa as diverse as planarians, crayfish, honeybees, and zebra fish (Hammer, 1997; Kusayama and Watanabe, 2000; Menzel et al., 1999; Panksepp and Huber, 2004). Such a system would be ideally suited for co-opting as a mechanism to ensure the appropriate motivations and behaviors as mating strategies became more complex, shifting from broadcast spawning to being oriented toward particular individuals (Parker, 1984). Once tied to reproduction, it is a short step to involvement in processes such as parental bonding that enhanced survival of offspring.

2. Animal models for the study of social bonding

In healthy humans, social contact can elicit a suite of physiological responses that are highly conserved and that may serve to reinforce the motivation to engage in such contact (Depue and Collins, 1999). In other words, these responses are rewarding (as defined by Ikemoto and Panksepp, 1999) in that they "elicit approach responses". Note that this definition does not imply "subjective positive hedonic effects". Thus, despite the fact that humans have established emotional terms for these responses such as feelings of warmth and security, comfort, trust, and ultimately, love, these emotions represent what has been termed "autonomic–motoric–cognitive states" (Kemper, 1987). Importantly, although the cognitive, subjective components probably are unique to humans, it is likely that other mammalian species experience aspects of the emotional/physiological components of what humans term love (Porges, 1998). This likelihood is supported by the observation that activation of central pathways associated with reward processing can occur in humans despite a lack of conscious perception (Berns et al., 1997). Thus, it is possible to employ animal models to examine certain aspects of the central processes underlying the formation and maintenance of pair bonds.

Rodents from the genera *Microtus* (voles) and *Peromyscus* (deer mice) have been used extensively in the study of social behavior including social bonding, parental behavior, mating behavior, aggression, stress responses, activation of sexual receptivity, and social influences on immune function (Carter et al., 1988; Curtis et al., 2001; Cushing and Carter, 2000; de Vries and Miller, 1998; Demas et al., 1999; Dewsbury, 1995; Heise and Van Acker, 2000; Insel et al., 1995; Kirkpatrick et al., 1994; Lonstein and De Vries, 2000; Ribble, 1992; Roberts et al., 1998; Stribley and Carter, 1999; Wang et al., 1997a; Williams et al., 1992b; Winslow et al., 1993). First proposed as a model system in the 1980s (Dewsbury, 1987; Getz et al., 1981), prairie voles (*M. ochrogaster*) have been the most commonly used species in studies on the formation of monogamous pair bonds.

Prairie voles (Fig. 1A) are small (~50 g) and easily bred in captivity providing an ideal animal model for examining social behavior. In addition, prairie voles are highly social and appear to seek out not just social interactions, but physical contact as well (Fig. 1B) (Shapiro and Dewsbury, 1990). Importantly, mated pairs of prairie voles are one of the few mammalian species that display pair bonding behavior. Field studies show that prairie voles display characteristics of monogamy such as biparental care of pups, sharing of a nest even beyond the breeding season, aggression toward strangers, and a tendency to travel together (Getz et al., 1981; Gruder-Adams and Getz, 1985; Hofmann et al., 1984). In the laboratory, both sexes form strong individual attachments manifested by a robust preference to associate with the familiar mate versus with a conspecific stranger. Importantly, such partner preferences can be readily quantified in an experimental setting (Fig. 1E) and provide a benchmark by which the effects of experimental manipulations can be assessed. Thus, prairie voles are an important extension of more traditional laboratory animals that do not exhibit such attachments. Furthermore, closely related vole species, such as montane (*M. montanus*) and meadow (*M. pennsylvanicus*) voles (Fig. 1D), are asocial (Fig. 1C) and differ only in their respective social structures.

3. Is dopamine involved in pair bond formation?

Activity of central dopamine systems is known to have profound effects on behavior. A variety of studies have implicated dopamine in stress responses (Abercrombie et al., 1989; Dunn, 1988), the formation of conditioned preferences (Kivastik et al.,