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Review

Neurobiology of social attachments

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ABSTRACT

Many types of social attachments can be observed in nature. We discuss the neurobiology of two types (1) intraspecific (with a partner) and (2) parental (with the offspring). Stimuli related to copulation facilitate the first, whereas pregnancy, parturition and lactation facilitate the second. Both types develop as consequence of cohabitation. These events seem to stimulate similar neural pathways that increase (1) social recognition, (2) motivation, reward; and (3) decrease fear/anxiety. Subregions of the amygdala and cortex facilitate social recognition and also disinhibition to decrease rejection responses. The interrelationship between MeA, BNST, LS may mediate the activation of NAcc via the mPOA to increase motivation and reward. Cortical areas such as the ACC discriminate between stimuli. The interaction between OT and D2-type receptors in NAcc shell facilitates intraspecific attachment, but D1-type appears to facilitate parental attachment. This difference may be important for maternal females to direct their attention, motivation and expression of attachment toward the appropriate target.

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1. Introduction

Social attachments are necessary in many species because they facilitate reproduction, increase survival, provide a sense of security and reduce feelings of stress and anxiety. Consequently, reproductive fitness and mental health depend to some extent on the capacity to form healthy attachments (Carter, 1998; Insel and Young, 2001). Many types of social attachments can be observed in nature. Some occur between opposite- and same-sex individuals, or between young and adult members of the same species; however, they can also occur between different species. In this review, we will explore two types only. One is referred to as "intraspecific attachment", and is typically observed between a male and a female around behaviors such as sexual partner preference and copulation

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that facilitate reproductive endpoints. The other is referred to as "parental attachment", and occurs between a parent and his/her young to facilitate survival of the offspring.

Intraspecific and parental attachments can occur either concomitantly or separately, but one is not required or sufficient for the other to occur. For example, an individual can be attached to his/her young and not to a partner, or vice versa. For these attachments to be displayed, animals must integrate external sensory signals with internal states and memories of previous experiences. Thus, to understand the neurobiology of attachment we must consider neural systems involved in social recognition, motivated behaviors, reward, memory and desinhibition. The aim of this review is to provide information on neural pathways underlying intraspecific and parental attachments. We begin by describing the objective measures of attachment in animal models. This is followed by a discussion of the evidence of the natural stimuli that facilitate attachments, and the putative neural systems that mediate the formation for each type.

2. What is attachment and how to study it?

Before describing the neural systems involved, it is important to understand the objective measures that indicate that one individual is attached to another. These measures are exclusively behavioral, and consequently, will vary from one species to another, although the end points served may be the same. In general, an *attachment* is a selective relationship with another individual (Carter, 1998; Insel, 2003), and in some species this selectivity is long-lasting. For example, monogamous voles show a long-lasting intraspecific attachment toward a partner they previously mated with or cohabited (usually for a 24-h period). The attachment is expressed when animals have the choice of two partners and select one of them to spend more time, copulate and reproduce with. The attachment may last for life and attached individuals are rarely observed to mate with other partners even following permanent separation from the original one (Getz et al., 1993) which suggests rigorous selectivity (the attachment is either displayed toward the known partner or nobody). In contrast, other species like rats can show selective, but relatively brief copulatory preferences induced by Pavlovian learning (Kippin and Pfaus, 2001; Coria-Avila et al., 2005, 2006). This type of preference is considered brief because it may last for few ejaculatory series before they change partners (Kippin et al., 1998; Kippin and Pfaus, 2001). However, partner-related stimuli may well be preferred during long periods of life (Pfaus et al., 2001). Nevertheless, the behavioral differences between species with short- or long-lasting sexual partner, copulatory, or mate preferences can help to understand the neurobiology of attachments that occur naturally or that occur as a consequence of a relatively contrived conditioning process.

Parental attachment is assumed when females or males display behaviors that indicate the willingness to nurse and protect the young. In some species, parental attachment is rigorously selective and long-lasting, whereas in other species selectivity is not that rigorous. For example, some precocial species like sheep may display selective maternal behavior exclusively toward offspring they recognize as theirs during the very first hours postpartum (Kendrick et al., 1998). However, rats can foster pups that are not their own even ten days after parturition (Grota, 1973), indicating that the maternal behavior they provide is not strictly selective to their own, but rather toward any comparable newborn. Still, parental attachments expressed by rats require recognition of certain features of the target individual (i.e. neonatal looking). Furthermore, some ungulate (von Keyserlingk and Weary, 2007) and primate species (Davenport et al., 1961; Dienske and Van Vreeswijk, 1987) show long periods of maternal care, whereas lagomorphs display short periods (Schulte and Hoy, 1997). Regardless of the species, changes in time spent with the young or modifications in the frequency of maternal behaviors may be correlated with disruption or development of the parental attachment. In general, behaviors such as nursing, retrieving, licking or grooming directed toward the offspring, as well as voluntary time spent with them, and defense against intruders, can be described as parental behaviors in mammals that indicate attachment to the young. In the case of intraspecific attachment, selective copulation, time spent or voluntary contact with other individual can be the usual manifestation of attachment (Carter et al., 1995), however, other behaviors such as grooming, licking and mate-guarding among others, may also indicate the presence of an attachment.

3. Factors that facilitate attachments

3.1. Natural stimuli for intraspecific attachment

Many reproductive events can trigger a cascade of physiological responses that facilitate the formation of intraspecific attachments, and a good example occurs in female rats. During non-reproductive periods, the levels of gonadotrophin-releasing hormone (GnRH) in the hypothalamus activate the release of luteinizing hormone (LH) and follicle stimulating hormone (FSH) in the pituitary gland (Schally et al., 1971), causing a steady increase of estrogens (E) during the cycle. However, during the phase of proestrus, there is an increase in the pulse amplitude and frequency of GnRH, causing a rapid increase of LH and FSH (Hoeger et al., 1999), which in turn, produce a surge of E, testosterone (T), and progesterone (P). This particular hormonal state leads to estrus behavior and ovulation (Davidson et al., 1968; Lisk and Barfield, 1975). When copulation occurs, the female rat is prepared not only to accept the male and receive sexual stimulation (clitoral and vaginocervical), but also her brain is in a hormonal state that facilitates learning. The effect of hormones, and sexual stimulation are required for female rats to develop conditioned partner preferences triggered by sexual stimuli (Parada et al., 2010; Corona et al., 2011; Parada et al., 2011; Pfaus et al., 2012).

Hormones and copulation affect behavior similarly in females of species that display selective and long-lasting preferences. For instance, female prairie voles can develop a partner preference for a familiar male if are allowed to cohabit with him for a 24-h period, but not during a period of 6 h. However, females that cohabit and are allowed to copulate during the 6 h period, develop partner preference for the familiar male relative to an unfamiliar male. This demonstrates that intraspecific attachments (also referred to as pair bonds) can occur as a consequence of long periods of cohabitation, and that copulation facilitates them (Williams et al., 1992), acting as a catalyst. Some experiments with rats have shown that ejaculation is the main rewarding catalyst that induces the formation of conditioned partner preferences in males (Kippin et al., 2001). In female rats, sexual reward is mainly achieved by pacing the frequency of sexual contacts with the male, which facilitates a conditioned partner preference (Coria-Avila et al., 2005).

There are stimuli other than genitosensory stimuli that facilitate the formation of intraspecific attachments. For example in male prairie voles, long periods of swimming are believed to be stressful. If voles are placed to cohabit for less than 6 h with a partner, attachments will not develop. However, if they are forced to swim and then are placed to cohabit for a period of 6 h, attachments are more likely to occur (DeVries et al., 1996; Carter, 1998). This is believed to be facilitated via the hormones that are released during the stress response (i.e. corticosteroids), since injections of corticosterone in males can also facilitate the formation of attachments that follow the injections (DeVries et al., 1996). The levels of plasma