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Comparative analysis of oxytocin receptor density in the nucleus accumbens: An adaptation for female and male alloparental care?

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ABSTRACT

Parental behavior is commonly displayed by progenitors. However, other individuals, genetically related (e.g. siblings, aunts, uncles) or not with the newborns, also display parental behavior (commonly called alloparental, or adoptive behavior). I hypothesize that species that live in family or social groups where other non-reproductive members (males and females) take care of infants, have brain adaptations to promote or facilitate that behavioral response. The present work revises the evidence supporting the hypothesis that high density of oxytocin receptors (OXTR) in the nucleus accumbens (NA) is one of those adaptations. All species known to have high NA OXTR show not only female, but also male alloparental care. Therefore, I predict that high NA OXTR could be present in all species in which juvenile and adult male alloparental behavior have been observed. Strategies to test this and other alternative working hypothesis and its predictions are presented.

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1. Behavioral responses toward newborns and infants by virgin naïve animals

When animals are exposed to newborns or infants, they can show a wide repertoire of behavioral responses (Numan et al., 2006; Olazábal et al., 2013a). For instance, animals can approach toward- or withdraw from- the newborn either immediately or after few minutes of sensory stimulation from a distance. Subsequently they can explore or avoid exploration of the young and, in case interaction with pups occurs, either shows protection and care (maternal behavior) or neglecting/infanticidal behavioral responses. The behavior of the animals depends on differences among species, their physiological stage (e.g. cycling, pregnant or lactating female), sex (male or female), age (e.g. juvenile, adolescent or adult), and emotional/affective state (e.g. fear, anxiety, aggressiveness, stress). The behavior and physiological conditions of the pups (e.g. temperament, nutrition) and the context of the interaction (e.g. a predator around), among other factors, also influence the final behavioral response (Bosch, 2013; Lonstein and De Vries, 2000; Olazábal et al., 2013a).

In the case of maternal behavior, most mammals are, at the end of pregnancy, hormonally stimulated to optimise their parental response (Numan et al., 2006; Olazábal et al., 2013a). It is well known that changes (commonly an increase) in estrogen/progesterone ratio, and increases in prolactin and oxytocin (OXT) facilitate maternal behavior (Numan et al., 2006; Olazábal et al., 2013a). In many mammalian or non-mammalian species, males and females that are not related to the young, can also display parental behavior (Olazábal et al., 2013a). That behavior, sometimes indistinguishable from the behavior of the progenitors, is called alloparental, pup-induced or adoptive behavior and will be the focus of the present review.

Many years ago, Leblond (1938), Noirot (1969), and Rosenblatt (1967) demonstrated that both mice and rats could be induced to display parental behavior by repeated exposures to newborns (pup-induced parental behavior). Daily exposures to a few pups were sufficient stimulation to induce parental behavior in most animals (Numan et al., 2006). Pup-induced parental behavior was also found in many other species of rodents (e.g. prairie voles, Roberts et al., 1998; and hamsters, Vella et al., 2005), and primates (e.g. marmosets, Barbosa and Da Silva Mota (2013)). The induction of parental behavior occurred sometimes immediately after the first exposure to pups (adult prairie voles and a few mice; Brown et al., 1996; Lucas et al., 1998; Olazábal and Young, 2005), or developed gradually after a few hours or days of repeated exposures (e.g. most mice and rats; Alsina et al., unpublished; Brown et al., 1996; Lucas et al., 1998; Rosenblatt, 1967).

Fathers, aunts, siblings and other non-related and non-reproductive animals commonly contribute to the care and protection

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of the offspring (Olazábal et al., 2013a) maintaining family or social groups together and safe. Pup-induced alloparental behavior is an adaptation that plays not only a reproductive, but also a social and ecological function (Abbott et al., 1998; Barbosa and Da Silva Mota, 2013; French, 1994; Hauber and Lacey, 2005; Mayer and Rosenblatt, 1979a,b; Olazábal et al., 2013a; Riedman, 1982; Santema and Clutton-Brock, 2012; Schubert et al., 2009; Thierry and Anderson, 1986; Watt, 1994). Therefore, the presence of female and male helpers (including unrelated individuals) in a family or social group depends on the reproductive and social strategy of the species (see Sections 6 and 7). For example, whether weanling animals (e.g. males) rapidly disperse or not from the nest area will determine the permanence, or not, of juvenile or adult males in the group.

2. Juvenile pup-induced alloparental behavior in altricial rodents: a role for oxytocin?

Altricial species produce young that cannot regulate their temperature, and have limited sensory and motor capabilities (Numan et al., 2006; Olazábal et al., 2013a). Therefore, their progenitors and care providers usually build a nest, retrieve pups (pick them up with their mouths and carry them) to that nest site, lick, clean, and protect them, and provide food and thermoregulation, adopting nursing postures (Numan et al., 2006; Olazábal et al., 2013a).

Interestingly, early studies from Bridges et al. (1974), Mayer and Rosenblatt (1979a,b), and Brunelli et al. (1985), among others (Stern, 1987), found that juvenile (20–22 days of age) weanling rats (males and females) exposed to pups displayed parental behavior with very short latencies (few hours to 2 days). Mayer and Rosenblatt (1979a,b) published a series of studies showing that weanling rats were very attracted to pups and spent most of the time in contact with them on the first exposure. However, after a few days (24–27 days of age), rats started to develop a neophobic or inhibitory behavioral response that resulted in pup avoidance or rejection (see also Fleming and Luebke, 1981). Juvenile parental behavior is thought to be an adaptation that permits juveniles to stay in the nest area acquiring experiences and sharing resources.

A few years later, a series of studies by Shapiro and Insel (1989) and Tribollet et al. (1992) found developmental changes in the density and distribution of OXT receptors (OXTR) in the rat brain from age 20 days to adulthood. OXT is a peptide of 9 aminoacids that has been extensively implicated in the physiology of reproduction (e.g. milk ejection pathway, uterus contraction during parturition). A series of studies in the 70's and 90's suggested that OXT also facilitated the onset of maternal behavior in rats and sheep (Kendrick et al., 1987; Pedersen et al., 1982). The sites where OXT acts in the brain to facilitate maternal behavior might differ among species. Several studies found evidence that supported OXT action in the ventral tegmental area (VTA), and the medial preoptic area (MPOA), among other brain regions (Numan et al., 2006; Pedersen et al., 1994). The action of OXT in these interconnected brain regions would promote release of dopamine in the nucleus accumbens (NA) facilitating active components of maternal behavior (Numan et al., 2006; Olazábal et al., 2013a; Pedersen et al., 1994).

The NA is critical for many behavioral processes including the processing of rewarding, aversive, novel and salient stimuli, the choice of adaptive behavioral responses, and the translation of emotions and motivations to actions, among other functions (Groenewegen et al., 1996; Kelley and Berridge, 2002; Olazábal et al., 2013b; Robbins and Everitt, 2002; Salamone and Correa, 2002). Newborn related stimuli are novel and salient for naïve animals, and likely have rewarding or aversive components that force them to take an adaptive behavioral response (e.g. attack, ignore, take care, withdraw). Therefore, the NA is critical in this initial stage of interaction with pups. It would processes and integrates several relevant information related to pups travelling to the NA via afferents from the hypothalamus, cortex and amygdala nuclei, and other brain regions, as described in detail in several previous reviews (Numan et al., 2006; Olazábal et al., 2013a,b).

Interestingly, Shapiro and Insel (1989) had found a decline in OXTR density in the (NA) from the age 20 days to adulthood. Because the NA was also known to be critical in several brain processes related to maternal behavior (Keer and Stern, 1999; Li and Fleming, 2003; Numan et al., 2005; Vernotica et al., 1999), I hypothesized that OXT in the NA might be mediating the rapid induction of alloparental behavior. A developmental decline in the expression of OXTR in the NA could explain the concurrent decline in the attraction toward newborns observed in adult rats (Mayer, 1983; Mayer and Rosenblatt, 1979a,b). Previous studies had also shown that ICV injections of OXT in juvenile rats increased the time these juveniles spent in contact with pups (Peterson et al., 1991). Then, a series of studies were developed in order to investigate the possibility that NA OXTR facilitated juvenile (see Section 3) and adult pup-induced parental behavior (Olazábal and Young, 2006a,b).

3. First comparative studies that supported NA OXTR role in alloparental behavior

In previous studies Insel and Shapiro (1992) had proposed that different distribution of OXTR and vasopressin (AVP) receptors in the brain reflected the reproductive and social strategies of species, for example the establishment of monogamous or promiscuous bonding. Following that way of reasoning, we investigated if differences in OXTR distribution in the brain, in particular in the NA, could explain why juveniles of different species behaved so differently when exposed to pups for the first time (Olazábal and Young, 2006a). We found that 4 species (meadow voles, mice, rats, and prairie voles) with different behavioral responses toward pups also differed in the distribution of OXTR in the brain. Using autoradiography for the radioactive ligand ^{125}I Ornithine Vasotocin Analog ([^{125}I]-OVTA, NEN/Perkin Elmer), we found that juvenile female prairie voles (spontaneously maternal) had more OXTR in the NA than rats (less spontaneously maternal), that also had higher NA OXTR than mice and meadow voles (non-maternal; Olazábal and Young, 2006a). We concluded that brain OXTR distribution could predispose juveniles from some species to be parental rapidly (Fig. 1). Specifically, we concluded that juveniles from species with higher OXTR in the NA could be rapidly induced to show allomaternal behavior.

A second experiment found that differences in NA OXTR could also be informative of individual differences in parental behavior within a species. Steve Phelps (Phelps and Young, 2003) had shown extraordinary diversity in AVP receptor (V1a) distribution in the brain of wild prairie voles that could be associated with behavioral variability in the population. We also found that OXTR distribution in prairie voles was extremely variable. A comparison of the time juvenile females spent in contact with pups, and the density of OXTR in the NA, revealed that higher OXTR in the NA juveniles had, longer time they spent in contact with pups (Olazábal and Young, 2006a). When OXTR in the NA of maternal and non-maternal adult female prairie voles were compared, the results also revealed that maternal females had higher OXTR in the NA than non-maternal animals. These differences in the density of OXTR were clearly brain region specific. For example, in other areas of the brain, such as the prelimbic cortex or the lateral septum, the density of OXTR was not different or was lower in maternal compared to non-maternal animals. Therefore, the expression of the

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