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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.

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

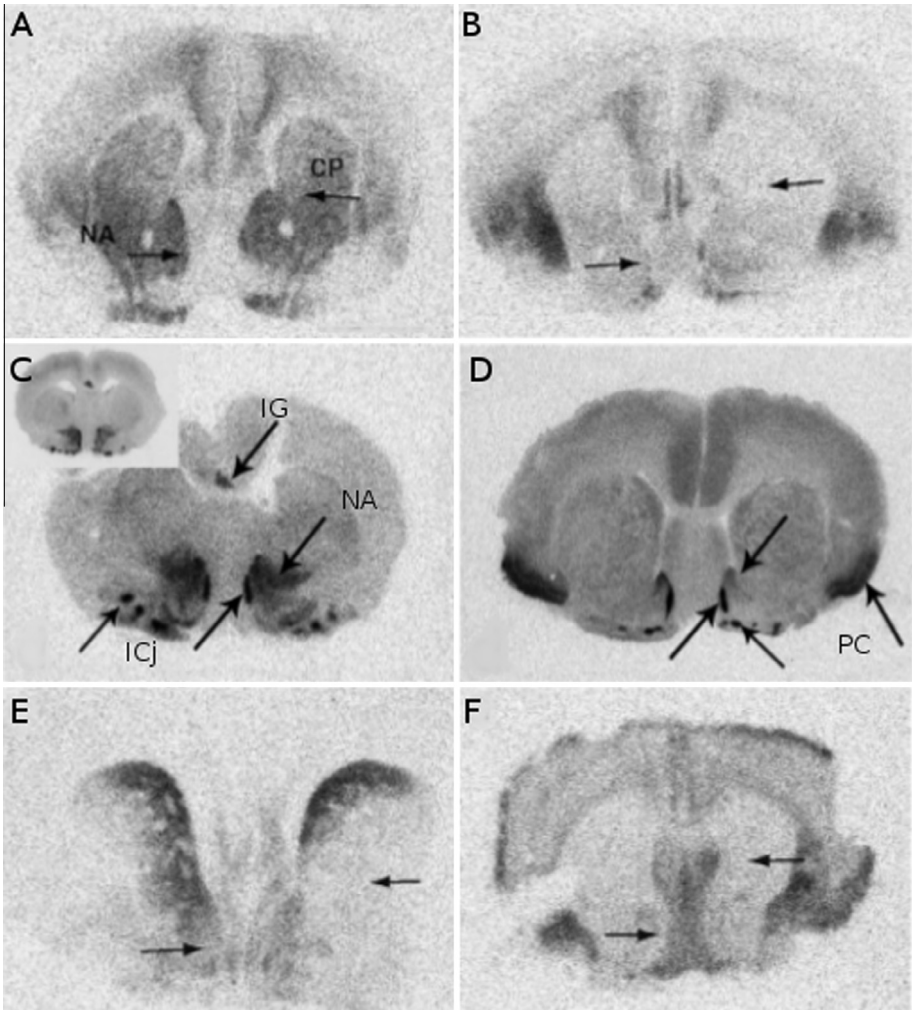

Fig. 1. Brain oxytocin receptor autoradiography. The figure shows autoradiographic signal for oxytocin receptor at the level of the nucleus accumbens (NA) in females of 6 different rodent species. ABEF are juvenile females. CD are adult females. (A) Prairie voles. (B) Meadow voles. (C) Naked mole rats (inset shows male binding). (D) Cape mole rats. (E) Rats, and (F) Mice. Arrows in ABEF shows the location of NA and caudate putamen (CP). Arrows in CD also show island of Calleja (minor and major, ICJ), indusium griseum (IG), and piriform cortex (PC). Pictures from C and D were taken from Telencephalic Binding Sites for Oxytocin and Social Organization: A Comparative Study of Eusocial Naked Mole-Rats and Solitary Cape Mole-Rats. Kalamatianos et al. Journal of Comparative Neurology (2010), and reproduced by permission of Wiley. Pictures from ABEF were taken from Species and individual differences in juvenile female alloparental care are associated with oxytocin receptor density in the striatum and the lateral septum. Olazábal and Young, Hormones & Behavior (2006), and reproduced by permission of Elsevier.

receptor was not up or down regulated in the whole brain in maternal or non-maternal animals.

Finally, female prairie voles infused with the OT receptor antagonist d(CH_2)^5,[Tyr(Me)^2,Thr^4,Orn^8,Tyr^9-NH_2]-vasotocin (Bachem) into the NA, but not the caudate putamen (control group), failed to show maternal behavior (Olazábal and Young, 2006b). In summary, comparative, developmental, individual differences, and pharmacological studies provided, for the first time, strong evidence that supported the hypothesis that OXT acted in the NA to facilitate MB. The main conclusion was that OXT, acting in the NA, was critical in the initial stages of the interaction between an individual and newborns, perhaps increasing their attraction toward pups, facilitating the spontaneous or rapid induction of maternal behavior in different contexts (Olazábal and Young, 2006b). It is unclear if the expression of the peptide and its projecting sites are conserved across vertebrate taxa (Kalamatianos et al., 2010; Freeman and Young, 2013). The possibility that species differences in OXT projections affects behavioral responses toward pups is appealing and deserve more attention. Similarly, it is important to consider in the present analysis that different pattern of release (i.e. somato-dendrytic, axonic) or diffusion of the peptide (Landgraf and Neumann, 2004) might also contribute to species or individual differences. However, the evidence clearly supports a significant variation in the distribution of the OXTR across species. Therefore, the analysis and discussion of the current review was limited only to the receptors.

4. Additional studies that supported NA OXTR function in alloparental care

Recently a series of comparative studies and genetic manipulations also provided additional support to the hypothesis that OXT facilitated parental care acting in the NA (Kalamatianos et al., 2010; Keebaugh and Young, 2011; Schorscher-Petcu et al., 2009). Keebaugh and Young (2011) found that viral vector infusions that increased OXTR in the NA of weanling females facilitated adult spontaneous maternal behavior in prairie voles. Overexpression of NA OXTR in adult females was not effective (Ross et al., 2009), suggesting that the presence of OXTR during development was important (Keebaugh and Young, 2011). However, according to these authors, the presence of OXTR during development was not

necessary to facilitate partner preference. It is still unclear why the presence of high levels of OXTR in the NA would be sufficient to facilitate one but not both behaviors, given that both are typical of the species and should be well established early in development. However, we must note that pair bonding in prairie voles is a process that develops slower (at least 8–12 h of continuous cohabitation with the opposite sex is needed) than parental behavior (spontaneous behavioral response), is dependent on olfactory information (the odor of the pups is not relevant for naïve male and female prairie voles), and then likely regulated by different mechanisms.

More recently, Kalamatianos et al. (2010) carried out a very elegant comparative study using two species of subterranean african mole rats, a solitary (cape mole rat) and a colonial (naked mole rat) species. They found that naked mole rats had high density of OXTR in the NA, while the related solitary species cape mole rat showed very low levels (Fig. 1). These authors also found that the NA was richly innervated by OXT fibers in naked, but not cape mole rats (Kalamatianos et al., 2010). Interestingly, naked mole rats live in complex colonies where only one female (queen) reproduces (copulating with 1–3 males), and many non-reproductive subordinates (females and males) cooperate with the caring activities.

Another study that investigated OXTR distribution in marmosets, a biparental primate species that live in family groups with rich social interactions and high levels of alloparental behavior by males and females (Abbott et al., 1998), also found high density of OXTR in the NA (Schorscher-Petcu et al., 2009). Altogether, these studies supported the hypothesis that high density of OXTR in the NA was an adaptation for alloparental care by related and unrelated non-reproductive animals living in family, or mixed sex social cooperative groups. However, I do not exclude the possibility that OXT also facilitate other forms of parental behavior in species with low density of OXTR in the NA as shown by Akther et al. (2013) in mice. Interestingly, these authors introduced human CD38 in the NA of CD38 knockout male mice using a lentiviral infection technique and found facilitation of paternal behavior. Therefore, OXT in the NA might facilitate different forms of parental behavior in males and females. Next section will discuss the possibility of sex differences in NA OXT function in alloparental care.

5. Is there a sex difference in NA OXT function in alloparental care?

The literature has strongly suggested the existence of sexual dimorphism in the behavioral effects of OXT and AVP (Carter, 2007; De Vries, 2008; Veenema et al., 2013; Wang et al., 2000). Briefly, OXT and AVP have been proposed to facilitate parental behavior and pair bonding in females and males respectively (Carter et al., 1995; Wang et al., 2000; Young and Wang, 2004; see Ophir et al., 2012 for an excellent discussion on this topic). Although those authors recognized that OXT and AVP could eventually facilitate same behaviors in both sex (Young and Wang, 2004), they proposed important sex differences in the mechanisms of action of OXT and AVP.

Sex differences in brain immunoreactivity for the peptide and receptor binding have been found in several species including rats and mice (Dhakar et al., 2013). However, these differences cannot be generalized to all species. Prairie voles, among other species, show no or only minor differences in brain V1aR/OXTR density or plasma concentration of these peptides (Bales et al., 2007; Kalamatianos et al., 2010; Olazábal and Young, 2008).

Several studies have also shown that the major behavioral effects of OXT release, treatment, and manipulation were similar in both males and females tested for social stressors, anxiety, and affiliative, among other behaviors (Engelmann et al., 1999; McGregor and Bowen, 2013; Sabihi et al., 2014; Snowdon et al., 2010).

Ophir et al. (2012) have also recently suggested that OXT acts in the NA to facilitate the establishment of partner preference not only in female, but also in male prairie voles. Besides, OXT has also been involved in the mediation of paternal behavior in several species (Akther et al., 2013; Bales et al., 2004; Gordon et al., 2010; Saito and Nakamura, 2011). Although the goal of this review is not discussing AVP role in parental behavior, we want to note that several studies have also shown that AVP modulates, not only paternal behavior (Wang et al., 1998), but also several aspects of maternal behavior (Bester-Meredith and Marler, 2012; Bosch, 2013; Bosch and Neumann, 2012). Therefore, I hypothesize that OXT in the NA facilitates both female and male pup-induced juvenile and adult alloparental behavior. Despite this historic bias in the field, several studies have started to pay more attention to OXT and AVP in both sexes. In next sections, I will describe why NA OXTR is more likely associated to male and female alloparental care than to female social monogamy, gregariousness or general group living.

6. OXTR in the NA: An adaptation for alloparental care or pair bonding?

The underlying question of this section is: what is the function and adaptive significance of high levels of OXTR in the NA?. Based in the extensive literature on OXT function in social and affiliative behavior, several groups of research led by Sue Carter (University of Illinois at Chicago), and Larry Young (Emory University at Atlanta), among others, have hypothesized that OXT and AVP action in the female NA and male ventral pallidum (VP), respectively, would participate in the establishment of partner preference, or pair bonding, in prairie voles and other mammalian species (Carter et al., 1995; Young et al., 1998). According to these authors, OXT action in the NA would be part of the rewarding processes that strengthen affiliation to the partner, and also facilitate other affiliative responses such as parental care. Freeman and Young (2013) hypothesized that the "*circuits that mediate the onset of maternal nurturing and infant attachment after parturition and during nursing have been exapted to give rise to the pair bond*". In contrast, male pair bonding would have developed in the context of AVP-mediated male territorial behavior (Freeman and Young, 2013). This particular hypothesis resulted in the assumption (not supported by the literature, see previous section) that OXT does not play a major or significant role in pair bonding or paternal behavior in males (idem for AVP in females). Besides, significant amounts of paternal/maternal and allopaternal/allomaternal care are present in non-monogamous species, suggesting the existence of independent mechanisms of adaptation for alloparental behavior and monogamy (Rymer and Pillay, 2014; Schubert et al., 2009).

Although the current review is not focused in AVP and pair bonding, the parallelism that exists in the literature between these two events require that we briefly discuss the evidence supporting that NA OXT and VP AVP are adaptations for pair bonding, and specifically pair bonding in females and males respectively. The original study of Insel et al. (1991), and Insel and Shapiro (1992), were done with the philosophical belief (inspired in Paul MacLean, Insel, 2003) that the best experiments are those that Nature has done for us. These authors proposed that different distribution of OXT and AVP receptors in the brain were relevant for the reproductive and social strategies of species, for example the establishment of monogamous or promiscuous bonding.

Following the idea about the advantage of using the experiments offered by Mother Nature, we reviewed several classic and new comparative studies and found some evidence that challenged the hypothesis that high level of OXTR in the NA (and also V1A receptors in the VP) is an adaptation for social monogamy or pair bonding. First, naked mole rats have high density of OXTR in the

NA (Kalamatianos et al., 2010) but are not considered a typical monogamous species. Second, two other species believed not to be monogamous, the singing mice (*Scotinomys teguina and Scotinomys xerampelinus*) and tucu-tuco (Beery et al., 2008), have high V1aR in the VP (Campbell et al., 2009). Third, no clear differences in AVP receptors in the VP were found in *Peromyscus californicus* (a monogamous species), and *Peromyscus maniculatus* (a promiscuous species, Insel et al., 1991). At that time the NA was not a research target for pair bonding or parental care, hence no OXTR in the NA was described. Fourth, Insel and Shapiro (1992) found no difference in NA OXTR between pine voles (monogamous), and meadow voles (promiscuous).

The absence of the expected binding in species that show partner preference can eventually be explained by alternative biological mechanisms that converged in the same behavior or function. However, the presence of high density of V1AR and OXTR binding in the VP and NA respectively in species that do not show social monogamy is difficult to explain. Would the presence of this high density of receptors be then directly related to partner preference and social monogamy?. An alternative hypothesis that will be developed in more detail in the next paragraphs was suggested in Olazábal and Young (2006a,b).

7. New predictions and perspectives

The alternative hypothesis is that the presence of OXTR in the NA might be an adaptation for alloparental care in certain family or social group conditions. I expect that cooperative species that require high tolerance toward young by unrelated males and females should have (or develop) special brain adaptations. Those adaptations would influence the behavior of the animals during development or throughout life, likely affecting not only their relationship with newborns and infants, but also with other members of their group, including their own parents and eventually (but not necessarily) also their partners. In particular, the presence of non-reproductive males in social or family groups, consequence of frequent immigration or delayed/no male dispersal (Getz et al., 2005; Griffin et al., 2003; Doolan and MacDonald, 1996), could be indicative of high NA OXTR in those species. However, these predictions do not exclude the possibility that OXT acts in the NA to promote parental or social behavior in species with low levels of OXTR in the NA as suggested by Akther et al. (2013) and Dölen et al. (2013).

Table 1 shows a strategy to test whether NA OXTR is more likely an adaptation for alloparental behavior or pair bonding. The table summarizes important behavioral features for several species, some of which have been tested for brain OXTR binding. Based on those features, it was predicted that if OXTR in the NA is an adaptation for pair bonding or social monogamy, *Peromyscus californicus*, dwarf hamsters (*Phodopus campbelli*), striped mice (*Rhabdomys pumilio*), and meerkats (*Suricata suricatta*) should more likely have high OXTR density in the NA. In contrast, if this is an adaptation for alloparental care and male tolerance to newborns in complex living family or social groups, only meerkats and striped mice are likely to have high NA OXTR. This prediction is based in the fact that in *P. campbelli* (dwarf hamsters) and *P. californicus* adult males do not show alloparental behavior. The behavior of naïve male juveniles has not been studied in *P. californicus*, and is rarely studied in other species.

If future experiments find contradictory evidence for OXTR in the NA and alloparental care, that is high OXTR in the NA in species that do not show alloparental care, my hypothesis would then also be challenged. Thus, careful receptor binding and behavioral studies in other species are needed. We must note that singing mice (*S. xerampelinus*), a species that has not been studied in detail, show some OXTR in the NA (Campbell et al., 2009). This binding is not comparable to that found in prairie voles, marmosets and naked mole rats, but might suggest some degree of complex social adaptation where male alloparental care could be expected. Studies in the laboratory have found high tolerant behavior in this species (Hooper and Carleton, 1976). Future comparative studies will likely reveal more information about the biological mechanisms underlying high levels of parental care in naïve males and females.

It is important to note two other main points. First, OXT is obviously not the only system that participates in the initial stages of interaction with pups, and even though OXTR in the NA might play a general role in affiliative behavior, OXT independent mechanisms may block the expression of alloparental care in some species (e.g. dwarf hamsters or *P. californicus*) or contexts. I believe in fact that OXT independent mechanisms are behind the blockage of spontaneous maternal behavior and induction of infanticidal behavior observed in some adult female prairie voles with high OXTR density in the NA (Olazábal and Young, 2006b). Second, as mentioned above for pair bonding, there could be OXT independent mechanisms that can also promote partner preference or alloparental

Table 1
Predictions of our working hypothesis.

Species	Social monogamy	Female/male delayed or no dispersal	Juvenile alloparental behavior (alien pups)	Female/male adult alloparental behavior	Non-reproductive family or social group	References
Peromyscus californicus	+	+	?	+/–	–	4,11,21
Dwarf Hamsters	+	–/+	–	–	–	17,18,28,29
Striped Mice	–	+	+	+	+	22,23,24,25
Meerkats	+	+	+	+	+	5,10,27
Naked Mole Rats*	–	+	+	+	+	3,12,13,20
Prairie Voles*	+	+	+	+	+	9,15,16,19
Marmosets*	+	+	+	+	+	1,26
Lab Mice	–	+/–	–	+/–	–	2,6,7,8,14

1. Barbosa and Da Silva Mota (2013), 2. Brown (1993), 3. Burda et al. (2000), 4. De Jong et al. (2012), 5. Doolan and MacDonald (1996), 6. Elwood (1986), 7. Gandelman (1973), 8. Gerlach (1990), 9. Getz et al. (2005), 10. Griffin et al. (2003), 11. Gubernick et al. (1994), 12. Jarvis (1981), 13. Kalamatianos et al. (2010), 14. Krackow (2003), 15. Lin et al. (2006), 16. Lucia et al. (2008), 17. McInroy et al. (2000), 18. Newkirk et al. (1997), 19. Olazábal and Young (2005, 2006a), 20. O'Riain and Faulkes (2008), 21. Ribble (1992), 22. Rymer and Pillay (2014), 23. Schoepf and Schradin (2012), 24. Schradin and Pillay (2003), 25. Schubert et al. (2009), 26. Snowdon and Ziegler (2007), 27. Stephens et al. (2005), 28. Vella et al. (2005), 29. Wynne-Edwards and Lisk (1987).

The table predicts density of OXTR in the NA in several species with different reproductive and social strategies. Italic letters represent high OXTR in the NA predicted by hypothesis supporting adaptation to partner preference, while Bold letters represent high OXTR in the NA predicted by hypothesis supporting adaptation to male/female alloparental care in family/social groups. Species in regular letters have already been studied and those with high OXTR in the NA are marked with an asterix. Plus and minus signs represent that the behavioral condition (male and female condition separated by a bar) is present or not, respectively, in that species. A question mark represents that the behavioral condition is unclear or not studied in detail.

care, so failure to find high OXTR in the NA of an alloparental species does not necessarily reject our hypothesis. However, finding of the opposite relationship (high OXTR in the NA and absence of alloparental care), as happened with social monogamy studies, would be an important challenge for our hypothesis. In that case we still should try to understand why is that enormous amount of OXTR in the NA present in some species, but not others. One possibility would be that additional OXT dependent or independent changes in other areas of the brain, acting in synchrony with OXT in the NA, are required for the occurrence of juvenile and adult male and female alloparental care in certain species. Therefore, more research on OXTR brain distribution in other species (in particular those shown in Table 1) is needed, in particular in males, but also at different ages (weanlings and adults). I hope that more contributions from independent laboratories and research groups will contribute to clarify some of these complex (sometimes contradictory) findings in this fascinating field of research.

After submitting the first version of this revision, we read a novel analysis of OXT role in mammalian sociality (Anacker and Beery, 2013). In that review, the authors concludes that OXT was likely to be involved in social selectivity, including increases in aggression toward social outgroups and decreased huddling with unfamiliar individuals, which may solidify group cohesion and protect against others. Obviously, the conclusions of the current manuscript are clearly different. I propose that some group-living conditions are sometimes consequence of increased tolerance in nest area or territory to unrelated (or related) young and adult alloparental males. Although Anacker and Beery (2013) hypothesis is very interesting, they did not analyse or discuss in detail the multiple group-living styles that exist in nature, and are just partially reflected in Table 1. In this review we do not imply a general non-aggressive prosocial effect for brain OXT, given that there is significant evidence showing that OXT release can facilitate aggressive behavior (Bosch et al., 2005; Bosch, 2013). However, I hypothesize that NA OXTR facilitates male and female alloparental behavior that indirectly increases tolerance to related or unrelated individuals. In addition, I want to point out that NA OXTR is just a small portion of the complex neural substrate where OXT acts to promote parental behavior (Bosch, 2013; Olazábal et al., 2013a,b).

I want to finish this review briefly describing the state of these investigations in humans. Human OXTR distribution in the brain has yet not been well described, and different affinity and/or selectivity of radioligands and antibodies in rodents, ungulates, and human added significant difficulties for comparative studies. Early studies by Loup et al. (1991) did not find OXTR in the NA of humans. However, the study of Loup et al. (1991) used a radioligand that was not as selective for human OXTR, and postmortem tissue was obtained in most cases from elder subjects. Efforts to develop compounds capable to be used with the positron emission tomography technique have so far failed (Smith et al., 2012). Recently, Boccia et al. (2013), using a monoclonal antibody, made an interesting contribution to our understanding of OXTR distribution in the human brain. This study also failed to find OXTR in the NA of two women brains. However, due to the problem of selectivity and specificity mentioned above, there is still some uncertainty about the real distribution of OXTR in the human brain (Boccia et al., 2013). However, we can expect that in few years, these technical problems will be solved. A careful analysis of behavior and OXTR brain distribution in more species might reveal important aspects of human biology. There are several studies (Bick and Dozier, 2010; Strathearn et al., 2009) that found higher OXT blood levels in more sensitive parents or in mothers interacting with infants (even unrelated infants). There are also some polymorphisms for the OXTR gene that have also been associated with more sensitive maternal behavior (Bakermans-Kranenburg and van Ijzendoorn, 2008; Feldman et al., 2012; Mileva-Seitz et al., 2013). Although this evidence can be considered somewhat preliminary, it is promising and might reveal how biological, social and contextual aspects affect the behavior and well being of care providers (progenitors, adoptive parents or helpers).

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