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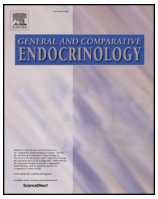

Variation in the density of oxytocin receptors in the brain as mechanism of adaptation to specific social and reproductive strategies

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ABSTRACT

Most species have predominant forms of social and reproductive behavior driven by many years of selection pressures and evolution. For example, rodent species can live in small or large groups, behave more tolerant or aggressively toward conspecifics (including newborns), and form or not bonds with other members of the group (including sexual partners). Any of those behavioral adaptations could result in good fitness for the species, but could also require compromises such as sharing resources, greater parental investment, increased risk of predation, etc. We propose that the oxytocin (OXT) system, among others neuroendocrine peptides, is at the basis of a neural mechanism that adapts and predisposes species to a particular social and reproductive form of living. In this review we will show evidence that the variability in the density of receptors for OXT (OXTR) in the nucleus accumbens (NAc) and the lateral septum (LS) predisposes species to adopt at least 4 different social and reproductive strategies in rodents. Large or medium size groups with lower conspecific spacing (preferred separation distance maintained by adult conspecifics), and high levels of promiscuity are characterized by low levels of OXTR in the NAc and LS (e.g. *Ratus norvegicus*, *Ctenomys sociabilis*, *Scotinomys teguina, Cavia porcellus*); small size groups with higher conspecific spacing and low levels of promiscuity are characterized by high OXTR in the NAc and the LS (e.g. *Peromyscus californicus*); large or medium groups with lower conspecific spacing and low levels of promiscuity characterized by high levels of OXTR in the NAc but low levels in the LS (e.g. *Microtus ochrogaster*, *Heterocephalus glaber, Microtus kikuchii*); and small or medium size groups with higher conspecific spacing and high levels of promiscuity characterized by low levels of OXTR in the NAc and high OXTR in the LS (e.g. *Mus musculus*, *Ctenomys haigi*, *Peromyscus maniculatus, Microtus pennsylvanicus, Microtus montanus*). Careful analysis of the distribution of OXTR, and other peptides receptors, in the brain can contribute to understand its function but also to predict reproductive and social strategies of species.

1. Diversity of social and reproductive strategies in rodent species

The typical social and reproductive behavior adopted by species is influenced by many years of selection pressures and ecological constraints. In addition, species are not static and can also be influenced by changes in their environment. Thus, diversity in behavior among species is generally higher than commonly recognized. There are multiple forms of association, interaction, and reproduction in all species that do not fit with any of the simplistic descriptions found in the literature (e.g. social/anti-social, prosocial/solitary, aggressive/non-aggressive, biparental/uniparental, monogamous/promiscuous). However, the species have a predominant social and reproductive behavior that can be clearly recognized and described (Olazábal and Young, 2006a; Lee and Beery, 2019). That is why, sometimes, descriptions of the behavior of species and individuals in the literature appear simplified.

Even though our idea is not to be exhaustive about the different features that better defines the life of the species, it can be recognized that rodent species can eventually live in small, medium or large mixed size groups, behave more tolerant or aggressively toward other conspecifics (including newborns), and form or not bonds with other members of the group (including sexual partners). Different combination of those behavioral features can result in many different reproductive and social strategies and good fitness for the species. However, benefits may also require compromises such as sharing resources, space, or nest, higher parental investment and cooperation among group members, increased risk of predation, etc. (Fryxell and Berdahl, 2018). Thus, for example, living in small family groups will require less sharing of resources but perhaps higher risk of predation, including killing of newborns in the absence of parents (Wolff, 1985). Then, a behavioral adaptation for that species could include

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territoriality, higher conspecific spacing, and aggressiveness toward conspecifics and potential predators. Obviously, there is variability within a species and not all animals of a certain species behave in the same way. However, both interspecific and intraspecific variability in behavior have been associated with differences in the distribution of peptide receptors in the brain (Insel et al., 1991; Insel and Shapiro, 1992; Francis et al., 2000; Olazábal and Young, 2006a, 2006b; Ophir et al., 2009).

2. Variation in oxytocin receptor density in the brain as a mechanism of adaptation

Oxytocin (OXT) is a hypothalamic peptide well known to play many physiological functions including, among others, promoting uterus contraction and milk ejection (Gimpl and Fahrenholz, 2001). However, OXT also acts in the brain to regulate parental, sexual, and aggressive behavior, stress and anxiety, among other functions (Gimpl and Fahrenholz, 2001). It is well known that OXT receptor (OXTR) is not equally distributed in the brain of the different species (Insel et al., 1991, Tribollet et al., 1992; Olazábal and Young, 2006a; Anacker and Beery, 2013, Olazábal, 2014, 2018). That variability in the distribution and density of OXTR in the brain is associated with different social and reproductive strategies of species (Insel et al., 1991; Insel and Shapiro, 1992; Olazábal and Young, 2006a; Beery et al., 2008; Campbell et al., 2009; Kalamatianos et al., 2010; Anacker and Beery, 2013). Besides, previous studies have shown that the variability in the distribution of OXTR among species can also be informative about variation in behavior within species (Olazábal and Young, 2006a, 2006b; Ophir et al., 2009). For example, a higher density of OXTR in the nucleus accumbens (NAc) is associated with a more rapid onset of parental responses in inexperienced males and females of several species, but also with higher contact with pups in juvenile prairie voles (*Microtus ochrogaster*, Olazábal and Young, 2006a, 2006b). In addition, higher OXTR in the NAc has also been associated with higher social bonds among conspecifics, including the formation of partner preference (Ophir et al., 2012; Liu and Wang, 2003). In some species and individuals, OXTR density in the NAc and the lateral septum (LS) was inversely correlated suggesting that OXTR in the LS could also play a role in the regulation of social behavior (Olazábal and Young, 2006a, 2006b). Beery et al. (2008), comparing two species of tuco tuco (*Ctenomys sociabilis* and *C. haigi*), found an association between low OXTR density in the LS in a species and higher social interaction or population density. However, the role of the interspecific variation of OXTR density in the LS is still not as well understood as is the case for the density of OXTR in the NAc.

In the present manuscript, we will review evidence that supports the idea that variation in the OXT system can be a mechanism used by evolution to adapt species to a certain social or reproductive strategy. Thus, understanding these neural mechanisms of adaptation we might be able to partially predict species reproductive and social behavior by just looking at the OXTR distribution in the brain. We reviewed evidence from many studies in several species carried out by different laboratories and the results suggested that the presence of different combination of OXTR expression in the NAc and LS could reveal important differences in the social and reproductive behavior of species (see Table 1 and Figs. 1–5).

3. Methods

We made a pubmed search using as keywords: oxytocin receptor and autoradiography and brain. The output was 186 articles that were later explored in detail to find descriptions of OXTR brain distribution in rodents. We also checked references of several review, research studies, and chapters (including our own previous publications) to look for descriptions of brain OXTR distribution in rodents (Olazábal and Young, 2006a, 2006b; Beery et al., 2008; Campbell et al., 2009; Beery et al., 2016). Our main analysis was based on studies that compared at

Table 1
Comparison of OXTR Autoradiographic Signal in 13 Rodent Species. The table summarize the intensity of OXTR autoradiographic signal in several brain regions from 13 rodents species as described in Tribollet et al. (1990); Insel et al. (1991); Insel and Shapiro (1992); Olazábal and Young (2006a, 2006b); Beery et al. (2008); Campbell et al. (2009); Kalamatianos et al. (2010); Chappell et al. (2016); Olazábal and Alsina-Llanes (2016). Brain regions and density of OXTR considered in this manuscript to separate species in 4 groups (shown in different gray scale) are represented in bold. H, M and L represents high, medium and low density of OXTR.

Oxytocin Receptor Density in the Brain of 13 Rodent Species

	R. norvergicus	*C. sociabilis*	*S. teguina*	*C. porcellus*	*M. musculus*	*M. pennsylvanicus*	*M. montanus*	*C. haigi*	*P. maniculatus*	*M. ochrogaster*	*H.glaber*	*M.kikuchii*	*P.californicus*
DS	H	L	L	L	L	L	L	L	L	H	L	L	M
NAc	L	L	L	L	L	L	L	L	L	H	H	H	H
LSd	L	L	M	L	H	H	H	H	H	M	L	L	H
LSv	L	L	L	L	H	H	H	H	M	L	L	L	H
BNST	H	M	H	L	M	L	L	H	H	H	H	L	M
MPOA	M	M	M	L	L	L	L	H	M	L	L	L	M
CA	H	M	H	L	M	H	H	M	H	H	H	M	H
BLA	H	M	M	L	M	H	M	H	M	H	M	L	M
MA	M	M	M	H	M	L	L	M	M	L	M	L	M
CoA	M	M	M	H	M	L	M	M	M	M	M	L	M
dHip	L	L	L	L	M	M	L	H	H	L	M	H	M
VMH	H	M	M	H	M	H	H	H	M	M	M	M	H

DS (Dorsal Striatum), NAc (Nucleus Accumbens), LSd/LSv (Lateral Septum dorsal/ventral), BNST (Bed Nucleus of the Stria Terminalis), MPOA (Medial Preoptic Area). CA (Central Amygdala), BLA (Basolateral Amygdala), MA (Medial Amygdala), CoA (Cortical Amygdala), dHip (dorsal Hippocampus), VMH (Ventromedial Nucleus of the Hypothalamus). L, M, and H stand for Low, Medium and High OXTR density. Different gray scales separate species with the same pattern of expression of OXTR in the Nac and LS.

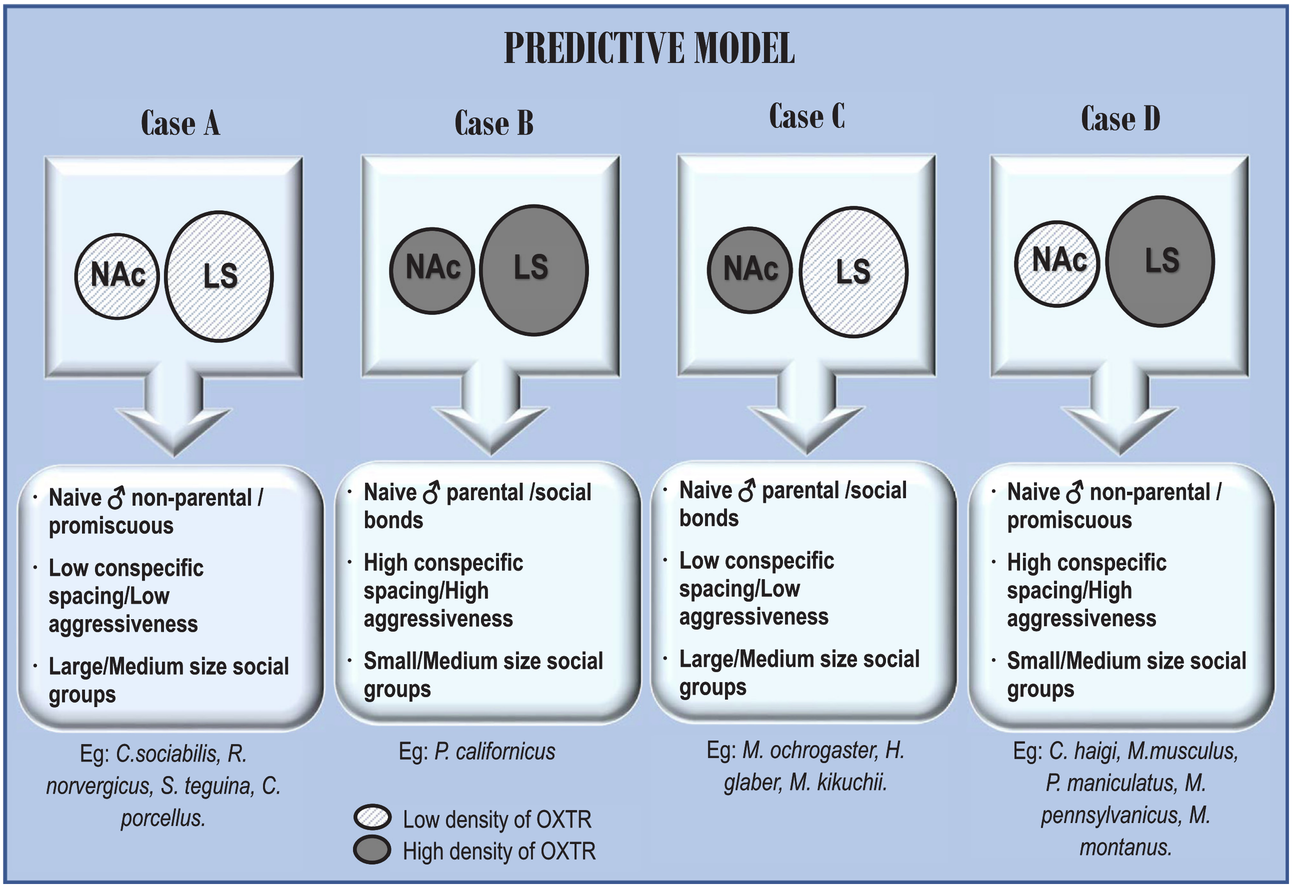

Fig. 1. Predictive model of four possible combinations (Case A–D) of OXTR expression in the nucleus accumbens (NAc) and lateral septum (LS). Dark diagrams represent high density of OXTR while light diagrams represent low density of OXTR. Behavioral features predicted by the model and examples of species in each case category are shown (see references in the text).

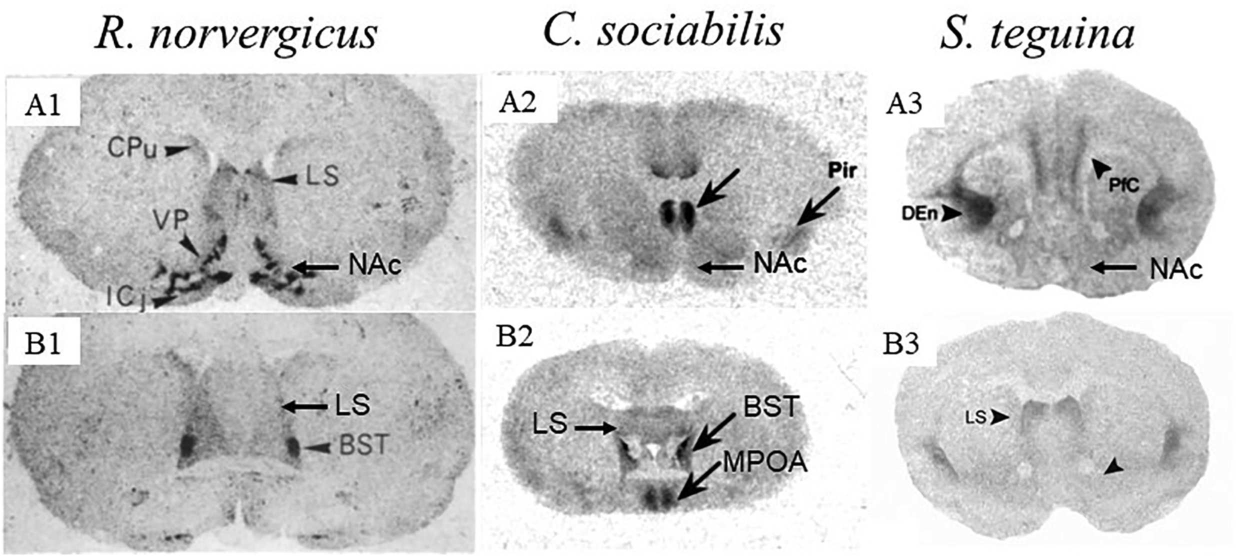

Fig. 2. Species with Low OXTR in NAc and LS. The figure shows autoradiographic signal for oxytocin receptor at the level of the nucleus accumbens (NAc, A1–3), and lateral septum (LS, B1–3) in *R. norvergicus* (A1–B1), *C. sociabilis* (A2–B2), and *S. teguina* (A3–B3). Arrows shows the location of NAc, LS, bed nucleus of the stria terminalis (BST), caudate putamen (CPu), and medial preoptic area (MPOA), among other brain regions. Pictures from A1–B1 were taken from Gonadal steroids regulate oxytocin receptors but not vasopressin receptors in the brain of male and female rats. An autoradiographical study. Tribollet et al. Brain Res. (1990) and reproduced by permission of Elsevier. Pictures from A2–B2 were taken from Oxytocin and vasopressin receptor distributions in a solitary and a social species of tuco-tuco (*Ctenomys haigi* and *Ctenomys sociabilis*). Beery et al. (2008). J. Comp. Neurol. and reproduced by permission of Wiley. Pictures from A3–B3 were taken from Central vasopressin and oxytocin receptor distributions in two species of singing mice. Campbell et al. (2009). J. Comp. Neurol. and reproduced by permission of Wiley.

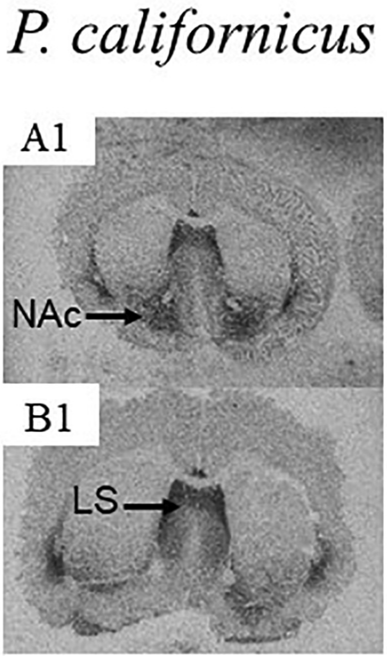

Fig. 3. Species with High OXTR in NAc and LS. The figure shows autoradiographic signal for oxytocin receptor at the level of the nucleus accumbens (NAc, A1), and lateral septum (LS, B1) in *P. californicus*. Arrows shows the location of NAc, and LS. Pictures were taken from an unpublished study in preparation.

least two species (Insel et al., 1991; Olazábal and Young, 2006a, 2006b; Beery et al., 2008; Campbell et al., 2009; Kalamatianos et al., 2010; Chappell et al., 2016). We qualitatively (using representative pictures) and quantitatively (using total values reported for the signal) compared the description of OXTR in the brain for the different species. We also made comparisons among different studies on the same species to better identify the intensity of the OXTR binding (e.g. in rats [*Ratus norvergicus*]; Freund-Mercier et al., 1987; Tribollet et al., 1988; Shapiro and Insel, 1989; Tribollet et al., 1990; Kremarik et al., 1993; Shelat et al., 1998; Olazábal and Young, 2006a; Lukas et al., 2010; Caughey et al., 2011; Dumais et al., 2013; Smith et al., 2017). We ended up with 18 rodent species in which brain OXTR distribution was described. We discussed evidence in all species but focused mainly in only 13 rodent species (see Table 1) in which there was more information about their social and reproductive behavior. Five rodent species (cape mole rats *[Georychus capensis],* Shaw's jird *[Meriones shawi],* golden hamster *[Mesocricetus auratus],* degu *[Octodon degus],* and long-tailed singing mouse *[Scotinomys xerampelinus]*) were also discussed although left out of the predictive model due to lack of behavioral information or clear description of OXTR signal in the NAc or LS. In some studies (Dubois-Dauphin et al., 1992; Tribollet et al., 1992), the publications showed high contrast poor quality pictures and were not used to prepare the figures that show representative sections of the OXTR autoradiographic signal in the different species. NAc OXTR in prairie voles and LS OXTR in the mice (*Mus musculus*) were used as references for high density, according to our previous studies (≥1000 dpm/mg) and consistent with other studies that confirmed high signal in those brain regions (Olazábal and Young, 2006a, 2006b; Ophir et al., 2012; Olazábal and Alsina-Llanes, 2016). In our studies, medium density was considered ≥ 400 < 1000 and low density was considered below 400 dpm. However, in other studies, important discrepancies were

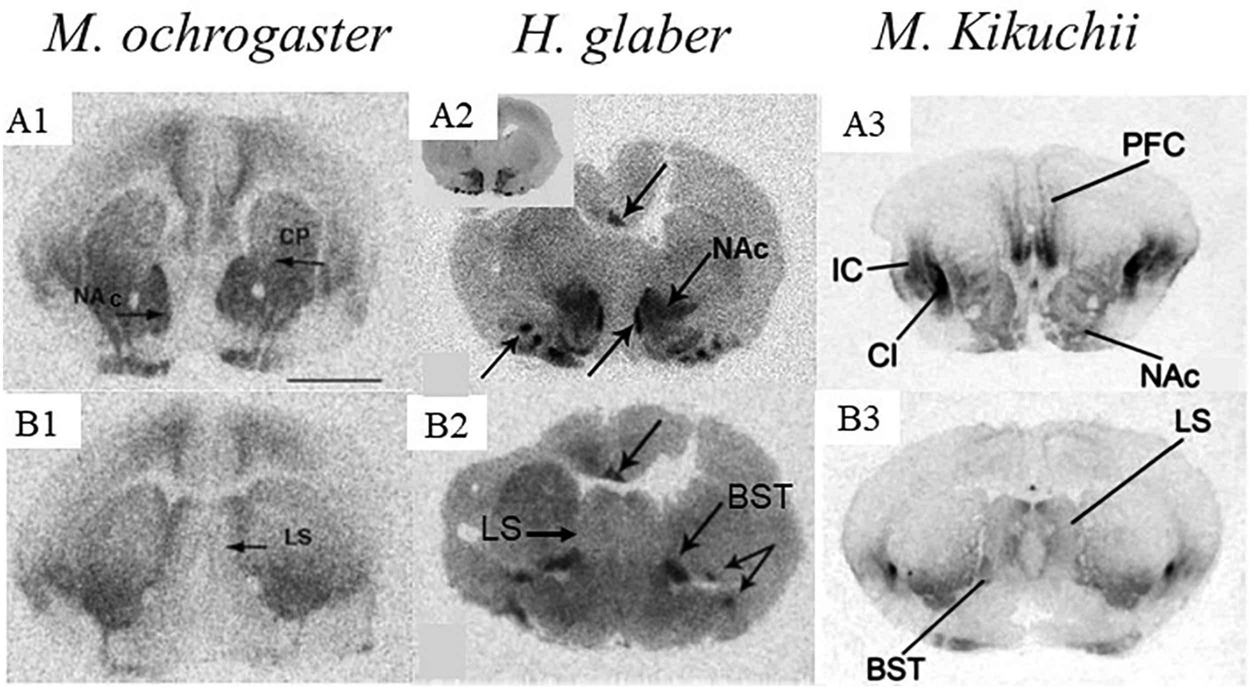

Fig. 4. Species with High OXTR in NAc and Low OXTR in LS. The figure shows autoradiographic signal for oxytocin receptor at the level of the nucleus accumbens (NAc, A1–3), and lateral septum (LS, B1–3) in *M. ochrogaster* (A1–B1), *H. glaber* (A2–B2), and *M. kikuchii* (A3–B3). Arrows shows the location of nucleus accumbens (NAc), LS, bed nucleus of the stria terminalis (BST), caudate putamen (CP), among other brain regions. Pictures from A1–B1 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, Horm. Behav. and reproduced by permission of Elsevier and Willey respectively. Pictures from A2 to B2 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. J. Comp. Neurol. (2010) and reproduced by permission of Wiley. Pictures A3–B3 were taken from Distributions of oxytocin and vasopressin 1a receptors in the Taiwan vole and their role in social monogamy. Chappell et al. (2016), J. Zool. and reproduced by permission of Wiley.

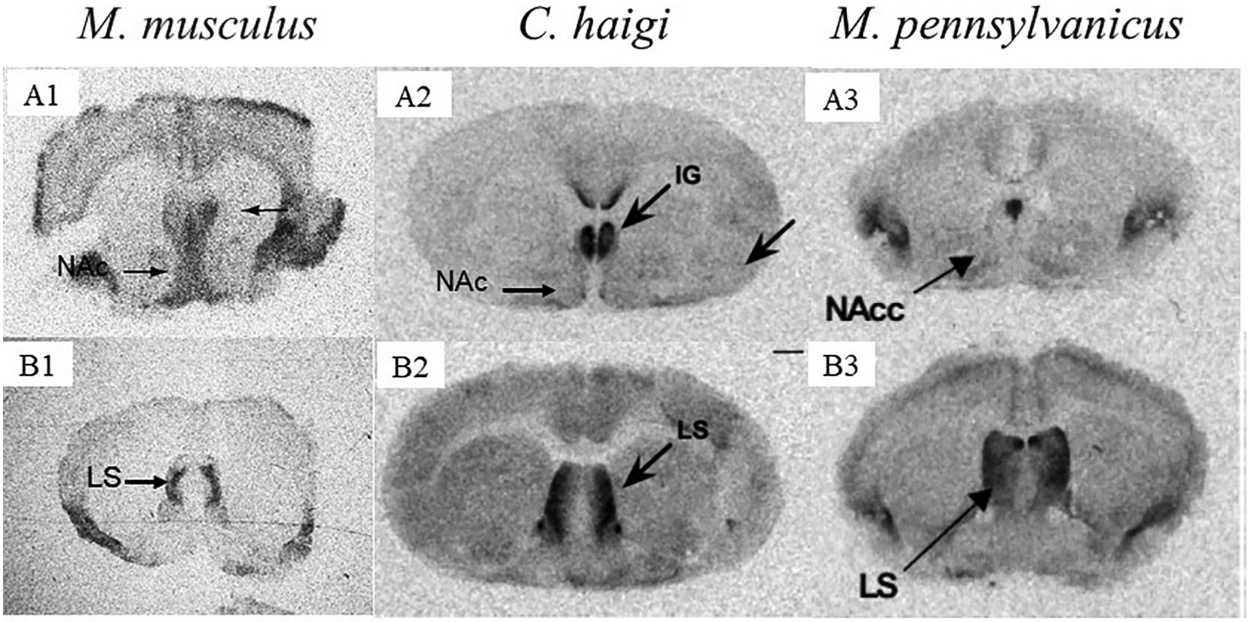

Fig. 5. Species with Low OXTR in NAc and High OXTR in LS. The figure shows autoradiographic signal for oxytocin receptor at the level of the nucleus accumbens (NAc or NAcc, A1–3), and lateral septum (LS, B1–3) in *M. musculus* (A1–B1), *C. haigi* (A2–B2) and *M. pennsylvanicus* (A3–B3). Arrows shows the location of NAc, LS, and indusium griseum (IG). Pictures from A1–B1 were taken from unpublished data and 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, Horm. Behav. and reproduced by permission of Elsevier. Pictures from A2–B2 were taken from Oxytocin and vasopressin receptor distributions in a solitary and a social species of tuco-tuco (*Ctenomys haigi* and *Ctenomys sociabilis*). Beery et al. (2008). J. Comp. Neurol. and reproduced by permission of Wiley. Pictures from A3–B3 were taken from Oxytocin and same-sex social behavior in female meadow voles. Beery and Zucker, Neuroscience, and reproduced by permission of Elsevier.

found in the total values of the reported signal, likely due to different time of film exposure, or different concentration of the radioligand used during the incubation step (Beery et al., 2008; Dumais et al., 2013). In those cases, it was only possible to make qualitative comparisons across studies. We looked at the relative differences in absolute values across all brain regions represented in the pictures shown in each study. Then, those representative pictures were compared with others from additional articles to decide in which category (high, medium or low) each region of the brain should be placed. Following those criteria, we were able to separate species in 4 main groups (Fig. 1).

4. The pattern of expression of OXTR in the nucleus accumbens and lateral septum is associated with the social and reproductive strategy of species

Analyzing the different possible combination of expression of OXTR (high, medium, low) published in the literature for the NAc, and LS in several rodent species, we could find at least 4 main groups that differed in at least four social and reproductive strategies: 1) the size of the groups or population density, 2) conspecific spacing (preferred separation distance maintained by adult conspecifics) and intraspecific aggressiveness, 3) rapid onset of parental behavior in inexperienced males, and 4) the establishment of social preferences or bonds. We are using here just two brain regions, known to be variable among species, and a few behavioral features to simplify the analysis. However, we consider that analyzing other brain regions, peptides systems, and behavioral features can significantly increase the chances of predicting properly the most common reproductive or behavioral strategy in a species. For example, species could also be grouped based in their different response to social stress, diurnal or nocturnal habits, behaviors based on social olfactory or visual stimuli, etc.

In the present manuscript we reviewed the literature and added some unpublished data to compare the distribution of OXTR in the NAc, and LS in the brain of rodent species that have been studied in detail to determine if OXTR density in those brain regions could help us to predict a certain pattern of social and reproductive behavior in species.

The 4 categories of OXTR pattern of expression discussed in this manuscript do not pretend to be exclusive or the only one that can be thought about. Besides each of these categories includes species that differ in several aspects of their reproductive and social behaviors not discussed in this manuscript. However, although the complexity of forms of living of species is greater than the groups that will be described here, we hope it will improve our understanding of the mechanisms that regulates social and reproductive behavior. Specifically, we hope to contribute to understand the role played by the OXT system, one of the neuroendocrine peptides more studied in social behavior (Carter et al., 2008), in shaping certain forms of social and reproductive lives.

Table 1 describes the intensity of OXTR labeling (autoradiographic signal) in several brain regions of 13 rodent species. Grouping animals according with the intensity of the signal for OXTR in the NAc and LS, we distinguished at least 4 clear combinations: Low OXTR NAc/Low OXTR LS (Tribollet et al., 1990; Tribollet et al., 1992; Beery et al., 2008; Campbell et al., 2009); High OXTR NAc/High OXTR LS (Duque-Wilckens et al., 2018); High OXTR NAc/Low OXTR LS (Olazábal and Young, 2006a, 2006b; Kalamatianos et al., 2010; Chappell et al., 2016); and Low OXTR NAc/High OXTR LS (Insel and Shapiro, 1992; Shapiro and Insel, 1992; Olazábal and Young, 2006a; Beery et al., 2008; Beery and Zucker, 2010). Grouping all these species, according with the pattern of expression of OXTR in the NAc and LS, several common behavioral features were also revealed in each group (Fig. 1). Large or medium size mixed sex groups with lower conspecific spacing, and high levels of promiscuity characterized by low levels of OXTR in the NAc and LS (e.g. *Ratus norvegicus*, *Ctenomys sociabilis*, short-tailed singing mouse *[Scotinomys teguina],* guinea pig *[Cavia porcellus]* Fig. 2); small size groups with higher conspecific spacing and very low levels of promiscuity (strictly monogamous) characterized by high OXTR in the NAc and the LS (e.g. California mouse *[Peromyscus californicus],* Fig. 3); large or medium size groups with lower conspecific spacing and low levels of promiscuity characterized by high levels of OXTR in the NAc but low levels in the LS (e.g. *Microtus ochrogaster*, naked mole rat *[Heterocephalus glaber],* Taiwan vole *[Microtus kikuchii],* Fig. 4); and small or medium size groups with higher conspecific spacing and high levels of promiscuity characterized by low levels of OXTR in the NAc and high OXTR in the LS (e.g. *Mus musculus*, *Ctenomys haigi*, deer mouse [*Peromyscus maniculatus],* meadow vole *[Microtus pennsylvanicus],* montane vole *[Microtus montanus],* Fig. 5). In the next section, we will briefly summarize similarities among the species in each group category and discuss how OXTR density in the brain might contribute to these similarities according to what it is known in the literature.

4.1. Low OXTR NAc/Low OXTR LS (e.g. Ratus norvegicus, Ctenomys sociabilis, Scotinomys teguina, Cavia porcellus)

According to our predictive hypothesis (Fig. 1), low density of OXTR in the NAc would be associated with lower social attachment and higher promiscuity, while low density in the LS associated with lower aggressiveness toward conspecifics, low conspecific spacing and higher density populations. We found that several species (*R. norvergicus, C. sociabilis*, *S. teguina, C. porcellus*) shared these characteristic behavioral features. They live in high or medium density populations, are considered gregarious or have low conspecific spacing, and more tolerant to conspecifics than other phylogenetically related species (Latané, 1969; Latané et al., 1971; Hooper and Carleton, 1976; Wagner and Manning, 1976; Willis et al., 1977; Lacey et al., 1997; Hennessy et al., 2006; Campbell et al., 2009). Besides, they are promiscuous and do not form strong bonds (Latané, 1969; Latané et al., 1971; Hooper and Carleton, 1976; Wagner and Manning, 1976; Beery et al., 2008; Blondel et al., 2009; Campbell et al., 2009; Davis et al., 2016). Finally, inexperienced male rats do not show paternal behavior rapidly, something that is likely valid also for *Ctenomys sociabilis, Scotinomys teguina, and Cavia porcellus.* Additionally, *Octodon degus* seems also to belong to this group. The only study that investigated OXTR brain distribution in this species described low levels of OXTR in the NAC but only medium levels of OXTR in the LS (Beery et al., 2016). They are known for living in non-kin social groups with high tolerance to conspecifics and high levels of promiscuity (Davis et al., 2016; Beery et al., 2016).

4.2. High OXTR NAc/High OXTR LS (e.g. Peromyscus californicus)

According to our predictive hypothesis, high density of OXTR in the NAc would be associated with higher social attachment, including pair bonding, and rapid onset of paternal behavior in inexperienced males and females, while high density in the LS would be associated with higher aggressiveness against conspecifics, higher conspecific spacing, and lower density populations. *P. californicus* form sexually exclusive monogamous pairs according to a detailed genetic analysis of progeny carried out for 2 years in natural conditions (Ribble, 1991). They also form small semi-permanent groups (pair and recent progeny, Ribble, 1990; 1992) and are more territorial than other phylogenetically related species such as white-footed mouse (*P. leucopus,* promiscuous species, Bester-Meredith et al., 1999). Besides, inexperienced males show rapid onset of paternal behavior (de Jong et al., 2013; Perea-Rodriguez et al., 2015; Horrell et al., 2017) and there is both male and female nest defense (Eisenberg, 1963). Males are also very aggressive and have very small intersexual superposition in territory (Gubernick and Alberts, 1987, 1989; Wolff, 1989; Ribble and Salvioni, 1990). This is the only species so far that clearly has this combination of OXTR receptor density in NAc and LS (see next section for discussion about *Microtus kikuchii*) and one of the few species reported clearly as strictly monogamous (Ribble, 1991; Chappell et al., 2016; Díaz-Muñoz and Bales, 2016). Perhaps the high aggressiveness and isolation of the pair reduce chances of sexual encounters outside the living pair.

4.3. High OXTR NAc/Low OXTR LS (e.g. Microtus ochrogaster, Heterocephalus glaber, Microtus kikuchii).

According to our predictive hypothesis, high density of OXTR in the NAc would be associated with higher social attachment, including pair bonding, and rapid onset of paternal behavior in inexperienced males and females, while low density in the LS would be associated with lower aggressiveness toward conspecifics, and higher density populations. These three species are different in many aspects but have also common features among them, and also with *P. californicus. M. ochrogaster* and *H. glaber* live in large or medium size groups, and even though they might show partner preference (Cho et al., 1999) they are not strictly monogamous (Solomon et al., 2004; Díaz-Muñoz and Bales, 2016). *M. ochrogaster* are found to live in pairs but also in groups of several adult males or females (Getz, 1963; Cochran and Solomon, 2000, Lucia et al., 2008) while *H. glaber* live in colonies and females can also copulate with 1–3 males (Kalamatianos et al., 2010). Both species show low conspecific spacing and low levels of aggressiveness toward conspecifics (Getz, 1962; Hofmann et al., 1984; Kalamatianos et al., 2010). Besides, both species form social bonds and show high levels of parental behavior in males, including spontaneous paternal behavior by inexperienced *M. ochrogaster* males (Olazábal and Young, 2006a, 2006b).

In the case of *M. kikuchii,* we have chosen to include this species in the present category, but it could also share features with *P. californicus* of the previous section. Even though some authors have reported that Taiwan voles are strictly monogamous (Wu et al., 2012), with low territorial overlapping with other conspecifics, as *P. californicus*, there is little detail, at least in English, about the behavior of this species (Wu et al., 2012). Besides, Lee et al. (2014) proposed that Taiwan voles were not strictly monogamous, there was certain territory overlap among males or females, and did not show partner preference. Analysis of OXTR density in the NAc and LS is also not clear in the study of Chappell et al. (2016). The representative pictures chosen by the authors show higher, or similar, density of OXTR in the NAc than in the LS. However, there is no information about the results of the comparison of OXTR density in the LS of prairie voles vs. Taiwan voles in that specific study (Chappell, 2016), something that would help to compare global OXTR binding in those two species. Therefore, we have so far included Taiwan voles in the same group as prairie voles assuming that Taiwan voles may actually have low levels of OXTR in the LS and show low promiscuity; assumptions that must be confirmed with future studies. If OXTR in the LS turns out to be high, then our prediction would be that they should be aggressive towards conspecifics and, more likely, strictly monogamous as *P. californicus*. Future studies will surely help us to better understand the behavior of Taiwan voles. Finally, although, to our knowledge, no study has described OXTR distribution in the brain of mandarin voles (*Lasiopodomys mandarinus*), several studies have measured OXTR mRNA or protein and found high levels of expression in the NAc (Wang et al., 2015, 2018). Mandarin voles are socially monogamous and also show high levels of paternal care (Wang et al., 2015, 2018). Levels of OXTR mRNA or OXTR protein in the lateral septum has not been reported.

4.4. Low OXTR NAc/High OXTR LS (e.g. Mus musculus, Ctenomys haigi, Peromyscus maniculatus, Microtus pennsylanicus, Microtus montanus).

According to our predictive hypothesis, low density of OXTR in the NAc would be associated with lower social attachment and lack of paternal behavior in inexperienced males, while high density in the LS would be associated with higher conspecific spacing, aggressiveness towards conspecifics, and lower density populations. Those features are shared by these five species as much as it is known. These species are in general described as promiscuous and with no paternal behavior displayed by inexperienced males (Lund, 1975; Vestal, 1977; McGuire and Novak, 1986; Shapiro and Dewsbury, 1990; Insel et al., 1991; Salo et al., 1993; Beery et al., 2008; Kappel et al., 2017). These species, in particular the males, are also generally considered aggressive (Eisenberg, 1962), maintain higher conspecific spacing than rats, and live in small or medium size groups (Vestal, 1977; Madison, 1980; Beery et al., 2008).

In the case of meadow voles, their higher aggressiveness is still not clear (Madison, 1980). Getz (1962) reported that meadow voles were intolerant of other individuals of its own species and avoided each other or fought when forced into an encounter. In this sense, they were also considered more aggressive than prairie voles (Getz, 1962; Pan et al., 2016). However, a recent study from Lee et al. (2019) suggests that female prairie voles are more aggressive than female meadow voles. Although it is possible that both species show high levels of aggressiveness in different context, it seems more research is needed to understand aggressiveness and tolerance to live in groups of prairie and meadow voles. Perhaps higher OXTR in the LS increases conspecific spacing, but not necessarily increasing aggressiveness.

Finally, golden hamsters and Shaẃs jirds also have low OXTR density in the NAC, but medium OXTR density in the LS (Dubois-Dauphin et al., 1992; Rabhi et al., 1999). Golden hamsters are well known for their territoriality, aggressiveness and solitary style of life, associated also with a promiscuous mating strategy (Delville et al., 2003). There is little behavioral information about captive or wild behavior of Shaẃs jirds but, they are also considered promiscuous, more aggressive and less social than gerbils (*Meriones unguiculatus*). However, some studies describe them as flexible and living both in solitary or large groups (Sales, 1972; Ghawar et al., 2015). More studies on Shaẃs jirds behavior and OXTR density in the brain are needed to better understand how OXTR distribution might affect the behavior of this species.

5. OXTR density in other areas of the brain

Although we have considered here only OXTR in the NAc and LS, we do not exclude the possibility that other areas of the brain could also contribute to our predictive model.

Although some brain regions show little variability among species (e.g. ventromedial nucleus of the hypothalamus or cortico-medial amygdala), other brain regions (e.g. dorsal hippocampus, dHip) show interesting changes that might also represent differences in other behavioral features among species. After these species were organized based in OXTR density in the NAc and LS, some of these groups (mainly the first two categories) also differed in the density of OXTR in the dHip. The hippocampus is a brain region that process spatial memory (Martin and Clark, 2007; Tomizawa et al., 2003) and differences in OXTR density in the hippocampus have been previously related to differences in socio-spatial memory (Campbell et al., 2009; Cilz et al., 2019). The first category, identified as promiscuous, living in high or medium density populations with low conspecific spacing, and more tolerant to conspecifics than other phylogenetically related species, also lack of significant OXTR density in the dorsal hippocampus (see Table 1). Species that are promiscuous and live in large and tolerant mixed sex social groups might no need to develop an oxytocin-mediated mechanism to remember where and who they encountered. In contrast, species that are territorial or highly aggressive toward conspecifics (second category) or establish prolonged bonds (third and fourth category), might need to remember who and where the encounters occurred (Leroy et al., 2018). Except for prairie and montane voles, all the other species had medium or high OXTR in the dHip. Whether the low or High OXTR expression in the dHip of these species is related to differences in social or socio-spatial memory (e.g. less or more need to remember where and who they encountered) need to be investigated further, but species comparisons clearly suggest a difference in the role of OXT in the dHip and a positive correlation between LS and dHip OXTR density. According to Campbell et al (2009), differences in OXTR density in the dHip might represent differences in their needs to remember location and identity of conspecifics, part of a neural mechanism for enhanced socio-spatial memory. Species use olfactory, auditory and visual sensory channels to detect, recognize, and remember the location of familiar individuals or strangers (Costanzo et al., 2009). Recently, Raam et al. (2017) found evidence that OXTR in the hippocampus is needed for appropriate social discrimination. Therefore, higher OXTR density in this brain region might reflect different selection pressures on the abilities to process and remember social information.

6. Additional comments on other rodent and non-rodent species

The present manuscript intended to analyze only rodent species and, in particular, those in which OXTR brain distribution or the behavior of the species is well known and has been described in the literature. However, we have also considered other species such as *Scotinomys xerampelinus,* but some particularities in the description of the distribution of OXTR, and the lack of available behavioral information made difficult to categorize this species. According to Campbell et al (2009), *S. xerampelinus* showed some, medium/low, OXTR in the NAc. However, when total values in the NAc are compared to OXTR density in the LS and hippocampus the density is clearly lower. According with our prediction, they might show some preference for familiar conspecifics or some level of paternal response toward newborns by inexperienced males, but NAc OXTR in this species is much lower than that observed in prairie voles, California mice, or Taiwan voles. Therefore, future studies that compare OXTR density in *S. xerampelinus* together with prairie voles, mice, or rats on the same assay might help us to better understand OXTR density in the brain of *S. xerampelinus,* and better predict their social and reproductive behavior. However, they should be aggressive toward conspecifics and live in small or medium size groups with low population density, and higher conspecific spacing, features that appear to agree with the report of Campbell et al (2009).

Additional studies in non-rodent species suggest that OXTR in NAc and LS might also predict most common reproductive and social strategy in other species. Although OXTR distribution analysis in the rodent brain do not necessarily translate or apply to non-rodent species (e.g. different selectivity for radioligands), there is promising evidence suggesting that it could be the case. For example, Marmosets (*Callithrix jacchus*) have been reported to establish social bonds, to be highly paternal, and live in large or medium social groups (Burkart and van Schaik, 2013; Wahab et al., 2015). This agrees with the behavioral features of prairie voles, and nake mole rats, but also with their OXTR distribution in the brain. Marmosets also have high OXTR in the NAc, but low OXTR in the LS (Schorscher-Petcu et al., 2009). However, as prairie voles, OXTR in the hippocampus appears to be very low suggesting that some other mechanism independent of OXT action in the hippocampus might also contribute to social memory in these species, or there is a behavioral feature specific for prairie voles and marmosets that has not been considered yet. Despite the presence of OXTR in the NAc, LS or dHip might predispose the species to certain behavioral adaptations; the absence of OXTR does not necessarily exclude other mechanisms. For example, cape mole rats are also territorial and aggressive despite they show low levels of OXTR in the LS (Kalamatianos et al., 2010). AVP is well known to affect aggressive behavior by acting in the LS (De Leon et al., 2002; Bester-Meredith et al., 1999; Leroy et al., 2018) and would influence partner preference acting in the ventral pallidum (Young et al., 2001). An obvious step ahead will be to incorporate the AVP system to the analysis presented here (Carter et al., 2008; Bosch and Neumann, 2012). We have also considered other species such as rabbits (*Oryctolagus cuniculus*), known to have very high OXTR in the LS and hippocampus, but not in the NAc (Jiménez et al., 2015). Our hypothesis would predict a high conspecific spacing, no paternal behavior by inexperienced males, promiscuity, absence of strong social bonds, but well-developed memory of nest location. Description of the reproductive and social behavior of rabbit seems also to agree with our predictions (Di Vincenti and Rehrig, 2016).

7. Within species variability

Finally, we want to note some aspects of variability that need to be considered when doing comparative studies. Early experiences might affect the density of OXTR in the brain during development, although not in the same way in all species (Wang and Young, 1997; Olazábal and Alsina-Llanes, 2016; Olazábal and Young, 2008; Perkeybile et al., 2019). Besides, gonadal hormonal changes, status, or environmental changes can affect or not OXTR density in the brain depending on the species (Mooney et al., 2015). However, within species variability in the density of OXTR in the brain can be sometimes as big as differences among species (Olazábal and Young, 2006a, 2006b). In fact, there is evidence that within variability in OXTR in the NAc and LS are also associated with behavioral consequences similar to those seen in comparative studies (Olazábal and Young, 2006a, 2006b). For example, higher density of OXTR in the NAc has been associated with more time spent in contact with pups in prepubertal prairie voles (Olazábal and Young 2006a) and more preference for partner in adult prairie voles (Ophir et al., 2012), while higher OXTR density in the LS in prairie voles has been associated with lower social investigation (Ophir et al., 2009). Therefore, the final OXTR density in the brain can be not only consequence of evolution but also due to environmental or experiences as mentioned in the introduction.

8. Final remarks

Comparative analysis of peptide receptor distribution, in particular OXTR, has been very helpful to understand the actions of peptides in the brain. However, this type of analysis not only can help us to understand reproductive and social behavior, but probably also differences in stress reactivity, social anxiety, and other aspects of OXT function (Beery et al., 2014; Duque-Wilckens et al., 2018). We strongly believe that there is enough evidence to start to predict most common differences in physiology (e.g. stress response) or behavior of the species by looking at the peptide receptor distribution in the brain. Despite the obvious variability within species and the effects of environmental changes on behavior, species still maintain clear differences in adaptation and in selection of a reproductive and behavioral strategy. However, the analysis presented in this manuscript has some limitations. Most studies published in the literature focused in few species and did not follow same protocols. In order to compare species from different studies more properly, future studies should be careful to follow similar protocols to those previously published. First, showing the displacement of signal is critical to know that the signal described in the study is selective for the targeted receptor; second, total values should be expressed in dpm/mg of tissue and appropriate standards used; and third, similar amount of days should be used to expose the radioactive slices to the film. Besides, there are limitations about the knowledge of the reproductive and social behavior of species. There are contradictory findings sometimes and, in other cases, no detailed information related to behavior of exotic non-traditional species. However, comparative behavioral studies together with the analysis of OXTR, and AVP receptors (and other systems) distribution in the same study might be particularly helpful to understand why species react different toward conspecifics, stressful stimuli (social or not), space limitations, sexual partners, shortage of resources, etc. This manuscript is just an example of how comparative neuroendocrinology and behavior could be informative about selection pressures that favored different reproductive and social styles of live.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

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