Paternal Behavior Is Associated With Central Neurohormone Receptor Binding Patterns in Meadow Voles (Microtus pennsylvanicus)

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Paternal and nonpaternal voles (microtus) have different arginine-vasopressin (AVP) and oxytocin (OT) receptor patterns in the extended amygdala, a neural pathway associated with parental behavior. Using receptor autoradiography, the authors examined whether AVP and OT receptor patterns were associated with facultative paternal behavior in either sexually and parentally inexperienced or experienced meadow voles (Microtus pennsylvanicus). Experienced, in contrast to inexperienced, males had less AVP binding in the lateral septum (LS), more AVP binding in the anterior olfactory nucleus (AON), and more OT binding in the AON, bed nucleus of the stria terminalis, LS, and lateral amygdala. Thus, specific AVP receptor patterns, which co-occur with paternal care in consistently paternal voles, also may be associated with paternal care (when present) in typically nonpaternal species. This study also demonstrated a possible relationship between OT receptor patterns and paternal state in male mammals.

Paternal care, in its broadest sense is defined as "all nongametic investments in offspring following fertilization" (Wittenberger, 1981). In rodents, the presence of paternal care is often associated with social living and harsh breeding conditions (Kleiman & Malcolm, 1981) and may be either a consistent or facultative feature of a given social system. For example, Peromyscus californicus (California mice) live in habitats with patchy resource bases and engage in consistent biparental care to increase offspring survivorship in this resource-poor environment (Gubernick, 1981). In contrast, typically nonparental rodents may also engage in parental care, but, rather than consistently occurring, facultative paternal behavior is usually expressed situationally to offset fitness costs associated with unpredictable social or seasonal changes; decreased access to mates or compromised offspring survivorship because of a patchy resource base, high predation risk, or increased offspring energy needs (Kleiman, 1977). Such facultative care has been reported in typically nonparental Peromyscus maniculatus (deer mice; Mihok, 1979), Marmota caligata (hoary marmots; Barash, 1975), and Peromyscus leucopus (white-footed mice; Schug, Vessey, & Underwood, 1992) during colder months.

To date, both the evolutionary rationale for paternal effort expenditure (Kleiman & Malcolm, 1981; Trivers, 1972) and the social and environmental regulation of paternal behavior expression (reviewed by Dewsbury, 1985) have been well elucidated for both consistently and facultatively paternal species. However, the neural pathways that mediate the expression of paternal behavior have been studied primarily in consistently paternal species (reviewed by Wang, Young, De Vries, & Insel, 1998). Thus, it is not yet known whether the same neurobiology regulates paternal behavior when it is facultatively, rather than consistently, initiated. Nevertheless, our understanding of the neurobiology that promotes paternal behavior has been greatly advanced by studies conducted in Microtus, an ideal genus in which to investigate the underlying neural circuits associated with the presence and absence of pair bonding and paternal behavior in closely related rodent species.

Initial studies demonstrated that sexually and parentally inexperienced monogamous Microtus ochrogaster (prairie voles) and nonmonogamous Microtus montanus (montane voles) showed considerable differences in arginine-vasopressin (AVP) and oxytocin (OT) receptor patterns in the extended amygdala (Insel & Shapiro, 1992; Insel, Wang, & Ferris, 1994). The extended amygdala neural pathway is composed of the accessory olfactory nucleus (AON), amygdala, bed nucleus of the stria terminalis (BNST), lateral septum (LS), and medial preoptic area of the hypothalamus (MPOA) and is important for the initiation of affiliative, mating, and parenting behaviors in several rodent species (reviewed by Newman, 1999). Because monogamous species often concomitantly exhibit paternal care, partner preferences, and stranger-directed aggression and nonmonogamous species do not, it has been suggested that receptor differences in this pathway reflect species differences in evolved patterns of social organization (Wang et al., 1998).

Since these first studies were published, a working model of the underlying neurobiology of male prairie vole social and affiliative...
behaviors has emerged. Behavioral research has shown that male prairie voles develop selective partner preferences after 24 hr of mated cohabitation with a female (Insel, Preston, & Winslow, 1995), and these behavioral changes are associated with enhanced paternal responsiveness (Bamshad, Novak & De Vries, 1994). Several pharmacological experiments have implicated a role for AVP (Winslow, Hastings, Carter, Harbaugh, & Insel, 1993) and OT (Cho, De Vries, Williams, & Carter, 1999) in male partner preference onset. Although a functional role for OT has not yet been investigated in regulating paternal behavior in voles, central administration of AVP into either the lateral ventricle or the LS enhances paternal behavior expression (Wang, Ferris, & De Vries, 1994).

Several lesion studies (bilateral bulbectomy in Kirkpatrick, Williams, Slotnick, & Carter, 1994; corticomedial and medial nuclei of the amygdala [MeAmyg] in Kirkpatrick, Carter, Newman, & Insel, 1994) in combination with a number of early gene (c-fos) expression (indexed by immunoreactivity [Fos-ir]), AVP-ir fiber density, and AVP messenger RNA (mRNA) peptide expression studies have also been helpful in indicating a likely role for specific neural pathways in regulating parental care in prairie voles. The importance of the extended amygdala is supported by increased Fos-ir in the MeAmyg (Kirkpatrick, Kim, & Insel, 1994) and MPOA (Wang, Hulihan, & Insel, 1997) after male interactions with pups. After mating and cohabiting with a female, males show increased AVP mRNA expression in BNST cell bodies and decreased AVP-ir fibers in the LS and lateral habenular nucleus (Bamshad et al., 1994; Wang, Smith, Major, & De Vries, 1994, but also see Lonstein & De Vries, 1999), and these differences are associated with increased paternal responsiveness (Bamshad et al., 1994).

The extended amygdala also contains significant numbers of AVP receptors (AON-amygdala-BNST-LS; Insel et al., 1994; Wang, Young, Liu, & Insel, 1997; Wang, Liu, Young, & Insel, 2000). Because paternal behavior is associated with increased synthesis and release of AVP (Bamshad et al., 1994), and central AVP receptor binding studies have found no detectable differences in receptor number or location between sexually inexperienced males and sires (Wang et al., 2000), it does not appear that a change in AVP receptor number is critical for the expression of consistent paternal behavior in prairie voles.

Although these studies delineate neural pathways involved in regulating consistent paternal behavior, exactly how neural systems act to facilitate parental behavior will vary by whether a species exhibits paternal behavior in a consistent or facultative manner. For example, unlike male prairie voles, most female rodents are neophobic as nulliparous adults (e.g., rats) and only become maternal peripartum (reviewed by Rosenblatt, 1990). The transition from neophobia to maternal behavior onset occurs concomitantly with greater OT receptor numbers in the extended amygdala late in pregnancy (Insel, 1986; Insel & Shapiro, 1992). For montane voles, which only exhibit maternal behavior peripartum, these behavioral changes are associated with greater numbers of OT receptors in the lateral amygdala (LatAmyg) compared with nulliparous females (Insel & Shapiro, 1992).

As stated earlier, exactly how (and which) neural systems act to regulate facultative paternal behavior has yet to be determined. However, behavioral and pharmacological research conducted in Microtus pennsylvanicus (meadow voles), a typically nonpaternal microtine species, provides a foundation by which to begin investigating the neural underpinnings of facultative paternal behavior regulation.

In some laboratory populations, meadow vole sires share nests with a mate rather than establishing separate nest sites (Storey, Bradbury, & Joyce, 1994), drive off intruding males (Storey, 1996; Storey, French, & Payne, 1995), demonstrate appreciable care for young (Dewsbury, 1983; Hartung & Dewsbury, 1979; Storey et al., 1994; Storey & Joyce, 1995; Storey & Snow, 1987; Wilson, 1982), and mate with an unfamiliar female without diminishing care for pups (Storey & Snow, 1987). Additionally, biparental care increases pup growth rates (Storey & Snow, 1987). More recently, it has been shown that sexually and parentally inexperienced adult meadow voles also exhibit appreciable paternal care (Parker & Lee, in press; Storey & Joyce, 1995), and housing under winter, short day (SD) lengths enhances this effect (Parker & Lee, in press).

Similar to prairie voles (Wang, Ferris, & De Vries, 1994), research in our laboratory has demonstrated a role for AVP in regulating meadow voles paternal state; central administration of AVP suppresses pup-directed aggression in previously aggressive males and promotes paternal behavior in previously pup-unresponsive males, and AVP antagonists block the onset of paternal behavior expression (Parker & Lee, 2001). However, administration of AVP does not induce paternal behavior in aggressive males, nor does it enhance paternal behavior expression in already paternal males. This finding suggests that other neural changes are involved in regulating paternal behavior expression, for example, changes in AVP (and/or OT) receptor number.

The goal of these experiments was to determine whether AVP and/or OT receptor binding density or location differed between sexually and parentally inexperienced (hereafter inexperienced) males and sexually and parentally experienced (hereafter experienced) males. After behavioral testing and central receptor autoradiography, inexperienced and experienced meadow voles were assessed for differences in AVP (Experiment 1) and OT (Experiment 2) receptor patterns in various neuroanatomical areas in the extended amygdala neural pathway.

General Method

Subjects

Subjects (Microtus pennsylvanicus), derived from wild-caught voles indigenous to northwestern Pennsylvania and southwestern New York, were born to breeding pairs in an established colony at the University of Michigan. Weanling meadow vole pups were removed from the dam and sire at 19 days of age and housed in same-sex sibling dyads in either long day (LD; 14 hr light/day) or short day (SD; 10 hr light/day) conditions. (LD and SD voles were evenly distributed across conditions, and independent t tests showed that LD and SD voles within each group showed no differences in regional receptor binding. Subsequently, all groups were collapsed across photoperiod to simplify additional analyses.) Subjects (total autoradiography n = 34; n = 24 for Experiment 1, n = 10 for Experiment 2) were housed in 26.67 × 21.59 × 13.97-cm polypropylene cages on pine shaving bedding with food (Purina Mouse Chow No. 5015, Ralston-Purina, St. Louis, MO) and water available ad libitum. Subject rooms were maintained at 21 ± 2°C with low ambient noise conditions. Subjects remained so housed until the beginning of the experimental procedure (at 11–13 weeks
of age). At this time, males were assigned to specific testing conditions. In Experiment 1, we examined whether the following groups showed similar or different regional AVP receptor patterns: (a) inexperienced, paternal males \((n = 6)\) compared with experienced, paternal males \((n = 6)\), (b) inexperienced, aggressive males \((n = 6)\) compared with inexperienced, pup-unresponsive males \((n = 6)\), and (c) all paternal males \((n = 12)\) compared with all nonpaternal males \((n = 12)\). In Experiment 2, OT receptor patterns were assessed in inexperienced, pup-unresponsive males \((n = 5)\) and experienced, paternal males \((n = 5)\).

**Paternal Behavior Testing**

As previously described (Parker & Lee, 2001, in press), the testing to sort males into groups was as follows. Inexperienced males (that received no social manipulation) were tested with an alien pup between 11 and 13 weeks of age. Experienced males were tested for paternal behavior with one of their own pups after 72 hr of postpartum pup exposure, after pairing with a female at 11 weeks of age, and cohabitation with their mate throughout pregnancy and delivery of the litter. Other than these differences, paternal behavior testing was identical for inexperienced and experienced males. Each male was placed in a novel polypropylene 48.26 × 26.67 × 20.32-cm cage with fresh bedding. Males were allowed to become familiar with the new environment for 5 min, and then a 2–5 day-old pup was introduced to the opposite end of the cage from the male. Each test was carried out during the lighted phase of the light cycle and was videotaped for 10 min with a Panasonic camera and wide-angle lens on a time-lapse VCR. Based on the experimenter’s rating, each male’s behavior was scored categorically as aggressive (rough handling or charging pup, resulting in pup vocalization or injury), unresponsive (brief investigatory sniffing or no contacting or interacting with pup), or paternal (grooming, huddling, and/or retrieving).

**Receptor Autoradiography**

After behavioral testing, subjects were anesthetized with halothane and decapitated. Brains were quickly removed, frozen on dry ice, and stored at \(-70^\circ C\) until sectioned. Brain slices of 20 µm were cut in a cryostat at 19 ± 1°C, slide mounted (Colorfrost/Plus slides, Fisher Scientific, Atlanta, GA), and stored at \(-70^\circ C\). Coronal sections were cut through four brain areas from rostral to caudal (see later discussion). Brain slices were thawed for 30 min at room temperature before commencement of the binding assay. AVP receptor autoradiography was performed using a highly selective linear AVP V1a receptor antagonist, \([125I]\)-phenylacetyl-D-Tyr(Me)-Phe-Gln-Asn-Arg-Pro-Arg-Tyr-NH₂ (New England Nuclear, Wellesley, MA; 2,200 Ci/mmol, 0.1 nmol). Slides were incubated in buffer (50 mmol Tris, 10 mmol magnesium chloride, 0.1% bovine serum albumin [BSA]) for 60 min, washed three times (8 min each) in buffer (50 mmol Tris, 100 mmol choline chloride, 0.1% BSA, 0.01% Triton X-100), and briefly dipped in double-distilled water. All buffer chemicals were obtained from Sigma Chemical (St. Louis, MO). Nonspecific binding was determined using 1-µM concentration of AVP, Cys-Tyr-Phe-Gln-Asn-Cys-Pro-Arg-Gly-NH₂ (Peninsula Laboratories, San Carlos, CA). The OT binding protocol was identical to the AVP binding protocol, except a highly selective \([125I]\)-ornithine vasotocin analog, d(CH₂)₅[Tyr(Me)]², Thr⁴, Orn¹⁰, \([125I]\) Tyr²-NH₂ (New England Nuclear; 2,200 Ci/mmol, 0.1 nM), was used to determine specific binding, and nonspecific binding was assessed using 1-µmol concentration of OT, Cys-Tyr-Ile-Gln-Asn-Cys-Pro-Leu-Gly-NH₂ (Peninsula Laboratories). Slides were dried under a stream of cool air, placed in film cassettes, and exposed to BioMax MR X-ray film (Amersham, Buckinghamshire, England) for 48 hr (AVP) or 24 hr (OT). In preliminary trials, X-ray films were developed after different lengths of exposure for both vasopressin and OT (e.g., 24 hr, 48 hr, and 72 hr) to determine a suitable exposure time that was in the linear response range of the film. Film optical densities were measured using Image J for the PC, a computerized imaging system from the National Institutes of Health.

**Data Analysis**

For each subject, nine sections per area per side of brain were analyzed (i.e., six specific binding sections and three nonspecific binding sections per area per side of the brain) by an experimenter who was unaware of subjects’ behavioral data. In a few cases, tissue sections were damaged during autoradiographic processing and were excluded from analysis by the mutual consent of two experimenters (each unaware of subjects’ experimental condition). Specific binding and nonspecific binding were averaged separately for each side of the brain, nonspecific binding was subtracted from specific binding for each side of the brain to yield total binding for left and right structural areas, and finally, left and right were averaged together to represent a single data point for each vole/area. Brain regions for image analysis were based on previous studies demonstrating an association between behavior and AVP or OT receptor binding conducted in various rodent species (Insel, 1986, 1990; Insel & Shapiro, 1992; Insel et al., 1994) and according to the areas that showed the most intense receptor binding in these experiments. For Experiment 1 (i.e., AVP receptor binding), the following brain regions that had considerable AVP binding were examined: AON, LS (anterior LS at the level of the vertical limb of the diagonal band; lateral, medial, and central measurements of the LS at the level of the anterior commissure), diagonal band, BNST, MeAmyg, and central amygdala (CeAmyg). For Experiment 2 (i.e., OT receptor binding), the AON, BNST, LS at the level of the vertical limb of the diagonal band, LaAmyg, and CeAmyg were examined. Data were analyzed separately for AVP and OT receptor autoradiography groups and are presented separately.

**AVP Statistical Analyses**

Using independent \(t\) tests, we assessed whether different types of paternal males (e.g., inexperienced, paternal vs. experienced, paternal) and different types of nonpaternal males (e.g., inexperienced, aggressive vs. inexperienced, pup-unresponsive) differed from each other. Because no significant differences in regional AVP receptor binding were found within either behavioral group, groups were collapsed within each behavioral category to simplify subsequent statistical analyses. Second, independent \(t\) tests were used to determine whether nonpaternal meadow voles and paternal meadow voles differed in AVP receptor binding for each neuroanatomical area.

**Results**

Paternal males showed more AVP receptor binding than nonpaternal males in the AON, \(t(20) = 2.192, p = .040\), and showed less AVP binding in the LS at the level of the diagonal band, \(t(21) = -2.890, p = .009\), and the lateral, \(t(15) = -2.583, p = .021\); central, \(t(15) = -2.501, p = .024\); and medial septum, \(t(15) = -2.697, p = .017\), at the level of the anterior commissure than did nonparental males (see Figures 1 and 2). No differences were found in the diagonal band (\(p = .771\), BNST (\(p = .852\), MeAmyg (\(p = .968\), or CeAmyg (\(p = .408\); see Figures 1 and 3).

**OT Statistical Analyses**

For OT receptor binding, independent \(t\) tests were used to determine whether inexperienced, pup-unresponsive males differed from experi-
enanced, paternal males in OT receptor distribution for each of the following neuroanatomical areas: AON, BNST, LS at the level of diagonal band, LatAmyg, and CeAmyg.

Results

Experienced, paternal males showed greater OT binding than inexperienced, pup-unresponsive males in the AON, \( t(8) = 2.389, p = .044 \); LS, \( t(8) = 7.550, p < .001 \); BNST, \( t(8) = 4.219, p = .003 \); and LatAmyg, \( t(8) = 2.665, p = .028 \) (see Figures 4 and 5). Although not statistically significant, OT receptor binding was elevated in the CeAmyg of experienced males (\( p = .095 \)), and it should be noted that two-tailed tests and low sample sizes may have masked a significant difference in OT binding for experienced males, relative to inexperienced males, in this area.

General Discussion

Data from Experiment 1 indicate that AVP receptor patterns in the extended amygdala are associated with paternal state in meadow voles. Specifically, paternal males demonstrate more receptor binding in the AON but less AVP receptor binding in various areas of the LS than nonpaternal males. In Experiment 2, sexually and parentally inexperienced and experienced males show regional differences in OT receptor distribution; paternal, experienced males have more OT receptor binding in the AON, LS, BNST, and LatAmyg and show a similar trend in the CeAmyg compared with nonpaternal, inexperienced males.

Whether or not activity in meadow vole AVP and OT neural pathways functions to generate the onset of paternal behavior remains unknown and awaits further investigation by other experimental techniques. Nonetheless, findings from experiments in
AVP AND OT RECEPTOR BINDING IN MALE MEADOW VOLES

Figure 2. Paternal meadow voles (filled bars) have higher arginine-vasopressin (AVP) binding in the anterior olfactory nucleus (AON) and lower AVP binding in the anterior lateral septum (ANTSEPTUM), lateral septum (LATSEPTUM), central septum (CENTSEPTUM), and medial septum (MEDSEPTUM) compared with nonpaternal males (open bars). Asterisks indicate a minimum significant difference (*p < .05) between paternal and nonpaternal males.

In the present studies, paternal behavior onset is marked by substantially lower AVP receptor binding in the lateral septum compared with nonpaternal males. This finding is similar to those observed in previous studies that have shown that characteristically paternal microtine species (i.e., prairie voles) show fewer AVP receptors in the LS compared with characteristically nonpaternal species (i.e., montane voles) in both sexually and parentally inexperienced and experienced states (Insel et al., 1994; Wang et al., 2000). In other nonpaternal rodents, it has been suggested that septal AVP may be involved in the acquisition and storage of information related to situations that invoke fear and anxiety (rats; Everts & Koolhaas, 1999), and higher levels of septal AVP (as indexed by AVP-ir) covary with increased aggressive behavior (mice; Compaan, Buijs, Pool, de Ruiter, & Koolhaas, 1993). Because the location of AVP receptor sites demarcates where endogenous peptides can exert their effects, perhaps the low septal AVP receptor binding that was observed for parental males reflects the diminished ability of AVP to induce aggressive and fearful behaviors in response to neonates, as was exhibited by aggressive and pup-unresponsive males with high septal AVP receptor binding. In this respect, it might be hypothesized that high numbers of AVP receptors in the septum exert inhibitory control over paternal behavior expression. Thus, down-regulation of AVP receptors in this site may exert a permissive effect on males and may allow them to respond to the specific social and environmental cues that induce paternal onset.

Paternal males also showed higher AVP receptor binding in the AON. Exactly why AVP receptor binding differs in this neuroanatomical area is unclear. However, because injections of AVP into the AON enhance social recognition in rats (Dluzen, Muraoka, Engelmann, & Landgraf, 1998), and bilateral bulbectomy reduces paternal behavior in prairie voles (Kirkpatrick, Williams, et al., 1994), it is possible that AVP receptors in the AON may play a significant role in recognizing pup odors during paternal states.

In addition to the observed differences in regional AVP receptor binding, sexually and parentally experienced males also show higher OT receptor binding in the AON, LatAmyg, CeAmyg, BNST, and LS compared with inexperienced males. These structures are part of the extended amygdala neural pathway that has been previously implicated in regulating maternal behavior onset in mammalian rodents (Fleming & Walsh, 1994; Numan & Sheehan, 1997). In several species, greater OT receptor binding in the BNST (female rats; Insel, 1986) and the LatAmyg (female montane voles; Insel & Shapiro, 1992) is associated with the onset of maternal behavior. Unfortunately, one limitation of our study is that we cannot distinguish between whether OT receptor binding differences in inexperienced and experienced voles are truly due to paternal state or whether they are produced by differences in the mating and cohabiting experience of sires compared with virgin males. Nonetheless, the possibility exists, and should be considered, that the observed differences in OT receptor binding in specific neuroanatomical sites may act to facilitate the onset of parental behavior in males.

Previous pharmacological experiments in inexperienced meadow voles have demonstrated a dose- and behavioral state-...
dependent effect of centrally administered AVP on aggressive and paternal behaviors (Parker & Lee, 2001). For baseline aggressive males, low (1 ng AVP), but not high (3 ng AVP), doses of AVP suppressed pup-directed aggression, but these same doses of AVP failed to induce paternal behavior. In pup-unresponsive males, 3-ng, but not 1-ng, doses of AVP promoted paternal behavior, and AVP antagonists administered to this group before 24 hr of unmated cohabitation with a female completely inhibited the reliable onset of paternal behavior. However, AVP injections did not enhance paternal behavior in already paternal voles. Previously, it was hypothesized that these results suggested that the receptor systems of these different baseline behavioral groups were not identical, and this possibility might account for the observed differential responses to AVP injection. Experiment 1 partially supports this assertion; inexperienced, paternal males do differ from inexperienced, aggressive and pup-unresponsive males in olfactory and septal AVP receptor binding, but the latter two groups do not differ from each other. Thus, it is not clear why AVP induces paternal behavior in pup-unresponsive, but not pup-aggressive, males. One possibility is that centrally administered AVP is acting not on AVP receptors but on OT receptors. This is supported by research that has shown that at low physiological doses exogenously administered AVP and OT primarily bind to their own receptors, but at high pharmacological doses AVP and OT exert behavioral effects by binding not only to their own but also to each other’s receptor sites (Barberis & Tribollet, 1996). Thus, the possibility that some of these behavioral effects were mediated through regional OT receptors cannot be ruled out. Unfortunately, no data are available on whether centrally administered OT induces changes in paternal state in meadow voles or any other rodent species. Nor is it known whether inexperienced, aggressive, pup-unresponsive, or paternal males differ in regional OT receptor binding. However, because differences in both AVP and OT receptor binding exist between sexually and parentally inexperienced and experienced males, determining whether meadow voles respond to central administration of OT and whether they demonstrate differences in regional OT receptor binding in all of the aforementioned inexperienced behavioral states merits further investigation.

In conclusion, these studies have demonstrated that specific central AVP and OT receptor patterns co-occur with paternal behavior in meadow voles. In particular, the presence of paternal behavior is associated with lower AVP receptor binding in the LS, an area of the brain associated with aggression (Compaan et al., 1993) and higher OT receptor binding in the extended amygdala in areas associated with maternal care (Fleming & Walsh, 1994; Numan & Sheehan, 1997). Although these studies mark a first step in identifying putative neural systems that regulate facultative paternal behavior, whether or not activity in meadow vole AVP and OT neural pathways functions to generate the onset of paternal behavior, and if so under which specific socioecological circumstances, remains unknown.

Figure 4. Photomicrographs of oxytocin receptor optical densities in extended amygdala structures of paternal and nonpaternal male meadow voles. A and B: anterior olfactory nucleus (AON); C and D: lateral septum (S) and bed nucleus of the stria terminalis (BNST) at the level of the anterior commissure; E and F: lateral and central amygdala (A).

Figure 5. Paternal, sexually, and parentally experienced meadow voles (filled bars) have greater oxytocin (OT) receptor binding in the anterior olfactory nucleus (AON), lateral septum (SEPTUM), bed nucleus of the stria terminalis (BNST), lateral amygdala (LATAMYGDALA), and central amygdala (CENAMYGDALA) compared with nonpaternal sexually and parentally inexperienced males (open bars). Asterisks indicate a minimum significant difference ($p < .05$) between paternal and nonpaternal males; dagger indicates a nonsignificant difference ($p < .10$) between paternal and nonpaternal males.
References


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