# Distribution of Oxytocin- and Vasopressin-Immunoreactive Neurons in the Brain of the Eusocial Mole Rat (*Fukomys anselli*)

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ABSTRACT

*Fukomys anselli*, also known as Ansell's mole rat, is a subterranean, highly social (so-called eusocial) rodent that lives in Africa. These mole rats typically form multigenerational families consisting of a single monogamous breeding pair and their nonreproductive offspring. Research on other mammals suggests that oxytocin (OT) and vasopressin (VP) as well as the distribution of OT- and VP-receptors may influence social behavior and pair bonding. Recent studies on eusocial naked mole rats have shown a possible relation between sociality and OT-immunoreactive (OT-ir) processes. In this study, we examined expression patterns of OT and VP in the brains of *F. anselli* and the common Sprague-Dawley (SD) laboratory rat. As in other species, the majority of OT-ir and VP-ir neurons was found in the paraventricular (Pa) and supraoptic (SO) nuclei, and scattered labeling throughout the preoptic and anterior hypothalamic areas. We found no difference in either quality or quantity of OT- and VP-ir neurons between individuals of different social and reproductive ranks. Equally unexpected was the finding of specific OT-immunoreactivity in neurons of the mammillary complex of *F. anselli* that was not found in SD rats. Further studies are needed to determine whether these mammillary OT-ir neurons are causally related to monogamy in *F. anselli* and whether these correlates of monogamy are found in other species. Anat Rec, 295:474–480, 2012. 

**Key words: monogamy; oxytocin; social recognition; caudal magnocellular nucleus; mole rat**

Abbreviations used: * = blood vessels; 3V = third ventricle; ACC = accessory magnocellular neurons in the anterior hypothalamus; AHA = anterior hypothalamic area; Arc = arcuate nucleus; BNST = bed nucleus of stria terminalis; CMC = caudal magnocellular nucleus; cp = cerebral peduncle; f = fornix; GT = ganglion trigeminale; LH = lateral hypothalamus; LM = lateral mammillary nucleus; LPO = lateral preoptica area; ME = median eminence; ML = medial mammillary nucleus, lateral part; MM = medial mammillary nucleus, medial part; MMn = medial mammillary nucleus, median part; MPA = medial preoptic area; MRe = mammillary recess, 3V; OT = oxytocin; opt = optic tract; Pa = paraventricular nucleus of the hypothalamus; PCMC = postmammillary caudal magnocellular nucleus; PFA = paraformaldehyde; Pit = hypophysis; pm = mammillary peduncle; SCh = suprachiasmatic nucleus; SO = supraoptic nucleus; SOr = supraoptic nucleus, rostral part; SOrch = supraoptic nucleus, retrochiasmatic part; SuM = supramammillary nucleus; sumx = supramammillary decussation; SN = substantia nigra; TMC = tuberal magnocellular nucleus; VMH = ventromedial hypothalamic nucleus; VP = vasopressin.

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## INTRODUCTION

*Fukomys anselli* are subterranean rodents (family Bathyergidae) that are native to Zambia. These rodents were formerly attributed to the genus *Cryptomys* (Kock et al., 2006). *F. anselli* has a unique social family organization. They live in large multigenerational families derived from one breeding pair (Burda, 1989). Offspring remain in the family as helpers to their parents and younger siblings, and do not breed. Unlike the short-term family helpers described in monogamous mammals or birds, these worker-like mole rats show long-lasting philopatry that overlaps several generations. This social structure is designated as eusocial and a rare phenomenon among mammals (Burda, 1995; Burda et al., 2000).

Under laboratory conditions, a new family group can be initiated by simply pairing two unfamiliar animals. The death or removal of a breeder results in reproductive quiescence in the family, which demonstrates that the mechanism constraining breeding in the family group also promotes incest avoidance (Burda, 1995). Female workers do not breed because they do not copulate. Previous work has shown that all nonbreeding family members are not sexually attractive to one another. Furthermore, this incest avoidance behavior is based on individual recognition and social memory, not semiochemical or behavioral suppression (Burda, 1995).

The exceptional social organization of these animals provides another opportunity for investigating social behaviors. Former researches on prairie voles suggest that telencephalic oxytocin (OT) receptors may contribute to the formation of monogamy (Young and Wang, 2004) and influence maternal care (Olazabal and Young, 2006a,b). Recently, marked differences in the distribution of telencephalic OT receptor binding sites between eusocial naked mole rats and solitary Cape mole rats have been revealed (Kalamatianos et al., 2010). The lack of OT and its receptors in the nucleus accumbens suggests a marginal oxytocinergic signaling in Cape mole rats. The authors speculate that this may correlate with their failing in long-lasting pair bonding behavior (Kalamatianos et al., 2010).

In many species vasopressin (VP) and vasotocin (VT) seem to be associated with pair bonding, parental, and dominance-subordinate behavior (Goodson and Baas, 2001). Many studies revealed consistent sex differences in vertebrate brains. The lateral septum in males has a higher VP-/VT-immunoreactivity of fibers than in females (de Vries and Panzica, 2006). Unexpected was the finding that in naked mole rats no reliable sex differences in VP innervation were found so far (Rosen et al., 2007). Because OT and VP are associated with social behaviors such as social recognition, pair bonding, affiliation, and maternal care (Winslow et al., 1993; Ferguson et al., 2000; Goodson and Bass, 2001; Bielsky et al., 2005; Lim and Young, 2006; Neumann, 2008), its distribution in the brains of male and female *F. anselli* was of interest. In this study, we document the topography of OT- and VP-ir neurons in the brains of eusocial *F. anselli* and investigate whether expression patterns deviate from already published data in other rodents and whether they are influenced by gender, breeding status, or age.

## MATERIALS AND METHODS

### Animals and Perfusion

All experimental procedures were conducted in accordance with National Institute's of Health guidelines and were approved by the relevant Institutional Animal Care and Use Committees. Two complete families of *F. anselli*, each consisting of seven members, were used ($n = 14$). For details on *F. anselli* husbandry, see Burda (1989). Four Sprague-Dawley (SD) rats, housed under standard laboratory conditions, were examined for comparison. SD rats were used specifically for topographical orientation in *F. anselli*, and not for quantitative comparison, due to considerable differences in body and brain size between the two species.

Animals were subjected to final narcosis, then transcardially perfused with heparinized saline for 10 min, followed by fixation with 4% paraformaldehyde (PFA) in 0.1 M phosphate buffer (PB) for another 10 min. Heads were removed and brains carefully dissected out of the skull. For cryoprotection, brains were then postfixed 4–6 hr in 4% PFA and soaked in sucrose-buffer solution (30% sucrose in PB, pH 7.4) over 1–2 days. Just prior to sectioning, brains were embedded in sucrose-gelatin (30% sucrose, 10% 300 bloom gelatin, in aqua bidest). These gelatin blocks were then fixed in sucrose-PFA solution (30% sucrose, 4% PFA in PB), trimmed, and marked for left/right discrimination in the coronal plane, via a longitudinal incision on the left side of the block. Coronal sections were made on a rotary cryotome (HM 340, MICROM, Heidelberg, Germany) at 60 μm.

### Immunohistochemistry

Free-floating sections were consecutively distributed into acrylic boxes with 18 compartments containing 0.01% sodium azide ($NaN_3$) PB and stored at 4°C. The sections of three compartments were stained with cresyl violet (BDH, Poole, England) and used for general topographical orientation.

Sections were then incubated overnight at room temperature with rabbit polyclonal anti-OT (DiaSorin [Immunostar]), Stillwater, MN, lot # 805355A, dilution 1:12,000) and rabbit polyclonal anti-AVP (DiaSorin [Immunostar]), Stillwater, MN, lot # 9226606, dilution 1: 8,000) solution in PB containing 0.1% bovine serum albumin (BSA, Sigma) and 0.3% Triton-X-100 (Sigma).

After rinsing in PB, sections were incubated for 90 min in the secondary antibody (biotinylated goat anti-rabbit; Vector Laboratories, Burlingame, CA; lot # K0505, dilution 1:400). Following rinsing in PB, sections were incubated for 120 min in a solution of Avidin-Biotin-Peroxidase Complex (ABC-Kit, Vectastain, Vector Laboratories, Burlingame, CA), diluted to a working solution of 1:800 in 0.3% Triton-X-100/BSA/PB. After rinsing in PB, sections were incubated in a 0.05% solution of 3,3′-diaminobenzidine (DAB, Sigma) in PB. To enhance the intensity of the reaction product, 1 mL of 1% nickel ammonium sulfate ($(NH_4)_2Ni\ (SO_4)_2$) and 1.25 mL of 1% cobalt chloride ($CoCl_2$) solution were added to 97.75 mL of DAB solution. After incubation, the DAB-reaction was initiated with 33 μL of 3% hydrogen peroxide solution. After 90 sec, the reaction was stopped in PB, and sections were rinsed five times in PB. The

sections were then mounted on chrom alum-coated slides, dried overnight at 37°C, and coverslipped with Eukitt®.

Immunohistochemical controls included 1) incubation of sections following preabsorption of the antibody with their related antigen or 2) omission of either the primary or secondary antibody. All of these control procedures resulted in a lack of immunoreactivity in the brain tissue.

### Topographical Analysis

We assessed the distribution, morphology, and number of OT- and VP-ir perikarya in the forebrain in each animal. The area examined extended from the rostral preoptic area to the posterior hypothalamus including the mammillary body. We documented the *F. anselli* brains and compared them among family members as well as with SD rats. Total numbers of OT- and VP-ir cells were counted for neuronal nuclei and scattered neurons in each telencephalic hemisphere.

Only OT- and VP-ir cells with a distinct nucleus were counted. Cell counts were analyzed by a two sample *t*-test (female vs. male; reproductive vs. nonreproductive) or two-way analysis of variance (ANOVA) (adult vs. subadult vs. juvenile) as between-subject factors, and brain region as the within-subject factor. We applied the neuroanatomical nomenclature used for rat by Paxinos and Watson (1998). Photomicrographs were taken with an Olympus BH2 and PM-10AD equipment, then imported into Adobe Photoshop 6.0 for digital labeling and the construction of images. No other changes were made in the image files.

## RESULTS

### OT-Immunoreactivity

In *F. anselli*, magnocellular OT-ir neurons were found in the hypothalamic paraventricular nucleus and the supraoptic nucleus, including the ventral and retrochiasmatic portions (Fig. 1). In addition, *F. anselli* exhibits numerous widespread accessory magnocellular OT-ir neurons throughout the hypothalamus. In detail, clusters of OT-ir cells were found in the bed nucleus of the stria terminalis (BNST), the medial preoptic area (MPA), anterior hypothalamic area (AHA), and the lateral hypothalamic (LH) area. No significant differences were found in the numbers of OT-ir neurons in all the regions investigated within the various categories of animals (concerning reproductive state, age, and gender) (Table 1).

Specifically, a population of OT-ir neurons was found in the periphery of the mammillary body of *F. anselli*. In all 14 *F. anselli* brains under study, the perikarya of these cells were present in the nucleus supramammillaris (SuM) and the caudal magnocellular nucleus (CMC) (Fig. 2). In SD rats, such magnocellular neurons were detected in the same area of the mammillary complex but showed no OT- or VP-ir (Fig. 3). The labeling of OT-immunoreactive neurons in the mammillary nuclei was specific but less intense than in supraoptic and paraventricular nuclei of *F. anselli*. Sporadically, axons could be observed but not the direction into which they run.

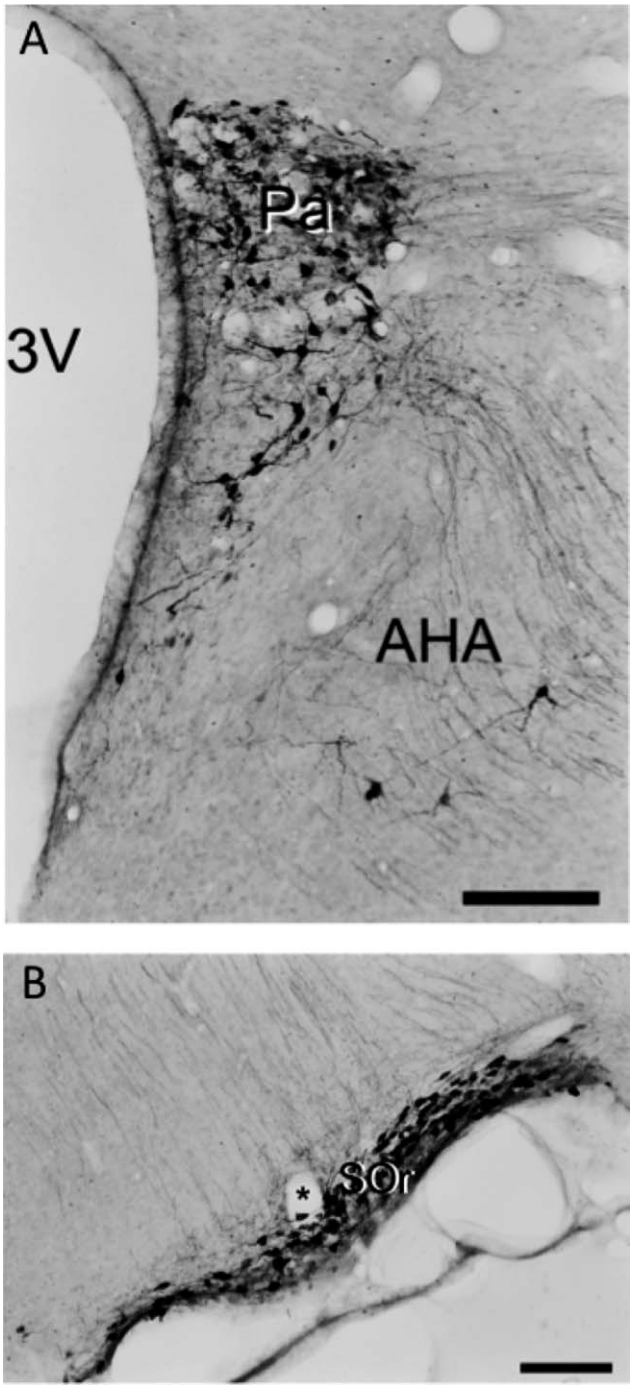


Fig. 1. Photomicrograph of magnocellular OT-ir neurons in the paraventricular hypothalamic nucleus (**A**) and supraoptic nucleus (**B**) of *F. anselli*. Medial is to the left. Scale bar = 200 μm (magnification: 100×).

### VP-Immunoreactivity

In *F. anselli*, dense clusters of magnocellular VP-ir cells were found in the ventral and the retrochiasmatic portions of the supraoptic nucleus (SO) and in the hypothalamic paraventricular nucleus (Pa). *Fukomys* brains also show numerous accessory magnocellular neurons in small

**TABLE 1. OT-immunoreactive cells in the brain of *Fukomys anselli***

| Status | Age | Sex | ID | Pa | $SO_r$ | $SO_{rch}$ | ACC | CMC | SuM |
|---|---|---|---|---|---|---|---|---|---|
| R | A | ♀ | $F_7$ | 200 | 234 | 16 | 22 | 263 | 114 |
| R | A | ♀ | $F_{11}$ | 195 | 138 | 46 | 22 | 147 | 22 |
| R | A | ♂ | $F_8$ | 209 | 203 | 17 | 23 | 131 | n/a |
| R | A | ♂ | $F_{10}$ | 173 | 127 | 26 | 24 | 108 | 26 |
| NR | A | ♀ | $F_{14}$ | 194 | 151 | 61 | 23 | 113 | 25 |
| NR | A | ♂ | $F_6$ | 202 | 199 | 29 | 27 | 310 | 68 |
| NR | A | ♂ | $F_2$ | 188 | 135 | 18 | 24 | 37 | 35 |
| NR | SA | ♀ | $F_4$ | 203 | 158 | 12 | 22 | 372 | 42 |
| NR | SA | ♀ | $F_{12}$ | 193 | 167 | 42 | 25 | 197 | 58 |
| NR | SA | ♀ | $F_1$ | 171 | 166 | 47 | 43 | 210 | 49 |
| NR | SA | ♂ | $F_3$ | 199 | 161 | 16 | 28 | 174 | 43 |
| NR | J | ♀ | $F_{13}$ | 179 | 126 | 24 | 28 | 181 | 34 |
| NR | J | ♀ | $F_9$ | 164 | 126 | 29 | 33 | 108 | 21 |
| NR | J | ♂ | $F_5$ | 177 | 140 | 30 | 18 | 82 | 33 |

Pa = hypothalamic paraventricular nucleus; $SO_r$ = supraoptic nucleus, rostral part; $SO_{rch}$ = supraoptic nucleus, retrochiasmatic part; ACC = accessory magnocellular neurons; A = adult; J = juvenile; NR = nonreproductive; R = reproductive; SA = subadult; ♀ = female; ♂ = male; $C_{1–14}$ = *Fukomys* specimens 1–14 ($F_{1–14}$); n/a: not applicable.

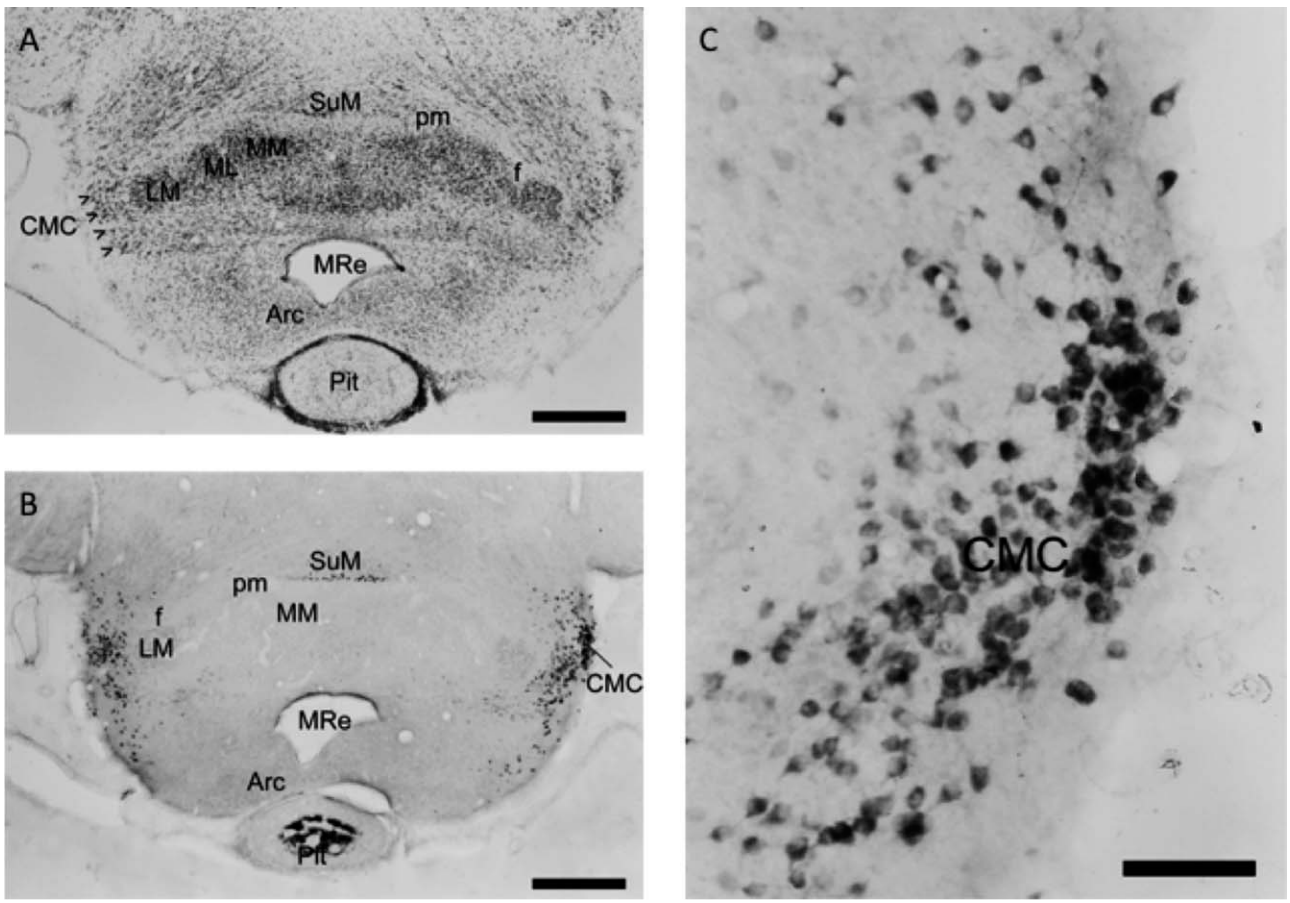


Fig. 2. Photomicrographs of the mammillary region in *F. anselli*. **A**: Cresyl violet stain. **B**: OT-ir cells in the supramammillary nucleus (SuM) and the CMC of *F. anselli*. **C**: OT-ir cells of (B) at higher magnification. Scale bars in (A) and (B) = 500 μm (magnification: 40×), (C) = 100 μm (magnification: 200×).

clusters throughout the MPA, BNST, AHA, and LH area. The majority of fibers originating from perikarya of the Pa and the SO are thick and project to the median eminence (ME) (Fig. 4). The suprachiasmatic nucleus contains a large number of parvocellular VP-ir cells (Fig. 4).

The distribution of the magnocellular VP-ir cells in *F. anselli* brains did not differ among family individuals. Similar to OT-immunoreactivity (OT-IR), no significant differences were found in the numbers of VP-ir neurons in all the regions investigated within the various

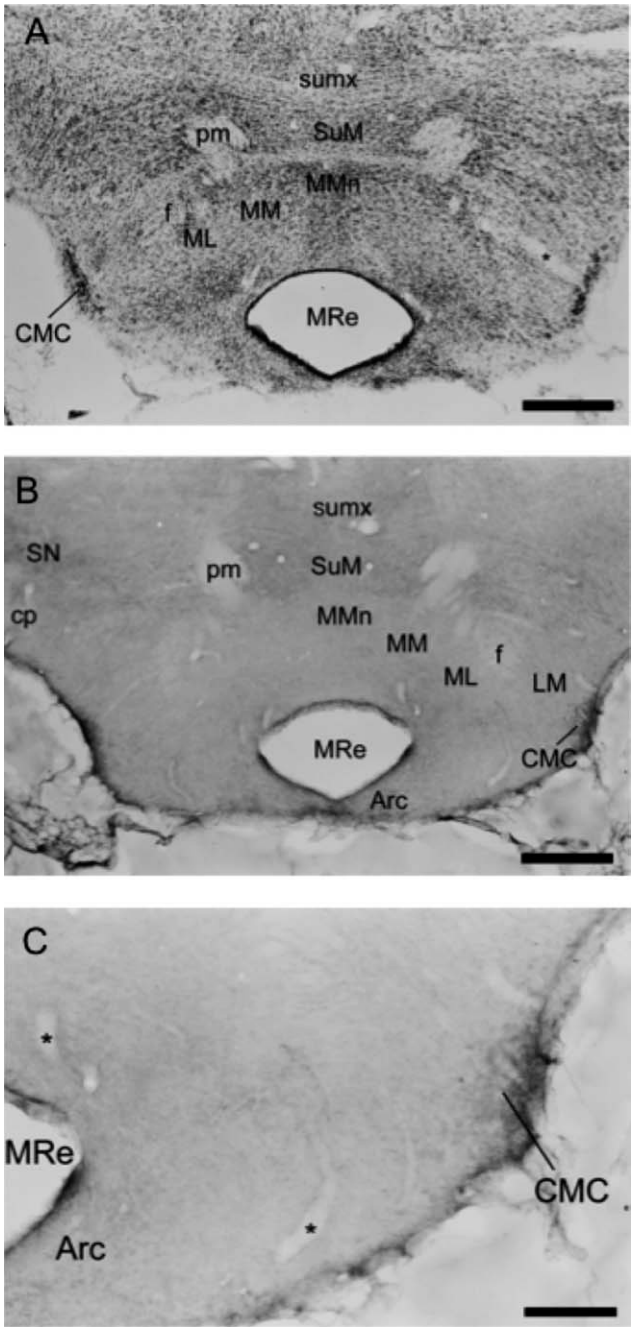


Fig. 3. Photomicrographs of the mammillary region in SD rats. **A**: Cresyl violet stain. **B**: This section was immunostained for OT but showed no immunoreactivity. **C**: Higher magnification of the CMC after OT immunostaining. Scale bars in (A) and (B) = 500 μm (magnification: 40×), (C) = 200 μm (magnification: 100×).

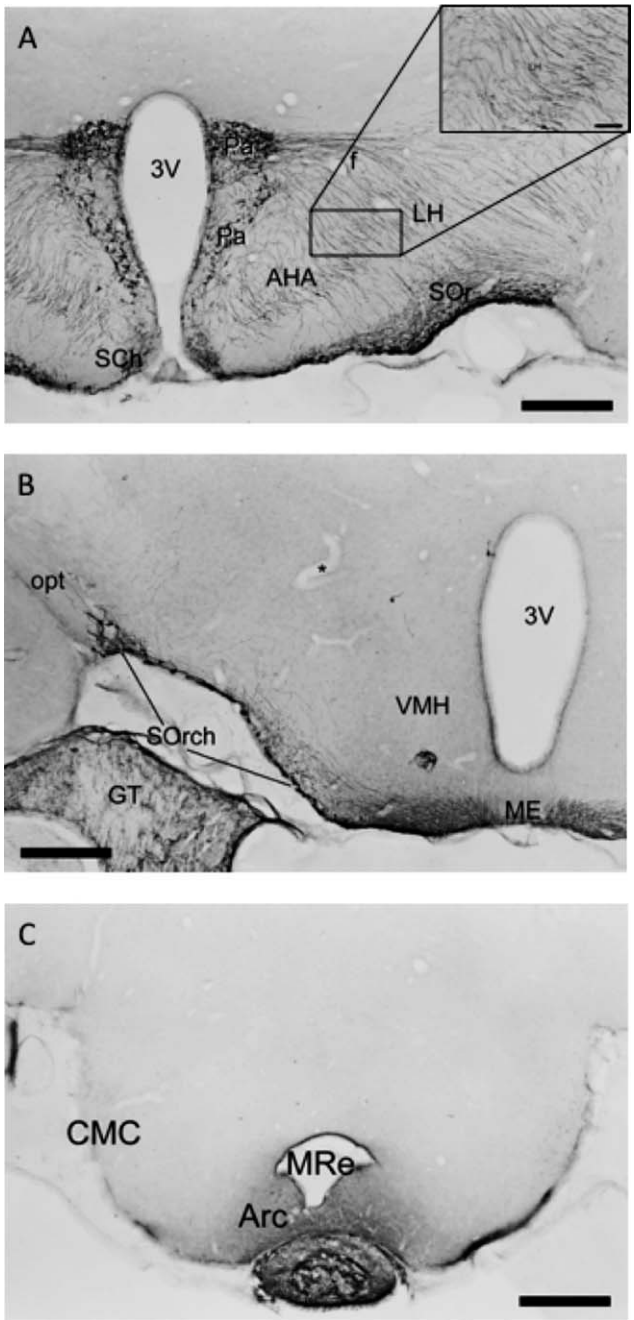


Fig. 4. Photomicrographs of (**A**) magnocellular VP-ir neurons in the paraventricular hypothalamic nucleus (Pa) of *F. anselli*. VP-ir fibers are shown in the boxed region at higher magnification. (**B**) VP-ir fibers in the median eminence. (**C**) This section was immunostained with anti-VP but showed no immunoreactivity in the CMC of *F. anselli*. Scale bars in (A–C) = 500 μm (magnification: 40×), inset = 100 μm (magnification: 200×).

categories of animals (concerning reproductive state, age, and gender) (Table 2). In addition, VP-IR was not found in the mammillary body (Fig. 4C).

## DISCUSSION

Previous research on diverse mammals indicates that oxytocinergic systems play an important role in the formation of social recognition, pair bonding, parental care, and nonsexual bonds (Insel and Shapiro, 1992; Kalamatianos et al., 2010). For social bonding to occur, individuals must have a capacity for social recognition, which includes the ability to distinguish family members from strangers (Ferguson et al., 2001). Indeed, this

**TABLE 2. VP-immunoreactive cells in the brain of *Fukomys anselli***

| Status | Age | Sex | ID | Pa | $SO_r$ | $SO_{rch}$ | ACC |
|---|---|---|---|---|---|---|---|
| R | A | ♀ | $F_7$ | 163 | 240 | 66 | 63 |
| R | A | ♀ | $F_{11}$ | 165 | 188 | 112 | 43 |
| R | A | ♂ | $F_8$ | 180 | 201 | 85 | 41 |
| R | A | ♂ | $F_{10}$ | 172 | 221 | 87 | 64 |
| NR | A | ♀ | $F_{14}$ | 198 | 236 | 99 | 60 |
| NR | A | ♂ | $F_6$ | 169 | 199 | 98 | 63 |
| NR | A | ♂ | $F_2$ | 204 | 234 | 85 | 39 |
| NR | SA | ♀ | $F_4$ | 177 | 216 | 63 | 43 |
| NR | SA | ♀ | $F_{12}$ | 171 | 210 | 94 | 59 |
| NR | SA | ♀ | $F_1$ | 171 | 184 | 80 | 78 |
| NR | SA | ♂ | $F_3$ | 184 | 171 | 61 | 68 |
| NR | J | ♀ | $F_{13}$ | 160 | 163 | 83 | 60 |
| NR | J | ♀ | $F_9$ | 153 | 176 | 74 | 58 |
| NR | J | ♂ | $F_5$ | 176 | 218 | 62 | 75 |

Pa = hypothalamic paraventricular nucleus; $SO_r$ = supraoptic nucleus, rostral part; $SO_{rch}$ = supraoptic nucleus, retrochiasmatic part; ACC = accessory magnocellular neurons; A = adult; J = juvenile; NR = nonreproductive; R = reproductive; SA = subadult; ♀ = female; ♂ = male; $C_{1–14}$, *Fukomys* specimens 1–14 ($F_{1–14}$).

ability has been also documented in *F. anselli* (Burda, 1995; Heth et al., 2004). Species-specific differences in the oxytocin receptor (OTR) distribution are associated with disparities in the level of social organization (Insel et al., 1991; Insel and Shapiro, 1992). Recently, in African mole rats, two species showing extreme differences in social organization and reproductive behavior have been investigated for telencephalic oxytocinergic binding sites. The study revealed that eusocial naked mole rats exhibit a considerably greater level of OTR binding than solitary Cape mole rats in many telencephalic areas, most notably in the nucleus accumbens (Kalamatianos et al., 2010). This study has identified and compared the distribution of OT-ir and VP-ir neurons in the brain of *F. anselli*, a less investigated but also eusocial mole rat.

The hypothalamo–hypophysial OT/VP system observed in *F. anselli* is similar to that seen in other rodents (Rhodes et al., 1981; Sofroniew, 1983; Schimchowitsch et al., 1989; Wang et al., 1996; Rosen et al., 2007, 2008) and encompasses immunoreactive somata in the hypothalamic paraventricular nucleus, supraoptic nucleus, and scattered accessory magnocellular neurons. However, OT-ir cell bodies in the supramammillary nucleus and CMC within the mammillary complex of *F. anselli* are an exception to this similarity. The finding of OT-ir cell bodies in the mammillary complex has not been seen in any other mammal so far, whereas OT binding sites in this region have been reported by Kremarik et al. (1995).

The CMC shows a small but prominent cluster of magnocellular cells at the lateral margin of the mammillary body. Close to the CMC and within the mammillary region, two additional magnocellular groups are found, the tuberal (TMC) and the postmammillary caudal magnocellular (PCMC) nuclei (Bleier and Byne, 1985). To date, these three magnocellular nuclei in the posterior hypothalamus have not been studied in detail. In rat, many of their neurons were found to express GABA (Vincent and Hökfelt, 1983) but OT-ir has not been detected in these nuclei before.

Further studies in rat have shown that GABAergic neurons of the CMC, TMC and PCMC project to the neocortex, striatum, and amygdala (Vincent and Hökfelt, 1983). Given that the neurons of the new OT-ir cell population found in the CMC more or less correspond with the GABAergic neurons found in this area, these OT-ir cells may use similar projections as the latter and thus influence neuronal mechanisms of social bonding on a telencephalic level. In our study, however, only perikarya have been investigated and OT-ir axons in the mammillary complex have been observed scarcely.

The studies published to date assume that receptor distribution is more relevant for social control than the immunoreactive-perikarya are. In this respect, it would be important to document the expression of OT-receptors, particularly in the potential target regions of the immunolabeled mammillary nuclei.

Although the sample size for the single categories of animals investigated was limited, we did not find any significant effect of gender, breeding status, or age on the number of OT-ir and VP-ir neurons in the brains of *F. anselli*.

Whether the peculiarities in OT-ir distribution reported here for *F. anselli* relate to monogamy and eusociality remains unclear. As Bathyergid mole rats comprise solitary as well as highly social species, further neurobiological comparison of *Fukomys anselli* to other Bathyergids with different social structures is needed. Special attention should be given to the connectivity of the perimammillary nuclei (CMC, TMC, and PCMC) with the neocortex, striatum, and amygdala to further validate hypotheses about the neurological basis of eusociality in mole rats.

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