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Research Article

Exposure to early life social complexity shapes vasopressin and galanin neural expression in the communal spiny mouse

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ABSTRACT

Early life social experiences shape the development of neural and behavioral phenotypes that persist into adulthood. Although prior research in rodents has demonstrated that early life isolation induces a variety of behavioral deficits, less work has assessed how *increased* social complexity during early life influences the neuroendocrine mechanisms of social behavior. The spiny mouse (*Acomys dimidiatus*) is ideal for examining the impact of rearing on offspring neurodevelopment. Spiny mice exhibit communal rearing in the wild, and thus young are exposed to non-kin during early life. Because spiny mice are precocial, they are able to engage in more dynamic social interactions early in life compared to altricial species, potentially enhancing the influences of early life social experiences on the development of the brain. Here we manipulated early life social complexity by rearing spiny mouse pups from birth to weaning with or without non-kin exposure. Once subjects reached adulthood, we collected brains and immunohistochemically labeled neural tissue to assess variation in expression of neurochemicals known to mediate multiple dimensions of social behavior: vasopressin, oxytocin, galanin, and dopamine. Although we observed no influence of rearing condition on oxytocin or dopamine cell numbers, we found that adult vasopressin cell numbers in the anterior hypothalamus were significantly lower and galanin fiber densities in the lateral hypothalamus were significantly higher in animals raised with non-kin. Given vasopressin's role in regulating aggression and galanin's role in modulating anxiety-like behavior, early life non-kin exposure may shape spiny mouse neurodevelopment in a way that facilitates communal living in adulthood.

Introduction

A notable sensitive period in social development is early in life when offspring are under the care of parents. Social isolation during early development often causes lifelong impacts to an individual (Lukkes et al., 2009, Shoji & Mizoguchi 2011). For example, in rats maternal separation during early life results in a variety of behavioral deficits in adulthood (Banqueri et al., 2017). Underlying neuroendocrine mechanisms are equally shaped by early social experience (Dimonte et al., 2023). For example, social isolation influences anxiety-like behavior in adult rats which is mirrored by changes to the hypothalamic–pituitary–adrenal axis and serotonergic system (Lukkes et al., 2009, Soga et al., 2015). Similarly, prairie voles raised either biparentally or with only a single mother show differences in both parental care and nonapeptide receptor distributions (Ahern & Young 2009, Hiura & Ophir, 2018).

Often researchers study the neurodevelopmental impacts of early life social environments using deficit-based models. However, less work has explored the role of *increased* social complexity or social enrichment during early life. Increased social complexity during early life in the form of communal rearing influences neural plasticity, social competency, anxiety-like behavior, and nonpeptide receptor densities (Branchi, 2009, Curley et al., 2009). Thus, here we ask: how does increasing social complexity during early life influence neurodevelopment?

To determine if early life social complexity shapes the neurodevelopment of neural systems that modulate social behavior, here we used the communally breeding spiny mouse *Acomys dimidiatus* (Brunjes

Abbreviations: ac, anterior commissure; AH, anterior hypothalamus; BNST, ned nucleus of the stria terminalis; f, fornix; fi, fimbria; Gal, galanin; int, internal capsule; LH, lateral hypothalamus; LV, lateral ventricle; MNPO, median preoptic nucleus; OT, oxytocin; PVN, paraventricular nucleus of the hypothalamus; SN, substantia nigra; TH, tyrosine hydroxylase; VP, vasopressin; VTA, ventral tegmental area; 3V, third ventricle.

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1990). Acomys are a subfamily within Murinae (Deomyinae), thus spiny "mice" are more closely related to Gerbillinae (gerbils) than to mice (Alhajeri et al., 2015; Fabre et al., 2012; Steppan and Schenk, 2017). Spiny mice live in large mixed-relation groups (Haughton et al., 2016) and show little aggression toward conspecifics (Fricker et al., 2022, Fricker & Kelly, 2024, Gonzalez Abreu et al., 2022). Additionally, this species exhibits a precocial developmental mode, which is rare in rodent species (Brunjes 1990, Dickinson et al., 2005). Precocial individuals are born more developed at birth than altricial species, which suggests they sense and process more environmental information in the early days of life than their altricial counterparts. Although a detailed, systematic characterization of the behavioral ecology of spiny mice (i.e., such as that for prairie voles) is lacking, field studies show that communal groups are comprised of multiple breeding adults and range in size from 12 to 46 individuals in desert environments and 60+ individuals in urban environments; further, spiny mouse groups typically have overlapping territories with one another (Shargal et al., 2000; Shkolnik 1966; Shkolnik & Borut, 1969). Thus, there is natural variation in social complexity for developing spiny mice in the wild, and there is a strong likelihood that young spiny mice will be exposed to and interact with both kin and non-kin conspecifics.

In the present study we raised spiny mouse pups either in the presence or absence of a non-kin breeding family. Prior research in spiny mice determined that while this rearing paradigm did not influence behavior in adulthood (quantified in two social contexts, an open field test, and a novel object test), rearing treatment did predict neural processing in adulthood: spiny mice raised in the presence of non-kin showed weaker lateral septal neural responses to a single novel conspecific, but stronger hypothalamic neural responses to a mixed-sex group (Wallace et al., 2025). Thus, here we additionally assessed if early life rearing in the presence of non-kin influenced adult expression profiles across a suite of cell-type specific neuronal populations throughout the brain that mediate aspects of social behavior: vasopressin (VP), oxytocin (OT), galanin (Gal), and tyrosine hydroxylase (TH).

To examine the influence of variation in the early social environment on VP and OT expression profiles in spiny mice, we quantified adult OT-ir cell numbers in the anterior hypothalamus (AH), bed nucleus of the stria terminalis (BNST), paraventricular nucleus of the hypothalamus (PVN), and median preoptic nucleus (MNPO) and quantified VP-ir cell numbers in the AH, BNST, and PVN. Although this study was largely exploratory, we predicted that, because OT and VP expression are influenced by the early life social environment in rats, mice, and prairie voles (Ceschim et al., 2021, Todeschin et al., 2009, Winkelmann-Duarte et al., 2007, Perkeybile & Bales, 2015, Bester-Meredith and Marler, 2001), we would observe differences in nonapeptide cell numbers in relation to early life social complexity in spiny mice. Specifically, we hypothesized that animals raised with non-kin exposure would exhibit higher cell numbers of BNST VP neurons, which may be important for facilitating grouping behavior Fricker & Kelly, 2024). Additionally, if AH VP facilitates aggressive behavior in spiny mice as it does in other rodents (Gobrogge et al., 2017, Albers 2012), then animals reared with less social experience with non-kin peers may exhibit greater number of VP neurons in the AH. Lastly, because there are notable sex differences in nonapeptide expression profiles in spiny mice (Kelly & Seifert, 2021) and because early-life social experiences often produce sex-dependent effects (Viveros et al., 2009, Rincón-Cortés 2023), we examined whether the early life rearing environment differentially influence VP and OT cell numbers in males and females, with no specific hypotheses.

Although Gal is primarily studied for its role in mediating feeding behavior (Kyrkouli et al., 1990), Gal has also been implicated in modulating anxiety-like behavior (Lyudyno et al., 2008, Tillage et al., 2021). Administration of a Gal antagonist to the BNST prior to an acute stressor (i.e., immobilization) attenuates typical behavioral and physiological stress responses exhibited by rats (Khoshbouei et al., 2002), and chemogenetic activation of Gal in lateral hypothalamic (LH) neurons decreases anxiety-like behavior in mice (Owens-French et al., 2022). Together, these studies suggest that Gal has anxiolytic properties. For a species that evolved to live in large groups, such as spiny mice, living amidst a larger group may be anxiety-reducing because of advantages including enhanced foraging efficiency, reduced predation, and collective traveling (Berdahl et al. 2018; Markham et al., 2015; Bettridge & Dunbar 2013). Therefore, we quantified Gal fiber densities in the BNST and LH and hypothesized that spiny mice raised with non-kin exposure would exhibit higher Gal densities compared to animals reared without non-kin exposure.

Lastly, because early life social experiences may influence an animal's motivation to interact with others, we also quantified TH cell numbers (i.e., presumably dopaminergic) in the ventral tegmental area (VTA) and substantia nigra (SN) – key nodes in reward circuitry (Ilango et al., 2014). In spiny mice, time spent engaging in prosocial behavior with a peer positively correlates with VTA TH neural responsivity, suggesting that dopaminergic signaling is sensitive to social context in spiny mice and that spiny mice find nonreproductive social interactions rewarding (Gonzalez Abreu et al., 2022). Thus, we hypothesized that spiny mice reared in socially complex environments would have greater TH cell numbers at least in the VTA.

Materials and methods

Animals

21 male and 13 female spiny mice (Acomys dimidiatus) age postnatal day (PND) 58–68 were used as subjects. Animals were from our breeding colony, which originates from breeders obtained from the captive-bred colony of Dr. Ashley w. Seifert (University of Kentucky). Pre-weaning, subjects were housed in Tecniplast GR 1800 double-decker polycarbonate rat cages (32 × 38 × 40 cm), whereas post-weaning, subjects were housed in standard rat polycarbonate cage (40 × 20 × 20 cm). All cages were lined with Sani-Chips bedding, and animals were provided with rodent igloos and shepherd shacks, as well as ad libitum food (Prolab RMH 1000) and water. The animal colony rooms were maintained on a 14-h light: 10-h dark cycle with an ambient temperature of 25 ± 2°C. All procedures were approved by the Institutional Animal care and Use Committee of Emory University

Experimental design

The aim of the present study was to determine how variation in the early life social environment influences neurodevelopment. The brain tissue used here came from spiny mice used in an experiment for which behavioral and immediate early gene neural data have been previously reported; for full experimental details, please see (Wallace et al., 2025). Briefly, all subjects were offspring of adult male and female spiny mice (sex assessed via anogenital distance) that were paired and housed in double-decker cages that contained a transparent Plexiglas barrier with 0.5 cm diameter holes. To examine how early life social complexity influences development, subjects were reared by their parents in either a complex or simple social environment. For the complex social environment, an unrelated "neighbor" breeding group, consisting of one adult male, one adult female, and a litter of pups less than PND 21, was housed on the opposite side of the Plexiglas barrier. Holes in the barrier allowed subjects to interact with their noses and paws with conspecifics in the neighbor group (see Fig. 1). For the simple social environment, the other side of the barrier was left empty, so subjects interacted only with their biological parents and siblings. All families consisted of 1 mother, 1 father, and 2–3 pups. Spiny mouse litters vary from 1 to 5 pups, with an average of 2–3 pups per litter. In the rare occurrence that more than 3 pups were born to a litter, litters were culled to 3 pups; this was done to minimize variation in litter size in the experiment while also attempting to maximize the number of families/litters that could be used for the study. Litters of only a single pup were excluded from the study and relocated into our colony. Subjects were weaned at PND 21 and moved

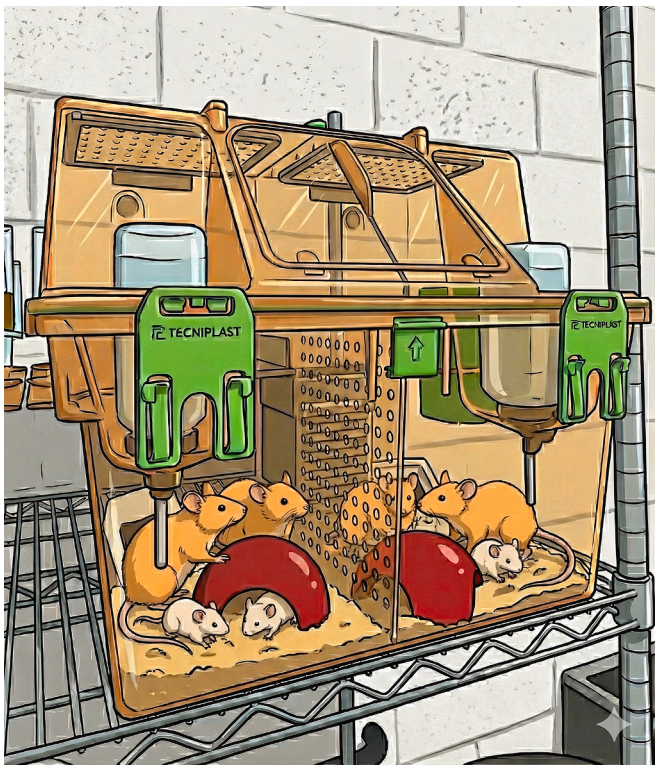

Fig. 1. Graphic created using Google Gemini Pro illustrating the cage setup, which allows for two families of spiny mice to live in a double decker cage with a transparent barrier containing holes dividing the cage in half.

into standard rat cages with their siblings; note that to avoid single-housing, subjects were housed in mixed-sex sibling groups of 2–3. At PND 58–68, subjects were euthanized via transcardial perfusion and brains were collected for subsequent analyses. Sample sizes: female complex-reared n = 6; male complex-reared n = 9; female simple-reared n = 7; male simple-reared n = 12. Sample sizes are imbalanced across groups due to the inability to control for which sex would be born to litters and for a lack of female births; in our colony, we have found that sex ratios at birth are male-biased (unpub. obs.).

Histology and immunohistochemistry

Subjects were overdosed on isoflurane and transcardially perfused with 0.1 M phosphate buffer saline (PBS) followed by 4% paraformaldehyde. Brains were post-fixed in 4% paraformaldehyde overnight prior to incubation in 30% sucrose for 48 h at 4°C. Brains were then frozen in Tissue-Tek O.C.T. and stored at −80°C until sectioning. Brains were sectioned into 3 series at 40um and processed via immunohistochemistry, using previously validated antibodies, as described in (Fricker et al., 2023a; Gonzalez Abreu et al., 2022, Kelly et al., 2022a). The second and third series of tissue were used for this study. Tissue was first rinsed in 0.1 M PBS and then incubated in a blocking solution (10% normal donkey serum + 0.03% Triton X-100 in PBS) for 1 h at room temperature. Tissue was then incubated for 48 h at 4°C in a primary antibody solution of 5% normal donkey serum and 0.03% Triton X-100 in PBS. The second series of tissue was labeled for TH and OT and used a rabbit anti-OT antibody (Abcam, #AB212193, 1:250) and mouse anti-TH antibody (Millipore, #MAB318, 1:1000). The third series of tissue was labeled for VP and Gal and used a guinea pig anti-VP antibody (Penninsula Labs, #T.5048.0050, 1:250) and a rabbit anti-Gal antibody (Invitrogen, #PA5-119131, 1:1000). After primary antibody incubation, tissue was rinsed in PBS. The third series of tissue underwent a biotinylating step; tissue was incubated in a solution containing 5% normal donkey serum, 0.03% Triton X-100, and a biotin SP donkey anti-guinea pig antibody (Jackson ImmunoResearch, #706-065-148, 1:125) in PBS for 1 h at room temperature followed by two 20 min rinses in 0.1 M PBS. All tissue was then incubated in a secondary antibody solution containing 5% normal donkey serum and 0.03% Triton X-100 in PBS for 2 h at room temperature in the dark. For the second series of tissue, secondary antibodies used were a donkey anti-rabbit conjugated to Alexa Fluor 594 (Thermo Fisher, A-21207, 1:250) and a donkey anti-mouse conjugated to Alexa Fluor 488 (Thermo Fisher, A-21202, 1:250). For the third series of tissue, secondary antibodies used were a donkey anti-rabbit conjugated to Alexa Fluor 594 (ThermoFisher, A-21207, 1:250) and a streptavidin 488 conjugate (Thermo Fisher, S-32354, 1:250). After rinses in PBS, tissue was mounted on subbed slides with Prolong Gold with DAPI. For representative images of immunostaining for OT, VP, Gal, and TH, see Fig. 2.

Neural quantification

Photomicrographs were taken using a Zeiss AxioImager II microscope fitted with an apotome. All imaging and quantification were conducted blind to condition. Because OT and VP cell groups are geographically distinct in the brain (Acher & Chauvet, 1995, Moore & Lowry, 1998, Rood & De Vries 2011), we did not use a region of interest (ROI) for cell counts and instead counted all immunoreactive cells present in a tissue section in the brain region of interest. Two images from two tissue sections were acquired at 10X for each cell group, with 120um between tissue sections for the BNST, MNPO, and AH. The VP and OT cell groups of the BNST, MNPO, and AH are relatively, and thus we totaled cells from the two images for each brain region for analyses. For the PVN, which is a fairly extensive nucleus, there were 320um between tissue sections (capturing rostral and caudal portions). There were no statistical differences between rostral and caudal PVN cell counts, so for analyses presented here we calculated an average of the cell counts from the two sections capturing the PVN as has been done previously (Fricker et al., 2023b; Kelly et al., 2022b; Kelly et al., 2017). Therefore, VP and OT cell numbers for the BNST, MNPO, and AH cell groups represent total numbers, whereas VP and OT cell numbers for the PVN cell group represent average cell numbers. Brain areas from which photomicrographs were acquired for VP and OT cell groups are shown in Fig. 3.

Gal labeling in the BNST and LH consisted mainly of fibers and thus optical density measurements were obtained for quantification. Two images were acquired at 5X from one hemisphere (left or right side was randomized across subjects) for each the BNST and LH, capturing rostral and caudal portions of the cell groups, with 240um between rostral and caudal sections. Images were converted to monochrome and the mean gray value was obtained for a standardized ROI fit over Gal-ir labeling in the center of the BNST or LH. Mean gray values were also obtained for each image from an area of tissue that expressed no Gal labeling (e.g., background). Background labeling was subtracted from the Gal labeling value for a final measurement of optical density. An average of the rostral and caudal optical density values were used for statistical analyses. Brain areas from which photomicrographs were acquired and ROIs for Gal-ir optical density measurements are shown in Fig. 4.

Because the TH cell groups of the SN and VTA span a substantial anterior-posterior distance in the brain, we acquired 3 images at 5X from one hemisphere (left or right side was randomized across subjects), with 240um between each tissue section. We applied standardized ROIs (i.e., the same sized ROI for each subject) to fit over TH-ir labeling in the center of the VTA and the center of the SN and counted cells within each ROI. Cell counts from the 3 images for each cell group were averaged for analyses. 2 males from the simple rearing environment condition and 2 males from the complex rearing environment condition were removed due to tissue damage or loss. Brain areas from which photomicrographs were acquired and ROIs for TH-ir cell counts are shown in Fig. 5.

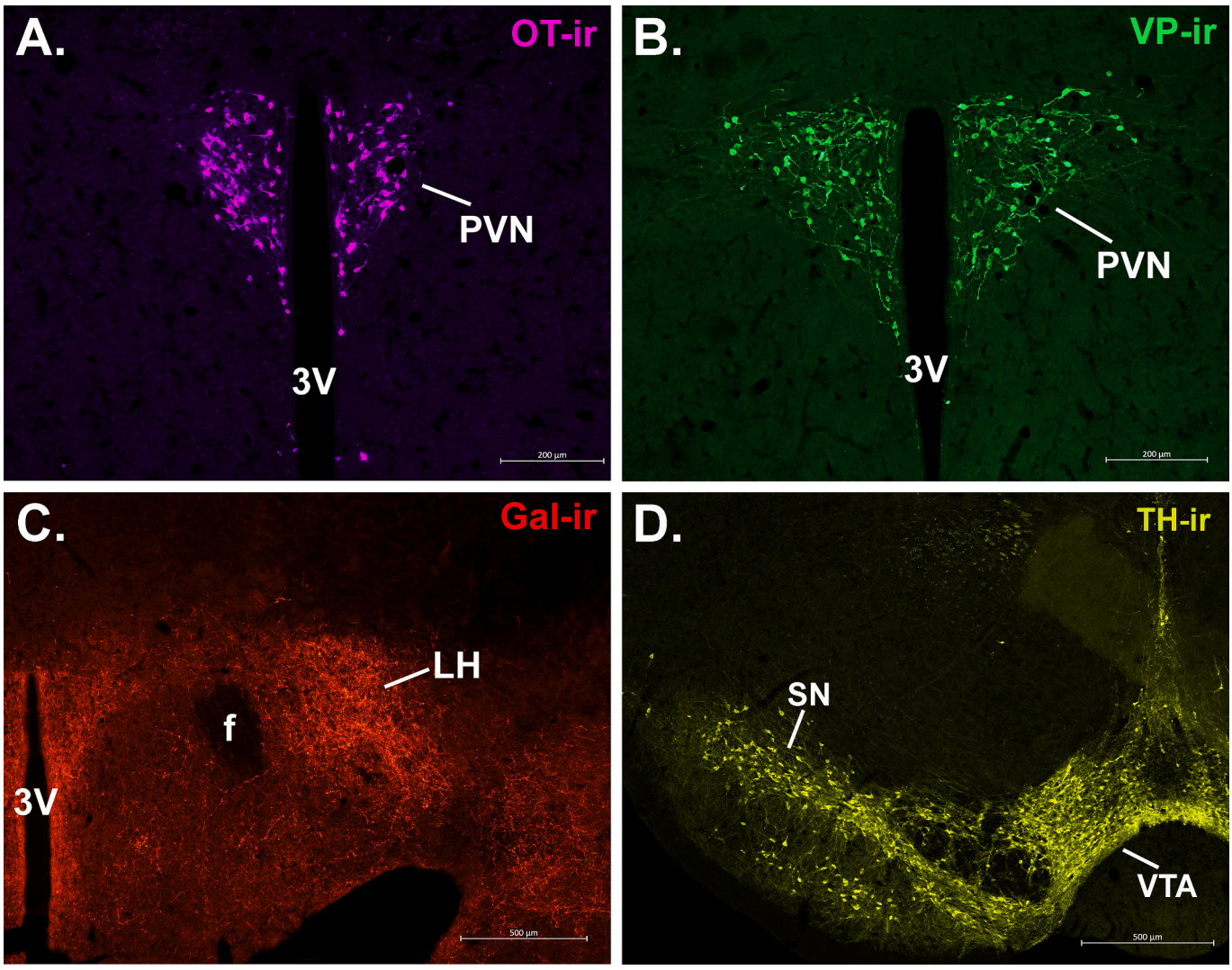

Fig. 2. Representative pseudocolored images from spiny mouse brain tissue of immunostaining of (A) oxytocin (OT) in purple, (B) vasopressin (VP) in green, (C) galanin (Gal) in red, and (D) tyrosine hydroxylase (TH) in yellow. 3 V, third ventricle; −ir, −immunoreactive; LH, lateral hypothalamus; PVN, paraventricular nucleus of the hypothalamus; SN, substantia nigra; VTA, ventral tegmental area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Statistics

Data for each cell group were analyzed using univariate general linear models (GLMs); multiple comparisons for all analyses were corrected using the Bonferroni procedure. Effect sizes were calculated using Cohen's d. We screened the data for outliers, defined as 3 standard deviations outside the mean, however, no outliers were identified. Data were analyzed using SPSS 29 (IBM Analytics, USA) and figures made using Prism 10 (GraphPad, USA).

Results

To examine the influence of early life social complexity on the neurodevelopment of systems involved in social behavior, anxiety, and reward in male and female spiny mice, for each cell group we conducted separate univariate GLMs with Sex (Male vs. Female) and Condition (Simple (i.e., reared with biological family) vs. Complex (i.e., reared with biological family and exposure to non-kin family)) as fixed factors and the cell group as the independent variable. A summary of *p*-values and effect sizes for the effects of Sex and Condition are presented below for each cell group (see Tables 1 and 2 for statistics).

Early life social complexity does not influence OT cell numbers

OT cell numbers were quantified for the BNST, MNPO, AH, and PVN. GLM analyses revealed no effect of Sex ($F_{(1,33)} = 0.041$; $p = 0.841$; Fig. 6A), Condition ($F_{(1,33)} = 1.045$; $p = 0.315$; Fig. 7A), and no interaction ($F_{(1,33)} = 0.993$; $p = 0.327$) for the BNST OT cell group. We found no effect of Sex ($F_{(1,33)} = 0.887$; $p = 0.354$; Fig. 6B), Condition ($F_{(1,33)} = 2.63$; $p = 0.115$; Fig. 7B), and no interaction ($F_{(1,33)} = 0.154$; $p = 0.689$) for the MNPO OT cell group. Similarly, analyses yielded no effect of Sex ($F_{(1,33)} = 0.284$; $p = 0.598$; Fig. 6C), Condition ($F_{(1,33)} = 0.375$; $p = 0.683$; Fig. 7C), and no interaction ($F_{(1,33)} = 0.170$; $p = 0.683$) for the AH OT cell group. Lastly, we also failed to observe an effect of Sex ($F_{(1,33)} = 0.561$; $p = 0.460$; Fig. 6D), Condition ($F_{(1,33)} = 0.345$; $p = 0.562$; Fig. 7D), or an interaction ($F_{(1,33)} = 1.817$; $p = 0.188$) for the PVN OT cell group. These findings suggest that the development of OT neuronal populations may be robust to variation in the number of social associations prior to weaning.

Spiny mice reared in simple social environments exhibit greater AH VP cell numbers

We quantified VP cell numbers for the BNST, AH, and PVN. A GLM

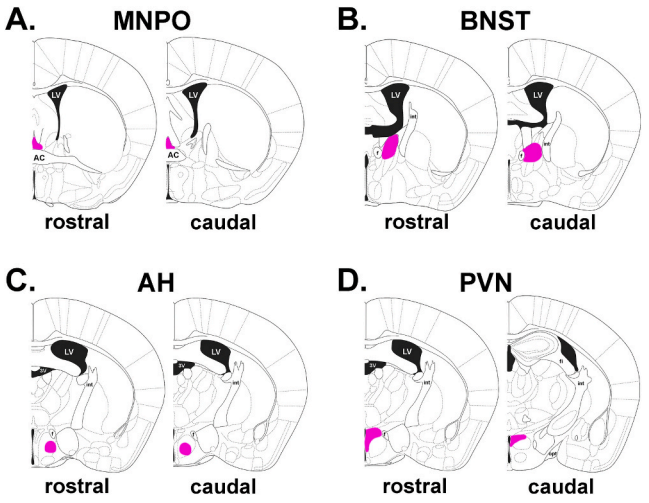

Fig. 3. Representative mouse brain atlas images (Allen Institute for Brain Science, 2011) with brain regions that express vasopressin- and/or oxytocin-producing neurons; please note that the spiny mouse brain is shaped slightly differently. Pink areas represent locations of vasopressin and/or oxytocin cells that were quantified for cell counts in the (A) median preoptic nucleus (MNPO), (B) bed nucleus of the stria terminalis (BNST), (C) anterior hypothalamus (AH), and (D) paraventricular nucleus of the hypothalamus (PVN). 3 V, third ventricle; AC, anterior commissure; f, fornix; fi, fimbria; int, internal capsule; LV, lateral ventricle; opt, optic tract. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

yielded a significant difference between males and females for VP neuronal number in the BNST ($F_{(1,33)} = 40.128$; $p < 0.001$; Fig. 8A), such that males exhibited significantly more VP-ir neurons than females, replicating a phylogenetically widespread sexual dimorphism in BNST VP anatomy across taxa (De Vries, 2008; Kelly & Goodson, 2013; Kelly & Seifert, 2021). However, we observed no effect of Condition ($F_{(1,33)} = 2.263$; $p = 0.143$; Fig. 9A) and no interaction between Sex and Condition ($F_{(1,33)} = 0.830$; $p = 0.370$) for the BNST VP cell group.

For the AH VP neuronal population, analyses yielded a main effect of Condition ($F_{(1,33)} = 25.598$; $p < 0.001$; Fig. 9B), showing that animals reared in the simple social environment exhibited more VP-ir neurons than spiny mice reared in the complex social environment. However, we found no effect of Sex ($F_{(1,33)} = 0.229$; $p = 0.635$; Fig. 8A) and no interaction between Sex and Condition ($F_{(1,33)} = 0.469$; $p = 0.499$) for the AH VP cell group.

Lastly, GLM analyses revealed no effect of Sex ($F_{(1,33)} = 0.028$; $p = 0.869$; Fig. 8C), Condition ($F_{(1,33)} = 1.053$; $p = 0.313$; Fig. 9C), and no interaction ($F_{(1,33)} = 0.033$; $p = 0.857$) for the PVN VP cell group.

Spiny mice reared in complex social environments exhibit greater LH gal fiber densities

Optical density values of Gal-ir were quantified in the BNST and LH. For BNST Gal, a GLM revealed no effect of Sex ($F_{(1,33)} = 0.063$; $p = 0.803$; Fig. 10A), Condition ($F_{(1,33)} = 3.705$; $p = 0.064$; Fig. 10C), and no interaction between Sex and Condition ($F_{(1,33)} = 2.874$; $p = 0.100$). However, for LH Gal we found a main effect of Condition ($F_{(1,33)} = 16.463$; $p < 0.001$; Fig. 10D), such that spiny mice reared in a simple social environment expressed less Gal-ir than those reared in a complex social environment. Analyses showed no effect of Sex ($F_{(1,33)} = 1.976$; $p = 0.170$; Fig. 10B) and no interaction between Sex and Condition ($F_{(1,33)} = 1.598$; $p = 0.216$) for LH Gal.

Early life social complexity does not influence TH cell numbers

Lastly, we examined TH cell numbers in the SN and VTA. A GLM yielded no effect of Sex ($F_{(1,29)} = 0.003$; $p = 0.957$; Fig. 11A), Condition ($F_{(1,29)} = 1.206$; $p = 0.282$; Fig. 11C), and no interaction ($F_{(1,29)} = 0.906$; $p = 0.350$) for the SN TH cell group. Similarly, we failed to observe an effect of Sex ($F_{(1,29)} = 0.200$; $p = 0.689$; Fig. 11B), Condition ($F_{(1,29)} = 2.524$; $p = 0.124$; Fig. 11D), or a interaction ($F_{(1,29)} = 1.494$; $p = 0.233$) for the VTA TH cell group. This suggests that engaging with unrelated conspecifics pre-weaning does not influence the development of dopaminergic cell groups involved in reward (Gonzalez Abreu et al., 2022; Keiflin et al., 2019; Luo et al., 2011).

Discussion

To assess long-term effects of increased social complexity during early life, in the current study we raised pups of the communal spiny mouse from birth to weaning in either the presence or absence of a non-kin breeding group. Upon adulthood, we immunohistochemically processed brain tissue and quantified cell numbers of OT, VP, and TH, and fiber densities of Gal. We found that while OT and TH neural populations were robust to the early life social environment, the VP neuronal population of the AH and the Gal population of the LH were sensitive to early life social complexity.

Vasopressin expression in the anterior hypothalamus is influenced by the early life social environment

We observed that spiny mice reared alongside non-kin exhibited significantly lower VP expression in the AH upon adulthood. VP in the AH is well known for promoting aggression in hamsters (Ferris et al., 1989) and prairie voles (Gobrogge et al., 2007). Although not necessarily specific to VP action in the AH, early life exposure to exogenous VP promotes adult aggression in prairie voles (Stribley & Carter, 1999). Together, these prior studies suggest that the lower VP neuronal

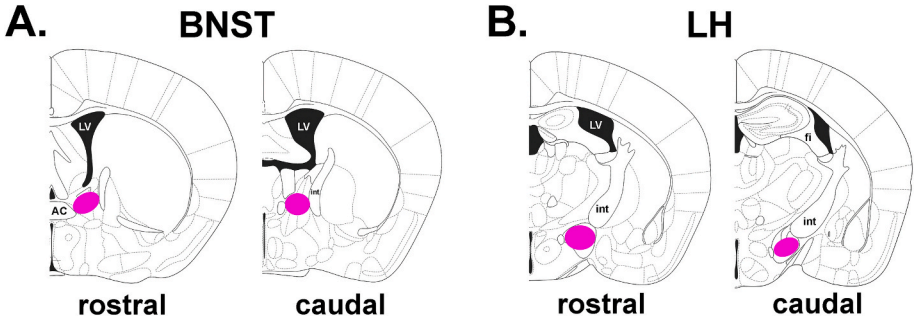

Fig. 4. Representative mouse brain atlas images (Allen Institute for Brain Science, 2011) with brain regions that express galanin (Gal) fibers; please note that the spiny mouse brain is shaped slightly differently. Pink areas represent regions of interest (ROIs) used to obtain optical density measurements of Gal-immunoreactive fiber densities in the (A) bed nucleus of the stria terminalis (BNST) and (B) lateral hypothalamus (LH). AC, anterior commissure; fi, fimbria; int, internal capsule; LV, lateral ventricle. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

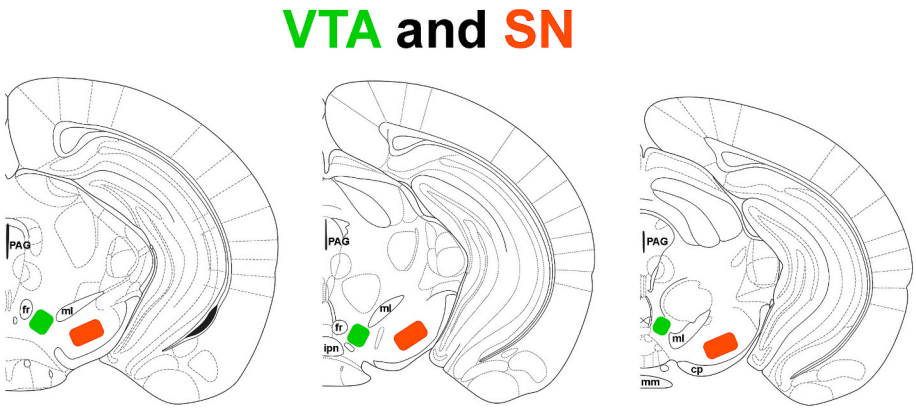

Fig. 5. Representative mouse brain atlas images (Allen Institute for Brain Science, 2011) with brain regions that express tyrosine hydroxylase (TH) neurons; please note that the spiny mouse brain is shaped slightly differently. Green areas represent regions of interest (ROIs) used to quantify TH cell numbers in the ventral tegmental area (VTA) and orange areas represent ROIs used to quantify TH cell numbers in the substantia nigra (SN). cp, cerebal peduncle; fr, fasciculus retroflexus; ipn, interpeduncular nucleus; ml, medial lemniscus; mm, medial mammillary nucleus; periaqueductal gray (PAG). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Pairwise comparisons for the main effect of Sex from univariate GLMs.

Cell group	Bonferroni corrected P-value	Effect size (Cohen's d)
BNST OT	0.841	0.044
MNPO OT	0.354	0.347
AH OT	0.598	0.090
PVN OT	0.460	0.210
BNST VP	***<0.001***	***1.843***
AH VP	0.635	0.067
PVN VP	0.869	0.081
BNST Gal	0.803	0.127
LH Gal	0.170	0.386
SN TH	0.957	0.005
VTA TH	0.689	0.135

Table 2
Pairwise comparisons for the main effect of Condition from univariate GLMs.

Cell Group	Bonferroni corrected P-value	Effect size (Cohen's d)
BNST OT	0.315	0.299
MNPO OT	0.115	0.652
AH OT	0.545	0.249
PVN OT	0.562	0.105
BNST VP	0.143	0.362
AH VP	***<0.001***	***1.885***
PVN VP	0.313	0.397
BNST Gal	0.064	0.535
LH Gal	***<0.001***	***1.287***
SN TH	0.282	0.368
VTA TH	0.124	0.550

densities observed in our socially complex-reared spiny mice could reflect adaptive changes to neural mechanisms that reduce adult aggression, thereby facilitating communal living. Because spiny mice generally exhibit little to no aggression (Fricker et al., 2022, Gonzalez Abreu et al., 2022, Fricker et al., 2025), we did not quantify aggression in subjects from this study, as reported in our previous publication (Wallace et al., 2025). However, consistent with findings in prairie voles (Madrid et al., 2024), anecdotally, spiny mice are more prone to chasing in social interactions if they are singly-, rather than group-, housed (unpub. obs.). Thus, it is feasible that early life experiences interacting with conspecifics may prepare a spiny mouse pup for exhibiting appropriate behavior for group-living once an adult. Indeed, lower aggression, especially when accompanied by higher gregariousness as observed in spiny mice (Fricker et al., 2022), is a phenotype that is likely beneficial for large group living (Treisman 1975, Papageorgiou &

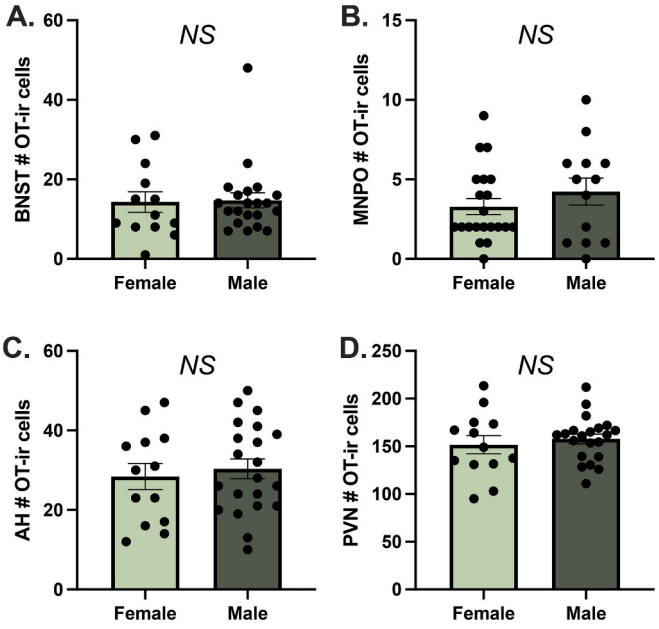

Fig. 6. Oxytocin-immunoreactive (OT-ir) cell numbers for female (light sage green) and male (dark sage green) spiny mice for the (A) bed nucleus of the stria terminalis (BNST) OT, (B) median preoptic nucleus (MNPO) OT, (C) anterior hypothalamus (AH) OT, and (D) paraventricular nucleus of the hypothalamus (PVN) OT cell groups. Data are represented as mean ± SEM. Dots represent individual data points. *NS* indicates no statistical significance. An asterisk indicates statistical significance of $p \leq 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Farine, 2020). For example, like the spiny mouse, the striped mouse exhibits communal rearing and little to no aggression towards group members (Schradin et al., 2004). And even in the eusocial naked mole rat, aggression is primarily demonstrated by the queen and typically functions to suppress reproduction of subordinates (Clarke & Faulkes, 2001). Further research on breeding, alloparental care, and aggression in this species will likely yield novel insights into the evolution of the neural mechanisms of communal living.

Although we observed an effect of the early life rearing environment on AH VP, we failed to observe any influence of the early life social environment on the VP cell groups of the PVN and BNST. Consistent

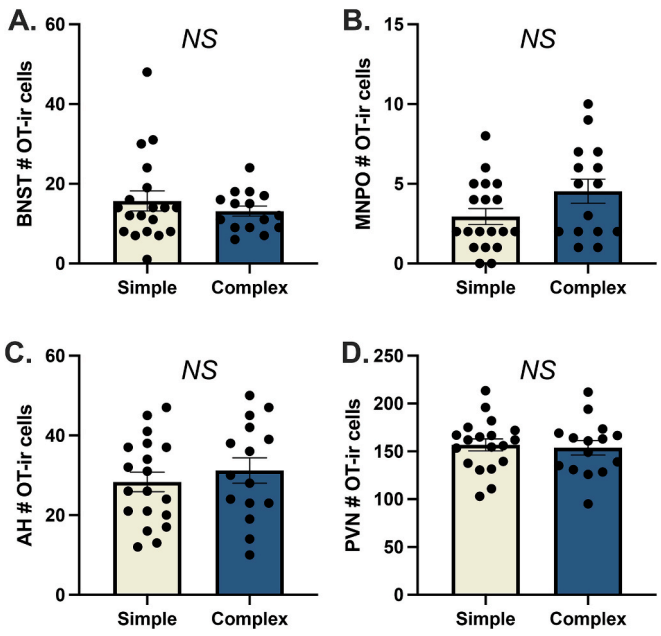

Fig. 7. Oxytocin-immunoreactive (OT-ir) cell numbers for spiny mice reared in Simple (beige) and Complex (blue) conditions for the (A) bed nucleus of the stria terminalis (BNST) OT, (B) median preoptic nucleus (MNPO) OT, (C) anterior hypothalamus (AH) OT, and (D) paraventricular nucleus of the hypothalamus (PVN) OT cell groups. Data are represented as mean ± SEM. Dots represent individual data points. *NS* indicates no statistical significance. An asterisk indicates statistical significance of $p \leq 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

with this, a study in prairie voles found that high or low parental contact throughout development did not influence PVN VP cell numbers (Perkeybile & Bales, 2015). Additionally, paternal absence or presence and variation in supplemental caregiving during the pre-weaning stage of early life in prairie voles also did not influence PVN or BNST VP cell numbers (Hiura et al., 2024). Although the PVN and BNST VP cell groups may be fairly robust to social environmental variation in the early life, at least the PVN VP cell group exhibits plasticity in adult animals. For example, the breaking of a pair bond and single housing for 1-month increases PVN VP cell numbers in male prairie voles (Sun et al., 2014) and Mongolian gerbils (Fricker et al., 2024a). Because the PVN VP cell group plays a crucial role in modulating the stress response (Herman & Tasker, 2016, Neumann & Landgraf, 2012), it is possible that plasticity in this neuronal population occurs with more drastic social environmental variation, such as being co-housed with conspecifics vs. complete social isolation. Indeed, we may not have observed any influence of the rearing environment in subjects in the present study because both conditions of being reared with parents and siblings and/or with neighboring, non-kin families likely are not stressful early life environments for spiny mice.

Vasopressin expression in the bed nucleus of the stria terminalis varies by sex

In our experiment, male spiny mice exhibited significantly more VP cells in the BNST than females. Sexual dimorphism in BNST VP neuronal expression is widely conserved across diverse taxa (De Vries 2008), and greater production of VP in the BNST of males is one of the most dramatic and most conserved sexual dimorphisms observed in the field of neuroendocrinology (Kelly & Goodson, 2013, De Vries 2004). Our finding of a sex difference in VP-ir BNST expression is consistent with our previous research showing that the only VP cell group to exhibit a sex difference in spiny mice is that of the BNST (Kelly & Seifert, 2021), a cell group that is strongly regulated by sex steroids (De Vries & Panzica 2006). In zebra finches, this dimorphism may serve to promote courtship behavior and offset the tendency for males to be more aggressive than females as demonstrated by a reduction in courtship and increase in aggression following antisense knockdown of BNST VP production (Kelly & Goodson, 2013). Additionally, antisense knockdown of BNST VP influences male, but not female, grouping behavior in zebra finches (Kelly et al., 2011, Kelly & Goodson, 2013). Similarly, in transgenic mice, the BNST VP also plays a more prominent role in social behavior in males than females, given that ablation of this cell group reduces social preferences in males, but not females (Rigney et al., 2019). It is unclear what function the sex difference in BNST VP neuronal densities may serve in spiny mice as this cell group has never been directly assessed. However, given that male and female spiny mice exhibit differences in social preferences (Wallace et al., 2025, Fricker et al., 2022), it is possible that the BNST VP cell group regulates aspects of social preference and/or affiliation in this species as it does in other species.

Galanin expression in the lateral hypothalamus is influenced by the early life social environment

In the present study, Gal expression was significantly higher in the LH of animals reared alongside non-kin. Although Gal in the LH is known to modulate locomotion (Qualls-Creekmore et al., 2017), we do not believe rearing treatment influenced locomotion behavior early in life as pup transverses along the central barrier of the home cage did not differ by rearing treatment (Wallace et al., 2025). Gal in the LH is also known for modulating feeding behavior as well (Qualls-Creekmore

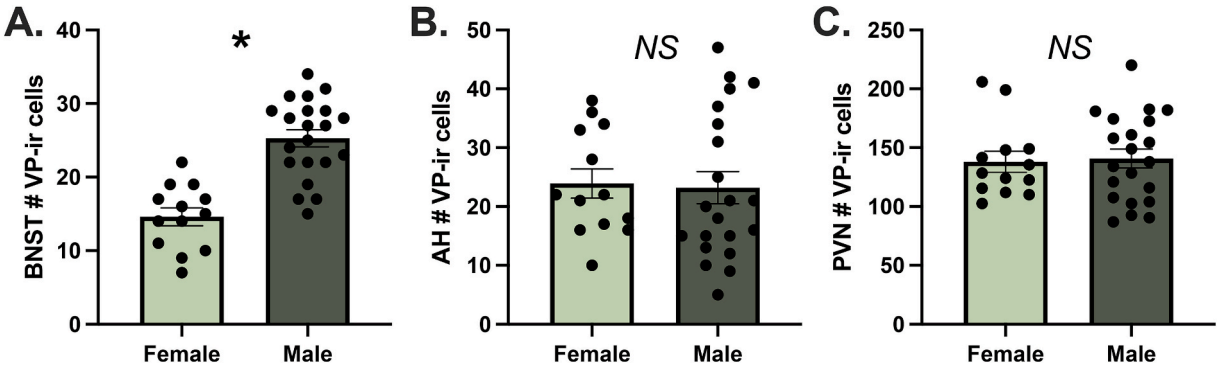

Fig. 8. Vasopressin-immunoreactive (VP-ir) cell numbers for female (light sage green) and male (dark sage green) spiny mice for the (A) bed nucleus of the stria terminalis (BNST) VP, (B) anterior hypothalamus (AH) VP, and (C) paraventricular nucleus of the hypothalamus (PVN) VP cell groups. Data are represented as mean ± SEM. Dots represent individual data points. *NS* indicates no statistical significance. An asterisk indicates statistical significance of $p \leq 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

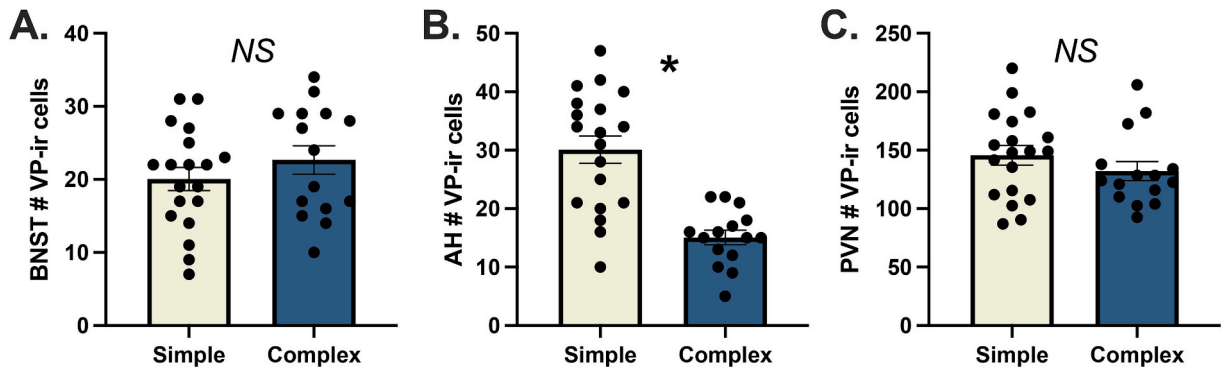

Fig. 9. Vasopressin-immunoreactive (VP-ir) cell numbers for spiny mice reared in Simple (beige) and Complex (blue) conditions for (A) bed nucleus of the stria terminalis (BNST) VP, (B) anterior hypothalamus (AH) VP, and (C) paraventricular nucleus of the hypothalamus (PVN) VP cell groups. Data are represented as mean ± SEM. Dots represent individual data points. *NS* indicates no statistical significance. An asterisk indicates statistical significance of $p \leq 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

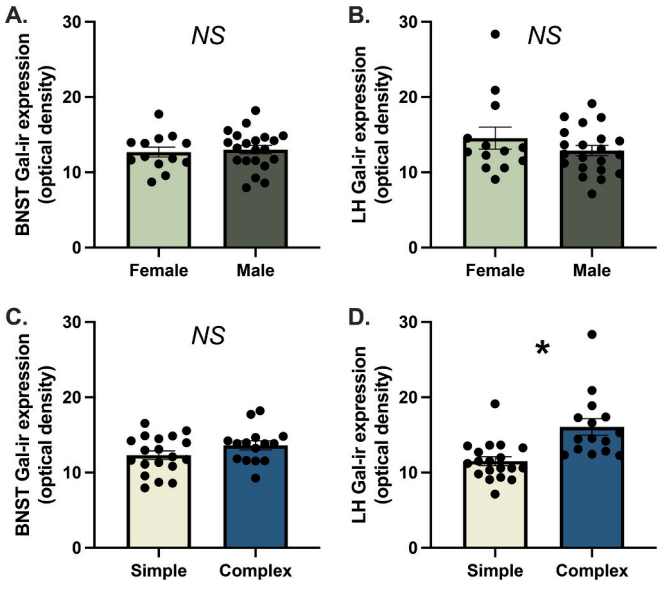

Fig. 10. Optical density measurements of galanin-immunoreactive (Gal-ir) fiber densities for female (light sage green) and male (dark sage green) spiny mice for the (A) bed nucleus of the stria terminalis (BNST) and (B) lateral hypothalamus (LH). Optical density measurements of Gal-ir fiber densities for spiny mice reared in Simple (beige) and Complex (blue) conditions for the (C) BNST and (D) LH. Data are represented as mean ± SEM. Dots represent individual data points. *NS* indicates no statistical significance. An asterisk indicates statistical significance of $p \leq 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

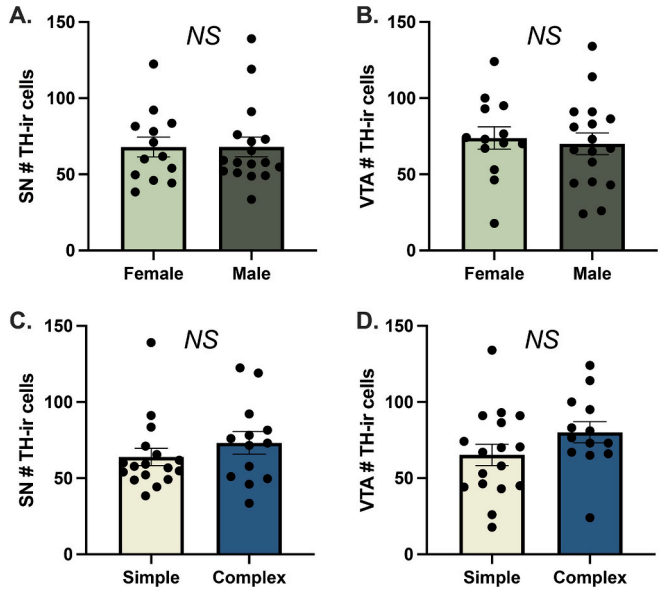

Fig. 11. Tyrosine-hydroxylase-immunoreactive (TH-ir) cell numbers for female (light sage green) and male (dark sage green) spiny mice for the (A) substantia nigra (SN) and (B) ventral tegmental area (VTA) TH cell groups. TH-ir cell numbers for spiny mice reared in Simple (beige) and Complex (blue) conditions for the (C) SN and (D) VTA. Data are represented as mean ± SEM. Dots represent individual data points. *NS* indicates no statistical significance. An asterisk indicates statistical significance of $p \leq 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

et al., 2017). Unfortunately, we did not obtain feeding or weight measurement for our subjects, and therefore further work is needed to investigate the role of communal rearing on feeding behavior and relevant underlying neural mechanisms. This is a possible area of future study for spiny mice, as this species exhibits food sharing with both related and unrelated conspecifics (Porter et al., 1981). Additionally, OT receptors in the nucleus accumbens of male spiny mice facilitate huddling with novel, same-sex peers *and* feeding behavior, demonstrating that a single cell type in a single brain region can be multi-purpose and have both social and nonsocial functions (Fricker et al., 2025).

In addition to Gal's metabolic functions, recent studies have implicated a role for this neurohormone in mediating anxiety-like behavior (Owens-French et al., 2022). For example, administration of a Gal receptor antagonist increases anxiety-like behavior in an open field task (Lyudyno et al., 2008), whereas chemogenetic activation of LH Gal neurons decreases anxiety-like behavior (Owens-French et al., 2022); together this suggests that LH Gal may have anxiolytic properties. Because spiny mice evolved to live communally in large groups, it is feasible that being reared in an environment with more conspecifics may help reduce anxiety, potentially via higher densities of LH Gal. Indeed, there is strength in numbers in relation to predator defense and collective foraging (Markham et al., 2015, Bettridge & Dunbar, 2013, Burger & Gochfeld, 2001, White, 2010, Vanthournout et al., 2016).

Alternatively, the higher LH Gal densities in socially complex-reared spiny mice could reflect the rewarding properties associated with interacting with a variety of conspecifics. Studies in rats and mice have shown that they will perform operant responses to receive electrical pulses within the LH (Fakhoury et al., 2016, Ide et al., 2017). Other studies have shown that, through GABA, the LH plays a primary role in

learning about reward-related cues (Sharpe et al., 2017). Further, we recently showed that the LH is not only involved in reward learning, but also likely modulates social learning in spiny mice (Roshko et al., 2025). Given that Gal can influence dopamine release (Tsuda et al., 1998), and it has been proposed that Gal may play a significant role in modulating the mesolimbic reward system (Robinson & Brewer, 2008), future studies could investigate whether the early life social environment-induced effects on LH Gal also affect Gal influences on dopamine signaling. Lastly, it is important to note that we do not know the source neurons from which the Gal fiber densities arose; thus, the fiber densities quantified may represent Gal fibers from LH neurons, but also from other LH neurons, such as those in the BNST.

Oxytocin and tyrosine hydroxylase expression are not influenced by the early life social environment

Here we observed no influence of pre-weaning social complexity on the cell numbers in any TH or OT cell group examined. As observed previously in this cohort of animals, manipulation of the early life environment by altering social complexity did not have a robust effect on social behavior once animals reached adulthood (Wallace et al., 2025). However, as assessed with an immediate early gene study, neural processing of novel social stimuli did significantly differ based on early life experience, such that the lateral septum, preoptic area, and PVN were more responsive to interactions with novel conspecifics in complex-reared animals compared to simple-reared animals (Wallace et al., 2025). This neural activity finding combined with the influence of our early life manipulation on VP and Gal discussed above demonstrate that spiny mice are sensitive to variation in early life social complexity. However, at least as assessed via the methods in the present study, we were unable to detect any influence of our manipulation on the development of OT or TH cell groups. Interestingly, previous work in spiny mice (Kelly & Seifert, 2021) identified sex differences in OT-ir expression in the MnPO, BST, and AH; however, no effects of sex were observed in the present study, which, although unlikely, could be due to different OT antibodies. Alternatively, variation in early life social complexity may have altered OT densities differentially in males and females, thereby eliminating typical sex differences in OT cell numbers (De Vries 2004).

Studies conducted in other species that manipulated the early life social environment have found an influence of variation in early life social experiences on OT cell groups in adulthood. For example, single-mother reared prairie voles exhibit more OT mRNA grain clusters in the PVN compared to pups reared with a mother and a father (Ahern & Young, 2009). Contradicting this finding, a study in mandarin voles found that paternal deprivation, as well as early social deprivation, resulted in less OT cells in the PVN (Feng et al., 2019). Whether these conflicting findings reflect species differences and/or methodological differences (i.e., labeling of mRNA vs. protein) remains unknown. Regardless, these studies demonstrate that the PVN OT neuronal population can be sensitive to early social experiences, depending on the species. Furthermore, our manipulation may not have been sufficiently dramatic to induce changes in PVN OT cell numbers, particularly if this cell group is especially sensitive to parental care given that all our subjects were reared by both a mother and father. Future studies in spiny mice could examine how rearing in a large communal group, with multiple alloparents, may influence the development of the PVN OT cell group. Lastly, because OT directly facilitates prosociality in several species, including spiny mice (Carcea et al., 2021, Gonzalez Abreu et al., 2022, Fricker et al., 2025, Marsh et al., 2021, Froemke & Young, 2021) and because the exhibition of prosociality is crucial to the success of spiny mice getting along in groups, OT cell numbers may be robust to variation in early social experiences to ensure a prosocial phenotype regardless of experience.

As with OT, it is possible that TH expression is unaffected by early life social rearing given its role in motivated social approach (Gonzalez Abreu et al., 2022), which is an adaptive behavior for a communal species like the spiny mouse (Fricker et al., 2022, Fricker et al., 2024b). We previously showed that VTA TH neurons are more responsive to social than nonsocial contexts in spiny mice (Gonzalez Abreu et al., 2022), so it is possible that degree of social experience may not influence the development of VTA TH neuroanatomy. VTA TH neural activity also positively relates to prosocial behavior with novel conspecifics in spiny mice (Gonzalez Abreu et al., 2022), however, we observed no differences in adulthood prosociality based on rearing condition (Wallace et al., 2025). Together, these findings strongly suggests that VTA TH cell numbers were simply unaffected by our early life manipulation in the present study. To our knowledge, the role of SN TH neurons in spiny mice is unknown. However, studies in rats and mice show that this dopaminergic cell group is also crucial for reward, including social reward (Ilango et al., 2014). Notably, many of the studies supporting early life influences on the dopaminergic reward system demonstrate changes in receptor expression (Han et al., 2012) or dopamine response to acute stimuli in adulthood (McWain et al., 2022, Yorgason et al., 2016, Karkhanis et al., 2014). In fact, early maternal separation, as well as early handling, does not influence TH cell numbers in the VTA or SN of rats (Madruga et al., 2006). Thus, further work in spiny mice on responses to acute stressors or rewarded behavior in adulthood may better capture changes in motivated behavior and mesolimbic reward circuitry influence by the early life social environment.

Limitations

Although we were able to represent both male and female spiny mice in our study, due to our inability to control the sex ratio of births, thus yielding relatively low sample sizes per condition when separating the sexes, our study is not ideally suited for specifically examining effects of sex on early life social environmental influences on the development of nonapeptide, Gal, and dopaminergic cell numbers and fiber densities. Therefore, future studies are required to conclusively determine whether early life social complexity differentially impacts male and female spiny mouse neural development. Similarly, we observed a few modest effect sizes for comparisons that failed to yield a significant p-value (e.g., MNPO OT, BNST Gal, and VTA TH) when examining effects of Condition on cell counts and fiber densities; this suggests that a larger sample size may have revealed differences between animals reared in Simple vs. Complex early life social environments for these cell groups. Additionally, because spiny mouse gestation is long for a rodent (i.e., ~45 days) and because females often do not immediately get pregnant with another litter of pups after giving birth, accumulating subjects was a long and arduous process. Therefore, to achieve a sufficient sample size in the present study, we allowed for variation in our experimental design, such that we included spiny mouse families with 2–3 pups per litter as opposed to an identical number of pups per litter, adding noise to our dataset. However, this exploratory study still shows that the early life social environment does influence at least some neural systems underlying social and anxiety-like behavior, and future studies can specifically examine how variation in group size or the number of siblings an individual is reared with influences neural development. Lastly, it is important to note that while the cell groups in which we observed significant differences based on early life social complexity (i.e., AH VP and LH Gal) are often linked to aggression and anxiety-like behavior, we did not quantify aggression or anxiety-like behavior in the present study. Thus, how the distinct neural profiles associated with early rearing condition observed here relate to behavior remains unknown, and we can only speculate that differences in AH VP could relate to differences in aggression and that differences in LH Gal could relate to differences in anxiety-like behavior. Future studies that directly assess relationships between these cell groups and relevant behaviors are required to determine whether early life social complexity influences the development of such neural systems, thereby influencing aggressive and anxiety phenotypes.

Conclusion

The present study demonstrates that early life social complexity has lifelong effects on neural circuitry underlying social behavior. Our findings that males and females raised in more socially complex environments have less AH VP may reflect a neurodevelopmental trajectory that promotes reduced aggression, thereby facilitating large group living. Similarly, the observed rearing effects on LH Gal expression may shape spiny mouse neurodevelopment in a way that enables social buffering of anxiety-inducing or stressful experiences. Importantly, both these changes may contribute toward a more successful navigation of complex communal environments in adulthood.

There are many timepoints in which to further explore social behavior-related neurodevelopment. In addition to early life, experiences during adolescence (Counotte et al., 2010) and adulthood (Fone & Porkess, 2008, Cacioppo & Hawkley, 2009) rewire the underlying neurocircuitry of social behavior. Further, in addition to the current paradigm manipulating social complexity with the addition of non-kin neighbors, we should also endeavor to examine how individual variation in parental care (Kelly et al., 2020) shapes neurodevelopment in communal rodents such as the spiny mouse; alloparental care is common in this species (Tučková et al., 2016; Makin & Porter, 1984) and the presence or absence of alloparents in addition to biological parents may influence neurodevelopment. Work of this nature may demonstrate intergenerational effects that persist beyond even the lifespan of one individual [7]. Future work on the effects of social rearing in the charismatic spiny mouse and other communal rodents may prove critical in understanding the evolution of the neural mechanisms that promote large-group living.

Ethics approval statement

All experiments comply with ARRIVE guidelines and all procedures were approved by the Institutional Animal Care and Use Committee of Emory University. The IACUC oversees compliance with the Guide for the Care and Use of Laboratory Animals, Eighth Edition, published by the National Research Council of the National Academies (National Research Council 2011). Emory University is an AAALAC fully accredited institution (Association for Assessment and Accreditation of Laboratory Animal Care International).

CRediT authorship contribution statement

Kelly J. Wallace: Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Hasun Noh:** Investigation. **Anna I. Bautista:** Investigation. **Alixandra Green:** Investigation. **Aubrey M. Kelly:** Writing – review & editing, Writing – original draft, Visualization, Supervision, Project administration, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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.

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Data availability

Data are available upon request from the corresponding author.

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