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Early social deprivation shapes neuronal programming of the social decision-making network in a cooperatively breeding fish

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Abstract

The early social environment an animal experiences may have pervasive effects on its behaviour. The social decision-making network (SDMN), consisting of interconnected brain nuclei from the forebrain and midbrain, is involved in the regulation of behaviours during social interactions. In species with advanced sociality such as cooperative breeders, offspring are exposed to a large number and a great diversity of social interactions every day of their early life. This diverse social environment may have life-long consequences on the development of several neurophysiological systems within the SDMN, although these effects are largely unknown. We studied these life-long effects in a cooperatively breeding fish, *Neolamprologus pulcher*, focusing on the expression of genes involved in the monoaminergic and stress response systems in the SDMN. *N. pulcher* fry were raised until an age of 2 months either with their parents, subordinate helpers and same-clutch siblings (+F), or with same-clutch siblings only (−F). Analysis of the expression of glucocorticoid receptor, mineralocorticoid receptor, corticotropin releasing factor, dopamine receptors 1 and 2, serotonin transporter and DNA methyltransferase 1 genes showed that early social experiences altered the neurogenomic profile of the preoptic area. Moreover, the dopamine receptor 1 gene was up-regulated in the preoptic area of −F fish compared to +F fish. −F fish also showed up-regulation of GR1 expression in the dorsal medial telencephalon (functional equivalent to the basolateral amygdala), and in the dorsolateral telencephalon (functional equivalent to the hippocampus). Our results suggest that early social environment has life-long effects on the development of several neurophysiological systems within the SDMN.

KEYWORDS
cooperative breeding, developmental plasticity, dopamine receptor, early social experience, glucocorticoid receptor, social decision-making network

1 | INTRODUCTION

Developmental plasticity is a form of phenotypic plasticity that allows animals to adjust their phenotype to the environment experienced early in life (West-Eberhard, 2003). The early social environment can affect the development of a wide range of phenotypic traits, including social behaviour (reviewed in Kasumovic & Brooks, 2011; Taborsky, 2017), cognition (Vardi et al., 2020), and life-history traits such as dispersal decisions (Fischer et al., 2017; Gustafsson & Sutherland, 1988), survival (Albon et al., 1987; Dijkstra et al., 1990) and reproductive effort (Antunes & Taborsky, 2020; Naguib et al., 2006). During early development, animals are sensitive to environmental information, which may be used to reduce uncertainty about the current and the expected, future environmental conditions (Panchanathan & Frankenhuis, 2016) and to fine tune phenotypic development accordingly (English et al., 2016; West-Eberhard, 2003). In the social domain, phenotypic adjustments are expected to evolve when social conditions are variable but predictable (English et al., 2016). Accordingly, the absence of appropriate social cues during early life, such as during social deprivation, can have negative consequences for social behaviour in adult life. For example, animals raised without parents can show a severe deficit in emotional regulation and performance in social interactions (Bertin & Richard-Yris, 2005), and they can have a reduced ability to learn socially (Lévy et al., 2003).

The early social environment can lead to persistent modulations of brain gene expression, with effects on neurophysiological states and behavioural phenotype (Champagne & Curley, 2005; Seckl, 2004). Such "brain programming" occurs when environmental influences during development induce long-term modifications of tissues and neurophysiological systems (Seckl, 2004). In rats, low-quality maternal care received during early development induces a higher corticosterone response to stress, and a down-regulation of glucocorticoid (GC) receptors in the hippocampus (Liu et al., 1997). Early-life effects on constitutive gene expression and neurophysiological state are accompanied by changes in an animal's social behaviour (reviewed in Sandi & Haller, 2015). These changes in neurophysiological states are mediated by different concentrations of hormones, which act as behavioural modulators/facilitators (Oliveira, 2004). Developmental changes in hormonal states (basal levels) may alter the probability of expressing certain behaviours and could be responsible for life-history specializations. For example, early social life stress induces an increase of plasma testosterone and higher expression of androgen and oestrogen receptors in the hippocampus and behavioural masculinization of female guinea pigs (*Cavia aperea f. porcellus*; Kaiser et al., 2003a).

The vertebrate social decision-making network (SDMN) is a highly conserved network of interconnected brain nodes from the forebrain and midbrain that processes and integrates social information and regulates the expression of social behaviour (Newman, 1999; O'Connell & Hofmann, 2011, 2012). Gene expression changes caused by early-life social experiences have been quantified in single SDMN regions, such as in the hippocampus of rats (Liu et al., 1997) or in the medial preoptic area (MPOA) of guinea pigs (Kaiser et al., 2003). However, information is encoded in a distributed manner across the SDMN nodes, such that particular social behaviours are better explained by the overall pattern of activation of the network rather than by a single node's activity (Goodson & Kabelik, 2009). Therefore, to understand which role the SDMN plays in early-life effects on social behaviour phenotypes, we need to quantify multiple pathways regulating social behaviour within multiple SDMN nodes concurrently (Teles et al., 2016; Vindas et al., 2018). While the long-term effects on gene expression after nonsocial early-life stressors have been quantified in multiple nodes of the SDMN (Vindas et al., 2018), such analysis in the social domain has been lacking.

Here we studied the effects of early social experience on gene expression in four selected nodes of the SDMN of the cooperatively breeding cichlid *Neolamprologus pulcher*. In recent decades, *N. pulcher* has become a widely studied model system for social evolution and the study of the neuro-endocrine mechanism underlying sociality (Taborsky, 2016a, 2016b; Wong & Balshine, 2011). *N. pulcher* live in size-structured social groups with a linear hierarchy between dominants and subordinates (Taborsky, 1984, 2016a, 2016b; Taborsky & Limberger, 1981), and individualized relationships and individual recognition between group members (B. Taborsky et al., unpubl. data). Group members are involved in hundreds of sociopositive and aggressive social interactions every day, and making appropriate social decisions in these interactions is an important determinant of fitness (Arnold & Taborsky, 2010; Taborsky et al., 2012; Taborsky & Oliveira, 2012). In *N. pulcher*, early social experience influences an individual's social competence (i.e., the ability of an individual to optimize its social behaviour depending on available social information; Taborsky & Oliveira, 2012), and alters brain gene expression (Taborsky et al., 2013). Fish raised in socially deprived conditions, that is with sibling brood mates only (−F), showed less submission after being attacked by dominants (Arnold & Taborsky, 2010; Nyman et al., 2017) and their GC receptor 1 (*gr1*) gene was down-regulated in the telencephalon (Nyman et al., 2017, 2018) compared to fish raised in a social group with parents, subordinates and same-clutch siblings (+F, i.e., reflecting natural group compositions). Moreover, a transcriptomic analysis revealed that −F and +F fish differed in their neurogenomic state of stress, and that in −F fish 96% of the 45 differently expressed genes were down-regulated (Nyman et al., 2020). Finally, in *N. pulcher* social rearing conditions induce life-long specialization into two divergent life-history strategies. −F fish help more in their natal territory and disperse earlier, but invest less in reproduction when they become independent breeders, whereas +F fish behave more submissively, remain philopatric and invest more in reproduction (Antunes & Taborsky, 2020; Fischer et al., 2017).

We used 8-year-old *N. pulcher*, which had been either raised with parents, one helper and brood mates (+F) or with brood mates only (−F) (Fischer et al., 2017). We microdissected the dorsolateral telencephalon (DL; functional equivalent of the mammalian hippocampus), the dorsomedial telencephalon (DM; functional equivalent of the mammalian basolateral amygdala), the ventral

subdivision of the ventral telencephalon (VV; functional equivalent of the mammalian lateral septum) and the preoptic area (POA). These four SDMN nodes were selected because of their known key role in regulating social behaviour, and because their development is sensitive to early-life experiences (Champagne, 2010; O'Connell & Hofmann, 2011; Vindas et al., 2018). The SDMN is sensitive to several neuro-endocrine systems, which are all important players in social decision-making of vertebrates (reviewed in Soares et al., 2010), including monoamines, GC and sex steroid signalling, as well as the nonapeptide system (O'Connell & Hofmann, 2012). We quantified the constitutive expression of three genes belonging to the monoaminergic system, which determines the valence of social interactions (O'Connell & Hofmann, 2011), as well as three genes of the hypothalamic–pituitary–interrenal (HPI) axis, which is the teleost stress response system. Furthermore, we quantified the expression of the DNA methyltransferase 1 (*dnmt1*) gene across the four brain nuclei from the SDMN to test the hypothesis that DNA methylation is involved in stable gene expression differences. DNA methylation can generate stable epigenetic marks associated with variations in gene expression (Razin, 1998) in response to early-life experience (Champagne, 2010; Denis et al., 2011). For instance, in rats, the down-regulation of the GR gene induced by low-quality maternal care (Liu et al., 1997) was accompanied by a significantly increased DNA methylation in the promotor region of this gene (Weaver et al., 2004).

2 | MATERIALS AND METHODS

2.1 | Study species

Neolamprologus pulcher is a cooperatively breeding cichlid fish endemic to Lake Tanganyika living in stable social groups with a size-based hierarchy consisting of a dominant breeder pair and up to 20 subordinate individuals acting as alloparental brood care helpers (Taborsky, 2016a, 2016b). In its natural habitat, *N. pulcher* can live up to 6–8 years (A. Jungwirth et al., unpubl. data). Depending on population of origin, it reaches standard lengths (SL; i.e., the length between the tip of the snout and the end of the caudal peduncle) of up to 5.5–7 cm. Until sexual maturity, which occurs around an age of 1 year and an SL of 3.0–3.5 cm, all subordinate group members delay dispersal from their natal groups and help raise the dominants' offspring. Helping behaviours include direct brood care in the form of egg cleaning and oxygen provisioning by fanning, territory maintenance, and defence against predators and space competitors (Balshine et al., 2001; Bruintjes & Taborsky, 2011; Heg & Taborsky, 2010; Taborsky, 1984, 1985, 2016b). Some subordinates stay as helpers at the natal territory long after sexual maturity, whereas others disperse quite soon afterwards (Stiver et al., 2004). Severe predation risk is assumed to have selected for sociality in *N. pulcher* (Heg et al., 2004; Taborsky, 1984), with social group composition being driven by variation in predation pressure, social needs and conflicts of interest (Groenewoud et al., 2016) between group members over rank positions, which can lead to the eviction of group members (Dey et al., 2013; Taborsky, 1985).

The social conditions *N. pulcher* experience during the first weeks of life, that is being reared with or without guarding older group members or being reared in large (a pair and many helpers) or small (a pair and one helper) groups, shape the later social phenotype and life history trajectory of offspring (Arnold & Taborsky, 2010; Fischer et al., 2015, 2017; Taborsky et al., 2012). Although fry and adults/helpers do not have social interactions with one another (Arnold & Taborsky, 2010), fry are intensively guarded by older group members against predators and space competitors, which enhances their survival (Brouwer et al., 2005). Apparently fry obtain cues of safety by being guarded, which translates directly into social experience in *N. pulcher*, because guarded fry show more social peer-to-peer interactions with their brood mates compared to unguarded fry (Arnold & Taborsky, 2010). It has been proposed that this effect occurs because guarded fry need to spend less time being vigilant, which frees time for interacting socially with peers. These differences in early-life social experiences then give rise to the above-mentioned specialization into two divergent social phenotypes, a submissive, more philopatric type that invests more in eggs per reproductive event, and a dispersive helper type with low investment per reproductive event (Antunes & Taborsky, 2020; Fischer et al., 2017).

2.2 | Brain atlas

Cichlids exhibit a large variety in brain anatomy (Gonzalez-Voyer et al., 2009; Pollen et al., 2007). Hence, a workable two-dimensional brain atlas of *N. pulcher* is necessary to identify the focal nodes of the SDMN. The atlas was developed in collaboration with co-authors M.C.T. and R.O. at the Instituto Gulbenkian de Ciência, Oeiras, Portugal. This research project was ethically reviewed and approved by the ORBEA (Animal Welfare Body) of the Instituto Gulbenkian de Ciência, and by the Portuguese National Entity that regulates the use of laboratory animals (DGAV - Direção Geral de Alimentação e Veterinária). All experiments conducted on animals followed Portuguese (Decreto-Lei no. 113/2013) and European (Directive 2010/63/EU) legislations concerning housing, husbandry and animal welfare. Surgeries were performed under MS222 anaesthesia, and every effort was made to minimize suffering. Four *N. pulcher* (two males and two females) were transcardially perfused, first with a phosphate-buffered saline solution (PB 0.2 M), to clear the vasculature, followed by a solution of paraformaldehyde (PFA, 2%) to fix the tissue, which killed the deeply anaesthetized fish. After the perfusion, the brains were removed from the skull, post-fixed for 1 h in PFA (2%) and transferred to a formalin solution (10%). After fixation, brains were dehydrated (Leica TP1020) and embedded in paraffin before they were cut into coronal sections at 10 µm and mounted on glass slides. The sections were then deparaffinized for 10 min at 70°C, rehydrated and stained with a Nissl staining protocol. After staining, the sections were dehydrated and coverslipped with DPX mounting medium (Merck; Simões et al., 2012). The brain regions of

N. pulcher were identified using the published *Oreochromis mozambicus* brain atlas as a guideline (Simões et al., 2012). We marked and identified the regions of interest within the forebrain and midbrain.

2.3 | Husbandry and rearing background of experimental fish

Early-life manipulations, rearing and the subsequent brain analyses were approved by the Veterinary Office of the Kanton Bern, Switzerland (licence no. BE 93/18). All fish used in the experiments were bred and housed at the Ethological Station Hasli of the Institute of Ecology and Evolution, University of Bern (licence no. BE 4/11, Veterinary Office of the Kanton Bern). The individuals used in this experiment were reared in two early social environments, either (i) with parents, one helper and same-aged siblings (+F treatment), or (ii) with same-aged siblings only (−F treatment). The early-environment treatments were applied for 62 days after larvae had reached the free-swimming stage, which occurs at 10 days of age (Fischer et al., 2017). Subsequently to the early-environment treatments, fish from all treatments were kept in same-age sibling groups in 100-L tanks. At an age of 200 days, all fish were subcutaneously tagged with coloured Visible Implant Elastomer (VIE) tags (Northwest Marine Technology Inc.) in the dorsal and caudal region. Tag colour and position (dorsal/caudal) were specific to the rearing treatment, parents-of origin and any previous tests the fish were used in. After the tagging, same-sex fish from a +F and a −F group were placed together in a 200-L tank. They were kept in these tanks for 8 years until their brains were taken for this experiment. All tanks were equipped with a 2-cm sand layer and a biological filter. The light–dark cycle was set to 13:11 hr with a 10-min dimmed light period in the morning and evening simulating the light conditions of Lake Tanganyika. Fish were fed *ad libitum* with commercial flake food TetraMin 5 days a week and frozen zooplankton at 1 day a week. Water temperature was maintained at 27 ± 1°C.

2.4 | Experimental fish

Twenty fish were microdissected, 10 −F and 10 +F fish, balanced for the two sexes within each treatment. As mentioned above, all experimental fish were kept in similar holding and social conditions after the early-life treatment for 8 years (±2 months). Experimental fish originated from a total of 14 independent breeding pairs (males: from 10 different pairs; females: from nine different pairs). Siblings from this laboratory population were individually marked after being used for other experiments, allowing the identification of an individual's history of usage during previous experiments. Whenever possible we used naïve fish for the current study, not used for any behavioural test over their lifetime. Seven out of the 20 fish used in this experiment have been used in a previous behavioural test that served to measure their cortisol levels (Antunes et al., 2021); from these seven fish there were four +F females, one −F female, one +F male and one −F male. After that test these fish had been back in their home tank for over 45 days and left undisturbed; this previous experience was included in our statistical analysis (see Statistical analysis).

2.5 | Candidate nodes of the SDMN

The hippocampus (functional equivalent of the DL in teleosts) plays an important role in learning, formation of episodic memories and mediating rewards. Early social experiences alter the expression of genes in this brain node from the HPI axis and dopaminergic system (Champagne, 2010; O'Connell & Hofmann, 2011). The basolateral amygdala (functional equivalent of the DM in teleosts) is involved in emotional behaviour (LeDoux, 2000; Moreno & González, 2007) and emotional learning (Portavella et al., 2002) using inputs from several sensory modalities. The lateral septum (functional equivalent of the VV in teleosts) is crucial for encoding stimulus salience and it is associated with the regulation of emotional reactivity and goal-orientated behaviours (O'Connell & Hofmann, 2011). The development of the VV is sensitive to early-life stress (Vindas et al., 2018), and maternal separation increases vasopressin$_{1A}$ receptor binding in rats (Lukas et al., 2010). The POA regulates a wide variety of social behaviour, such as aggression, sexual behaviour and parental care (O'Connell & Hofmann, 2011). Maternal care quality and the stability of the early social environment alter the expression of sex steroid receptors in the MPOA (Champagne et al., 2006; Kaiser et al., 2003b).

2.6 | Tissue collection and RNA extraction

Fish were killed with an overdose of MS222 (Sigma-Aldrich) and decapitated within 2 min after catching them from their home tanks. Fish heads were embedded in Tissue-Tek (optimal cutting temperature compound, OCT; Sakura), rapidly frozen on dry ice and stored at −80°C until further processing. Subsequently, using disposable R35 microtome blades (Feather) fish heads were sectioned in the coronal plane at 250 µm using a Hyrax C 60 cryostat (Carl Zeiss) and mounted on glass microscope slides. Microdissections were performed under a WILD M3C stereoscope using a 24G sample corer tool (Fine Science Tools) while microscope slides were placed on a cold plate (±−25°C). The collected tissue was combined per brain region per individual in DNA/RNA Shield (Zymo Research) and stored at −80°C until further processing. To lyse the tissue, a Proteinase K digestion was performed for 2 h at 55°C. Total RNA was extracted in accordance with the protocol for the Quick-RNA MicroPrep kit (Zymo Research). To prevent genomic DNA contamination, RNA samples were treated with DNase I (Zymo Research) during the isolation procedure. After the extraction, RNA was quantified using a QuBit RNA HS assay kit (ThermoFischer Scientific) following the company's protocol on a QuBit 2.0 fluorometer machine (ThermoFischer Scientific; sample RNA concentration ranged from 10 to 236 ng µl^{-1}). RNA extractions were unsuccessful in 12 out of

80 samples. RNA samples were reverse transcribed to cDNA using an iSCRIPT cDNA synthesis kit (Bio-Rad).

2.7 | Candidate genes

To study the effects of early social environment on the development of the selected SDMN nuclei, we analysed the constitutive expression of six genes belonging to two signalling pathways. (i) For the monoaminergic pathway, we analysed the expression of the dopaminergic receptors *drd1* and *drd2*, and the expression of the serotonin transporter (*sert*). The *drd1* gene regulates aggression (mammals: Bondar & Kudryavtseva, 2005), reward perception and learning (fish: Messias, Paula, et al., 2016; Messias, Santos, et al., 2016), whereas the *drd2* gene regulates aggression, social bonds, partner preference and learning (mammals: Young & Wang, 2004). In *N. pulcher*, *drd2* modulates aggression, submission and affiliative behaviour (D. F. Antunes et al., unpubl. data). The *sert* gene is responsible for removing serotonin from the synaptic cleft, determining the magnitude and duration of the influence of serotonin on its receptors (Holmes, 2008; Puglisi-Allegra & Andolina, 2015). Expression of *sert* is associated with dominance in fish; dominant zebrafish up-regulate *sert* expression (Filby et al., 2010). (ii) For the HPI axis, we analysed the expression of *gr1*, mineralocorticoid receptor (*mr*) and corticotropin releasing factor (*crf*). The *gr1* gene is the orthologue to the mammalian *gr* (Arterbery et al., 2011) and is a key component for vertebrate stress responses. It is involved in the negative feedbacks leading to a shutdown of cortisol production and thus the termination of stress responses (Rothuizen et al., 1993). Early social deprivation causes *gr1* downregulation in *N. pulcher* (Nyman et al., 2017). The *mr* gene, which has a 10-fold higher sensitivity to GCs than *gr*, is involved in regulating basal cortisol concentrations (Greenwood et al., 2003). In fish, *crf* expression stimulates the excretion of GCs from the POA in response to stressors, and it has effects on the anterior pituitary (Joëls & Baram, 2009). Early-life manipulation of the HPI axis, by exposing juveniles to cortisol or *gr* antagonist, caused an up-regulation of *mr* and down-regulation of *crf* in the telencephalon of *N. pulcher* (Reyes-Contreras et al., 2019). Furthermore, early social deprivation induced an upregulation of *crf* in whole brain analyses of *N. pulcher* (Taborsky et al., 2013). To investigate if the differences in constitutive gene expression were associated with stable DNA methylation, we analysed the expression of *dnmt1*, which is responsible for the maintenance of DNA methylation marks (Denis et al., 2011; Yi & Goodisman, 2009). Early social experience induces differential expression of DNMT1 in the hippocampus in rodents (reviewed in Champagne, 2010). All genes were analysed for all four selected SDMN nodes, except *crf*, which was only quantified in the POA, because we were mostly interested in the stimulating effect of *crf* on GC production, which occurs in this brain node. The expression of 18s was quantified as a house-keeping gene (Kasper et al., 2018; Nyman et al., 2017).

2.8 | Gene phylogenies

Gene phylogenies for *dnmt1*, *sert*, *drd1*, *drd2* and *crf* were preformed to analyse their homology between *N. pulcher*/*Neolamprologus brichardi* sequences and other vertebrate groups. Sequences from *N. brichardi* were used because for this species an annotated genome is available (Brawand et al., 2015), and *N. brichardi* is closely related to *N. pulcher*; they belong to the same species complex (Brawand et al., 2015; Duftner et al., 2007). Sequences for DNMT1, SERT, Drd1, Drd2 and CRF from humans (*Homo sapiens*), Norway rats (*Rattus norvegicus*), domestic hens (*Gallus gallus*), African clawed frogs (*Xenopus laevis*), green anoles (*Anolis carolinensis*), zebrafish (*Danio rerio*) and the cichlid *N. brichardi* were obtained from the National Center for Biotechnology Information (NCBI) GenBank. For information on the sequences used see Table S1). The sequences were aligned by CLUSTAL W and a neighbour-joining tree was calculated with 5000 bootstrappings, and the evolutionary distances were calculated by the maximum composite likelihood method (Tamura et al., 2004) using MEGA X (Kumar et al., 2018) (https://www.megasoftware.net/). All ambiguous positions were removed for each sequence pair (pairwise deletion) and the final data set had a total of: *dnmt1*: 105,121 positions; *sert*: 6850 positions; dopamine receptors: 9447 positions and *crf*: 10,198 positions. The sequences of the *gr1* and *mr* genes of *N. pulcher* are homologous to those of all other major vertebrate taxa (O'Connor et al., 2013).

2.9 | Quantitative real-time PCR

Primers for *gr1*, *crf*, *mr* and 18s were as in Taborsky et al., (2013), whereas the primers for the other genes (*dnmt1*, *drd1*, *drd2* and *sert*) were designed using PRIMER-BLAST (NCBI) from the sequences of *N. brichardi* available at the NCBI GenBank. The primer sequences are given in Table S2. During the testing of the newly designed primers, PCR (polymerase chain reaction) products were sequenced and underwent BLAST (NCBI) to confirm their specificity to the targeted genes. To determine the amplification efficiency (E), the absence of primer dimers and the specificity of the amplification for each primer pair, quantitative PCR (qPCR) experiments and melting curves (50–90°C) were run using standard curves for 5 × 10-fold dilutions (of all brain RNA) in triplicate (Aubin-Horth et al., 2012). The primers (Microsynth) and 1 µl of sample cDNA was prepared on a 96-well plate (Greiner Bio-one) and used for a qPCR experiment using 5× HOT FIREPol EvaGreen qPCR Mix Plus ROX (Solis BioDyne) on an ABI PRISM 7000 (Applied Biosystems). All cDNA samples were run in triplicate together with no-template controls. To verify that only a single-amplified product was produced and to confirm the absence of primer dimers, melting curves were performed for each replicate. Cycle thresholds (Ct) for each sample were then used to calculate gene expression for each individual brain following the formula $\frac{1}{(1+E)^{Ct}}$. Relative expression was then normalized to the reference gene (18s) (Pfaffl, 2001).

2.10 | Statistical analysis

Statistical analyses were performed using the software R version 3.5.2. For some samples, gene expression data were not used for one or more genes because the coefficient of variation (CV) of the three replicates was too large and we removed them from the analysis (a CV cut-off of 5% was used as quality control). Principal component analyses (PCAs) were performed to reduce the complexity of the gene expression data set and thus to obtain a neurogenomic profile, that is a distinct gene expression profile in the brain reflecting early-life experiences (Robinson et al., 2008; Zayed & Robinson, 2012), (i) from all four SDMN candidate nodes and all individuals and (ii) for each SDMN node separately. The PCAs on all four nodes included all individual samples for the four SDMN nodes (POA: $N = 11$; VV: $N = 12$; DM: $N = 13$; DL: $N = 11$) with *sert*, *drd1*, *drd2*, *gr1* and *mr* as variables; only these five genes were quantified in all four SDMN nodes, using the R function "prcomp" from the package "stats" version 4.0.3. CRF was excluded from this PCA as its expression was solely quantified in the POA; *dnmt1* was also excluded from this analysis, because we only could use expression data of three individuals in the VV (see above). Loadings of each gene on each principal component (PC) were determined, and the PC scores for each individual fish were calculated. The separate PCAs on the four nodes included the following genes: PCA on POA: *sert*, *drd1*, *drd2*, *dnmt1*, *gr1*, *mr* and *crf*; PCA on VV: *sert*, *drd1*, *drd2*, *gr1* and *mr*; PCA on DM and PCA on DL: *sert*, *drd1*, *drd2*, *dnmt1*, *gr1* and *mr*. Using the package "lme4" version 1.1–23 (Bates et al., 2015), linear models (LMs) were fitted on the PC scores of the individuals to analyse the influence of the early social environment on neurogenomic profiles, when differences in the PCA were found by visual inspection. This was only the case for the POA.

The effects of early social environment treatments (+F and −F) on the expression of each gene within each SDMN candidate region were analysed by fitting linear mixed effects models (LMMs). All initial LMMs contained rearing treatment, previous usage in other studies (binary factor) and sex as fixed effects. Previous usage refers to the seven fish that were used in a previous experiment (mentioned above), to account for the effects of the additional experience of these fish. Sex and previous experience were removed from the initial model in the course of model simplification through backwards selection (Bates et al., 2015). To control for the genetic background (some experimental fish were bred from the same parents), parental identity was included as a random factor in all initial models. In the case that parental identity explained zero variation, the random term was removed and linear models were fitted (Bates, https://stat.ethz.ch/pipermail/r-sig-mixed-models/2014q3/022509.html). The assumptions of normality of the error term were checked by Shapiro–Wilk tests, and visual inspection of quantile–quantile plots of model residuals to detect skew and kurtosis, as well as Tukey–Anscombe plots to check for homogeneity of variance. Gene expression levels were log-transformed to fit normality assumptions. Outliers were identified and removed by calculating Cook's distance of the model residuals using the function "cooks.distance" from the package "stats" version 4.0.3. Forty-six outliers were removed out of 341 observations across the four SDNM regions.

TABLE 1 Loadings of the different genes on the first two principal components (PCs) of (a) a PCA on all four analysed SDMN regions together ($N = 52$), and (b) a PCA on the POA region only ($N = 14$)

SDMN node	Gene	PC1	PC2
(a) All SDMN regions	*sert*	0.450	−0.425
	drd1	0.477	−0.339
	drd2	0.494	−0.072
	gr1	0.474	0.307
	mr	0.313	0.776
	Variance explained	71.9%	18.8%
(b) POA	*sert*	0.414	−0.255
	crf	0.225	0.919
	drd1	0.406	−0.073
	drd2	0.414	−0.120
	dnmt1	0.391	−0.054
	gr1	0.422	−0.158
	mr	0.330	0.201
	Variance explained	77.5%	11.5%

3 | RESULTS

3.1 | Gene phylogenies

The DNA sequences for *dnmt1*, *sert*, *crf* and *drd1* and *drd2* from *Neolamprologus brichardi* were homologous to members of five vertebrate classes, including other teleost fish, amphibians, reptiles, birds and mammals (see Figures S1–S4).

3.2 | Early social environment effects on neurogenomic profiles

3.2.1 | Across SDMN nodes

We used PCA to analyse the variance in the neurogenomic profile (expression of five genes) across the individual data points in all four SDMN nodes ($N = 52$). The first two PCs explained 90.7% of the variance (PC1: 71.9%; PC2: 18.8%; Table 1). All five genes included in this analysis loaded positively on PC1 (*sert*, *drd1*, *drd2*, *gr1* and *mr*), whereas the monoaminergic pathway (*sert*, *drd1* and *drd2*) loaded negatively and the stress axis (*gr1* and *mr*) loaded positively on PC2. Plotting the neurogenomic profiles by SDMN node revealed that the four nodes overlapped along PC1 but clustered separately along PC2, indicating distinct neurogenomic profiles (Figure 1). Plotting the PCA scores separately by early social environment along PC1 and PC2, there were no apparent treatment differences (see Figure S5).

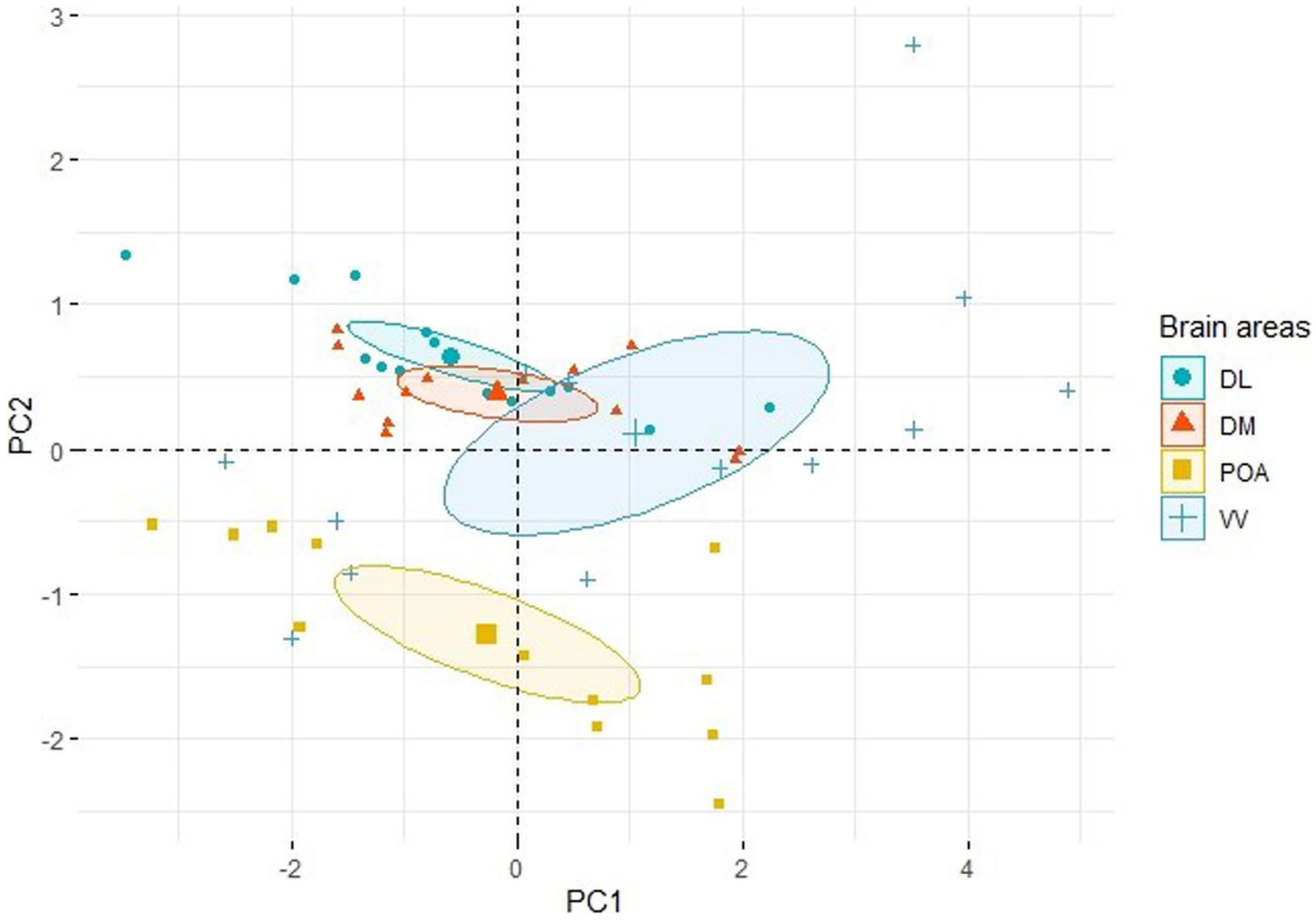

FIGURE 1 Gene expression profiles (neurogenomic profiles) along the first two principal components of the PCA for all four SDMN nodes together (see Table 1), plotted by brain node. Turquoise dots: dorsolateral telencephalon (DL); red triangles: dorsomedial telencephalon (DM); yellow squares: preoptic area (POA); blue crosses: ventral part of the ventral telencephalon (VV). Large symbols represent means along PC1 and PC2, while small symbols are the individual data points

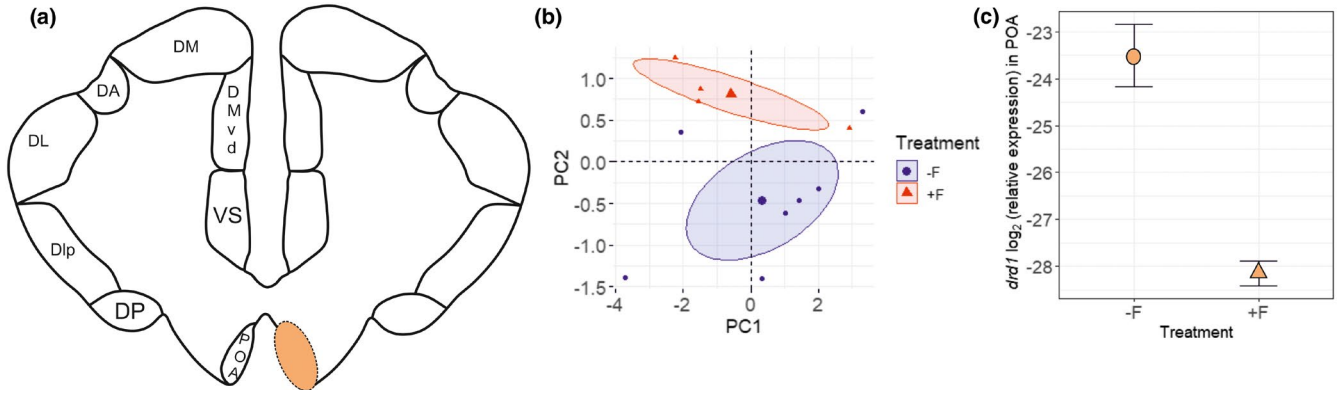

FIGURE 2 Effects of early social environment on neurogenomic profile and gene expression in the POA. (a) Schematic representation of *Neolamprologus pulcher* telencephalon and diencephalon including the POA (highlighted in orange). Brain region abbreviations: Dm, dorsomedial telencephalon; DA, dorsoanterior telencephalon; DL, dorsolateral telencephalon; DLp, posterior subdivision of the dorsal telencephalon; DP, posterior part of the dorsal telencephalon; POA, preoptic area; VS, supracommissural part of the ventral telencephalon; DMvd, ventral part of the dorsal subdivision of the dorsomedial telencephalon. (b) Relationship between the neurogenomic profiles along PC1 and PC2 of the PCA on the POA only, plotted separately by early-life treatment; blue circles: −F individuals, red triangles: +F individuals; larger symbols represent the mean values, while small symbols are individual data points. (c) Relative mean expression of the D1R gene in the POA for −F and +F individuals: means ± *SE* are shown; circle: −F; triangle: +F

3.2.2 | Within SDMN nodes

We further analysed the neurogenomic profiles of each of the four candidate SDMN regions separately using PCAs. Visual inspection of the PCA results showed that the neurogenomic profile of the POA differed between early social treatments along PC2, but not PC1 (LM on the PC2 scores: df =9; T = 3.05, p = .013, Figure 2b). The first two PCs explained 89.1% of the variance (PC1: 77.5%; PC2: 11.5%; Table 1). All seven genes loaded positively on PC1, whereas *sert*, *drd1*, *drd2*, *dnmt1* and *mr* loaded negatively and *crf* and *gr1* loaded positively on PC2. The neurogenomic profiles of the remaining three SDMN regions did not differ between fish from different early social environments (see Table S3, Figure S6).

3.3 | Early social environment effects on single gene expression

In fish reared without parents and a helper (−F), the *gr1* gene was up-regulated in the DM (Table 2; Figure 3c) and DL (Table 5; Figure 3d) relative to +F fish, but this gene did not differ in the other two SDMN regions (POA: Table 3; VV: Table 4). The *drd1* gene was up-regulated in the POA of −F fish (Table 3; Figure 2c) and tended to be up-regulated in −F fish in the VV (Table 4; Figure 3b). Early social environment did not influence the expression of *mr*, *drd2*, *sert* and *dnmt1* in the SDMN regions (DM: Table 2; POA; Table 3; VV: Table 4; DL: Table 5), or the expression of *crf* in the POA (Table 3).

4 | DISCUSSION

We analysed the neurodevelopmental effects of early social deprivation on the monoaminergic and stress response systems across four brain regions belonging to the SDMN to investigate the underlying neuronal mechanisms of early-life effects on social behaviour. We first established that the sequences for *sert*, *dnmt1*, *crf* and dopamine receptors of *Neolamprologus brichardi*, a congener of *Neolamprologus pulcher* belonging to the same species complex (Duftner et al., 2007), are homologous to the sequences from important vertebrate classes ranging from other teleost fish to humans. We then showed that early social experience can alter the neurogenomic profile regarding genes belonging to the HPI axis and monoaminergic system in the POA, as well as the expression of *gr1* in the DM and of *drd1* in the POA. *dnmt1* was not differently expressed between early-life treatments. Our results suggest that early social environment induced life-long neurophysiological reprogramming.

Early social deprivation from brood care by adults had life-long effects on the neurogenomic profile of the POA in *N. pulcher*. The POA has often been the focus of studies on the regulation of social and reproductive behaviours (Burmeister et al., 2005; Weitekamp et al., 2017) because of its projections to several regions of the limbic system (O'Connell & Hofmann, 2011). For instance, electrical stimulation of the POA elicits courtship behaviour and reduces aggression in bluegill sunfish (*Lepomis macrochirus*; Demski & Knigge, 1971). The development of the POA is sensitive to early-life experiences, as early-life stress caused by instability in social groups causes an up-regulation of oestrogen and androgen receptors in guinea pigs (Kaiser et al., 2003a). Here we showed that early social deprivation from adult care permanently alters the neurogenomic profile of the POA through changes in the monoaminergic and stress response systems. Such changes of the neurogenomic profile may alter the responsiveness of the POA through a change in the number of receptors (Oliveira, 2009), leading to long-lasting changes in behavioural states (Cardoso et al., 2015). Early social deprivation from adult care reduces social competence in *N. pulcher* reared in the −F treatment (Arnold & Taborsky, 2010; Nyman et al., 2017). The changes to the neurogenomic profile of the POA presented here could be responsible for the reduced social competence shown in previous studies. Furthermore, the life-long changes in the POA might be responsible for changes in physiological states, as the POA has projections to the hypothalamus (Folgueira et al., 2004), which regulates adenohypophysis activity (Wendelaar Bonga, 1997). Early social deprivation from adult care reduced the basal cortisol levels in *N. pulcher* reared in the −F treatment (Antunes et al., 2021); the neurogenomic profile alteration of the POA found in the current study might be responsible for maintaining these physiological state differences observed in our previous study.

Monoaminergic activity, particularly the activity of the dopaminergic and serotonergic systems, plays a crucial role in regulating behaviour (Soares et al., 2010; Winberg & Thörnqvist, 2016). In mice, for instance, short-term maternal separation up-regulates *drd1* in the hippocampus (Köhler et al., 2019), and females with smaller social networks show an up-regulation of dopaminergic production (Lopes & König, 2020). Similarly to other neurological systems, during early-life monoaminergic systems require appropriate social stimulation to achieve normal development. In our study, *drd1* expression in the POA was up-regulated in −F fish and *drd1* tended to be more highly expressed in the VV, whereas *drd2* and *sert* expression was not affected by the early-life treatment. In *N. pulcher*, −F fish are known to incur fewer social interactions than +F fish during their social experience phase in the first 2 months of life (Arnold & Taborsky, 2010), and to develop poorer social competence (Taborsky et al., 2012). These reduced numbers of social interactions during early development might have caused higher dopaminergic release during development in −F fish, and therefore might have impaired the ability of −F fish to determine the valence of social interactions. Indeed, in *N. pulcher* dopaminergic activity regulates social interactions by altering submission, aggression and affiliation within group members (D. F. Antunes et al., unpubl. data). Therefore, this impairment might be responsible for the reduced social competence reported in these fish (Fischer et al., 2017; Taborsky et al., 2012). Thus, we hypothesize that *drd1* activity is an important regulator of social competence. A more exhaustive study on the role of *drd1* activity on the regulation of social competence is necessary to confirm our hypothesis, using a combination of pharmacological manipulation of the dopaminergic system with a neuronal activity study.

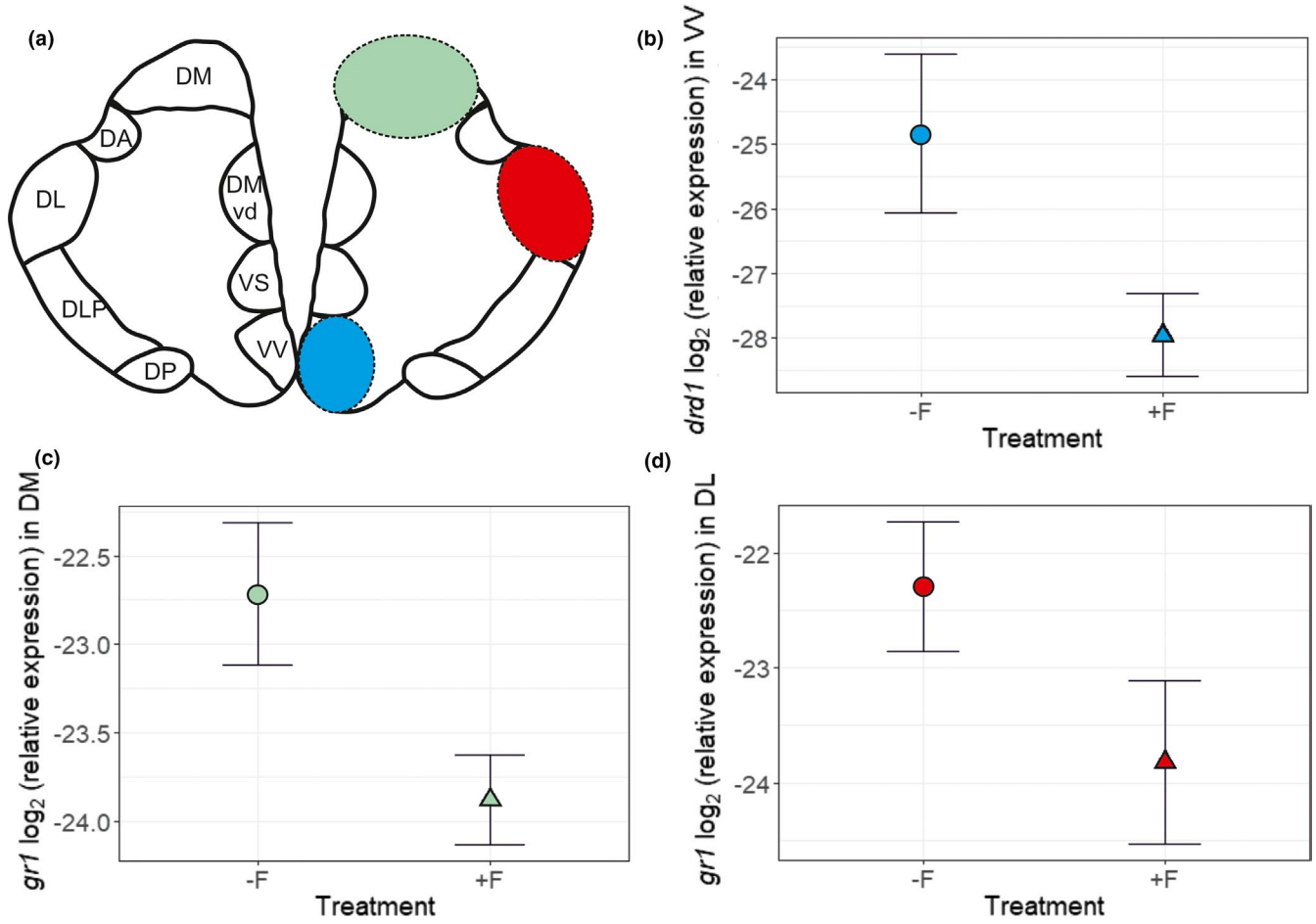

FIGURE 3 Early social environment effects on gene expression in the telencephalon. (a) Schematic representation of *Neolamprologus pulcher* telencephalon including the VV (lateral septum in mammals, in blue), DM (basolateral amygdala in mammals, in green) and DL (hippocampus in mammals, in red). Brain regions abbreviations: DM, dorsomedial telencephalon; DA, dorsoanterior telencephalon; DL, dorsolateral telencephalon; DLp, posterior subdivision of the dorsal telencephalon; DP, posterior part of the dorsal telencephalon; VV, ventral subdivision of the ventral telencephalon; VS, supracommissural part of the ventral telencephalon; DMvd, ventral part of the dorsal subdivision of the dorsomedial telencephalon. (b) Relative expression of the *drd1* gene in the VV for −F and +F individuals. (c) Relative expression of the *gr1* gene in the DM for −F and +F individuals. (d) Relative expression of the *gr1* gene in the DL for −F and +F individuals. In (b)–(d), means ± *SE* are shown. Circles: −F individuals: triangles: +F individuals

TABLE 2 Model results of the effects of early social experience on the relative expression of six candidate genes in the DM region

Gene	Factor	Estimate ± SE	*df*	*t*	*p*-value
gr1 (LM) *N* = 10	Treatment	−1.165 ± 0.545	8	−2.14	*.003*
sert (LMM) *N* = 13	Treatment	0.27 ± 1.687	6.9	0.16	.877
drd1 (LMM) *N* = 13	Treatment	−0.427 ± 1.4	5.6	−0.31	.771
drd2 (LMM) *N* = 12	Treatment	−0.94 ± 1.313	7.8	−0.72	.495
dnmt1 (LMM) *N* = 13	Treatment	−0.4 ± 0.584	7.1	−0.69	.515
mr (LMM) *N* = 11	Treatment	0.237 ± 1.079	4.8	0.22	.834

p-values < .05 are highlighted in italics.

The development of the HPI axis is under strong social influence (Spencer, 2017). Socially deprived vertebrates, including *N. pulcher*, can have lower GC baselines (Antunes et al., 2021) or extended stress responses (Clarke, 1993; Veenema, 2009), accompanied by lower expression of GC receptors (*gr1*) in the telencephalon (Nyman et al., 2017). Early social experience had life-long effects on the *N. pulcher* stress response axis, as the 8-year-old individuals used in this study had up-regulated expression of *gr1* in the DM and DL of −F individuals. The basolateral amygdala (i.e., the functional equivalent of the DM) is responsible for the regulation of anticipatory stress, and it plays a role in dampening the effects of chronic stress (reviewed in Jankord and Herman (2008)). In rats, maternal

TABLE 3 Model results of the effects of early social experience on the relative expression of seven candidate genes in the POA region

Gene	Factor	Estimate ± *SE*	*df*	*T*	*p*-value
gr1 (LM) *N* = 13	Treatment	−1.674 ± 1.358	11	−1.23	.194
sert (LMM) *N* = 12	Treatment	34.443 ± 268.185	6	0.13	.902
drd1 (LM) *N* = 9	Treatment	−4.649 ± 0.981	7	−4.74	*.0003*
drd2 (LMM) *N* = 12	Treatment	−2.859 ± 1.760	6.1	−1.62	.154
dnmt1 (LMM) *N* = 12	Treatment	−0.505 ± 0.653	6.2	−0.77	.467
crf (LM) *N* = 9	Treatment	0.381 ± 0.361	7	1.06	.249
mr (LMM) *N* = 11	Treatment	0.855 ± 0.579	4.4	1.48	.207

p-values < .05 are highlighted in italics.

TABLE 4 Model results of the effects of early social experience on the relative expression of five candidate genes in the VV region

Gene	Factor	Estimate ± *SE*	*df*	*t*	*p*-value
gr1 (LM) *N* = 11	Treatment	−0.367 ± 1.884	12	−0.19	.827
	Sex	7.108 ± 1.884	12	3.77	*.0006*
sert (LMM) *N* = 12	Treatment	−1.334 ± 1.798	7.2	−0.74	.481
drd1 (LMM) *N* = 11	Treatment	−3.502 ± 1.601	6.6	−2.18	.067
drd2 (LMM) *N* = 16	Treatment	−1.811 ± 2.563	9.1	−0.70	.497
mr (LMM) *N* = 11	Treatment	0.017 ± 0.010	5.9	1.68	.145

p-values < .05 are highlighted in italics.

TABLE 5 Model results of the effects of early social experience on the relative expression of six candidate genes in the DL region

Gene	Factor	Estimate ± SE	*df*	*T*	*p*-value
gr1 (LM) *N* = 11	Treatment	−1.776 ± 0.391	8	−4.538	*<.001*
	Previous experiences	−2.467 ± 0.391	8	−6.305	*<.001*
sert (LMM) *N* = 14	Treatment	0.063 ± 2.462	7.3	0.026	.98
drd1 (LMM) *N* = 12	Treatment	−1.983 ± 1.139	6.7	−1.74	.127
drd2 (LM) *N* = 13	Treatment	−0.757 ± 0.756	11	−1.001	.287
dnmt1 (LMM) *N* = 11	Treatment	−0.103 ± 0.768	7.9	−0.135	.896
mr (LMM) *N* = 13	Treatment	−0.061 ± 0.835	6.6	−0.074	.943

p-values < .05 are highlighted in italics.

separation during early development increased baseline corticosterone concentration and down-regulated intranuclear GR expression in the basolateral amygdala (Hegde et al., 2020). The hippocampus (i.e., the functional equivalent of the DL) plays an important role in mediating stress responses (Fuchs et al., 2001), due to its high concentration of receptors for GCs (de Kloet et al., 1998), and it modulates GC excretion through a negative feedback loop. The altered constitutive *gr1* expression of *N. pulcher* in the DM and DL might be the result of chronic stress from early-life social deprivation of adult care. Similarly to our results, in rats the quality of maternal care has long-term effects on the offspring's stress responsiveness and brain *gr* expression. Lower tactile stimulation by mothers leads to a higher stress responsiveness in offspring and a down-regulation of *gr* in their hippocampus (van Hasselt et al., 2012; Liu et al., 1997). The direction of early social stress on hippocampal *gr* expression might be species-specific, however, because it goes in opposite directions in fish and rats.

While our results are apparently in line with findings of whole brain analysis (Taborsky et al., 2013), the results from our study might seem contradictory to those of Nyman et al. (2017, 2018), who showed a *gr1* down-regulation in socially deprived *N. pulcher* when analysing the entire telencephalon. The difference between our and previous results is probably explained by the different specificity of the analysed regions in the two studies: here we found differences in the DM and DL, whereas the telencephalon analysed by Nyman et al. (2017, 2018) contains many different nodes of the SDMN (O'Connell & Hofmann, 2011), which may all have their own specific expression patterns of *gr1*. Analysing gene expression from whole brain might be beneficial for determining the overall neurogemonic state, but a further analysis of region-specific expression is necessary to nail down the effects of early-life experiences on neurodevelopment more precisely. Such region-specific expression differences have been documented previously in another fish species, the cichlid *Astatotilapia burtoni* (Greenwood et al., 2008).

Early social environment did not alter the expression of other stress-related candidate genes (*mr* and *crf*). Due to a whole genome duplication, *N. pulcher* has two GC receptors, *gr1* and *gr2* (Arterbery et al., 2011; O'Connor et al., 2013). Previous results showed that the early social environment alters expression of the *gr1* gene (Nyman et al., 2017; Taborsky et al., 2013), but not of the *gr2* gene in *N. pulcher* (Taborsky et al., 2013), which is why we focused only on *gr1* in this study.

The *dnmt1* gene was not differentially expressed between early social environment treatments. DNA methylation can generate stable epigenetic marks, which may persistently alter gene activity (Yi & Goodisman, 2009). The *dnmt1* gene is responsible for maintaining DNA methylation (Denis et al., 2011; Yi & Goodisman, 2009). For instance, DNMT1 expression regulates DNA methylation of the brain-derived neurotrophic factor in mice (*Mus musculus*) in response to early-life adversity (Kundakovic et al., 2015). We did not find evidence that the observed differences in early-life brain reprogramming could be regulated through the activity of *dnmt1*, which could be responsible for keeping DNA methylation stable. However, this does not mean that stable DNA methylation as a regulatory mechanism can be excluded, as methylation could differ in the promotor regions of our genes of interest. A detailed DNA methylation analysis of the promotor regions of the differentially expressed genes would be necessary to exclude the role of stable DNA methylation on early-life reprogramming. Alternatively, other epigenetic or neural mechanisms might be responsible for the transcriptional differences between early-life treatments.

The current study highlights the importance of early social experience on brain development. Long-term early environment effects arise when the available information is most relevant to animals at an early stage (Panchanathan & Frankenhuis, 2016), leading to the development of phenotypes that are better adapted to the envisaged, future conditions (Dufty et al., 2002; Uller, 2008). Such predictive adaptive responses (PARs) may arise in environments with variable but autocorrelated conditions, in which the available information predicts later conditions (Fawcett & Frankenhuis, 2015). If we consider how the offspring might have perceived their early environment, the presence of parents in the +F condition could have provided early-life cues of higher local density and consequently higher future local competition, but also higher current safety due to the presence of adult individuals that defend them against predators (Brouwer et al., 2005). By contrast, the fish raised without parents (−F condition) received very little information regarding their current and future environment, making their early environment highly uncertain. Even though adult *N. pulcher* do not directly interact with the developing offspring (Arnold & Taborsky, 2010), the presence of adults during early ontogeny is important for the offspring to learn about the danger posed by heterospecific fish (Watve & Taborsky, 2019). In its natural setting, *N. pulcher* group sizes are very variable within a population ranging from three to 20 or more individuals, but group size is predictable across years (Heg et al., 2005). Similar to our treatment, *N. pulcher* offspring raised in larger groups show more submission than fish that were raised in smaller groups (Fischer et al., 2015), highlighting the importance of the presence of adults early in life. Therefore, plasticity in response to cues of rearing group size, mediated by the developmental reprogramming of neurophysiological systems regulating social interactions, could be adaptive. Group size and structure affect the number and diversity of social interactions of an individual (Kappeler, 2019; Kappeler et al., 2019; Rooke et al., 2020). Therefore, reprogramming of the dopaminergic system and HPI stress axis, which are crucial for regulating social interactions (Sandi & Haller, 2015; Skuse & Gallagher, 2009), should match future group size and social environment. We propose that socially induced PARs might be regulated through constitutive changes to the dopaminergic system and stress response axis.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTION

DFA, NAH and BT designed the study. DFA, MCT and RFO did the brain atlas. DFA, MCT and CF established the microdissection method and for the study species. DFA and MZ conducted the laboratorial work. DFA and BT analyzed the data. DFA wrote the first draft of the manuscript. All authors revised and edited the manuscript.

DATA AVAILABILITY STATEMENT

Data files with gene expression values have been deposited at Dryad (https://doi.org/10.5061/dryad.0p2ngf20m).

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