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Research article

Modulation of Adult Neuro- and Gliogenesis in the hyperpallium and mesopallium of pigeons (*Columba livia* f.d.)

Julia Mehlhorn [a,*], Ilias-Dimitrios Karlaftis [a], Serap Kurutas [a], Katrin Amunts [b,c], Svenja Caspers [a,c], Christina Herold [b]

[a] Institute for Anatomy I, Medical Faculty & University Hospital Düsseldorf, Heinrich-Heine-University Düsseldorf, Germany
[b] C. & O. Vogt Institute of Brain Research, Medical Faculty & University Hospital Düsseldorf, Heinrich-Heine-University Düsseldorf, Germany
[c] Institute of Neuroscience and Medicine (INM-1), Research Centre Jülich, Germany

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ABSTRACT

In birds, adult neurogenesis is more widespread compared to mammals. It has been linked to spatial cognition and behavioral flexibility relying on networks involving the hippocampus and the song system. However, its significance in other brain regions remains poorly understood. To test whether environmental and behavioral experiences differentially affect neurogenesis beyond those networks, we exposed adult pigeons (*Columba livia* f.d.) to different housing conditions and spatial-cognition related experiments after 5-bromo-deoxyuridine treatment to label active cell division. Pigeons received training in spatial-orientation tasks (operant chamber or homing) and were either housed permanently in a pigeon indoor loft or allowed to fly freely. Three months later, brains were collected and immunohistochemically processed to examine neuro- and gliogenesis in the meso- and hyperpallium, two regions relevant to sensory and associative processing with heterogeneous levels of adult cell generation. We show that training and housing conditions alter neurogenesis with specific regional effects. Training and outdoor experiences had stimulating effects, though not consistently. Adult gliogenesis showed a different pattern, with lowest levels observed in loft pigeons without training. The different experimental conditions further altered newborn cells in various ways along the anterior-posterior brain axis, with differences occurring primarily at posterior levels. Overall, the findings demonstrate that adult neuro- and gliogenesis represent a mechanism through which the brain integrates internal states and external experiences to dynamically adjust its functional organization.

1. Introduction

Adult neurogenesis involves the proliferation, differentiation, migration, and integration of new neurons into existing neural circuits, contributing to neural plasticity, learning, memory, and potentially brain repair [1–8]. In mammals, adult neurogenesis rates are low and presumably restricted to a few neurogenic niches: the subgranular zone of the hippocampal dentate gyrus and the subventricular zone (SVZ) of the lateral ventricles [9–11]. Additional studies have reported small hotspots of neurogenic activity in the mammalian hypothalamus, neocortex, amygdala, striatum and substantia nigra [11–13].

It has been reported that adult neurogenesis shows region-specific functional specialization: in the hippocampus, it appears to regulate specific aspects of cognitive and affective processing, whereas newborn neurons generated in the SVZ in birds have been shown to contribute to olfactory function and reproductive behavior [14,15]. However, the extent and functional significance of adult neurogenesis in other brain regions, not only in the human brain, remain subjects of ongoing research and debate [13]. Because cellular numbers are altered in neurodegenerative diseases, and stimulation of neurogenesis could potentially counteract or ward off disease or aging effects, the neurogenic niches have drawn a lot of attention. Still, the fact that adult mammalian neurogenic activity is weak and locally restricted has hampered research in this field [12]. Besides, conflicting findings have been reported in human studies, reflecting not only the limited availability of (healthy) brain tissue but also fundamental methodological constraints. Direct investigation of neurogenesis in the human brain is inherently challenging, as it relies largely on rare post-mortem tissue, which is often of variable quality and derived from individuals with heterogeneous life histories, limiting control over critical factors such as

* Corresponding author.
E-mail address: julia.mehlhorn@hhu.de (J. Mehlhorn).

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age, health status, and environmental exposure [16,17]. At the same time, non-invasive in vivo approaches currently lack the spatial and cellular resolution required to reliably detect and quantify newly generated neurons or to link them to specific functional outcomes. These limitations make it difficult to establish causal relationships or to systematically investigate the influence of individual variables [18]. Animal models remain indispensable because they enable controlled experimental manipulation, longitudinal analysis, and direct investigation at the cellular-level, thereby providing mechanistic insights that remain largely inaccessible in human studies.

In recent years, a growing number of researchers have turned their attention to alternative model organisms that display a distinct pattern of neurogenic activity - birds. Neuroscientific studies in several bird species have experienced a surge during the last decade and have helped to deepen our understanding of structural, functional and evolutionary processes shaping the vertebrate brain [19–25]. Even though the avian forebrain differs macroscopically from the mammalian forebrain, the underlying microstructure, including circuitry, cell morphology and cytoarchitecture, shows a high degree of similarity [21,26]. Thus, birds have turned into a valuable, complementary model system for neuroscientific research and have been proposed as suitable models for studying neurodegenerative processes that contribute to cognitive decline in humans [11,27,28].

Adult neurogenesis in birds was first demonstrated by Goldman and Nottebohm [29] in the high vocal center (HVC) of canaries using radioactively labelled thymidine. HVC is a specific forebrain nucleus of songbirds in the caudal nidopallium and newly generated neurons are seasonally recruited into HVC to support vocal motor learning, song repertoire modification, and social communication [8,29,30]. Studies on songbirds provided the first clear evidence that adult-born neurons functionally integrate into discrete, behaviorally relevant circuits Further studies verified neurogenesis during lifetime for a variety of bird species in nearly all telencephalic subdivisions with hotspots at the ventricular zones (VZ) [6,11,29,31,32]. This suggests that adult neurogenesis is a widespread phenomenon in this vertebrate class and that this form of plasticity appears to be a fundamental characteristic of the avian forebrain [33]. Barnea and Pravosudov [28] than pointed out that birds are a very suitable model system for studying adult neurogenesis - a view later reinforced by Herold and colleagues [11], who performed a comparative study of striatal adult neurogenesis in pigeons, mice, macaques and humans. All together, these findings provide an excellent opportunity to explore the basic biology and functional significance of adult neurogenesis.

To better understand how adult neurogenesis is influenced by environmental factors that shape region-specific brain plasticity, animal models are required in which cognitive challenges, behavior, and environmental stressors can be experimentally controlled while preserving biological relevance. In birds, a lot of neuroscientific studies have been conducted in pigeons, thus they became an important model organism in cognition research and neuroscience [34]. Previous brain morphological studies in pigeons have shown high levels of plasticity that depend on environmental conditions, particularly in areas crucial for spatial orientation. While Melleu et al. [6]. and Mazengenya et al. [35]. showed high numbers of proliferating cells in several brain regions of pigeons, research of our own group has delivered a detailed analysis of regional patterning of adult neurogenesis including maturation stages of diverse neuronal and glial cells along the anterior-posterior axis of the forebrain [11,29,32].

Meanwhile many external and internal factors have been identified that alter adult neurogenesis. For example, steroid hormones critically modulate song-related neuronal circuits in songbirds [33,36–39]. In male canaries, elevated testosterone increases neuron numbers in the HVC [30,33,40,41], while estrogens promote neuronal differentiation and migration [38]. Beyond that hormonal control, adult neurogenesis in the songbird forebrain is additionally dynamically driven by active vocal (motor) practice, social interactions, and seasonal environmental demands [37,42].

Another important factor is aging, which is associated with a marked decline in adult neurogenesis in songbirds [43], while physical activity enhances cell proliferation and neurogenesis, at least in mice, particularly in the hippocampus [44,45]. A stimulating environment, complex social structure and positive social experiences further promote adult neurogenesis in birds and mammals [42,46–51]. Chronic stress and elevated cortisol levels as well as social isolation inhibit adult neurogenesis and negatively affect various stages of neurogenesis, including the proliferation, differentiation, and survival of new neurons within both the song-control nuclei and the hippocampal formation [50–54].

However, it remains unclear how these factors interact with each another, how adult neurogenesis is regulated and what role it plays in brain plasticity and behavior. In songbirds adult neurogenesis is largely investigated within the compartmentalized context of specialized vocal control circuits, but it remains less clear how experience-dependent plasticity operates across non-vocal, broader sensory and associative pallial regions.

To disentangle specific effects of environmental or cognitive stimuli on adult neuro- and gliogenesis levels, we systematically studied the influence of different housing conditions and experimental trials in subregions of the hyper- and mesopallium of five groups of homing pigeons *(Columba livia* f.d.). Both regions are important for processing visual or other sensory-related information and had shown heterogeneous levels of adult cell generation in pigeons [32]. In addition, the different subregions of the hyperpallium, historically named avian “Wulst”, and the mesopallium, as part of the dorsal ventricular ridge (DVR), are involved in the integration and processing of sensory and other information, supporting spatial cognition, motor control and higher sensory functions [55–63]. Our experimental design was thus guided by specific functional predictions:

First, because the hyperpallium is generally involved in visual sensory processing and the densocellular hyperpallium, in particular, represents a key node within the thalamofugal visual pathway and serves as a link between the hyperpallium and the hippocampal formation [55,57,62], we predicted that tasks imposing high visual processing and spatial orientation demands, such as 2D discrimination tasks in operant chambers or 3D navigational homing, would generally enhance adult neurogenesis and selectively triggers the densocellular part of the hyperpallium relative to the apical and intercalated hyperpallium.

Second, given that the mesopallium acts as a multisensory integration hub and receives trigeminal somatosensory input from the beak during tactile interactions, we predicted elevated adult neurogenesis in the mesopallium in response to pecking-based cognitive training in an operant chamber.

Third, we expected free-flying birds to exhibit higher levels of adult neurogenesis compared to birds restricted to the loft. This prediction was based on the greater variety and complexity of sensory stimuli and environmental experiences encountered during free flight.

Fourth, we expected individual homing to represent the most challenging condition in terms of learning and spatial orientation and, consequently, to be associated with particularly high levels of adult neurogenesis.

By testing these region- and experience-specific expectations, we aimed to clarify whether adult neurogenesis operates as a uniform, widespread phenomenon or as a finely tuned cellular mechanism supporting localized, activity-dependent plasticity in the avian forebrain. Thereby, we presume that adult neurogenesis constitutes a central cellular mechanism through which the brain integrates internal states and external experiences to dynamically reorganize its functional architecture. Rather than representing a mere correlate of plasticity, it can be conceptualized as an evolutionarily conserved, development-like program that persists into adulthood to support ongoing adaptation. From this perspective adult neurogenesis emerges as a key substrate for cognitive flexibility, linking environmental demands to affective, emotional, and motivational processes. Accordingly, identifying how

specific experiential factors and distinct brain regions contribute to this process is essential for advancing a more mechanistic and functionally resolved understanding of brain plasticity beyond the current literature. To address this question, we carried out comparative analysis quantifying newly generated cells in the subregions of the hyperpallium and the mesopallium.

2. Material And methods

2.1. Animals, treatments and experimental conditions

Five groups of homing pigeons (*Columba livia* f.d.), in total 49 birds were analysed, were raised in the same loft. All pigeons were adults and between 10 and 19 months old. During the whole time, food and water were provided ad libitum. An overview of the different groups and conditions is presented in Table 1.

The Loft Control pigeons (LCG n = 10, 7 females, 3 males) stayed permanently in the loft without access to free outdoor flight and served as our control group. They had no experiences in pigeon races or behavioural experiments. The size of the loft (195 cm×190 cm x 200 cm) enabled the pigeons to fly inside.

The Loft + Box pigeons (LBG, n = 10, 4 females, 4 males, 2 unknown sex) stayed permanently in the loft, but had to complete a spatial learning task in a standard operant chamber (skinner box). Training in the operant chamber comprised spatial memory/orientation tasks (with geometric features and symbols as stimuli) which are established for testing orientation behaviour in a 2D space [64]. During learning a hand-shaping phase occurred, in which the animals were trained to obtain food from the dispenser. This was followed by an autoshaping procedure, in which the animals learned to peck at a neutral stimulus displayed on the touchscreen to receive food from the dispenser. The subsequent learning phase involved conditioning to a specific stimulus. During the test phase, various combinations and arrangements of geometric and color-stimuli were presented (see Mehlhorn and Rehkämper [64], for details). Depending on the animal's performance, the behavioural tests took about eight to twelve weeks (Table 1). The task was easy to perform and served solely as a two-dimensional learning task until a predefined criterion was reached (successful pecking in 32 out of 40 trials (80%)). The Outdoor + Loft + Box group (OLBG, n = 10, 4 females, 6 males) had daily access to free outdoor flight and participated in pigeon races facing distances from 25 to 300 km in their first year of life. In addition, they were trained in the same learning task as the LBG group.

Learning performance was analyzed retrospectively for both groups and no differences between groups were detected (General Linear Model, $F(1, 8) = 0.13$, $p = 0.723$).

The Outdoor + Loft + Homing group (OLHG, n = 10, 6 females, 4 males) had daily access to free outdoor flight and participated in pigeon races facing distances from 25 to 300 km in their first year of life. In addition, OLHG pigeons received individual homing training for three weeks, during which they were released alone rather than in a group, with three releases from each cardinal direction (12 flights in total) in a distance of 30 km from their home loft at initially unknown locations (Table 1).

Outdoor + Loft pigeons (OLG, n = 9, 5 females, 4 males) neither participated in races, nor received any spatial training or other behavioural experiments but had daily access to free outdoor flight. Parts of the data from the OLG are already published [32]. Data from BrdU/S100ß staining of the OLG were obtained from an additional group of pigeons that were housed under the same conditions as the OLG group, because this staining was incorporated into the study design at a later stage.

Before the beginning of experiments, all pigeons were initially injected i.m. with 5-bromo-deoxyuridine (BrdU; 50 mg/kg) on three consecutive days (Table 1). BrdU has been established as a reliable marker for adult newborn cells and the simultaneous use of cell-type specific markers allows the immunohistochemical identification of newly generated cells [65–69].

To cover the same experimental periods for all groups, BrdU injections of LCG and OLG pigeons were performed at the start of the regulated housing conditions and animals were perfused 10–12 weeks after injection to cover a comparable time frame to the other groups (see 2.3).

The study was approved by the Committee on the Ethics of Animal Experiments of the state of North Rhine-Westphalia, Germany (Ref. 84–02.04.2014.A345).

2.2. Immunohistochemistry

10–12 weeks after BrdU injection, all animals were euthanized with pentobarbital (70 mg/100 g) and immediately perfused with saline solution and 4% paraformaldehyde. Subsequently the brains were removed and postfixed overnight in 4% paraformaldehyde and 30% sucrose. After 24 h in cryoprotection (30% sucrose in phosphate buffer), the brains were frozen and completely serially sectioned in 40 μm thick coronal sections (Leica SM 2000R/Reichert-Jung, Germany). This resulted into ten series of sections per brain with 400 μm in between each section in each series for future storage.

For the investigation of adult-born mature neurons, glial cells and neuronal precursor cells, we used the following markers BrdU (anti-BrdU; 1:200; Abcam Cat# ab6326, RRID:AB_305426), NeuN (anti-NeuN; 1:1000; Millipore Cat# MAB377, RRID: AB_2298772), S100β (anti-S100β; 1:500; Abcam Cat# ab52642, RRID:AB_882426) and doublecortin (anti-DCX; 1:500; Abcam Cat# ab18723, RRID:AB_732011).

Neuronal Nuclei (NeuN) is a protein localized within the nuclei of neurons in regions of low chromatin density, as well as in the perinuclear cytoplasm and a reliable neuronal marker for mature neurons [70].

The S100 calcium-binding protein β (S100β) is a multifunctional protein expressed in the nucleus and cytoplasm, where it plays key roles

Table 1
Schedule for the experimental groups.

Pigeon group (G)/Week	1	2 - 9	10 - 12
Loft Control (LCG)	BrdU 3x	Living inside the loft	Perfusion
Loft + Box (LBG)	BrdU 3x	Geometric feature training	Perfusion
Outdoor + Loft + Box (OLBG)	BrdU 3x	Geometric feature training	Perfusion
Outdoor + Loft + Homing (OLHG)	BrdU 3x	Homing training	Perfusion
Outdoor + Loft (OLG)	BrdU 3x	Free flying	Perfusion

in cell cycle regulation and differentiation [71]. Within the brain S100ß is expressed in astrocytes and oligodendrocytes serving as a well-established marker for glial cells [72,73]. Triple-Staining with antibodies against BrdU, NeuN and S100ß allowed us to identify newborn adult neurons and glial cells (Fig. 1A-F).

DCX is a microtubule-associated protein that is expressed during the maturation of adult newborn neurons and thus in many advanced precursor cells or at an early post-mitotic stage of immature neurons [74–76]. It has been widely accepted as an indicator for adult neurogenesis and neuronal plasticity and serves as a valuable complement to BrdU labelling [68,77]. Here, larger, multipolar and triangular shaped cells (DCX-tri) represent a higher matured state compared to small, bipolar and ovoidal shaped cells (DCX-ov) (Fig. 1G+H).

For each analysis, relevant sections of one series (about 25–35 sections in total) were immunohistochemically processed for fluorescent triple-labelling detection of BrdU, NeuN and S100ß. A second series was processed for fluorescent double-labelling detection of doublecortin and BrdU. Each of the used sections was analysed/quantified for the meso- and hyperpallium and followed the protocol of previous studies [29,32]. All antibodies were validated by control rounds without the primary or the secondary antibody and confirmed specific binding in previous studies [29,32].

2.3. Data acquisition and analysis

The sections were scanned at 20x magnification with a fluorescent microscope system (AxioScan.Z1, Zeiss Germany) and analyzed using ZEN Blue Edition (Zeiss, Germany). The determination of atlas levels and delineation of brain regions for all sections was done in accordance with the *Stereotaxic atlas of the brain of the pigeon* [58] and publications by Atoji and Wild [78], Atoji et al. [57,79], and Herold et al. [80]. The following telencephalic brain regions were analysed (Fig. 2): apical part of the hyperpallium (HA), intercalated part of the hyperpallium (HI), densocellular part of the hyperpallium (HD) and mesopallium (M) as a whole. The area of each region was determined in mm^2. Using the ZEN counting tool, the immunoreactive cells BrdU +, BrdU + /NeuN +, BrdU + /S100ß +, DCX + (ovoidal (DCXov) or triangular (DCXtri) shaped) were counted manually for each individual region (Fig. 1). Thus, the cell density as a value for each region of the number of immunoreactive cells per mm^2 was determined. This number of immunoreactive cells/area (mm^2) was averaged for each analysed region for a regional-specific profile and different atlas levels to analyse anterior-posterior differences in neurogenesis.

For analysis of the anterior-posterior axis of the different regions, the number of immunoreactive cells was investigated for the following atlas

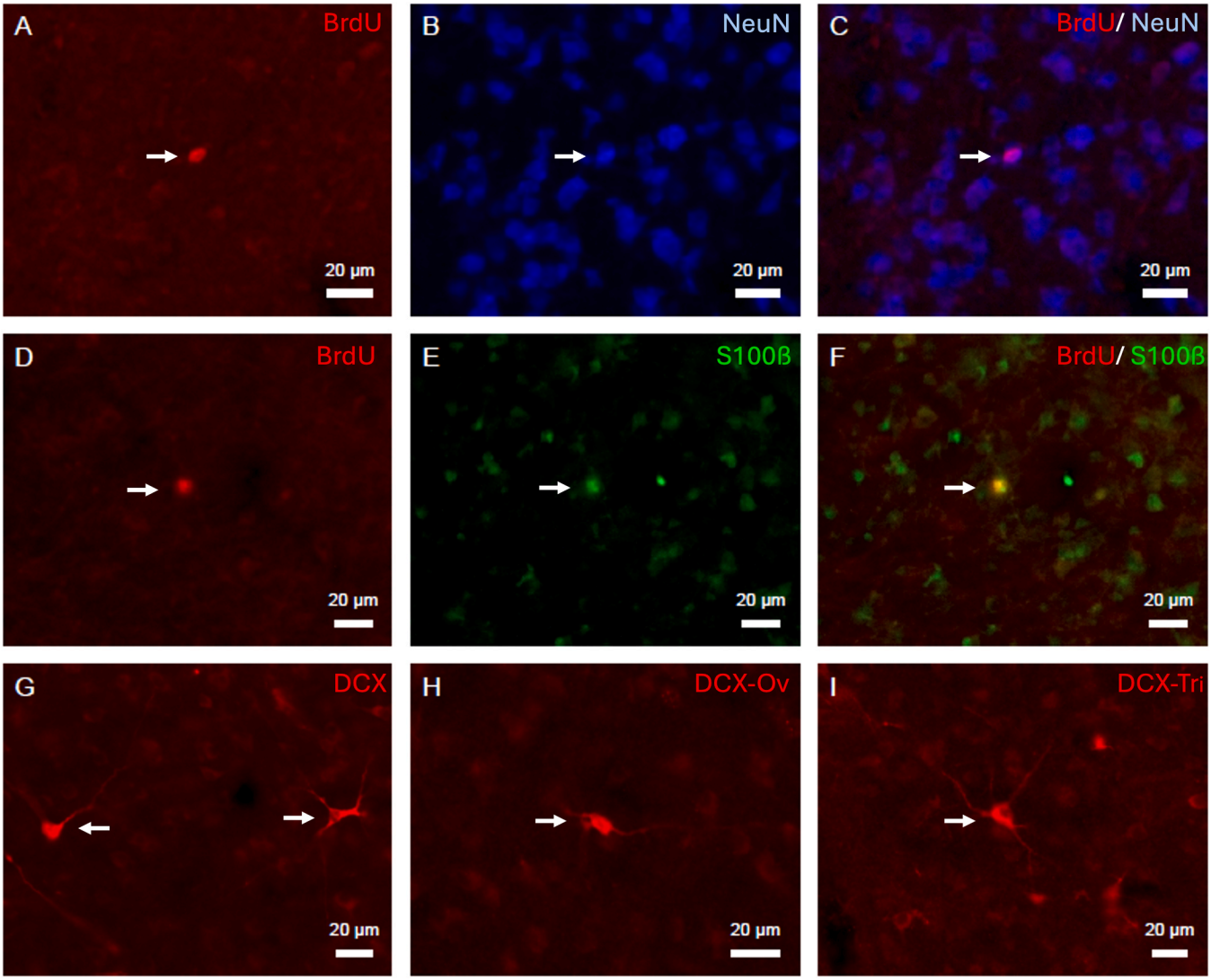


Fig. 1. Triple-labelling with BrdU, NeuN and S100ß (A-F) and DCX labelling (G-I) for identifying newborn and immature cells. A) + D) BrdU positive cell, B) NeuN positive cell, C) double labelled BrdU/NeuN positive cell, E) S100ß positive cell, F) double labelled BrdU/NeuN positive cell, G) DCX positive cells, H) DCX positive and ovoidal shaped cell, H) DCX positive and triangular shaped cell.

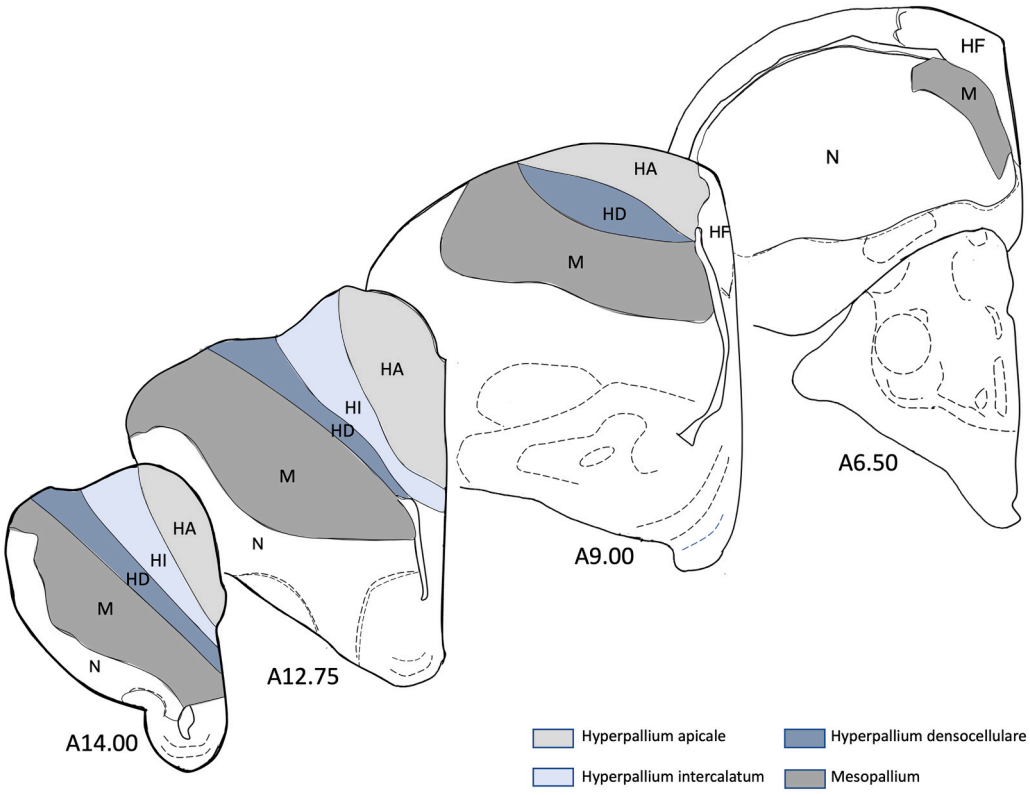


Fig. 2. Schematic illustrations of coronal sections through the left hemisphere of the pigeon brain, representing four atlas levels from anterior to posterior, highlighting the regions analyzed in this study. Atlas levels referring to Karten and Hodos [58].

levels (±500 μm, [58]): A 14.00, A 12.75, A 11.50, A 10.25, A 9.00 and A 7.75 (without HI). For M, data was investigated for the atlas levels (±500 μm) A 14.25; A 12.75; A 11.25; A 9.75; A 8.25; A 6.75; A 5.50.

For subsequent analysis of group differences, normal distribution of the data was tested using the Shapiro-Wilk test, revealing an inhomogeneous mixture of normally and non-normally distributed datasets for the different immunohistochemically processed markers and groups. Consequently, non-parametric tests were utilized for the analysis. For comparisons of cell densities between experimental groups, a Kruskal-Wallis test was used followed by pairwise comparisons using the Mann-Whitney U-test in case of significance. We adjusted the α level to account for multiple pair-wise tests using the Bonferroni correction; the α level was thus set to 0.005 (α = 0.05 / 10 tests) for pair-wise comparisons.

To investigate differences of cell densities between groups along the anterior-posterior axis, we used Linear Mixed Models. The atlas level was treated as a continuous variable to model linear spatial trends respectively comparing slopes between groups. Group (LCG, LBG, OLBG, OLHG, OLG) was included as a fixed between-subject factor, and the interaction between group and atlas level was specified to test for group-specific differences along the axis. Individual animals were included as a random intercept to account for inter-individual variability in baseline cell density. To model the correlation between repeated measurements within individuals across atlas levels, an autoregressive covariance structure of order 1 (AR (1)) was used to account for decreasing correlations between measurements with increasing distance across atlas levels. Pairwise differences between group-specific slopes were assessed by re-parameterizing the mixed-effects model with different reference categories and by evaluating linear contrasts of fixed-effect estimates. For visualization, model-based predicted values (fixed effects only) were extracted from the linear mixed-effects model. Given the significant group × atlas level interaction, post hoc comparisons were conducted to assess group differences at individual atlas levels using estimated marginal means and Bonferroni correction for multiple testing ($p < 0.05$) as implemented in the post-hoc procedure of the statistical software SPSS.

The statistical analysis of the data sets was carried out using the software package SigmaPlot/SigmaStat version 12.0 (Systat Software Inc., USA) and IBM SPSS Statistics, Version 31.0 (IBM Corp., USA). Figs. 5 and 7 were prepared using the AI-assisted tools ChatGPT and NotebookLM.

3. Results

3.1. Region-specific changes of neurogenic cell activity in different pigeon groups

In all analysed brain structures independent of group, BrdU labelled cells (newly generated cells per se), newborn neurons (BrdU/NeuN double labelling) and newborn glial cells (BrdU/S100ß double labelling) were found (Figs. 3 and 4, Table 2, Table S1). The same applies to immature neurons, i.e. DCX labelled cells. All investigated brain regions showed DCX positive cells, including the more matured, multipolar, triangular-shaped DCX-positive cells and the less matured, bipolar, ovoidal-shaped DCX-positive cells (Figs. 3 and 4, Table 2, Table S1).

The numbers of cells for each neurogenic marker in cells/mm^2 for each structure is presented in Table 2 and corresponding bar charts (Fig. 3). For greater clarity, the differences of the means between the groups are visualized in matrices (Fig. 4). Fig. 4 shows the pairwise group comparisons as semi-diagonal matrices. Each matrix displays the p-value and the exact difference between the means (row minus column, green: difference is positive, red: difference is negative). The more intense the color tone, the greater the difference compared to the reference group. Generally, the overall comparison of cell densities among all groups and cell types revealed significant differences in the analysed brain regions based on Kruskal-Wallis tests. Post-hoc pairwise

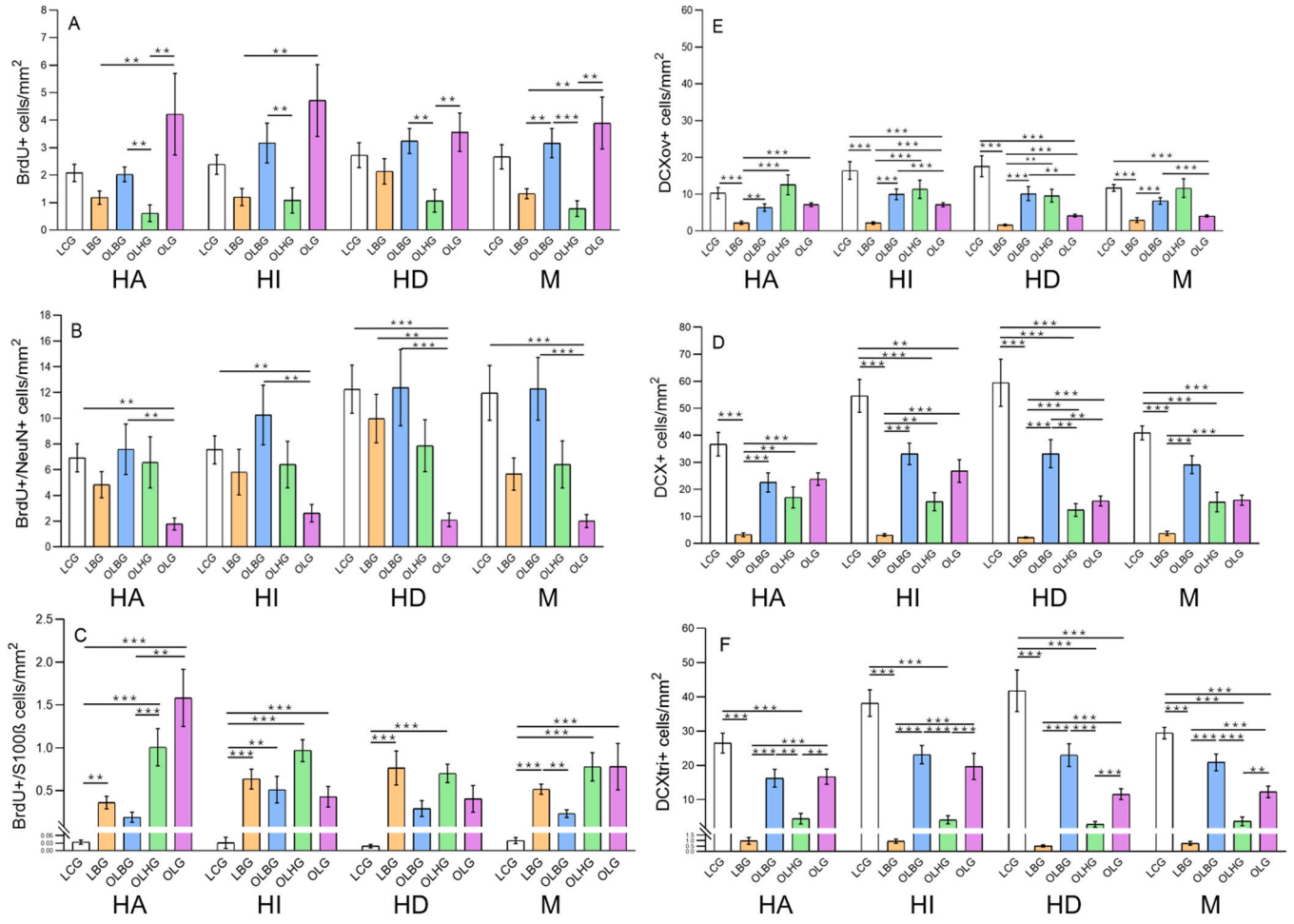


Fig. 3. Distribution of immunoreactive cells/mm^2 of five different pigeon group in four different regions of the telencephalon. (A) BrdU + , (B) BrdU + /NeuN + , (C) BrdU + /S100ß + , (D) DCX + , (E) DCXov + (ovoidal shaped cells), (F) DCXtri + triangular shaped cells. Y axis in (C) and (F) is built with two segments for better visualization ((C) break at 0.07 cells/mm^2, (F) break at 1.6 cells/mm^2). HA Hyperpallium apicale, HD Hyperpallium densocellulare, HI Hyperpallium intercalatum, LBG Loft + Box group, LCG Loft Control group, OLG Outdoor + Loft group, OLBG Outdoor + Loft + Box group, OLHG Outdoor + Loft + Homing group, M Mesopallium. Bars represent mean ± SE. Asterisks indicate significant differences (Mann-Whitney U-test, **$p < 0.01$, ***$p < 0.001$).

comparisons using Mann-Whitney U tests then revealed several significant pairwise differences between the individual groups and between the analysed regions (Figs. 3, 4, Table 2). The detailed statistical outcomes are presented in Table S1, while the following text focuses only on the main differences.

As mentioned above, regional differences were evident in absolute cell densities across the four analysed pallial subdivisions. However, several consistent group-specific patterns were observed. For BrdU-positive cells, densities were consistently highest in the Outdoor + Loft group and lowest in the Outdoor + Loft + Homing group across all four regions. In contrast, the distribution of newborn neurons showed an opposite pattern, with the Outdoor + Loft + Box group generally exhibiting the highest densities, whereas the Outdoor + Loft group showed markedly lower values and consistently represented the lowest group across the four regions. For newborn glial cells, densities were highest in the two outdoor groups, Outdoor + Loft and Outdoor + Loft + Homing, while the Loft Control group consistently showed the lowest values across all three hyperpallial regions and the mesopallium. A particularly highly consistent pattern was observed for immature neurons (DCX-positive cells). Across all four regions, the Loft Control group exhibited the highest DCX-positive cell densities, whereas the Loft + Box group showed by far the lowest values. The same group-specific pattern was also evident for the DCXov and DCXtri populations. Thus, despite substantial regional variation in the absolute densities of the different cell populations, the relative ranking of the experimental groups was remarkably consistent across the hyperpallial subregions and the mesopallium.

Overall, the intercalated and densocellular hyperpallium mostly showed higher densities of newborn neurons (BrdU/NeuN-positive cells) than the apical hyperpallium, with densocellular hyperpallium displaying particularly high values in the Loft Control group, the Loft + Box group and the Outdoor + Loft + Box group. In contrast, BrdU-positive cells lacking additional markers were relatively similar across the four regions, although densities tended to be somewhat higher in the intercalated hyperpallium and mesopallium in the Outdoor + Loft group and somewhat lower in the whole hyperpallium and mesopallium in the Outdoor + Loft + Homing group (Fig. 3, Table 2). In all analysed brain regions except the densocellular hyperpallium the Outdoor + Loft group showed significantly more BrdU + cells compared to the Loft + Box group (Figs. 3, 4, Table 2, Table S1).

Generally, all hyperpallial regions as well as the mesopallium showed the lowest number of new neurons in the Outdoor + Loft group and the highest density in the Outdoor + Loft + Box group (Fig. 3, Table 2). Both groups were kept under identical conditions, but the Outdoor + Loft + Box group additionally performed the spatial task in the Skinner box. The Outdoor + Loft + Box group, together with the Loft Control group, exhibited higher numbers of newborn neurons and pronounced differences in the densocellular hyperpallium and mesopallium compared to the apical hyperpallium and intercalated hyperpallium (Figs. 3, 4, Table 2, S1).

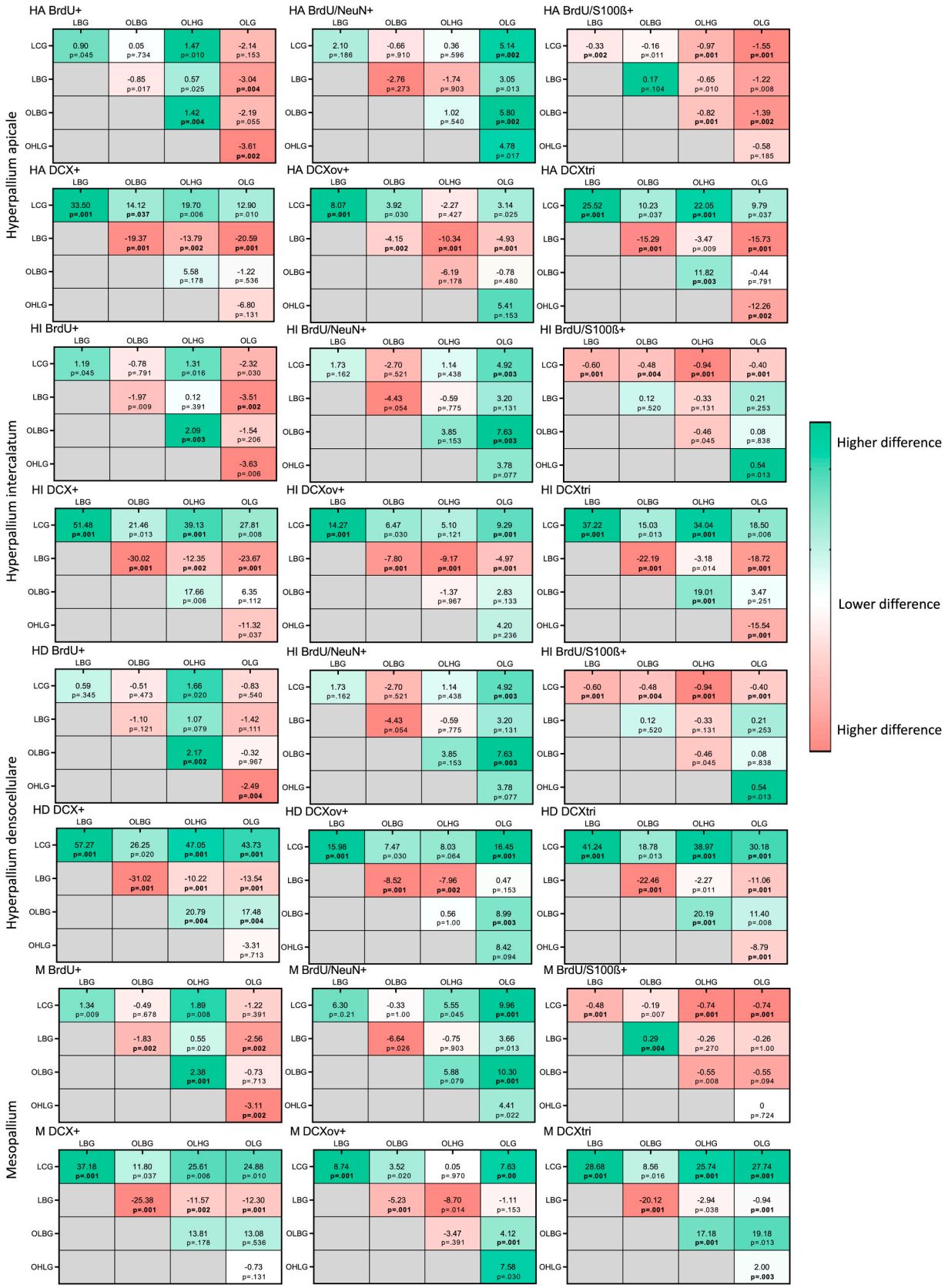


Fig. 4. Distribution of immunoreactive cells/mm^2 of five different pigeon groups in four different regions of the telencephalon. Each matrix displays the p-value and the exact difference between the means (row minus column, green: difference is positive, red: difference is negative). HA Hyperpallium apicale, HD Hyperpallium densocellulare, HI Hyperpallium intercalatum, LBG Loft + Box group, LCG Loft Control group, OLG Outdoor + Loft group, OLBG Outdoor + Loft + Box group, OLHG Outdoor + Loft + Homing group, M Mesopallium. Significant p-values in bold, the α-level was set to $p < 0.005$).

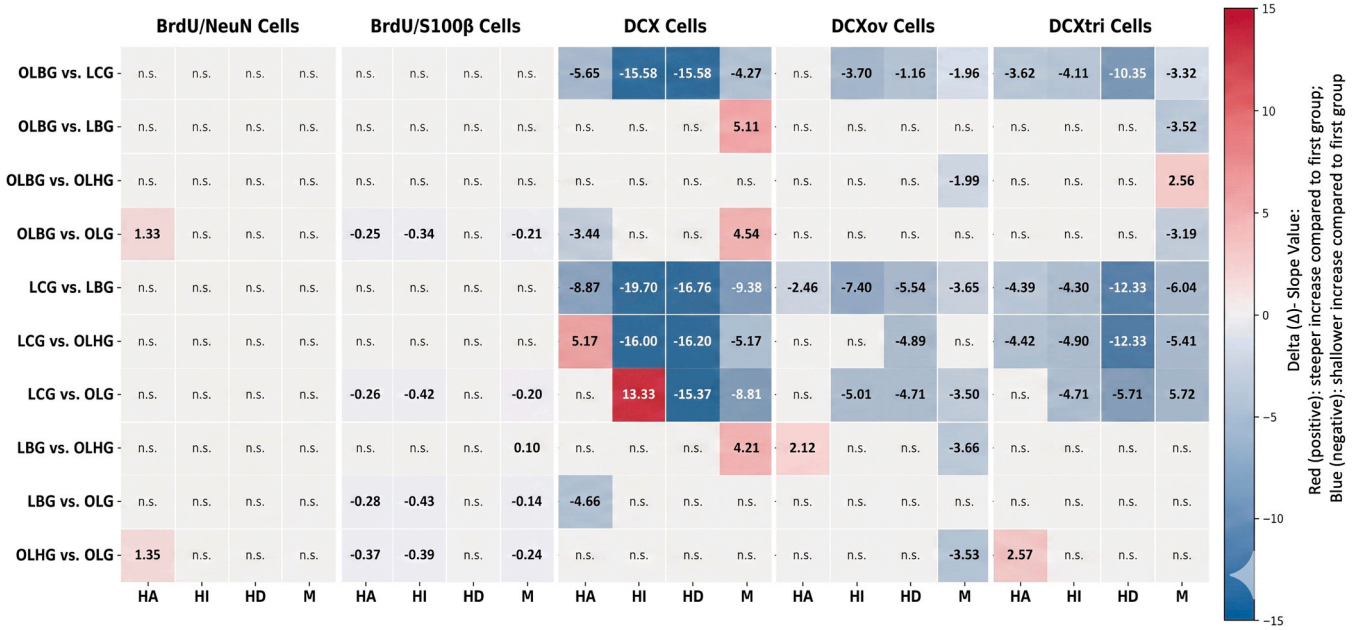


Fig. 5. Pairwise group comparisons of rostrocaudal cell density gradients (Δ-slopes) across brain structures and cell types. The multi-panel heatmap displays the model-based Δ-slope values derived from the linear mixed-effects model analyzing cell density changes across different atlas levels from rostral to caudal. Each panel represents a distinct cell marker or combination: BrdU/NeuN (newborn neurons), BrdU/S100ß (newborn glial cells), DCX (immature neurons), DCXov (ovoidal shaped, less matured immature neurons), and DCXtri (triangular shaped, more matured immature neurons). Rows represent the ten unique pairwise group comparisons, and columns the analyzed brain regions: Hyperpallium apicale (HA), Hyperpallium intercalatum (HI), Hyperpallium densocellulare (HD), and Mesopallium (M). The divergence color scale indicates the direction and magnitude of the difference in linear slopes between the first-listed and second-listed group in each row comparison: Red (positive) Δ-slope values indicate a steeper increase (or less pronounced decrease) in cell density across atlas levels from rostral to caudal in the second-listed group compared to the first-listed group. Blue (negative) Δ-slope values indicate a shallower increase (or more pronounced decrease) in cell density in the second-listed group compared to the first-listed group. n.s.: non-significant difference after post-hoc test. HA Hyperpallium apicale, HD Hyperpallium densocellulare, HI Hyperpallium intercalatum, LBG Loft + Box group, LCG Loft Control group, OLG Outdoor + Loft group, OLBG Outdoor + Loft + Box group, OLHG Outdoor + Loft + Homing group, M Mesopallium. This figure was prepared using the AI-assisted tools NotebookLM.

The distribution of BrdU/S100β-positive cells showed a different regional pattern and the number of newly generated glial cells was generally lower compared to newborn neurons or BrdU + cells. The highest densities were found in the apical hyperpallium of the Outdoor + Loft group and the Outdoor + Loft + Homing group (Fig. 3, Table 2). Furthermore, in the mesopallium, the Loft + Box group showed significant higher levels of newborn glial cells compared to the Outdoor + Loft + Box group (Figs. 3, 4, Table 2, S1). In all analysed regions the Loft Control Group showed the lowest densities of newborn glial cells. This became evident in comparison with all other groups for all regions except the Outdoor + Loft + Box group.

The highest density of immature neurons was found in the intercalated and densocellular hyperpallium, whereas the apical hyperpallium and the mesopallium showed lower values. The most pronounced differences to the other groups were observed in the Loft Control Group, while the lowest cell density was found in the Loft + Box group (Figs. 3, 4, Table 2, S1). The Loft Control group showed significant more DCX positive cells than the Loft + Box group in all regions, except in the apical hyperpallium, compared to the Outdoor + Loft + Homing group and the Outdoor + Loft. The Loft + Box group not just displayed significantly fewer DCX-positive cells than the Loft Control group, but also compared to all other groups and nearly all other analyzed structures. Additionally, in the densocellular hyperpallium, the Outdoor + Loft + Box group exhibited higher numbers of immature neurons compared to the Outdoor + Loft + Homing group and the Outdoor + Loft group (Figs. 3, 4, Table 2, S1). In the apical hyperpallium, the highest cell density of ovoidal shaped DCX + cells was observed in the Outdoor + Loft + Homing group and the lowest in the Loft + Box group compared to all other groups. In the other regions the expression pattern was different. Here, the highest number of DCXov cells was found in Loft Control individuals and the lowest again in Loft + Box individuals. Additionally, in the densocellular hyperpallium, as well as in the mesopallium, the Outdoor + Loft + Box group displayed a higher number of cells than the Outdoor + Loft group (Figs. 3, 4, Table 2, S1). The number of triangular shaped DCX positive cells exceeded the number of ovoidal shaped cells in the Loft Control group, the Outdoor + Loft + Box group and the Outdoor + Loft group (Figs. 3, 4, Table 2, Table S1). In the other two groups (Loft + Box group and Outdoor + Loft + Homing group), we determined more ovoidal shaped cells. The highest density of DCXtri cells was found in in all regions in the Loft Control group and the lowest cell density in the Loft + Box group. Accordingly, we found the most pronounced differences here compared to the other groups. In contrast to the number of ovoidal shaped cells, where the Outdoor + Loft + Homing group showed higher counts than the other three groups with outdoor flying opportunities, this group exhibited lower numbers for DCXtri (Figs. 3, 4, Table 2, S1).

3.2. *Cell densities along the rostrocaudal axis*

3.2.1. *Group-specific differences across atlas levels*

To estimate the differences across the rostro-caudal axis, a linear mixed-effects analysis was performed at different atlas levels from rostral to caudal. Here, the delta (Δ)-slope represents the difference in the linear slopes of all the pairs of groups. A multi-panel heatmap of these pairwise interactions across all brain regions and cell types had been compiled to provide a compact visualization (Fig. 5). It displays the model-based Δ-slope values derived from the linear mixed-effects model analyzing cell density changes across different atlas levels from rostral to caudal. The divergence color scale indicates the direction and magnitude of the difference in linear slopes between the first-listed and second-listed group in each row comparison: red (positive) Δ-slope values indicate a steeper increase (or less pronounced decrease) in cell

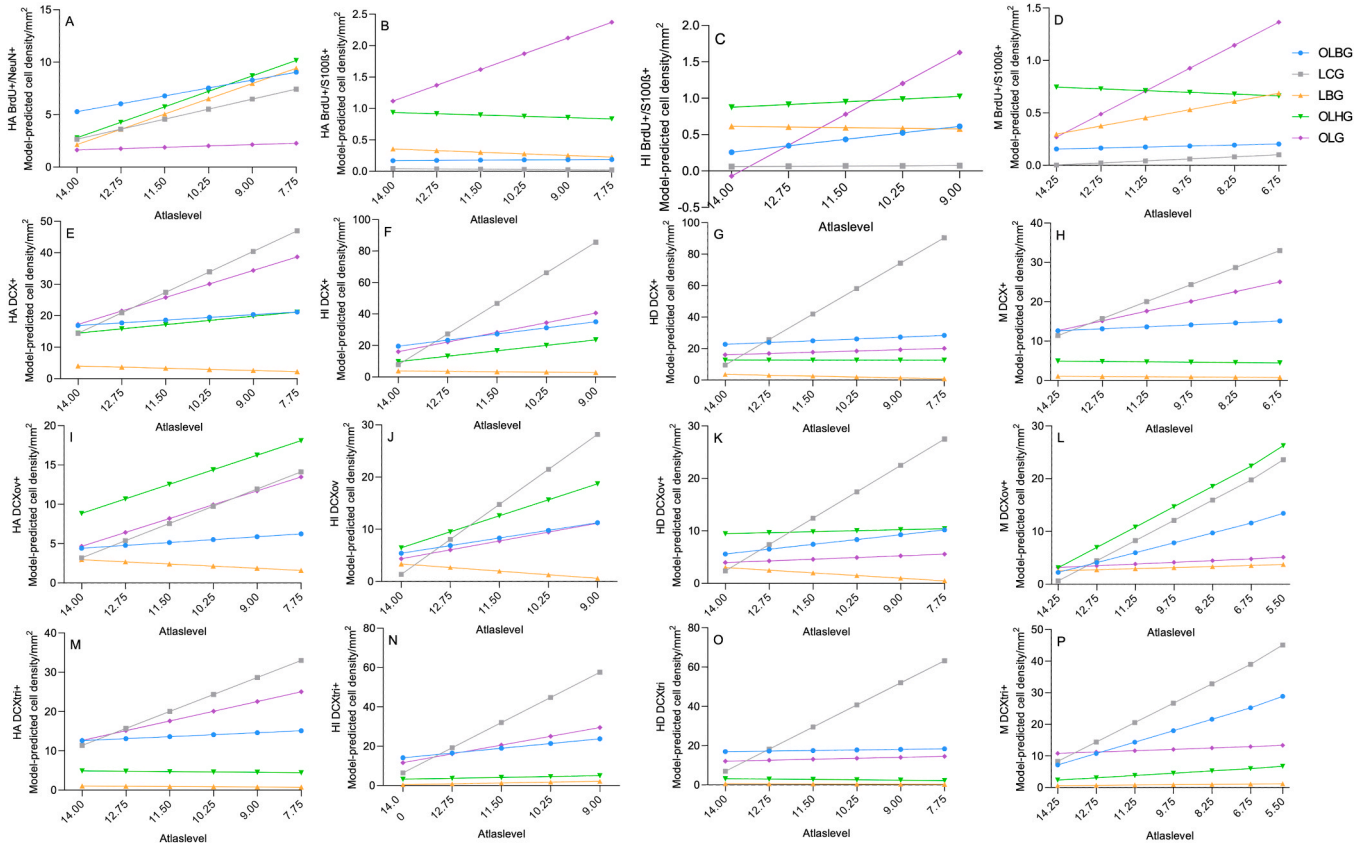


Fig. 6. Model-based predicted values from the fixed effects of the linear mixed-effects model for the rostrocaudal axis. Lines represent model-predicted cell density (Y-axis) across atlas levels derived from the linear mixed-effects model. HA Hyperpallium apicale, HD Hyperpallium densocellulare, HI Hyperpallium intercalatum, LBG Loft + Box group, LCG Loft Control group, OLG Outdoor + Loft group, OLBG Outdoor + Loft + Box group, OLHG Outdoor + Loft + Homing group, M Mesopallium. Statistical results see text and Table S1.

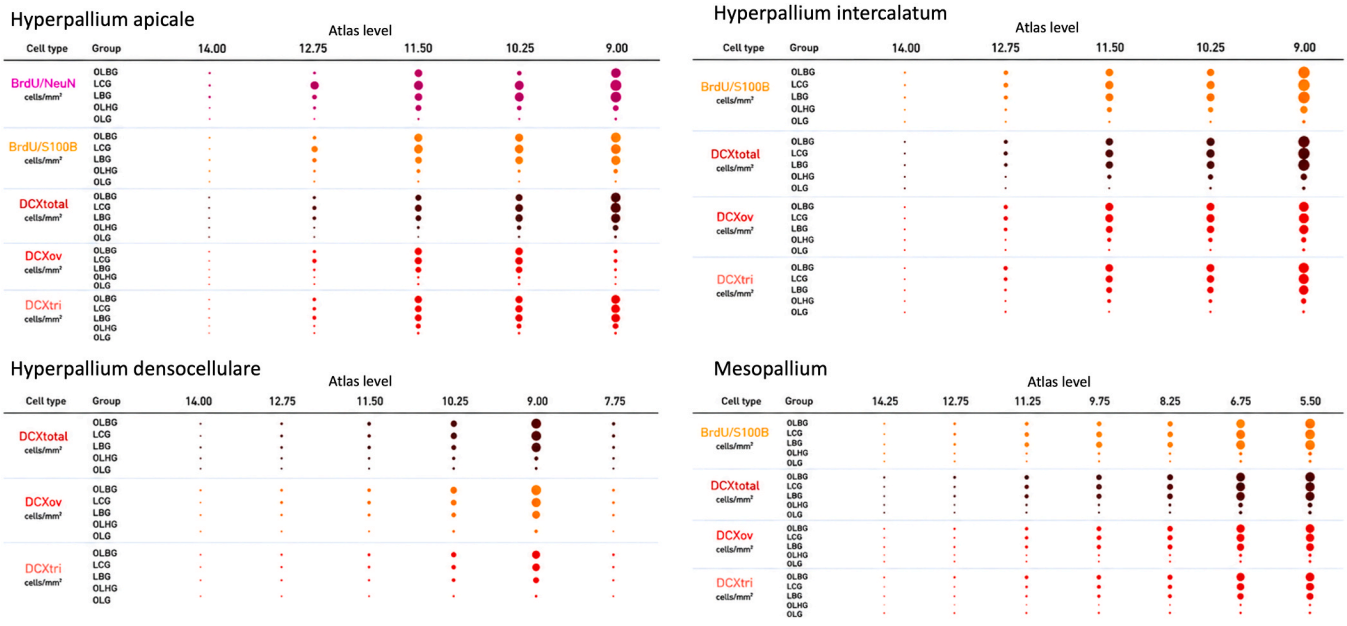


Fig. 7. Dot-density grid of the spatial distribution of adult neurogenesis and gliogenesis markers along the rostrocaudal axis. The dot plots illustrate the densities (cells/mm²) of the cell markers across different atlas levels for the Hyperpallium apicale, Hyperpallium intercalatum, Hyperpallium densocellulare, and Mesopallium. The size of each dot is proportional to the cell density in the respective region and group. LBG Loft + Box group, LCG Loft Control group, OLG Outdoor + Loft group, OLBG Outdoor + Loft + Box group, OLHG Outdoor + Loft + Homing group. This figure was prepared using the AI-assisted tool ChatGPT.

density across atlas levels from rostral to caudal in the second-listed group compared to the first-listed group. Blue (negative) Δ-slope

Table 2
Distribution of BrdU + , BrdU + /NeuN + , BrdU + /S100ß + , DCX + , DCXov and DCXtri cells/mm^2 in different telencephalic regions of five pigeon groups: LBG Loft + Box group, OLG Outdoor + Loft group, OLBG Outdoor + Loft + Box group, OLHG Outdoor + Loft + Homing group, HA Hyperpallium apicale, HD Hyperpallium densocellulare, HI Hyperpallium intercalatum, LCG Loft Control group, M Mesopallium. Values are mean ± SEM.

BrdU cells without any other marker/ mm^2					
	LCG	**LBG**	**OLBG**	**OLHG**	**OLG**
HA	2.08 ± 0.3	1.18 ± 0.2	2.03 ± 0.3	0.61 ± 0.3	4.22 ± 1.5
HI	2.39 ± 0.4	1.20 ± 0.3	3.17 ± 0.7	1.09 ± 0.5	4.71 ± 1.3
HD	2.73 ± 0.5	2.14 ± 0.5	3.24 ± 0.5	1.07 ± 0.4	3.56 ± 0.7
M	2.67 ± 0.5	1.33 ± 0.2	3.16 ± 0.5	0.78 ± 0.3	3.89 ± 0.9
BrdU/NeuN cells/ mm^2					
	LCG	**LBG**	**OLBG**	**OLHG**	**OLG**
HA	6.93 ± 1.1	4.83 ± 1.0	7.58 ± 2.0	6.57 ± 2.0	1.79 ± 0.5
HI	7.55 ± 1.1	5.82 ± 1.7	10.25 ± 2.3	6.40 ± 1.8	2.62 ± 0.7
HD	12.25 ± 1.9	9.98 ± 1.9	12.37 ± 3.0	7.86 ± 2.0	2.10 ± 0.5
M	11.96 ± 2.1	5.66 ± 1.2	12.30 ± 2.4	6.41 ± 1.8	2.00 ± 0.5
BrdU/S100β cells/ mm^2					
	LCG	**LBG**	**OLBG**	**OLHG**	**OLG**
HA	0.03 ± 0.0	0.36 ± 0.1	0.19 ± 0.1	1.01 ± 0.2	1.58 ± 0.3
HI	0.03 ± 0.0	0.63 ± 0.1	0.51 ± 0.2	0.97 ± 0.1	0.43 ± 0.1
HD	0.02 ± 0.0	0.76 ± 0.2	0.29 ± 0.1	0.70 ± 0.1	0.40 ± 0.2
M	0.04 ± 0.0	0.52 ± 0.1	0.23 ± 0.0	0.78 ± 0.2	0.78 ± 0.3
DCX cells/ mm^2					
	LCG	**LBG**	**OLBG**	**OLHG**	**OLG**
HA	36.70 ± 4.4	3.201 ± 0.7	22.58 ± 3.6	17.00 ± 3.9	23.80 ± 2.3
HI	54.59 ± 6.1	3.101 ± 0.5	33.13 ± 4.0	15.46 ± 3.3	26.78 ± 4.2
HD	59.42 ± 8.7	2.15 ± 0.3	33.17 ± 5.2	12.37 ± 2.4	15.69 ± 1.8
M	40.89 ± 2.6	3.71 ± 0.8	29.09 ± 3.4	15.28 ± 3.6	16.01 ± 1.9
DCXov cells/ mm^2					
	LCG	**LBG**	**OLBG**	**OLHG**	**OLG**
HA	10.28 ± 1.5	2.21 ± 0.5	6.37 ± 1.0	12.56 ± 2.7	7.14 ± 0.5
HI	16.43 ± 2.4	2.17 ± 0.4	9.97 ± 1.4	11.34 ± 2.5	7.14 ± 0.5
HD	17.62 ± 2.8	1.63 ± 0.2	10.15 ± 1.9	9.59 ± 1.8	1.17 ± 0.4
M	11.71 ± 0.9	2.97 ± 0.7	8.19 ± 0.9	11.66 ± 2.6	4.08 ± 0.3
DCXtri cells/ mm^2					
	LCG	**LBG**	**OLBG**	**OLHG**	**OLG**
HA	26.50 ± 2.9	0.98 ± 0.3	16.27 ± 2.6	4.45 ± 1.5	16.71 ± 2.2
HI	38.17 ± 3.9	0.95 ± 0.2	23.14 ± 2.7	4.13 ± 1.2	19.67 ± 3.8
HD	41.76 ± 6.1	0.52 ± 0.1	22.98 ± 3.3	2.79 ± 0.9	11.58 ± 1.6
M	29.43 ± 1.7	0.75 ± 0.2	20.87 ± 2.5	3.69 ± 1.3	12.26 ± 1.7

values indicate a shallower increase (or more pronounced decrease) in cell density in the second-listed group compared to the first-listed group. Fig. 6 represents the model-based predicted cell densities across atlas levels, given a significant group × atlas level interaction. Detailed values, including statistical outcomes, are listed in Table S2 and S3. Comparable to paragraph 3.1., the following text focuses on the main differences supplemented by the detailed statistical values.

There are no significant differences in the slope or density of BrdU-positive cells (newborn cells, but not neurons or glial cells) along the rostral-caudal axis between groups (Table S3). This means that the spatial distribution of BrdU positive cells across atlas levels is similar between groups ($p > 0.05$).

The comparison of the regression lines of the different groups for *BrdU/NeuN positive cells (newborn neurons)* revealed significant differences in the apical hyperpallium (Figs. 5, 6, Table S2, S3). Here, the increase of cell density from rostral to caudal was less steep in the Outdoor + Loft group compared with the Outdoor + Loft + Box group and Outdoor + Loft + Homing group.

The data for *BrdU/S100ß positive cells (newborn glial cells)* showed significant rostrocaudal gradients in all analysed regions except the densocellular hyperpallium (Figs. 5, 6, Table S2, S3). Most notably, the Outdoor + Loft group showed a stronger increase of the density of BrdU/S100ß positive cells from rostral to caudal in all analysed brain regions (except the densocellular hyperpallium) and compared to all other groups. Additionally, in the mesopallium, the Outdoor + Loft + Homing group showed a steeper rostrocaudal gradient compared to the Loft + Box group (Figs. 5, 6, Table S2, S3).

The comparison of the regression lines of the different groups for *immature neurons (DCX positive cells)* revealed significant different rostrocaudal gradients in all analysed brain structures. Here, the Loft Control group showed a more pronounced increase of cell density in the total number of DCX positive cells from rostral to caudal in all analysed brain regions and compared to nearly all other groups (Figs. 5, 6, Table S2, S3). An exception was observed in the apical hyperpallium, where the gradient in the Loft Control group was less steep compared to the Outdoor + Loft + Homing group, and in the intercalated hyperpallium, where the gradient in the Outdoor + Loft group was steeper. Additionally, the cell density in the apical hyperpallium of the Outdoor + Loft group increased with atlas level from rostral to caudal compared to the Outdoor + Loft + Box group and the Loft + Box group (Figs. 5, 6, Table S2, S3). In the mesopallium, the Outdoor + Loft + Box group showed also a shallower rostrocaudal gradient, now compared to the Loft + Box group and again to the Outdoor + Loft group (Figs. 5, 6, Table S2, S3) while the Outdoor + Loft + Homing group showed a less pronounced rostrocaudal cell density gradient than the Loft + Box group.

Regarding the rostrocaudal gradient for the *less matured DCX positive and ovoidal shaped cells*, it was shown that they differed significantly in the analysed brain structures with differential expression pattern. It becomes apparent that the Loft Control group showed again a more pronounced increase of cell density of DCXov positive cells from rostral to caudal in all analysed brain regions and compared to most of the other groups (Figs. 5, 6, Table S2, S3). Additionally, the rostrocaudal gradient of cell density in the hyperpallium apicale of the Loft + Box group was less steep compared with the Outdoor + Loft + Homing group. In the mesopallium, the rostrocaudal gradient of the Outdoor + Loft + Homing group was also steeper than that of the Loft + -Box group, the Outdoor + Loft group and the Outdoor + Loft + Box group (Figs. 5, 6, Table S2, S3).

Similar to the DCXov cells, the comparison of the regression lines of the different groups for the *more matured DCX positive and triangular shaped cells* revealed significant differences in all analysed brain structures (Figs. 5, 6, Table S2, S3). Here, the Loft Control group showed similar results to the DCX positive and ovoidal shaped cells with a more pronounced rostrocaudal cell density increase in all analysed brain regions and compared to most of the other groups. Additionally, the Outdoor + Loft group showed a steeper increase in cell density from the rostral to the caudal apical hyperpallium compared to the Outdoor + Loft + Homing group and the Loft + Box group. Once again, the expression pattern in the mesopallium is different: here, the Outdoor + Loft + Box group stands out and showed a steeper rostrocaudal gradient than the Outdoor + Loft + Homing group, the Outdoor + Loft group and the Loft + Box group (Figs. 5, 6, Table S2, S3).

3.2.2. *Group-specific differences in cell density at individual atlas levels*

Detailed values (means±SE) per group, atlas level, region and cell type were listed in Fig. S2 and Table S4. A dot-density-grid of the spatial distribution across all brain regions and cell types was compiled for compact visualization and is presented in Fig. 7. The size of each dot is proportional to the cell density in the respective region and group. Given a significant group × atlas level interaction (see 2.3 and 3.2.1), post hoc comparisons were conducted to assess group differences at individual atlas levels. Fig. 8 represents a statistical heatmap and summarizes the results of the post hoc comparisons based on estimated marginal means, assessing group differences at individual atlas levels. Statistical significance is color-coded by group dominance (Green: first group shows a

		14.00	12.75	11.50	10.25	9.00	7.75			14.00	12.75	11.50	10.25	9.00	7.75
	OLBG vs. LCG								OLBG vs. LCG						
	OLBG vs. LBG								OLBG vs. LBG						
Hyperpallium	**OLBG vs. OLHG**								**OLBG vs. OLHG**						0.009
apicale	OLBG vs. OLG						0.022	Hyperpallium	OLBG vs. OLG						
BrdU/NeuN+	LCG vs. LBG							apicale	**LCG vs. LBG**					0.011	0.012
	LCG vs. OLHG					0.044		DCXov+	LCG vs. OLHG						
	LCG vs. OLG						0.037		LCG vs. OLG						
	LBG vs. OLHG								**LBG vs. OLHG**				0.040	<0.001	<0.001
	LBG vs. OLG								**LBG vs. OLG**					0.009	0.049
	OLHG vs. OLG					0.015	0.009		OLHG vs. OLG						
	OLBG vs. LCG								**OLBG vs. LCG**					0.002	
	OLBG vs. LBG								OLBG vs. LBG						
	OLBG vs. OLHG								OLBG vs. OLHG						
Hyperpallium	**OLBG vs. OLG**	0.032			0.021	<0.001	<0.001	Hyperpallium	OLBG vs. OLG						
apicale	LCG vs. LBG							intercalatum	**LCG vs. LBG**					<0.001	
BrdU/S100ß+	**LCG vs. OLHG**		0.044		0.01	0.038		DCXov+	LCG vs. OLHG						
	LCG vs. OLG	0.009			0.006		<0.001		**LCG vs. OLG**					0.046	
	LBG vs. OLHG								LBG vs. OLHG						
	LBG vs. OLG				0.036	<0.001	<0.001		LBG vs. OLG						
	OLHG vs. OLG					<0.001	<0.001		OLHG vs. OLG						
	OLBG vs. LCG								**OLBG vs. LCG**					<0.001	0.012
	OLBG vs. LBG								**OLBG vs. LBG**					0.003	
	OLBG vs. OLHG								OLBG vs. OLHG						
Hyperpallium	**OLBG vs. OLG**			<0.001	0.022			Hyperpallium	OLBG vs. OLG						
intercalatum	LCG vs. LBG							densocellulare	**LCG vs. LBG**					<0.001	0.027
BrdU/S100ß+	LCG vs. OLHG							DCXov+	**LCG vs. OLHG**					<0.001	
	LCG vs. OLG			<0.001	0.002				**LCG vs. OLG**					<0.001	
	LBG vs. OLHG								LBG vs. OLHG						
	LBG vs. OLG				0.014				LBG vs. OLG						
	OLHG vs. OLG								OLHG vs. OLG						
	OLBG vs. LCG								**OLBG vs. LCG**						0.009
	OLBG vs. LBG								OLBG vs. LBG						
	OLBG vs. OLHG								**OLBG vs. OLHG**						<0.001
Mesopallium	**OLBG vs. OLG**						<0.001	Mesopallium	OLBG vs. OLG						
BrdU/S100ß+	LCG vs. LBG							DCXov+	**LCG vs. LBG**					0.005	<0.001
	LCG vs. OLHG	0.037	0.044		0.01				LCG vs. OLHG						
	LCG vs. OLG						<0.001		**LCG vs. OLG**					0.014	<0.001
	LBG vs. OLHG								**LBG vs. OLHG**					0.006	<0.001
	LBG vs. OLG						<0.001		LBG vs. OLG						
	OLHG vs. OLG						<0.001		**OLHG vs. OLG**					0.016	<0.001
	OLBG vs. LCG					0.016	0.023		OLBG vs. LCG						
	OLBG vs. LBG								OLBG vs. LBG						
	OLBG vs. OLHG								OLBG vs. OLHG						
Hyperpallium	OLBG vs. OLG							Hyperpallium	OLBG vs. OLG						
apicale	**LCG vs. LBG**				0.010	<0.001	<0.001	apicale	**LCG vs. LBG**		0.005	0.038			
DCX+	**LCG vs. OLHG**					<0.001		DCXtri+	**LCG vs. OLHG**		0.044	0.045			
	LCG vs. OLG								LCG vs. OLG						
	LBG vs. OLHG								LBG vs. OLHG						
	LBG vs. OLG				0.021	<0.001	<0.001		**LBG vs. OLG**			0.034			
	OLHG vs. OLG								**OLHG vs. OLG**			0.041			
	OLBG vs. LCG					<0.001			OLBG vs. LCG						
	OLBG vs. LBG								**OLBG vs. LBG**				0.045		
	OLBG vs. OLHG								OLBG vs. OLHG						
Hyperpallium	OLBG vs. OLG							Hyperpallium	OLBG vs. OLG						
intercalatum	**LCG vs. LBG**				0.012	<0.001		intercalatum	**LCG vs. LBG**				0.003	<0.001	
DCX+	**LCG vs. OLHG**					0.014		DCXtri+	**LCG vs. OLHG**				0.004	<0.001	
	LCG vs. OLG					0.049			LCG vs. OLG						
	LBG vs. OLHG								LBG vs. OLHG						
	LBG vs. OLG								LBG vs. OLG						
	OLHG vs. OLG								OLHG vs. OLG						
	OLBG vs. LCG					<0.001	<0.001		**OLBG vs. LCG**					<0.001	<0.001
	OLBG vs. LBG								OLBG vs. LBG						
	OLBG vs. OLHG							Hyperpallium	OLBG vs. OLHG						
Hyperpallium	OLBG vs. OLG							densocellulare	OLBG vs. OLG						
densocellulare	**LCG vs. LBG**					<0.001	0.001	DCXtri+	**LCG vs. LBG**					<0.001	<0.001
DCX+	**LCG vs. OLHG**					<0.001	0.001		**LCG vs. OLHG**					<0.001	<0.001
	LCG vs. OLG					<0.001	0.009		**LCG vs. OLG**					<0.001	0.005
	LBG vs. OLHG								LBG vs. OLHG						
	LBG vs. OLG								LBG vs. OLG						
	OLHG vs. OLG								OLHG vs. OLG						
	OLBG vs. LCG					0.022	<0.001		**OLBG vs. LCG**				0.023		<0.001
	OLBG vs. LBG						<0.001		**OLBG vs. LBG**					<0.001	<0.001
	OLBG vs. OLHG								**OLBG vs. OLHG**					<0.001	<0.001
Mesopallium	**OLBG vs. OLG**						0.010	Mesopallium	**OLBG vs. OLG**					<0.001	
DCX+	**LCG vs. LBG**					<0.001	<0.001	DCXtri+	**LCG vs. LBG**	0.010		0.041	<0.001	<0.001	<0.001
	LCG vs. OLHG					0.012	<0.001		**LCG vs. OLHG**		0.018		<0.001	<0.001	<0.001
	LCG vs. OLG						<0.001		**LCG vs. OLG**				<0.001	<0.001	<0.001
	LBG vs. OLHG								LBG vs. OLHG						
	LBG vs. OLG								LBG vs. OLG						
	OLHG vs. OLG								OLHG vs. OLG						

Fig. 8. Statistical heatmap of significant group differences in cell density across the rostro-caudal axis. The matrix displays significant differences between experimental groups across six defined atlas levels (from rostral A14.00 to caudal A7.75; mesopallium: from A14.25 to A5.50) and five different cell types/cell markers. Statistical significance is color-coded by group dominance (Green: first group > second group; Blue: second group > first group). Color intensity reflects the p-value significance levels ($p < 0.001$ for high intensity, $p < 0.01$ for medium intensity, $p < 0.05$ for lower intensity), with non-significant results left uncolored (white). LBG Loft + Box group, LCG Loft Control group, OLG Outdoor + Loft group, OLBG Outdoor + Loft + Box group, OLHG Outdoor + Loft + Homing group.

higher cell density, Blue: second group shows a higher cell density). Color intensity reflects the p-value significance levels ($p < 0.001$ for high intensity, $p < 0.05$ for lower intensity), with non-significant results left uncolored (white). The following section highlights the main findings.

Newborn neurons (BrdU/NeuN positive cells):

Atlas level specific post hoc comparisons of BrdU/NeuN positive cells revealed that group differences in the density of BrdU/NeuN-positive cells were restricted to posterior atlas levels A 9.00 and A 7.75 and to the apical hyperpallium (Figs. 7, 8, Fig. S2, Table S4). Specifically, the Outdoor + Loft + Homing group exhibited higher cell densities than the Outdoor + Loft group and the Loft Control group at atlas level A 9.00, whereas the Outdoor + Loft group showed higher cell densities than all other groups, except the Outdoor + Loft + Homing group, at the more posterior atlas level A 7.75.

Newborn glial cells (BrdU/S100ß positive cells):

Regarding newborn glial cells, post hoc comparisons revealed atlas-level-specific group differences in cell density at several atlas levels in all regions except the densocellular hyperpallium (Figs. 7, 8, Fig. S2, Table S4). Notably, in the apical hyperpallium and mesopallium, group differences were confined to anterior and posterior atlas levels, but not at intermediate levels (A 11.50 and A 11.25). In contrast, in the intercalated hyperpallium, group differences were observed only at intermediate atlas levels (A11.50 and A10.25). Particularly the Outdoor + Loft group exhibited high cell densities in the apical hyperpallium at the most anterior atlas level A 14.00 and the more posterior atlas levels A10.25, A 9.00 and A 7.75. The Outdoor + Loft + Homing group in particular showed higher cell numbers at atlas level A 9.00 in the apical hyperpallium compared to the Loft Control group and there are similar expression patterns for the Outdoor + Loft group in the mesopallium. Here, particularly high values of were determined at A 6.75. Similar to the apical hyperpallium, the Loft Control group rather showed low numbers of newborn glial cells not just at posterior atlas levels of the mesopallium, but also in general and also in the intercalated hyperpallium.

Immature neurons (DCX positive cells):

Post hoc comparisons of cell densities of DCX positive cells along the rostrocaudal axis showed significant group differences in all analysed brain regions, but just at posterior atlas levels (Figs. 7, 8, Fig. S2, Table S4). Most obviously, the Loft Control group showed consequently higher cell numbers at posterior atlas levels compared to the other groups in all regions. Additionally, the Outdoor + Loft + Box group showed a higher cell density compared to the Loft + Box group and the Outdoor + Loft group at atlas level A 6.75. In the apical hyperpallium there are also high cell numbers in the Outdoor + Loft group at posterior atlas levels A 10.25, A 9.00 and A 7.75.

DCX positive and ovoidal shaped cells:

Here, pairwise comparisons demonstrated again most of significant group differences at posterior atlas levels (Figs. 7, 8, Fig. S2, Table S4). The high number of cells already observed in DCX positive cell total values in the Loft Control is also reflected here. The Loft Control group showed high numbers of ovoidal shaped DCX positive cells, particularly at posterior atlas levels. Notably, the Loft + Box group showed significantly lower cell densities compared to the other groups. This became more obvious at the posterior atlas levels, where the other groups rather showed increased cell numbers. The mesopallium showed quite heterogeneous expression pattern of the groups at posterior atlas levels. At atlas level A 6.75, next to the Loft + Box group, the Outdoor + Loft group showed a lower cell density, although their DCXov number in the apical hyperpallium was high. At atlas level A 5.50, not only the Loft Control group, but the Outdoor + Loft + Homing group exhibited high numbers of cells (Figs. 7, 8, Fig. S2, Table S4).

DCX positive and triangular shaped cells:

In contrast to the other cell types, there are significant differences in the densities of DCX positive and triangular shaped cells in the apical hyperpallium and mesopallium at more anterior and intermediate atlas levels (Figs. 7, 8, Fig. S2, Table S4). Generally, the Loft Control group showed the highest values and the Loft + Box group the lowest. In the intercalated and densocellular hyperpallium, group differences were observed at the more posterior atlas levels A 10.25, A 9.00 and A 7.75. The mesopallium showed a heterogeneous expression pattern across atlas levels. There were several significant differences in cell densities at all atlas levels except the rostral atlas level A 14.25. One common feature is, that the Loft Control group generally has a higher cell density than the other groups. The Outdoor + Loft + Box group showed the second highest cell number with a peak at atlas level A 6.75.

4. Discussion

The present study investigated adult neurogenesis and gliogenesis in the hyper- and mesopallium in homing pigeons under different housing conditions and/or experimental experiences, including spatial cognitive training. The results showed evidence of adult neurogenesis and gliogenesis, regardless of the group or examined region. Despite this, the number of newborn cells (both neurons and glia) and immature neurons varied considerably. The study revealed a heterogeneous distribution of both across the meso- and hyperpallial regions dependent on environmental factors and conditions.

Overall, the number of immature neurons (DCX+) consistently outnumbered the number of newborn mature neurons (BrdU+/NeuN+) and newborn glial cells (BrdU+/S100ß+). Pigeons that underwent cognitive training (operant chamber or homing tasks) had a higher number of newborn neurons compared to those that lived in the loft and flew outdoors without undergoing further tasks. This implies a positive effect of cognitive training on adult neurogenesis. Pigeons that performed in the operant chamber exhibited a moderate number of newborn neurons and immature cells, whereas pigeons with additional outdoor flight access showed higher levels, indicating the stimulatory effects of physical activity on adult neurogenesis. Surprisingly, pigeons that permanently lived in the safe space of the loft without outdoor experiences or cognitive training showed comparable numbers of newborn neurons to those in the other conditions. They further exhibited the highest numbers of immature neurons of all groups, which points to additional environmental influences for adult neurogenesis.

Adult gliogenesis on the other side, revealed a different pattern. Here, the highest number of newborn glial cells was detected in pigeons that lived in the loft condition with outdoor flight access and in pigeons that were trained in homing, while pigeons that lived only in the loft without any training exhibited the lowest levels of gliogenesis in all analysed regions.

Previous studies already demonstrated a high level of adult neurogenesis and plasticity in different regions of the pigeon brain [6,11,29,32,35]. However, these studies largely describe the existence and general modulation of neurogenesis without disentangling how specific, ecologically relevant experiences shape region-specific responses. The current study moves beyond this by systematically linking distinct experiential factors to differential patterns of neurogenesis in defined pallial regions. Our results support the view that adult neurogenesis potentially contributes to the maintenance of neural plasticity and might be associated with the capacity of birds to respond rapidly and flexible to environmental changes and requirements. While it is well known that adult neurogenesis in birds follows distinct, highly regulated patterns that depend on different external and internal factors like environmental conditions, stress, hormone level, age, sex, seasonality, physical activity, social context and (song) behavior [8,32,43,45,48,49,51,52,81,82], our study adds a more detailed perspective and provides important new insights by experimentally isolating and directly comparing key influencing factors within a unified design. Specifically, our findings provide new evidence that the mesopallium and hyperpallium do not respond uniformly to external and behavioral stimuli but exhibit region-specific sensitivity to particular combinations of experience. This allows a more precise characterization of how adult neurogenesis is functionally

embedded in adaptive responses. We refine the current understanding of adult neurogenesis from a broadly regulated phenomenon to a more targeted, experience-dependent mechanism that supports flexible behavioral adaptation. Based on our study design, we could establish a link between specific ecological demands and local plasticity. This expands the field beyond general modulation effects toward a more integrative and functionally differentiated framework.

4.1. Group-specific cell densities

4.1.1. Newborn neurons

Generally, all pigeons that underwent cognitive training, regardless of whether it was in the Skinner box or individual homing, consistently showed a higher number of newly generated neurons compared to pigeons that received no training but flew outside the loft. This suggests that cognitive training per se has a sustaining effect on the formation of new neurons. Notably, even pigeons that lived permanently in the loft without training maintained moderate to high levels of neurogenesis, suggesting that while baseline levels are preserved under standard conditions, training provides an additional stimulatory effect.

Our results support the general concept that adult neurogenesis is dynamically regulated by learning and experience across vertebrates. In mammals, this relationship has been studied primarily in the hippocampus, where higher performance in spatial learning tasks such as the Morris water maze is associated with increased dentate gyrus neurogenesis, suggesting that newly generated neurons are recruited into circuits supporting spatial memory [83–86]. Comparable experience-dependent regulation has been described in birds, where adult neurogenesis is linked to song learning in songbirds and to spatial memory demands in food-caching species [28,29,37,46,48,81,87]. In songbirds, the experience-dependent recruitment and long-term survival of newborn neurons in forebrain nuclei such as the HVC are dynamically regulated by vocal motor learning, song repertoire maintenance, and seasonal social interaction [30,81]. However, whether similar principles apply to other pallial regions remained largely unresolved. Our findings extend the latter by demonstrating that experience-dependent adult neurogenesis is not restricted to the hippocampal formation or specialized song-control nuclei, but also occurs in the hyperpallium and mesopallium. Importantly, the effects were region- and experience-specific. In the hyperpallium, the densocellular hyperpallium shows higher responses compared to the apical or intercalated hyperpallium (see also 4.2.), indicating that different pallial subregions differ in their sensitivity to environmental and behavioral challenges.

Although learning experiences of any kind seem to have a positive effect on hyperpallial and mesopallial adult neurogenesis, there are differences regarding the type of learning experiences, and that, for example, three-dimensional landmarks have a higher impact compared to digital learned orientation signs. Thus, we must distinguish between distinct learning types, training and experience. Adult neurogenesis is shaped not simply by learning per se, but by the specific cognitive demands and ecological relevance of the experience.

One question remains: why did birds that lived in the loft and had access to daily outdoor flight, yet received no additional training, show the lowest levels of adult neurogenesis for matured neurons compared to all other groups? Moreover, the direct comparable group that lived permanently inside the loft even exhibited higher levels, which also contrasts with the results of learning or environmental stimuli. At least in the densocellular hyperpallium and the mesopallium, the loft-only group displayed nearly identical matured neuron numbers to the box-trained and outdoor-flying groups. One possible explanation can be derived from the results of the two different stimulation experiments. First, training in the operant chamber preserved newly matured neurons. The same would be true for pigeons that underwent homing training, although the effects were less pronounced. Second, mature neurons were also sustained by social housing and stable groups, whereas birds living in a less restricted environment with more spatial freedom but without extra training did not require these additional neurons. This would also explain why these birds show the highest number of non-determined BrdU + cells. According to Kempermann's [88] "neurogenic reserve" hypothesis for the mammalian hippocampus, proposing a persistent pool of neurons that can be recruited when animals face new stimuli, a similar reserve may exist in non-hippocampal regions of birds, given their generally higher neurogenic activity and number of neurogenic niches [6,11,32,81]. In addition, in mammals it has been suggested that training may first enhance the survival of young granule cells in the hippocampus but with prolonged training subsequently trigger their elimination. The dynamic regulation of cell death may ensure that granule cells involved in memory consolidation are maintained, while newly generated neurons that have completed their functional role are removed to allow the integration of additional naïve neurons [85,89]. This regulation, however, likely depends on the type of training, whereas in the Loft Control pigeons, this "making space" process may not occur, because no training or learning task was performed.

However, social factors on the one hand and differences in physical activity on the other hand should not be neglected: Studies in zebra finches showed that social housing can increase neurogenesis and promote survival of older neurons [42,90] which aligns with the conditions of the current study, because all pigeons lived in stable social groups. Additionally, Outdoor + Loft + Box pigeons show higher values of newborn cells than Loft + Box pigeons. Pigeons of the Outdoor + Loft + Box group do not get just far more spatial and navigational experience, outdoor flying inevitably leads to greater exercise and thus to a substantially higher level of physical activity. A stimulatory effect of physical activity on neural precursor cell proliferation at least in the dentate gyrus of mammals has been already demonstrated [44,91] and more recent work has reported that even short periods of increased activity are sufficient to enhance neuronal precursor cell proliferation [45,92]. Thus, physical activity may be a factor that influenced adult neurogenesis in all of our groups that had access to outdoor flying and/or homing. However, the fact that pigeons with outdoor flying and box-training showed higher adult neurogenesis than pigeons with outdoor flying but no extra training, suggests that the learning experience was more important for adult neurogenesis and that higher physical activity per se does not seem to preserve or stimulate adult neurogenesis in the hyper- and mesopallium to any distinct degree.

4.1.2. Immature neurons

Generally, the quantity of DCX + cells was higher than that of BrdU + /NeuN + cells. The distribution of ovoidal or triangular-shaped cells varied between groups and the data showed both regional and group specific differences. The Loft Control group showed the highest number of DCX + cells, pigeons of the Loft + Box group the lowest. Triangular-shaped cells outnumbered ovoid-shaped cells in the Loft Control group, Outdoor + Loft group and Outdoor + Loft + Box group, whereas Loft + Box and Outdoor + Loft + Homing individuals displayed the opposite pattern, suggesting that different experimental/environmental inputs may shift the balance between immature and migrating neurons. Again, high levels were detected in the Loft Control birds, suggesting that additional factors like e. g. stress might account for lower levels in the other groups.

In addition to adult born neurons, DCX can be also expressed in adult, non-newly generated cell populations in the brain, marking sites of neuronal plasticity per se [93]. It is therefore possible that the large number of immature neurons does not necessarily indicate recent cell generation. Thus, animals kept under stable, unchanging conditions, like those in the Loft Control group, may accumulate a high degree of plasticity, characterized by a substantial pool of immature cells that remain in a kind of quiescent 'waiting' state. In line with the "neurogenic reserve" hypothesis, these cells could then be recruited when sudden events or environmental changes occur.

4.1.3. Newborn glial cells

In contrast to adult neurogenesis, a different pattern emerged for gliogenesis which occurred at lower levels, reflected in lower S100b/BrdU cell numbers. Interestingly, adult gliogenesis was not affected by external stimuli to the same extent as adult neurogenesis. Animals of the Outdoor + Loft group exhibited the highest numbers of newborn glial cells, whereas pigeons of the Loft Control group showed the lowest levels. Thus, our results suggest that adult gliogenesis is stimulated by experience, largely independent of its specific nature. Outdoor flying provides a large amount of three-dimensional spatial information and seems to be sufficient to enhance gliogenesis in the meso- and hyperpallium, indicating that specialized or structured training, at least regarding the tasks of this study, is not required to induce adult glial cell generation in the meso- and hyperpallium. The higher values observed in all groups compared to Loft Control pigeons can be also a result of greater levels of physical activity or sensory stimulation. Studies in mice have demonstrated that physical activity is associated not just with increased neurogenesis but also increased gliogenesis in the frontoparietal cortex, the striatum and the hippocampus [94–96]. The comparatively lower values observed in the Loft Control group may therefore be explained by the animals' restricted range of movement. The size of the loft permitted limited flight, but this is not comparable to unrestricted free outdoor flight.

Adult gliogenesis has been much less studied compared to neurogenesis, but accumulating evidence highlights its importance for brain plasticity, homeostasis, and repair [97,98]. In particular, astrocytes are susceptible to plasticity, and induce and stabilize synapses, regulate the concentration of various molecules, and support neuronal energy metabolism. The gliogenic domains in the ventricular and subventricular zones tend to be quiescent under homeostasis, and their regulation is achieved by intrinsic and extrinsic factors, including physical exercise, environmental enrichment, and dietary restriction [99,100]. Our data indicate that gliogenesis, like neurogenesis, is influenced by different conditions, but occurs to some degree independently. In the meso- and hyperpallium, physical activity might be more crucial for gliogenesis. Nevertheless, these cells may be involved in regulating neural activity and plasticity. Today, glial cells are viewed as essential players in brain circuitry. Understanding their role in modulating neuronal activity and repair may help clarify how and why new neurons are generated in the brain [101,102].

4.1.4. Stress as an underestimated factor?

As noted above, the high number of newborn and immature neurons in the Loft Control group was unexpected, as was the comparatively low number observed in the Loft + Box group. Additionally, pigeons in the Outdoor + Loft + Homing group that underwent individual flight training exhibited relatively low numbers of both newborn and immature neurons. Along with the flight outside the loft or handling for box-training or homing, differential, unintended stress exposure may have contributed to differences between these groups such as handling by experimenter, Skinner-box, predator exposure and environmental stress. We may therefore hypothesize that stress acts as an additional factor, which should be addressed in future studies. Stress can negatively affect adult neurogenesis both in mammals and in birds [52,53,82]. Loft only pigeons were likely less exposed to stress because they never faced any threats compared to pigeons that left the loft. Flying outdoors involves contact with potential predators, which has recently been shown, at least in the hippocampus, to negatively affect cell proliferation and maturation in black capped chickadees [54]. Findings in songbirds also indicate that elevated corticosterone levels, social isolation, or predator-induced fear significantly suppress cell proliferation and neuronal recruitment both in the song-control system and the hippocampal formation [53,54]. The comparatively lower densities of mature newborn neurons observed in our outdoor-flying and homing groups may reflect similarly transient, non-experimental stress exposure during free flight or handling, suggesting the view that stress acts as a potent negative regulator of avian neuroplasticity across distinct pallial networks.

4.2. Region-specific functional considerations

Our results revealed pronounced, region-specific differences across the different groups, demonstrating that learning- and/or experience-dependent adult neurogenesis in birds extends beyond the hippocampal formation. We show for the first time, that the hyper- and mesopallium exhibit distinct patterns of experience-dependent modulation pointing to a more widespread and functionally differentiated network of plasticity in the avian forebrain than previously recognized.

Regarding the hyperpallium and newborn neurons, this applies mostly to the densocellular hyperpallium that showed higher values than the apical or intercalated hyperpallium in all groups except in the Outdoor + Loft group, while the mesopallium showed comparable values to the densocellular hyperpallium. The distribution of immature neurons was more heterogeneous: Loft Control, Outdoor + Loft and Outdoor + Loft + Box pigeons showed the highest cell density in the intercalated and densocellular hyperpallium, while the other two groups showed higher density in the apical hyperpallium and the mesopallium. For newborn glial cells, it is noticeable that the Outdoor + Loft group had very high values in the apical hyperpallium, while the distribution is somewhat more uniform in the other groups.

Generally, our results confirm the functional specialization of the analysed brain regions and point to distinct functional demands. Apparently, there are different needs for plasticity in these regions and the observed differences might be aligned with the sensory modalities involved: the densocellular hyperpallium which is involved in distinct visual processing showed higher densities in Loft + Box and Outdoor + Loft + Box pigeons with a high amount of two-dimensional visual stimulation from the skinner box training. This may indicate that these visual stimuli were predominantly processed in this region and that mature neurons in the densocellular hyperpallium are of particular functional relevance within the visual system. To encode visual information via the thalamofugal visual pathway into memory, the densocellular hyperpallium is connected with the hippocampal formation [57,79,103,104]. Previous work has suggested that visual information relevant for behaviors such as migration or homing is conveyed not only to the dorsolateral hippocampal formation but also to the densocellular hyperpallium and that this region even represents the main connecting structure between the hyperpallium and the dorsolateral and dorsomedial hippocampal [79,104–106]. Taking this into account, one would have expected the Outdoor + Loft + Homing group also have high values here, but this is not the case. On the other hand, box training with orientation cues in combination with free flight seems to sustain adult born neurons in these regions. Nevertheless, the densocellular hyperpallium appears to rely on a higher degree of plasticity, whereas the apical or intercalated hyperpallium may depend more on a stable, conserved circuitry.

The mesopallium is neurochemically and anatomically subdivided into seven subregions which serve as critical relay stations within the tectofugal, auditory, multisensory, limbic, and trigeminal systems [63,78,107,108]. Fibers projecting from the densocellular hyperpallium into the adjacent mesopallium have also been described [6]. Thus, the migration of newborn cells into this region is conceivable and may provide an explanation for the increased occurrence of newly generated mature neurons that migrated into the mesopallium during an earlier immature stage. The higher adult neurogenesis in Outdoor + Loft + Box pigeons compared with Outdoor + Loft + Homing and Outdoor + Loft pigeons may reflect increased pecking-related somatosensory stimulation during Skinner-box tasks, given that parts of the mesopallium are known to process somatosensory input from the beak [78]. Supporting this, Gaede et al. [22]. showed that regions adjacent to or overlapping with the mesopallium respond to tactile stimulation and that the avian forebrain contains somatotopic representations of body surfaces.

However, when interpreting our data from the hyperpallium and mesopallium, it is important to consider that there are actually two competing models of avian pallial organization. The more traditional "distinction hypothesis" treats the Wulst (hyperpallium) and the dorsal ventricular ridge (DVR) as fundamentally separate cell populations with different developmental and molecular identities [56]. In contrast, the "continuum hypothesis" argues that dorsal (Wulst) and ventral (DVR) regions are highly similar, sharing molecular profiles and gene co-expression modules linked to development, synaptic transmission, signaling, and neurogenesis [20] Similar data in different regions, as observed in the densocellular hyperpallium and the mesopallium may not only indicate comparable neuronal functions under these specific learning or training conditions, but could rather support the view that the meso- and hyperpallium are a dorsoventral continuum with regional specializations within a shared pallial sheet resulting from the migration of cells of different origins [20,25].

4.3. Rostrocaudal progression of adult neuro- and gliogenesis

Only a limited number of studies have addressed functional differences along the rostrocaudal axis of the avian brain, despite evidence regarding anterior-posterior variations in adult neurogenesis in the hippocampal formation [29,82,109,110]. In this context, examining adult neurogenesis along the rostrocaudal axis provides a means to link cellular plasticity to large-scale organizational patterns. Rather than being uniformly distributed, region-specific changes in neurogenesis along the axis may indicate how different parts of the pallium are selectively engaged by distinct functional demands. By focusing on the hyperpallium and mesopallium, our study therefore goes beyond hippocampus-specific descriptions and addresses whether experience-dependent plasticity follows systematic processing-related principles within the avian forebrain. Unlike in rodents, the rostral-migratory-stream, a pathway described through which newly generated neurons migrate from the subventricular zone to the olfactory bulb, has not yet been identified in birds. This is relevant because the rostral-migratory-stream represents a key mechanism for targeted neuronal integration in mammals; whether newly generated cells in birds may follow different migratory routes or rely on alternative strategies for incorporation into existing circuits, is not finally clarified. Instead, the reported pronounced neurogenic niche "hotspots" near the ventricular zones are distributed at different positions along the anterior–posterior axis with distinct migratory pathways in pallial regions and the olfactory bulb [6,32,111]. In addition, in mammals, the hippocampus can be compartmentalized into multiple functional domains along the longitudinal and medio-lateral (humans) and dorsal-ventral axis (rodents), respectively [23,112–117]. This is similar to the avian hippocampal formation which exhibits different functional subdivisions along the rostrocaudal axis and different rates of adult neurogenesis [23, 29,80]. According to these findings, we aimed to take a deeper look into hyperpallial and mesopallial regions, as they show highly specialized functional domains along the longitudinal axis as well [21,26]. For example, large parts of the pigeon hyperpallium are integrated into higher visual processing, but data obtained at atlas level A 14.00 also encompassed portions of a rostrally located somatosensory area. However, in none of the groups did the rostral part show a distinguishable effect for newborn neurons but the visual parts did. Here, group differences resulted mainly from the posterior atlas levels. Those differences were primarily reflected in alterations of the rostrocaudal gradient of cell density rather than uniform shifts in absolute values. Regarding the newborn neurons in the apical hyperpallium, the Outdoor + Loft group exhibited a significantly less pronounced slope increase across atlas levels compared to all other groups, indicating a relative flattening of the rostrocaudal gradient. In contrast, newborn glial cells showed the steepest slope increase in Outdoor + Loft pigeons, suggesting a specific effect at posterior levels. So, gliogenesis was specifically increased at posterior levels in the apical hyperpallium of this group.

Interestingly, Loft Control pigeons consistently demonstrated a steeper slope increase across atlas levels for DCX in the apical hyperpallium, indicating a group-specific alteration in the distribution of immature neurons. This is underlined by the analysis of individual atlas levels of this structure. Here, pigeons of the Loft Control group showed a higher number of immature neurons at the posterior apical hyperpallium compared to the other groups. This suggests an internal functional differentiation, but the precise nature or role remains to be determined.

Generally, posterior regions of the hyperpallium and mesopallium appear to show a greater capacity for producing and integrating new neurons, or a higher functional demand related to internal regional specialization, particularly under stable environmental conditions. In contrast, when additional demands such as learning tasks or homing, are introduced, anterior regions become engaged. This supports the idea that adult neurogenesis may contribute to adaptive behavioral stability and that the functional role of newly generated neurons depends on their site of integration within the brain [118].

4.4. Further considerations

Homing pigeons are widely used to study learning, memory and decision-making, supported by extensive behavioural and anatomical data [19,21,34,119,120]. Regarding adult neurogenesis, most studies have focused on the hippocampus, but the relevance of adult neurogenesis in other pallial regions as a contributing-factor to avian cognitive abilities has not been fully estimated until now. The heterogeneity of our findings suggests that adult neurogenesis is not uniformly involved across all higher cognitive functions processed in the hyperpallium and mesopallium. Instead, our results point toward a more selective and context-dependent role, with a particular relevance for spatial cognition, processing of experiences and brain plasticity.

Although our study was primarily designed to investigate the effects of different learning and spatial experiences on adult neurogenesis, important factors independent of these variables emerged retrospectively. Both, physical activity and stress appear to be factors that should not be underestimated and likely exert a substantial influence on our results. Another important factor concerns the influence of individual life history on adult neurogenesis. Do prior experiences affect adult neurogenesis, and might extensive exposure to diverse stimuli or experiences confer advantages later in life? Our results at least point in this direction, suggesting that prior experience may exert a modulatory influence on plasticity.

While songbirds represent a highly specialized avian model in which adult neurogenesis is functionally compartmentalized within dedicated song-control nuclei [28,37], non-songbirds like pigeons display a more widespread distribution of adult-born neurons across sensory and multimodal pallial regions. This comparative perspective suggests that adult neurogenesis is an evolutionarily conserved cellular substrate across birds that has been recruited for distinct functional specializations, ranging from vocal motor learning in songbirds to spatial orientation and multimodal sensory integration in non-songbirds.

As proposed by Herold et al. [11], we would expect that in pigeons and likely other birds, effects based on environmental changes, hormones, stress, sex, cognition, or pharmacological manipulation, may become more prominent compared to mammals. This is also supported by Rueda-Alana et al. [24] who showed that developmental neurogenesis programs differ across taxa. If adult neurogenesis reuses developmental mechanisms, the capacity for and modulation of adult neurogenesis and the successful integration of newborn neurons depend also on developmental rules, not just neuron production. However, newborn neurons may acquire their functional identity through post-mitotic maturation and circuit integration, not only through lineage. Neuronal identity can emerge late and remain plastic [25].

Our study supports the suggestion, that adult neurogenesis could be the ultimate cellular process that integrates elements from both the

internal and external environment to adjust brain functions. It can be understood as an evolutionarily conserved, development-like program that supports cognitive flexibility and probably the processing of affective, emotional and motivational signals.

Author contributions

JM and CH designed the study. JM wrote the original version of the manuscript. JM, IK, and SK collected the data. JM and IK analysed the data and prepared the figures. CH, KA and SC contributed to the interpretation of the results. All authors critically reviewed the final version of the manuscript and provided comments. All authors contributed to the article and approved the submitted version.

CRediT authorship contribution statement

Julia Mehlhorn: Writing – original draft, Visualization, Validation, Supervision, Investigation, Formal analysis, Data curation, Conceptualization. **Ilias-Dimitrios Karlaftis:** Writing – review & editing, Visualization, Formal analysis, Data curation. **Serap Kurutas:** Formal analysis, Data curation. **Katrin Amunts:** Writing – review & editing, Project administration. **Svenja Caspers:** Writing – review & editing, Project administration. **Christina Herold:** Writing – review & editing, Validation, Supervision, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the author(s) used ChatGPT and NotebookLM for preparing Fig. 5+7. The author(s) reviewed and edited the output as needed and take full responsibility for the content of the published article.

Declaration of Competing Interest

The authors declare that they have no competing interests.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.bbr.2026.116557.

Data availability

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

References

[1] J.R. Kirn, F. Nottebohm, Direct evidence for loss and replacement of projection neurons in adult canary brain, J. Neurosci. 13 (1993) 1654–1663, https://doi.org/10.1523/JNEUROSCI.13-04-01654.1993.
[2] F. Doetsch, C. Scharff, Challenges for brain repair: Insights from adult neurogenesis in birds and mammals, Brain Behav. Evol. 58 (5) (2001) 306–322, https://doi.org/10.1159/000057572.
[3] B.W. Lindsey, V. Tropepe, A comparative framework for understanding the biological principles of adult neurogenesis, Prog. Neurobiol. 80 (2006) 281–307, https://doi.org/10.1016/j.pneurobio.2006.11.007.
[4] J. Balthazart, G. Boseret, A.T.M. Konkle, L.L. Hurley, G.F. Ball, Doublecortin as a marker of adult neuroplasticity in the canary song control nucleus HVC, Eur. J. Neurosci. 27 (2008) 801–817, https://doi.org/10.1111/j.1460-9568.2008.06059.x.
[5] G. Kempermann, New neurons for 'survival of the fittest, Nat. Rev. Neurosci. 13 (2012) 727–736, https://doi.org/10.1038/nrn3319.
[6] F.F. Melleu, T.S.D. Santos, C.L. De Oliveira, J. Marino-Neto, Distribution and characterization of doublecortin-expressing cells and fibers in the brain of the adult pigeon (Columba livia), J. Chem. Neuroanat. 47 (2013) 57–70, https://doi.org/10.1016/j.jchemneu.2012.10.006.
[7] S.M. Braun, S. Jessberger, Adult neurogenesis: mechanisms and functional significance, Development 141 (10) (2014) 1983–1986, https://doi.org/10.1242/dev.104596.
[8] E.A. Brenowitz, K.L. Lent, K.E. Miller, D.J. Perkel, Adult neurogenesis is necessary for functional regeneration of a forebrain neural circuit, Proc. Natl. Acad. Sci. U. S. A. 121 (28) (2024) e2400596121, https://doi.org/10.1073/pnas.2400596121.
[9] Z. Nicola, K. Fabel, G. Kempermann, Development of the adult neurogenic niche in the hippocampus of mice, Front. Neuroanat. 9 (2015) 53, https://doi.org/10.3389/fnana.2015.00053.
[10] G. Hussain, R. Akram, H. Anwar, F. Sajid, T. Iman, H.S. Han, C. Raza, J.G. De Aguilar, Adult neurogenesis: a real hope or a delusion? Neural Regen. Res. 19 (1) (2024) 6–15, https://doi.org/10.4103/1673-5374.375317.
[11] C. Herold, E. Karsli, N. Delhaes, J. Mehlhorn, H. Bidmon, K. Amunts, Adult Striatal Neurogenesis-A Comparative Approach Between Pigeons, Mice, Macaques, and Human, J. Comp. Neurol. 533 (11) (2025) e70107, https://doi.org/10.1002/cne.70107.
[12] M.P. Jurkowski, L. Bettio, K.W. E, A. Patten, S.Y. Yau, J. Gil-Mohapel, Beyond the Hippocampus and the SVZ: Adult Neurogenesis Throughout the Brain, Front. Cell. Neurosci. 14 (2020) 576444, https://doi.org/10.3389/fncel.2020.576444.
[13] M. Alonso, A.C. Petit, P.M. Lledo, The impact of adult neurogenesis on affective functions: of mice and men, Mol. Psychiatry 29 (8) (2024) 2527–2542, https://doi.org/10.1038/s41380-024-02504-w.
[14] G. Gheusi, H. Cremer, H. McLean, G. Chazal, J.D. Vincent, P.M. Lledo, Importance of newly generated neurons in the adult olfactory bulb for odor discrimination, Proc. Natl. Acad. Sci. USA 97 (2000) 1823–1828, https://doi.org/10.1073/pnas.97.4.1823.
[15] B.W.-M. Lau, S.-Y. Yau, T.M.C. Lee, Y.-P. Ching, S.-W. Tang, K.-F. So, Effect of corticosterone and paroxetine on masculine mating behavior: possible involvement of neurogenesis, J. Sex. Med. 8 (2011) 1390–1403, https://doi.org/10.1111/j.1743-6109.2010.02081.x.
[16] G. Kempermann, F.H. Gage, L. Aigner, H. Song, M.A. Curtis, S. Thuret, H.G. Kuhn, S. Jessberger, P.W. Frankland, H.A. Cameron, E. Gould, R. Hen, D.N. Abrous, N. Toni, A.F. Schinder, X. Zhao, P.J. Lucassen, J. Frisén, Human Adult Neurogenesis: Evidence and Remaining Questions, Cell. Stem Cell. 23 (1) (2018) 25–30, https://doi.org/10.1016/j.stem.2018.04.004.
[17] P.J. Lucassen, N. Toni, G. Kempermann, J. Frisen, F.H. Gage, D.F. Swaab, Limits to human neurogenesis-really? Mol. Psychiatry 25 (10) (2020) 2207–2209, https://doi.org/10.1038/s41380-018-0337-5.
[18] N. Ho, J. Hooker, A. Sahay, vivo imaging of adult human hippocampal neurogenesis: progress, pitfalls and promise, Mol. Psychiatry 18 (2013) 404–416, https://doi.org/10.1038/mp.2013.8.
[19] M. Shanahan, V.P. Bingman, T. Shimizu, M. Wild, O. Güntürkün, Large-scale network organization in the avian forebrain: a connectivity matrix and theoretical analysis, Front. Comput. Neurosci. 7 (2013) 89, https://doi.org/10.3389/fncom.2013.00089.
[20] G. Gedman, B. Haase, G. Durieux, M.T. Biegler, O. Fedrigo, E.D. Jarvis, As above, so below: Whole transcriptome profiling demonstrates strong molecular similarities between avian dorsal and ventral pallial subdivisions, J. Comp. Neurol. 529 (12) (2021) 3222–3246, https://doi.org/10.1002/cne.25159.
[21] O. Güntürkün, K. von Eugen, J. Packheiser, R. Pusch, Avian pallial circuits and cognition: A comparison to mammals, Curr. Opin. Neurobiol. 71 (2021) 29–36, https://doi.org/10.1016/j.conb.2021.08.007.
[22] A.H. Gaede, P.H. Wu, D.B. Leitch, Variations in touch representation in the hummingbird and zebra finch forebrain, Curr. Biol. 34 (12) (2024) 2739–2747, https://doi.org/10.1016/j.cub.2024.04.081.
[23] F.N. Madison, V.P. Bingman, T.V. Smulders, C.R. Lattin, A bird's eye view of the hippocampus beyond space: Behavioral, neuroanatomical, and neuroendocrine perspectives, Horm. Behav. 157 (2024) 105451, https://doi.org/10.1016/j.yhbeh.2023.105451.
[24] E. Rueda-Alaña, Evolutionary convergence of sensory circuits in the pallium of amniotes, Science 387 (6735) (2025) eadp3411, https://doi.org/10.1126/science.adp3411.
[25] B. Zaremba, Developmental origins and evolution of pallial cell types and structures in birds, Science 387 (6735) (2025) eadp5182, https://doi.org/10.1126/science.adp5182.
[26] M. Stacho, A cortex-like canonical circuit in the avian forebrain, Science 369 (2020) 1585, https://doi.org/10.1126/science.abc5534.
[27] O. Güntürkün, R. Pusch, J. Rose, Why birds are smart, Trends Cogn. Sci. 28 (3) (2024) 197–209, https://doi.org/10.1016/j.tics.2023.11.002.
[28] A. Barnea, V. Pravosudov, Birds as a model to study adult neurogenesis: bridging evolutionary, comparative and neuroethological approaches, Eur. J. Neurosci. 34 (2011) 884–907, https://doi.org/10.1111/j.1460-9568.2011.07851.x.
[29] S.A. Goldman, F. Nottebohm, Neuronal production, migration, and differentiation in a vocal control nucleus of the adult female canary brain, Proc. Natl. Acad. Sci. U. S A. 80 (1983) 2390–2394, https://doi.org/10.1073/pnas.80.8.2390.
[30] J.R. Kirn, B. O'Loughlin, S. Kasparian, F. Nottebohm, Cell death and neuronal recruitment in the high vocal center of adult male canaries are temporally related

to changes in song, Proc. Natl. Acad. Sci. U. S. A. 91 (17) (1994) 7844–7848, https://doi.org/10.1073/pnas.91.17.7844.
[31] C. Herold, P. Schlömer, I. Mafoppa-Fomat, J. Mehlhorn, K. Amunts, M. Axer, The hippocampus of birds in a view of evolutionary connectomics, Cortex 118 (2019) 165–187, https://doi.org/10.1016/j.cortex.2018.09.025.
[32] J. Mehlhorn, N. Niski, K. Liu, S. Caspers, K. Amunts, C. Herold, Regional Patterning of Adult Neurogenesis in the Homing Pigeon's Brain, Front. Psychol. 13 (2022) 889001, https://doi.org/10.3389/fpsyg.2022.889001.
[33] S. Rasika, A. Alvarez-Buylla, F. Nottebohm, BDNF Mediates the Effects of Testosterone on the Survival of New Neurons in an Adult Brain, Neuron 22 (1) (1999) 53–62, https://doi.org/10.1016/s0896-6273(00)80678-9.
[34] O. Güntürkün, M.C. Stüttgen, M. Manns, Pigeons as a model species for Cognitive neuroscience, E-Neuroforum 20 (2014) 86–92, https://doi.org/10.1515/s13295-014-0057-5.
[35] P. Mazengenya, A. Bhagwandin, P. Nkomozepi, P.R. Manger, A.O. Ihunwo, Putative adult neurogenesis in two domestic pigeon breeds (Columba livia domestica): Racing homer versus utility arneau pigeons, Neural Regen. Res. 12 (7) (2017) 1086–1096, https://doi.org/10.4103/1673-5374.211187.
[36] A. Louissaint, S. Rao, C. Leventhal, S.A. Goldman, Coordinated Interaction of Neurogenesis and Angiogenesis in the Adult Songbird Brain, Neuron 34 (6) (2002) 945–960, https://doi.org/10.1016/s0896-6273(02)00722-5.
[37] F. Nottebohm, The road we travelled: Discovery, choreography, and significance of brain replaceable neurons, Ann. N. Y. Acad. Sci. 1016 (2004) 628–658, https://doi.org/10.1196/annals.1298.027.
[38] D.W. Lee, G. Fernando, R.S. Peterson, T.A. Allen, B.A. Schlinger, Estrogen mediation of injury-induced cell birth in neuroproliferative regions of the adult zebra inch brain, Dev. Neurobiol. 67 (8) (2007) 1107–1117, https://doi.org/10.1002/dneu.20399.
[39] S. Bathina, U.N. Das, Brain-derived neurotrophic factor and its clinical implications, Arch. Med. Sci. 11 (6) (2015) 1164–1178, https://doi.org/10.5114/aoms.2015.56342.
[40] F. Nottebohm, M.E. Nottebohm, L. Crane, J.C. Wingfield, Seasonal changes in gonadal hormone levels of adult male canaries and their relation to song, Behav. Neural Biol. 47 (2) (1987) 197–211, https://doi.org/10.1016/s0163-1047(87)90327-x.
[41] J.R. Kirn, The relationship of neurogenesis and growth of brain regions to song learning, Brain Lang. 115 (1) (2010) 29–44, https://doi.org/10.1016/j.bandl.2009.09.00.
[42] D. Lipkind, F. Nottebohm, R. Rado, A. Barnea, Social change affects the survival of new neurons in the forebrain of adult songbirds, Behav. Brain Res. 133 (1) (2002) 31–43, https://doi.org/10.1016/s0166-4328(01)00416-8.
[43] V. DeWulf, S.W. Bottjer, Age and sex differences in mitotic activity within the zebra finch telencephalon, J. Neurosci. 22 (10) (2002) 4080–4094, https://doi.org/10.1523/JNEUROSCI.22-10-04080.2002.
[44] H. van Praag, G. Kempermann, F.H. Gage, Running increases cell proliferation and neurogenesis in the adult mouse dentate gyrus, Nat. Neurosci. 2 (1999) 266–270.
[45] O. Leiter, S. Seidemann, R.W. Overall, B. Ramasz, N. Rund, S. Schallenberg, T. Grinenko, B. Wielockx, G. Kempermann, T.L. Walker, Exercise-induced activated platelets increase adult hippocampal precursor proliferation and promote neuronal differentiation, Stem Cell. Rep. 12 (2019) 667–679.
[46] A. Barnea, F. Nottebohm, Seasonal recruitment of hippocampal neurons in adult free-ranging black-capped chickadees, Proc. Natl. Acad. Sci. U. S. A. 91 (23) (1994) 11217–11221, https://doi.org/10.1073/pnas.91.23.11217.
[47] A.M. Stranahan, D. Khalil, E. Gould, Social isolation delays the positive effects of running on adult neurogenesis, Nat. Neurosci. 9 (4) (2006) 526–533, https://doi.org/10.1038/nn1668.
[48] L.D. LaDage, T.C. Roth, V.V. Pravosudov, Hippocampal neurogenesis is associated with migratory behaviour in adult but not juvenile sparrows (Zonotrichia leucophrys ssp, Proc. R. Soc. B 278 (1702) (2010) 138–143, https://doi.org/10.1098/rspb.2010.0861.
[49] F.F. Melleu, M.V. Pinheiro, C. Lino-de-Oliveira, J. Marino-Neto, Defensive behaviors and prosencephalic neurogenesis in pigeons (Columba livia) are affected by environmental enrichment in adulthood, Brain Struc. Funct. 221 (2016) 2287–2301, https://doi.org/10.1007/s00429-015-1043-6.
[50] K. Santiago Gonzalez, T. Boswell, T.V. Smulders, Functional Differentiation along the Rostro-Caudal Axis of the Avian Hippocampal Formation, Brain Behav. Evol. 100 (2) (2025) 67–79, https://doi.org/10.1159/000542207.
[51] M.M. Holmes, Social regulation of adult neurogenesis: A comparative approach, Front. Neuroendocr. 41 (2016) 59–70.
[52] T.V. Smulders, The Avian Hippocampal Formation and the Stress Response, Brain Behav. Evol. 90 (1) (2017) 81–91, https://doi.org/10.1159/000477654.
[53] A.E.M. Newman, S.A. MacDougall-Shackleton, Y. An, B. Kriengwatana, K. K. Soma, Corticosterone and dehydroepiandrosterone have opposing effects on adult neuroplasticity in the avian song control system, J. Comp. Neurol. 518 (18) (2010) 3662–3678, https://doi.org/10.1002/cne.22395.
[54] L.E. Witterick, S. Davidge, E.C. Hobbs, S.A. MacDougall-Shackleton, M. Clinchy, L.Y. Zanette, Fear of Predators Suppresses Neurogenesis in the Brains of Wild Songbirds, Integr. Org. Biol. 7 (1) (2025) obaf037, https://doi.org/10.1093/iob/obaf037.
[55] T. Shimizu, H.J. Karten, Immunohistochemical analysis of the visual wulst of the pigeon (Columba livia), J. Comp. Neurol. 300 (1990) 346–369, https://doi.org/10.1002/cne.903000307.
[56] A. Reiner, Revised nomenclature for avian telencephalon and some related brainstem nuclei, J. Comp. Neurol. 473 (2004) 377–414, https://doi.org/10.1002/cne.20118.
[57] Y. Atoji, S. Sarkar, J.M. Wild, Differential projections of the densocellular and intermediate parts of the hyperpallium in the pigeon (Columba livia), J. Comp. Neurol. 526 (1) (2018) 146–165, https://doi.org/10.1002/cne.24328.
[58] H.J. Karten, W. Hodos, A Stereotaxic Atlas of the Brain of the Pigeon, Johns Hopkins Press, 1967.
[59] G.F. Striedter, The telencephalon of tetrapods in evolution, Brain Behav. Evol. 49 (4) (2014) 179–213, https://doi.org/10.1159/000112991.
[60] P. Ahumada-Galleguillos, M. Fernandez, G.J. Marin, J.C. Letelier, J. Mpodozis, Anatomical organization of the visual dorsal ventricular ridge in the chick (Gallus gallus): Layers and columns in the avian pallium, J. Comp. Neurol. 523 (2015) 2618–2636, https://doi.org/10.1002/cne.23808.
[61] A. Calabrese, S.M. Woolley, Coding principles of the canonical cortical microcircuit in the avian brain, Proc. Natl. Acad. Sci. U. S. A 112 (2015) 3517–3522, https://doi.org/10.1073/pnas.1408545112.
[62] M. Fernandez, P. Ahumada-Galleguillos, E. Sentis, G. Marin, J. Mpodozis, Intratelencephalic projections of the avian visual dorsal ventricular ridge: Laminarly segregated, reciprocally and topographically organized, J. Comp. Neurol. 528 (2020) 321–359, https://doi.org/10.1002/cne.24757.
[63] M. Fernandez, R. Reyes-Pinto, C. Norambuena, E. Sentis, J. Mpodozis, A canonical interlaminar circuit in the sensory dorsal ventricular ridge of birds: The anatomical organization of the trigeminal pallium, J. Comp. Neurol. 529 (2021) 3410–3428, https://doi.org/10.1002/cne.25201.
[64] J. Mehlhorn, G. Rehkaemper, The orientation of homing pigeons (Columba livia f. d.) with and without navigational experience in a two-dimensional environment, PLOS ONE 12 (11) (2017) e0188483, https://doi.org/10.1371/journal.pone.0188483.
[65] H.G. Kuhn, H. Dickinson-Anson, F.H. Gage, Neurogenesis in the dentate gyrus of the adult rat: age-related decrease of neuronal progenitor proliferation, J. Neurosci. 16 (6) (1996) 2027–2033, https://doi.org/10.1523/JNEUROSCI.16-06-02027.1996.
[66] R.S. Nowakowski, S.B. Lewin, M.W. Miller, Bromodeoxyuridine immunohistochemical determination of the lengths of the cell cycle and the DNA-synthetic phase for an anatomically defined population, J. Neurocytol. 18 (1989) 311–318, https://doi.org/10.1007/BF01190834.
[67] G. Kempermann, D. Gast, G. Kronenberg, M. Yamaguchi, F.H. Gage, Early determination and long-term persistence of adult-generated new neurons in the hippocampus of mice, Development 130 (2) (2003) 391–399, https://doi.org/10.1242/dev.00203.
[68] J. Balthazart, G.F. Ball, Endogenous versus exogenous markers of adult neurogenesis in canaries and other birds: advantages and disadvantages, J. Comp. Neurol. 522 (2014) 4100–4120, https://doi.org/10.1002/cne.23661.
[69] A. Cattan, A. Ayali, A. Barnea, The cell birth marker BrdU does not affect recruitment of subsequent cell divisions in the adult avian brain, Biomed. Res. Int. (2015) 126078, https://doi.org/10.1155/2015/126078.
[70] V.V. Gusel'nikova, D.E. Korzhevskiy, NeuN As a Neuronal Nuclear Antigen and Neuron Differentiation Marker, Acta Nat. 7 (2) (2015) 42–47.
[71] D. Ehninger, G. Kempermann, Neurogenesis in the adult hippocampus, Cell. Tissue Res. 1 (1) (2008) 243–250, https://doi.org/10.1007/s00441-007-0478-3.
[72] V.L. Savchenko, J.A. McKanna, I.R. Nikonenko, G.G. Skibo, Microglia and astrocytes in the adult rat brain: Comparative immunocytochemical analysis demonstrates the efficacy of lipocortin 1 immunoreactivity, Neuroscience 96 (1) (2000) 195–203, https://doi.org/10.1016/s0306-4522(99)00538-2.
[73] K. Hernández-Ortega, A.A. Canul-Euan, J.M. Solis-Paredes, H. Borboa-Olivares, E. Reyes-Muñoz, G. Estrada-Gutierrez, I. Camacho-Arroyo, S100B actions on glial and neuronal cells in the developing brain: an overview, Front. Neurosci. 18 (2024) 1425525, https://doi.org/10.3389/fnins.2024.1425525.
[74] A. Denoth-Lippuner, S. Jessberger, Formation and integration of new neurons in the adult hippocampus, Nat. Rev. Neurosci. 22 (2021) 223–236, https://doi.org/10.1038/s41583-021-00433-z.
[75] G. Kempermann, H. Song, F.H. Gage, Neurogenesis in the Adult Hippocampus, Cold Spring Harb. Perspect. Biol. 7 (9) (2015) a018812, https://doi.org/10.1101/cshperspect.a018812.
[76] R. Knoth, I. Singec, M. Ditter, G. Pantazis, P. Capetian, R.P. Meyer, V. Horvat, B. Volk, G. Kempermann, Murine features of neurogenesis in the human hippocampus across the lifespan from 0 to 100 years, PLoS. One 5 (1) (2010) e8809, https://doi.org/10.1371/journal.pone.0008809.
[77] J.P. Brown, S. Couillard-Després, C.M. Cooper-Kuhn, J. Winkler, L. Aigner, H. G. Kuhn, Transient expression of doublecortin during adult neurogenesis, J. Comp. Neurol. 467 (1) (2003) 1–10, https://doi.org/10.1002/cne.10874.
[78] Y. Atoji, J.M. Wild, Afferent and efferent projections of the mesopallium in the pigeon (Columba livia), J. Comp. Neurol. 520 (4) (2012) 717–741, https://doi.org/10.1002/cne.22763.
[79] Y. Atoji, J.M. Wild, Projections of the densocellular part of the hyperpallium in the rostral Wulst of pigeons (Columba livia), Brain Res. 1711 (2019) 130–139, https://doi.org/10.1016/j.brainres.2019.01.001.
[80] C. Herold, Distribution of neurotransmitter receptors and zinc in the pigeon (Columba livia) hippocampal formation: a basis for further comparison with the mammalian hippocampus, J. Comp. Neur. 522 (2014) 2553–2575, https://doi.org/10.1002/cne.23549.
[81] E.A. Brenowitz, T.A. Larson, Neurogenesis in the adult avian song-control system, Cold Spring Harb. Perspect. Biol. 7 (6) (2015) a019000, https://doi.org/10.1101/cshperspect.a019000.
[82] B.A. Robertson, L. Rathbone, G. Cirillo, R.B. D'Eath, M. Bateson, T. Boswell, P. W. Wilson, I.C. Dunn, T.V. Smulders, Food restriction reduces neurogenesis in the avian hippocampal formation, PLoS. One 12 (12) (2017) e0189158, https://doi.org/10.1371/journal.pone.0189158.

[83] E. Drapeau, W. Mayo, C. Aurousseau, M. Le Moal, P.V. Piazza, D.N. Abrous, Spatial memory performances of aged rats in the water maze predict levels of hippocampal neurogenesis, Proc. Natl. Acad. Sci. U. S. A 100 (24) (2003) 14385–14390, https://doi.org/10.1073/pnas.2334169100.
[84] J. Gil-Mohapel, P.S. Brocardo, W. Choquette, R. Gothard, J.M. Simpson, B. R. Christie, Hippocampal neurogenesis levels predict watermaze search strategies in the aging brain, PloS. One 8 (9) (2013) e75125, https://doi.org/10.1371/journal.pone.0075125.
[85] B. Leuner, E. Gould, T.J. Shors, Is there a link between adult neurogenesis and learning? Hippocampus 16 (3) (2006) 216–224, https://doi.org/10.1002/hipo.20153.
[86] M. Opendak, E. Gould, Adult neurogenesis: a substrate for experience-dependent change, Trends Cogn. Sci. 19 (3) (2015) 151–161, https://doi.org/10.1016/j.tics.2015.01.001.
[87] D.F. Sherry, J.S. Hoshooley, Seasonal hippocampal plasticity in food-storing birds, Philos. Trans. R. Soc. Lond. B Biol. Sci. 365 (1542) (2010) 933–943, https://doi.org/10.1098/rstb.2009.0220.
[88] G. Kempermann, The neurogenic reserve hypothesis: What is adult hippocampal neurogenesis good for? Trends Neurosci. 31 (4) (2008) 163–169, https://doi.org/10.1016/j.tins.2008.01.002.
[89] A. Olariu, K.M. Cleaver, L.E. Shore, M.D. Brewer, H.A. Cameron, A natural form of learning can increase and decrease the survival of new neurons in the dentate gyrus, Hippocampus 15 (6) (2005) 750–762, https://doi.org/10.1002/hipo.20097.
[90] E. Adar, F. Nottebohm, A. Barnea, The relationship between nature of social change, age, and position of new neurons and their survival in adult zebra finch brain, J. Neurosci. 28 (20) (2008) 5394–5400, https://doi.org/10.1523/JNEUROSCI.5706-07.2008.
[91] G. Kronenberg, K. Reuter, B. Steiner, M.D. Brandt, S. Jessberger, M. Yamaguchi, G. Kempermann, Subpopulations of proliferating cells of the adult hippocampus respond differently to physiologic neurogenic stimuli, J. Comp. Neurol. 467 (4) (2003) 455–463, https://doi.org/10.1002/cne.10945.
[92] R.W. Overall, T.L. Walker, O. Leiter, S. Lenke, S. Ruhwald, G. Kempermann, Delayed and transient increase of adult hippocampal neurogenesis by physical exercise in DBA/2 mice, PLoS. One 8 (2013) e83797, https://doi.org/10.1371/journal.pone.0083797.
[93] H.P. Lipp, L. Bonfanti, Adult neurogenesis in mammals: variations and confusions, Brain Behav. Evol. 87 (2016) 205–221, https://doi.org/10.1159/000446905.
[94] J. Li, Y.H. Ding, J.A. Rafols, Q. Lai, J.P. McAllister, Y. Ding, Increased astrocyte proliferation in rats after running exercise, Neurosci. Lett. 386 (3) (2005) 160–164, https://doi.org/10.1016/j.neulet.2005.06.009.
[95] M. Uda, M. Ishido, K. Kami, M. Masuhara, Effects of chronic treadmill running on neurogenesis in the dentate gyrus of the hippocampus of adult rat, Brain Res. 1104 (2006) 64–72.
[96] L. Saur, P.P. Baptista, P.N. de Senna, M.F. Paim, P. do Nascimento, J. Ilha, P. B. Bagatini, M. Achaval, L.L. Xavier, Physical exercise increases GFAP expression and induces morphological changes in hippocampal astrocytes, Brain Struct. Funct. 219 (1) (2014) 293–302, https://doi.org/10.1007/s00429-012-0500-8.
[97] Z. Rusznák, W. Henskens, E. Schofield, W.S. Kim, Y. Fu, Adult Neurogenesis and Gliogenesis: Possible Mechanisms for Neurorestoration, Exp. Neurobiol. 25 (3) (2016) 103–112, https://doi.org/10.5607/en.2016.25.3.103.
[98] J. Martins-Macedo, A.J. Salgado, E.D. Gomes, L. Pinto, Adult brain cytogenesis in the context of mood disorders: From neurogenesis to the emergent role of gliogenesis, Neurosci. Biobehav. Rev. 131 (2021) 411–428, https://doi.org/10.1016/j.neubiorev.2021.09.030.
[99] A.C. Delgado, A.R. Maldonado-Soto, V. Silva-Vargas, D. Mizrak, T. von Känel, K. R. Tan, A. Paul, A. Madar, H. Cuervo, J. Kitajewski, C.S. Lin, F. Doetsch, Release of stem cells from quiescence reveals gliogenic domains in the adult mouse brain, Science 372 (6547) (2021) 1205–1209, https://doi.org/10.1126/science.abg8467.
[100] K.T. Baldwin, D.L. Silver, Expanding gliogenesis, Science 372 (6547) (2021) 1151–1152, https://doi.org/10.1126/science.abj1139.
[101] A. Kriegstein, A. Alvarez-Buylla, The glial nature of embryonic and adult neural stem cells, Annu. Rev. Neurosci. 32 (2009) 149–184, https://doi.org/10.1146/annurev.neuro.051508.135600.
[102] B. Steiner, G. Kronenberg, S. Jessberger, M.D. Brandt, K. Reuter, G. Kempermann, Differential regulation of gliogenesis in the context of adult hippocampal neurogenesis in mice, Glia 46 (1) (2004) 41–52, https://doi.org/10.1002/glia.10337.
[103] W. Clark, M. Colombo, Seeing the Forest for the Trees, and the Ground Below My Beak: Global and Local Processing in the Pigeon's Visual System, Front. Psychol. 13 (2022) 888528, https://doi.org/10.3389/fpsyg.2022.888528.
[104] D. Heyers, I. Musielak, K. Haase, C. Herold, P. Bolte, O. Güntürkün, H. Mouritsen, Morphology, biochemistry and connectivity of Cluster N and the hippocampal formation in a migratory bird, Brain Struct. Funct. 227 (8) (2022) 2731–2749, https://doi.org/10.1007/s00429-022-02566-y.
[105] N. Patzke, M. Manns, O. Güntürkün, P. Ioalè, A. Gagliardo, Navigation-induced ZENK expression in the olfactory system of pigeons (Columba livia), Eur. J. Neurosci. 31 (2010) 2062–2072, https://doi.org/10.1111/j.1460-9568.2010.07240.x.
[106] A. Rastogi, Y. Kumari, S. Rani, V. Kumar, Phase inversion of neural activity in the olfactory and visual systems of a night-migratory bird during migration, Eur. J. Neurosci. 34 (2011) 99–109, https://doi.org/10.1111/j.1460-9568.2011.07737.x.
[107] T. Nakamori, K. Sato, Y. Atoji, T. Kanamatsu, K. Tanaka, H. Ohki-Hamazaki, Demonstration of a neural circuit critical for imprinting behavior in chicks, J. Neurosci. 30 (2010) 4467–4480, https://doi.org/10.1523/JNEUROSCI.3532-09.2010.
[108] W. Clark, M. Chilcott, A. Azizi, R. Pusch, K. Perry, M. Colombo, Neurons in the pigeon visual network discriminate between faces, scrambled faces, and sine grating images, Sci. Rep. 12 (2022) 589, https://doi.org/10.1038/s41598-021-04559-z.
[109] H.L. Payne, G.F. Lynch, D. Aronov, Neural representations of space in the hippocampus of a food-caching bird, Science 373 (2021) 343–348, https://doi.org/10.1126/science.abg2009.
[110] M.C. Applegate, K.S. Gutnichenko, E.L. Mackevicius, D. Aronov, An entorhinal-like region in food-caching birds, Curr. Biol. 33 (12) (2023) 2465–2477, https://doi.org/10.1016/j.cub.2023.05.031.
[111] A. Alvarez-Buylla, J.M. Garcia-Verdugo, A.S. Mateo, H. Merchant-Larios, Primary Neural Precursors and Intermitotic Nuclear Migration in the Ventricular Zone of Adult Canaries, J. Neurosci. 18 (3) (1998) 1020–1037, https://doi.org/10.1523/JNEUROSCI.18-03-01020.1998.
[112] H.-W. Dong, L.W. Swanson, L. Chen, M.S. Fanselow, A.W. Toga, Genomiceanatomic evidence for distinct functional domains in hippocampal field CA1, Proc. Natl. Acad. Sci. U. S. A. 106 (11794) (2009) e11799, https://doi.org/10.1073/pnas.0905641106.
[113] S. Ohara, S. Sato, K.-I. Tsutsui, M.P. Witter, T. Iijima, Organization of multisynaptic inputs to the dorsal and ventral dentate gyrus: Retrograde trans-synaptic tracing with rabies virus vector in the rat, PloS. One 8 (2013) e78928, https://doi.org/10.1371/journal.pone.0078928.
[114] B.A. Strange, M.P. Witter, E.D. Lein, E.I. Moser, Functional organization of the hippocampal longitudinal axis, Nat. Rev. Neurosci. 15 (2014) 655–669, https://doi.org/10.1038/nrn3785.
[115] C. Anacker, R. Hen, Adult hippocampal neurogenesis and cognitive flexibility-linking memory and mood, Nat. Rev. Neurosci. 18 (2017) 335–346, https://doi.org/10.1038/nrn.2017.45.
[116] A. Plachti, S.B. Eickhoff, F. Hoffstaedter, K.R. Patil, A.R. Laird, P.T. Fox, K. Amunts, S. Genon, Multimodal Parcellations and Extensive Behavioral Profiling Tackling the Hippocampus Gradient, Cereb. Cortex. 29 (11) (2019) 4595–4612, https://doi.org/10.1093/cercor/bhy336.
[117] S. Genon, B.C. Bernhardt, R. La Joie, K. Amunts, S.B. Eickhoff, The many dimensions of human hippocampal organization and (dys)function, Trends Neurosci. 44 (12) (2021) 977–989, https://doi.org/10.1016/j.tins.2021.10.003.
[118] C.L. Pytte, S. George, S. Korman, E. David, D. Bogdan, J.R. Kirn, Adult neurogenesis is associated with the maintenance of a stereotyped, learned motor behavior, J. Neurosci. 32 (20) (2012) 7052–7057, https://doi.org/10.1523/JNEUROSCI.5385-11.2012.
[119] O. Güntürkün, T. Bugnyar, Cognition without cortex, Trends Cogn. Sci. 20 (2016) 291–303, https://doi.org/10.1016/j.tics.2016.02.001.
[120] D. Scarf, K. Boy, A. Uber Reinert, J. Devine, O. Güntürkün, M. Colombo, Orthographic processing in pigeons (Columba livia), Proc. Natl. Acad. Sci. U. S. A. 113 (2016) 11272–11276, https://doi.org/10.1073/pnas.1607870113.