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Full-Length Research Article

Morphological Differences in Superior Colliculus of Adult and Juvenile African Grasscutter (*Thryonomys swinderianus*)

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Summary: Rodents have provided insight to specific aspects of neural organization including morphology, function, development, and evolution in mammalian species. The superior colliculus (SC) also referred to as rostral colliculus has been studied in several mammals, including nonhuman primates. The SC has been considered a visual motor integration center of the CNS. Under-explored species such as the African Grasscutter (AGC), a semi nocturnal rodent species, exhibits peculiar SC-regulated behaviors in the wild including arrest and freezing abilities in response to predators. This study morphologically assessed differences in the SC of adult and juvenile AGCs. Six AGCs (adult/ juvenile, n = 3) were procured for this study. Brains were harvested and morphologic characteristics including histology, histometry (pyramidal soma size and perimeter) and cell distribution in the SC of AGCs were assessed and quantified. Data obtained were analyzed using GraphPad Prism and computer running imaging software (AmScope and ImageJ, USA). Comparison of morphologic characteristics of SC revealed similarities and variations between the AGCs age groups: SC presented with similar histoarchitectural organization; pyramidal cell soma characteristics and cell distribution showed a significant ($p < 0.05$) difference between the AGCs with higher mean value in the juvenile. This study has demonstrated a basic histoarchitectural organization of the superior colliculus in adult and juvenile African Grasscutter; thus, points to conserved architectural organization across rodent species. Observed differences could be attributed to variations in cellular functionality with response to developmental neurogenesis and synaptic refinement between the rodents. Findings are of potential benefit in understanding neurodevelopmental variations that influence functional capabilities across different age group.

Keywords: *Cell distribution, Histoarchitectural organization, Histometric characteristics, Pyramidal cells, Rodents, Superior colliculus*
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INTRODUCTION

Mammalian species, most especially rodents, have provided an opportunity to study specific aspects of neural organization including morphology, function, development, and evolution as they relate to variations in peripheral morphology, sensory specialization and cognitive ability, with only rat and mice accounting for about 40% of the neural research (Manger et al., 2008). Previous researches have reported that rat and mice brain lack the complexity of the human brain and much is yet to be understood about specific contributions of brain to even simple behaviors (Krubitzer et al., 2011).

The Thryonomys swinderianus (African Grasscutter, AGC) is a common rodent of Africa and the largest rodent species after the African porcupine. A peculiar response behavior exhibited by the AGC include its skilled swimming and arrest or freezing ability when in context with a potential threat (Akpan et al., 2009). One region of the mammalian brain responsible for this behavior is the midbrain, specifically the rostral colliculus, also referred to as the superior colliculus (SC). This brain structure has been established to be part of the network of brain areas involved in spatial visual attention, through the implementation of motor consequences; thus, considered a visual motor integration center of the central nervous system (Krauzlis et al., 2013; Wheatcroft et al., 2022). The superior colliculus (SC) has been studied in numerous mammalian species, including nonhuman primates (Basso and May, 2017). In mammalian species, the SC is a laminarized structure; organized into distinct layers on the basis of its neuronal distribution, connectivity, and functional properties (Liu et al., 2022).

As such, comparative assessments utilizing basic anatomical approaches, within and across rodents, especially the underexplored and non-laboratory reared species like the AGCs, are important and could be essential in providing basic understanding of neuroanatomical features, thereby narrowing the gap between basic and translational neuroscience research. Therefore, this study morphologically assessed differences in the SC of adult and juvenile AGCs.

MATERIALS AND METHODS

Ethical Approval: Ethical approval for this study was obtained from Ahmadu Bello University Ethics Committee on animal use and care with the approved number ABUCAUC/2023/108.

Experimental Animals: Six apparently healthy rodents - *Thryonomys swinderianus* (AGC), comprising of three adult and three Juvenile (adult 350-450 days old; juvenile 65-72 days old; Ibe et al., 2017) were obtained from Okiki Farm in Lokoja, Kogi State, Nigeria and transported using locally fabricated wooden animal cages to the Department of Human Anatomy Animal House, Ahmadu Bello University, Zaria, Kaduna State, Nigeria and housed under standard laboratory conditions (12-hrs light/dark). The AGCs were allowed to acclimatize to the novel environment for three days before commencement of the study.

Experimental Design: The six rodent species (N=6) (three adult AGCs and three juvenile AGCs) were weighed, euthanized using chloroform inhalation and decapitated. Brains were extracted out by removal of cranial and facial bones including the meninges using thumb forceps and a pair of scissors. Morphologic observations were made and midbrain region was identified. Dissected brains were subsequently fixed in 10% formal saline for further studies (Fig. 1).

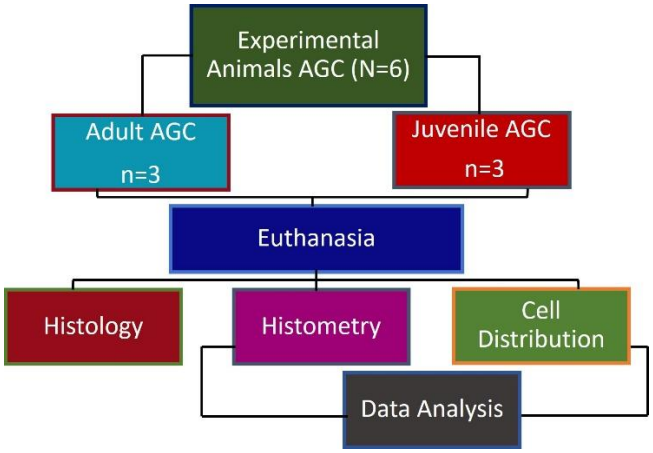

Figure 1:
Experimental Design

Histological Studies: The harvested post-fixed brain samples were grossed coronally at the level of superior colliculus between the cerebrum and cerebellum to reveal the upper part of the midbrain (right and left superior colliculus). Tissue sections were subsequently processed for light microscopic examination and stained with Hematoxylin and Eosin (H&E) according the method described by Feldman and Wolfe (2014) and Suvarna et al. (2019) to demonstrate general histoarchitectural features. Stained tissue sections were examined using a light microscope and a computer running image processing software (AmScope MT *version* 3.0.0.5, USA) at a magnification of ×40, ×100 and ×250 respectively. A dissecting microscope with computer running image processing software (AmScope MT *version* ×64,4.10.17192) was used at ×20 to map out the entire coronal section of the midbrain. Regional identification was guided by the Rat Brain Atlas, (Paxinos and Watson, 2013). All tissue processing and light microscopic procedures were conducted in the Histology Unit and Microscopy and Stereology Research Laboratory in the Department of Human Anatomy, ABU, Zaria.

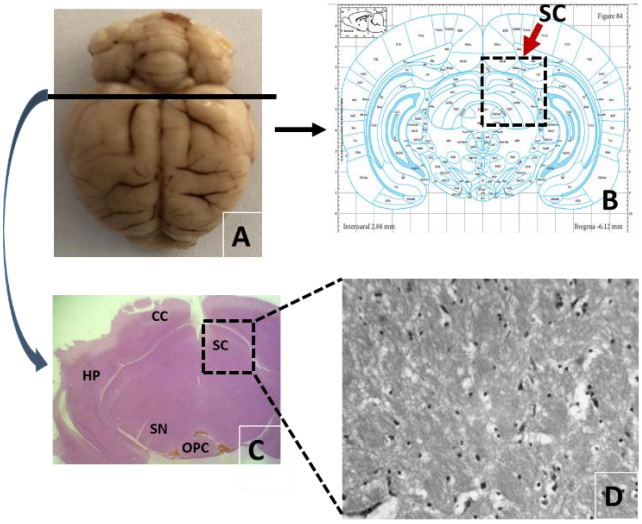

Plate 1:
Coronal section of the midbrain identifying region of study (superior colliculus).
A = AGC brain plain of section (black line); B= Illustration and location of SC on brain atlas; C= Coronal section of SC; D= Inset from plate C, illustrating histology of SC; SC =Superior colliculus; CC= Cerebral Cortex; HP= Hippocampus; SN = Substantia nigra; OPC=Optic Chiasma.

Histometric Assessments: Histometric assessment was conducted according to the method described by Agbon et al. (2021) for 2D estimation of size of structures on micrographs and was performed to estimate the soma size (area and perimeter) of the pyramidal cells in a specific region of interest; the deep layer of superior colliculus, using a light microscope (HM-LUX, LeitzWetzlar, Germany) with a 25/ 0.5 × objective (× 250 magnification), a micrometer slide (1 mm graduated in 0.01 mm units; that is divided into 100 µm units) and a computer running imaging software (AmScope MT *version* 3.0.0.5, USA). Three (3) H&E-stained histological sections of the superior colliculus per AGC, across the age groups (adult and juvenile), were captured as digital micrographs. The digital micrographs were imported to the imaging software and the AmScope imaging software polygon tool was used to measure the areas and perimeters of selected pyramidal neurons. To minimize bias, pyramidal cells from different fields for each tissue slide were selected for the measurement.

Cell Density Quantification: The quantification of cell density (distribution) in SC laminae of adult and juvenile

AGCs was conducted by adopting the method described by Agbon et al. (2022). This involved assessing micrographs (captured at × 250 magnification) using a computerized image analysis software (ImageJ, NIH, US) according to the manufacturer's instruction. Captured micrographs of SC laminae (the Zo layer excluded to avoid bias based on its very narrow extent, dorso-ventrally) were imported into ImageJ software and converted to 16 bits. Threshold was calibrated to select cells (Color: Black and White with color space: HSB). The image was converted to binary format and cells were counted automatically. The mean count values of data obtained were computed and statistically analyzed.

Data Analysis

Data obtained from measurements were analyzed using the statistical software GraphPad Prism (version 9.3.1, Boston, USA), result presented in charts and expressed as mean ± S.E.M. The presence of significant differences among means of the groups were determined using independent *t-test*. Values were considered statistically significant when $p < 0.05$

RESULTS

Histological Examinations: At lower magnification of ×20, coronal section of midbrain region in both adult and juvenile AGCs revealed a dorsal part known as tectum and ventral part known as tegmentum. The tectum is composed of two elevations identified as superior colliculus bounded superiorly by the cerebral cortex and inferiorly by the substantia nigra and optic chiasma. A centrally located cerebral aqueduct and periaqueductal gray were also observed in the section (Figure 3).

At a high magnification of ×100, the SC presented with three distinct layers base on predominant histoarchitectural features; identified as superficial layer (SL) with densely distributed cells; an intermediate layer (IML) with interspersed reticulations within cells, and a deep layer (DL) with sparse distribution of cells (Plate 1).

At a closer magnification (× 250), the three layers were presented with six distinct laminae. The SL was presented with two laminae (Zo and SuG), IML presented with only one laminae (Op) and DL presented with three laminae (InG, DpG and DpWh). Histoarchitectural features in these laminae including neuronal and glial cells were compared between the adult and juvenile AGCs (Plate 2).

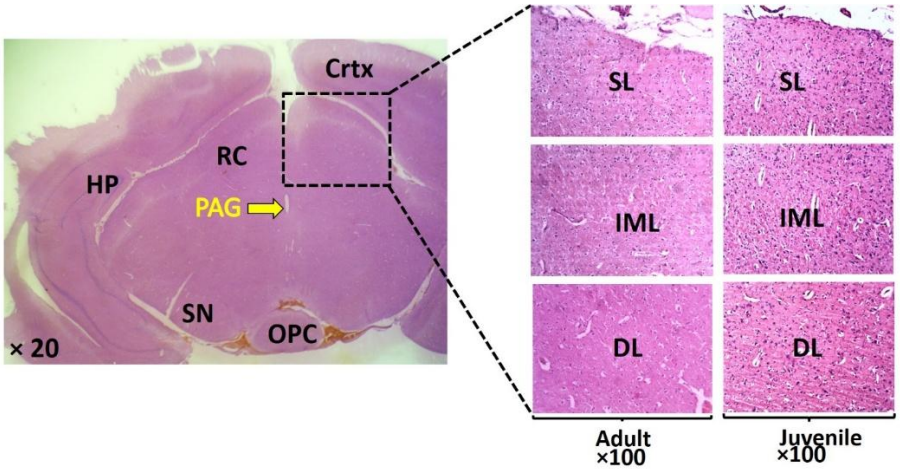

Plate 2:
Coronal section of AGC brain illustrating the three zonal layers of SC. (H & E)
SC =Superior colliculus; CC= Cerebral Cortex; HP= Hippocampus; SN=Substantia nigra; OPC=Optic Chiasma, PAG; Periaquiductal Grey and ceberbral aqueduct; SL=Superficial Layer; IML= Intermediate Layer; DL=Deep Layer

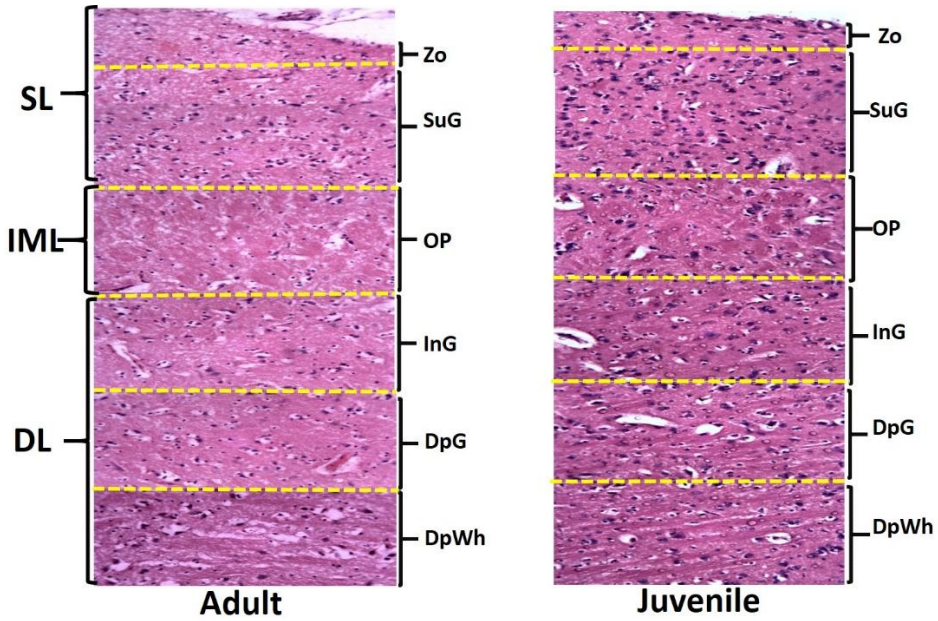

Plate 3:
Stacked micrographic representation of laminae in the superior colliculus of adult and juvenile AGCs . H &E × 250
Zo *= Zonal layer;* ***SuG****= Superficial Gray;* ***OP****= Optic layer;* ***InG*** *= Inner Gray;* ***DpG****= Deep Gray;* ***DpWh****= Deep White*

The Zo (stratum zonal; layer lining the SC) is observed to be thin, and contain cells that are sparsely distributed and arranged in a horizontal order. The size of this lamina appeared to be reduced in the adult AGC. The SuG (stratum griseum superficiale) contains clusters of cells with varying shapes and size including pyramidal and stellate cells. The Op (Optic laminae) is composed of mostly white matter reticulations. Contains fewer cells identified as pyramidal and stellate/ oligodendrocytes.This laminar seperates the superficial from the deep laminar.The InG (Inner grey) and DpG (Deep grey) contains numerous cells including pyramidal.The two laminae have similar histoarchitecture with no observable delineation between the laminae. The DpWh (Deep white) lies immediately above the periaquiductal grey and contains reticulations. Cells observed were pyramidal, with stellate cells surrounded by empty spaces.

A general observation in the histotoarchitecture of the SC laminae presented with larger cells and dense reticulations in juvenile AGCs compared to the adult (Plates 4 and 5).

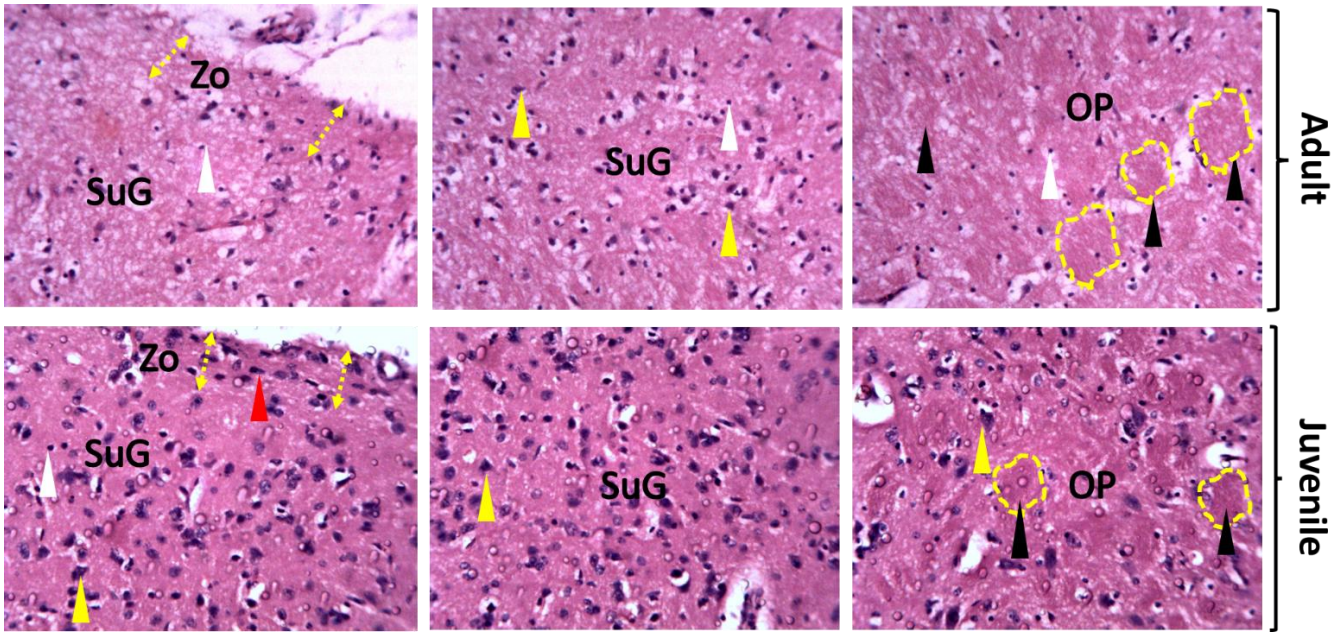

Plate 4:
Superior colliculus of Adult and Juvenile AGCs. H & E. X250
Zo = Zonal layer; SuG= Superficial Gray; OP= Optic layer; Black arrow head=White matter reticulation; red arrow head=horizontal cell; Yellow arrow head=Pyramidal cell; White arrow head=Stellate cell\Oligodendrocyte

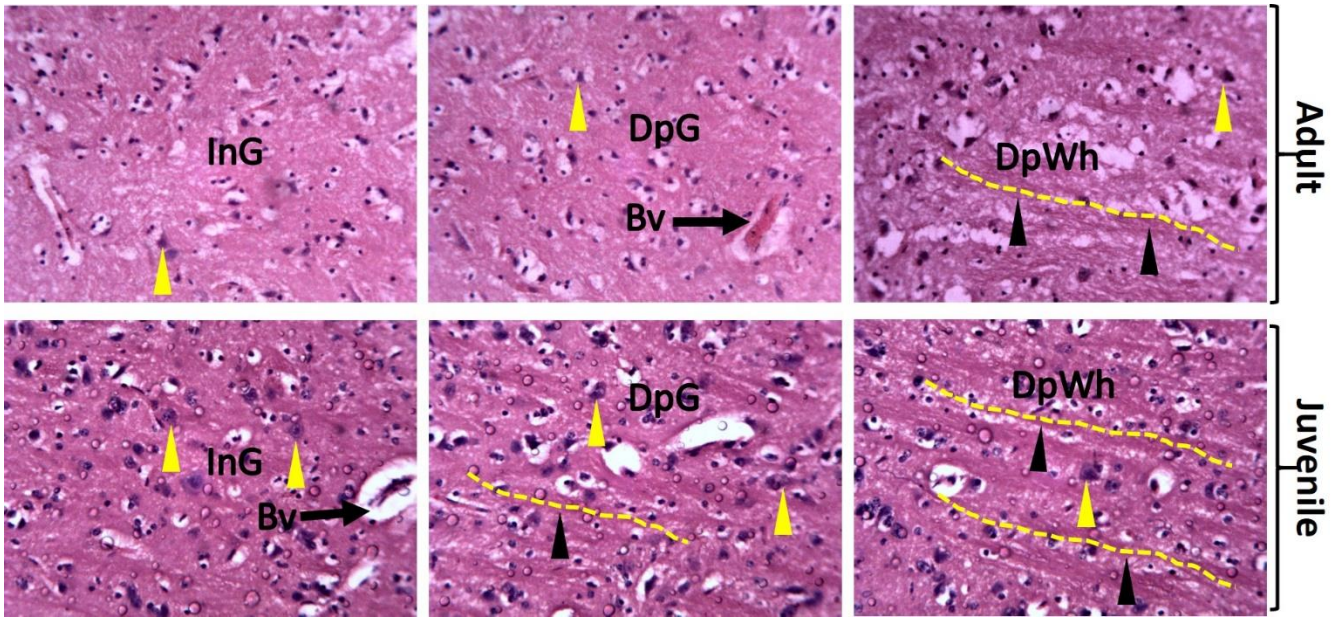

Plate 5:
Superior colliculus of Adult and Juvenile AGCs. H & E. × 250
InG = Inner Gray; DpG=Deep Gray; DpWh= Deep White; Black arrow head=White matter reticulation; Yellow arrow head=Pyramidal neuron; Black arrow=Blood vessel.

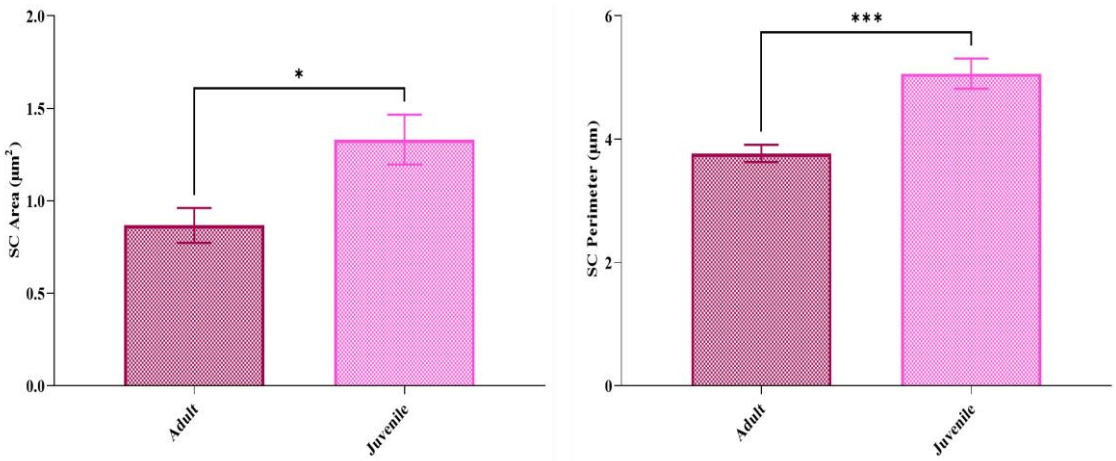

Figure 2:
SC soma area and perimeter comparison between adult and juvenile African Grasscutter
n=6, Mean ± SEM, Independent sample *t*-test, *=p< 0.05; ***=p< 0.001 when adult was compared to juvenile. SC= Superior colliculus.

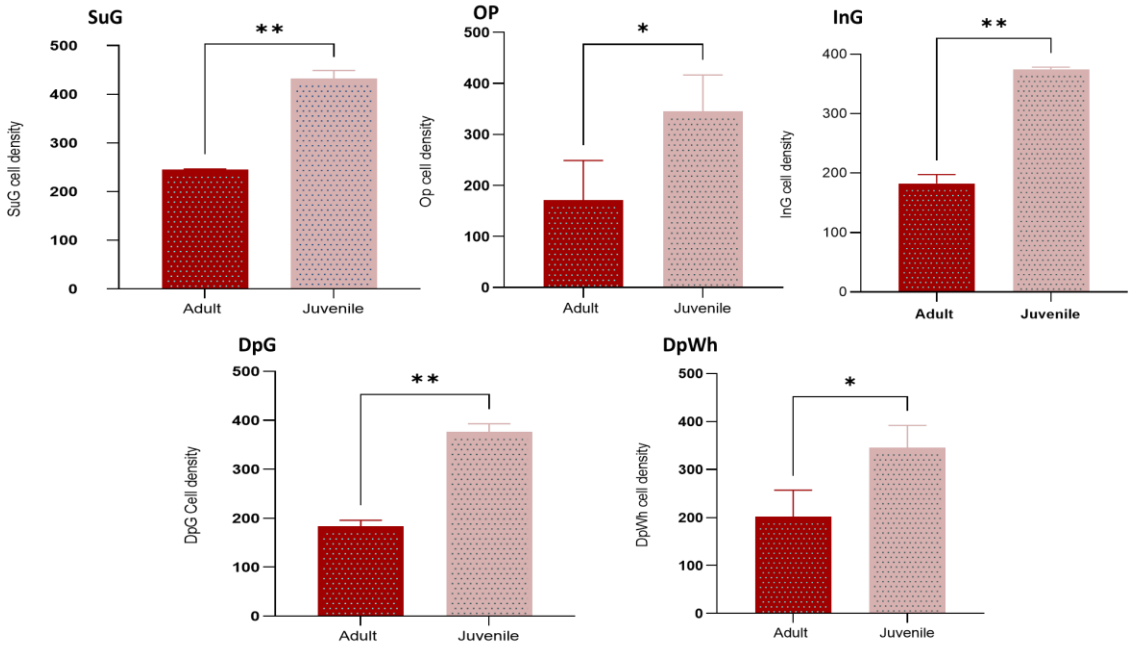

Figure 8:
Cell density quantification in SC Laminar of adult and juvenile AGCs
Mean ± SEM, Independent sample *t*-test, *=p<0.05, **=p<0.01 when adult was compared to juvenile
SuG= Superficial Gray; OP= Optic layer; InG = Inner Gray; DpG= Deep Gray; DpWh= Deep White

Histometric Characteristics: Histometry was conducted to estimate the cell body (soma) area and perimeter of pyramidal cells in the Deep Layer of SC across the age group. Histometric characteristics revealed a statistically significant (p< 0.05) difference, with juvenile AGCs having higher mean values when compared to the adults (Figure 2).

Cell Distribution: Quantification of cell distribution from sections of the selected SC laminae revealed a significant difference. Across the laminae, juvenile AGCs presented with higher (p<0.05) mean values when compared to the adult (Figure 3).

DISCUSSION

In this study, morphologic features of the SC, particularly the histoarchitecture of the laminae was assessed microscopically and compared between the adult and juvenile AGCs.

The observed histoarchitectural features of the AGC midbrain with ventral tegmental and dorsal tectal parts, and related structures are similar with the architectural organization across mammalian species (Singh, 2009; Agbon et al., 2022; Agbon et al., 2024). The elevated tectum in which the SC is situated is consistent with other rodents including rat and mouse (Ruchalski and Hathout, 2012; Zhang 2018). This organization facilitates similar functions in response to SC regulated behavior including visual and auditory processing which are critical for survival and adaptation (Stein and Rowland, 2011).

The characteristics demonstration of three distinct layers of the SC; SL, IML and DL is in line with reports on the histoarchitectural organization in mammalian SC; the SC is a laminarized structure with several layers (May, 2006). Six

distinct laminae were observed on the basis of their predominant histoarchitectural features (Zo, SuG, Op, InG, DpG and DpWh). These findings reflect a complex organization of the SC that is consistent across various mammalian species, including rodents. Liu *et al.* (2022) reported the SC as an organized mesencephalic structure, composed of several laminae on the basis of neuronal distribution patterns, connectivity and functional properties. Mensah-Brown and Garey (2006) recorded six laminae in the rostral colliculus of camels and associated this architecture to a well-developed visual system; suggesting a good eyesight in the camel. However, this study is at variance with reports on some rodent; Paxinos and Watson (2007) that observed seven laminae in rat. The observed cytoarchitectural variations could be tied to species specificity or to methods and technique used.

Cytoarchitectural features identified within the SC laminae with heterogenous cell morphologies including horizontal, pyramidal and stellate; neurons and glia cells are in line with the reported cytoarchitectural characteristics of the colliculi in mammals (Wang et al., 2010; Gale and Murphy, 2014; Ibe et al., 2019). The presence of sparsely distributed cells with interspersed reticulations in the Op lamina of AGCs agrees with the reported architecture in a rodent species, mouse (Cang, 2018). Functionally, Op lamina has been associated with a unique behavioral response to environmental threat (Xie et al., 2021). Findings are indicative of AGC's similar functional activity to other rodents, with an ability to freeze in confront with a potential threat. This behavior is critical for the survival of the AGC from potential predators in its habitat being a seminocturnal rodent in West Africa (Adu et al., 2017). Xie et al. (2021) and Wheatcroft (2022) reported that inhibition or excitation of neuronal cells in the Op lamina elicit or impairs the freezing ability of rodent specie.

Histometric measurements or 2D estimation have been used to assess and compare certain histological characteristics (Asuquo et al., 2007). It serves as an imperative tool that provide basis for assessment of histological observations, thereby making statistical analysis easier (Huda and Zaid, 2007; Agbon et al., 2024). Histometric estimation of AGC pyramidal cell soma size within the Dp layers of SC with remarkably higher values in the juvenile is suggestive of variations in pyramidal cell sizes which could be attributed to variations in cellular activity and functionality with respect to SC regulated behaviors. The interplay between structural and functional factors significantly influences regional variations in neuronal sizes across biological species (Djouhri and Lawson 2004; Savage et al., 2007; Partanen and Achim, 2022). Structurally, neuronal size has been associated with brain size of a species, and physiologic activity of a neuron correlates with size of the neuron (Harding 2013; Agbon et al., 2023). In this study, the higher histometric values of pyramidal neurons in juvenile SC could be attributed to the physiologic activity of the neurons, especially on-going developmental needs associated with SC regulated behaviors including learning and environmental exploration. These morphological variations are critical for survival and adaptation in the species' natural environment. This finding is in line with the reports of Agbon et al. (2024) that observed differences in histometric characteristics of pyramidal neurons in certain brain regions of compared rodent species including Wistar rat and Guinea pig.

Cell density or distribution is essential in maintaining balance and normal functioning of a biological system (Feinberg and Meister, 2015; Agbon et al., 2024). The presence of remarkable differences in cell distribution of the SC laminae AGCs age group; higher cell distribution in the juvenile AGCs is in line with the report of Ibe et al. (2019). This observation could be attributed to variations in cell functionality as the AGC matures; neuronal cells undergo significant growth and differentiation with increased synaptic connectivity during early postnatal life (Hardwick, 2014). Observations are suggestive of active cellular communication in response to excitatory stimuli between neurons in juvenile AGCs, which is necessary for survival at early stages of development and adaptive related behavior associated with environmental exploratory and familiarization (Yamamuro, 2020). However, in adult AGCs cell distribution and connections may have been eliminated through the process of pruning, and the cellular architecture of the SC is more refined, more stable and efficient. Across species, the relative abundance of neuronal density in different brain regions correlates with neural functionality and behavior (Williams and Herrup, 1988 and Herculano-Houzel et al., 2009). Therefore, juvenile AGCs could be said to engage their SC more compared to the adults.

In conclusion, this study has demonstrated a basic histoarchitectural organization of the superior colliculus in adult and juvenile African Grasscutter; thus points to conserved architectural organization across rodent species. Observed differences could be attributed to variations in cellular functionality with response to developmental neurogenesis and synaptic refinement between the rodents. Findings are of potential benefit in understanding the interplay between neurodevelopmental variations and functional capabilities across different age group. Studies including neurobehavioral studies (visual acuity), the identification of specific cell types and stereological quantification are required to support the precision of this findings.

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