GROSS MORPHOLOGY OF THE CEREBRUM AND BRAINSTEM OF THE ADULT AFRICAN GRASSCUTTER (*THRYONOMYS SWINDERIANUS*—TEMMINCK, 1827)

Ibe, C. S., Ikpegbu, E., Ogbonnaya, O.

Department of Veterinary Anatomy, Michael Okpara University of Agriculture, Umudike
Nigeria

ibe.chikera@mouau.edu.ng

ABSTRACT

In order to meet the increasing protein and income demand in Africa due to the rapid population growth, wildlife, such as the African grasscutter, is currently bred and domesticated as microlivestock. This study is one of the series on the brain morphology of this very large rodent, aimed at providing information that is lacking in the literature. Here, the gross anatomy of the cerebrum and brainstem in nine adult African grasscutters is described. The cerebral cortex was smooth, devoid of gyri and sulci, thus, placing the rodent in the lissencephalic group of mammals. However, blood vessels on the cortex created arterial and venous impressions. The cortex was asymmetrically-tapered oval in shape. The rostral and caudal colliculi were exposed through the cerebral transverse fissure. The rostro-caudal extent of the *corpus callosum* was from the mid-point of the frontal and parietal lobes, to a point just rostral to the occipital lobe. The rostral colliculi were grossly smaller than the caudal colliculi. The oculomotor and trochlear nerves emerged from the ventral midbrain, rostral to the pons. The pons

was exceptionally large; it was pre-trigeminal. On either side of the ventral median fissure of the *medulla oblongata* were conspicuous pyramids. The trapezoid bodies were also conspicuous. These, and other findings, will be useful in future phylogenetic comparison of rodent brain morphology.

Key words: African grasscutter; brainstem; cerebrum; *medulla oblongata*; trapezoid body

INTRODUCTION

The current estimate of the global human population is 7 billion, and expected to be 9.3 billion by the year 2050, with Africa recording the highest value [3]. This demographic upheaval exerts pressure on food supply, including animal protein. According to Auzel and Wilkie [1], at least 20 % of the animal protein source in Africa is obtained through hunting and fishing. Thus, wildlife represents a substantial source of animal protein and income for a large part of the rural populations on the continent. The

African grasscutter is a wild rodent. However, to meet the current protein decline in Nigeria, the rodents are currently bred and domesticated as microlivestock. Unfortunately, the behaviour of the rodent is not well known, as the biology is still being studied. Knowledge of the biology of the African grasscutter is necessary to provide a near-natural habitat for the rodent in captivity. This is one of the reasons the brain of the African grasscutter was studied.

The morphology of mammalian brains has recorded wide diversity. The morphology of the cerebrum varies in mammals. In higher mammals, the cerebral cortex is convoluted, forming ridges called gyri and troughs called sulci. Such mammals with a convoluted cerebral cortex are said to be gyrencephalic, while those with smooth cerebral cortex are said to be lissencephalic. The convolutions permit more cortical surface areas to be contained in the same volume of the cranial vault [10]. Studies have revealed that the shape of the cerebral cortex vary in different animals, although spherical in humans. Peng et al. [26] reported that the shape of the cerebral cortex of the African ostrich is an obtuse triangle. Ibe et al. [13] observed a diamond-shaped cerebral cortex in the adult African giant pouched rat.

The brainstem is made up of the *medulla oblongata*, the pons and the midbrain, though some authors include the thalamus as part of the brainstem [12]. The thalamus serves as the gateway between the brainstem and the cerebrum, such that all incoming information (except olfaction) approaches the cerebrum through the thalamus [18]. The thalamus has also been linked to cerebral arousal [18]. The midbrain, which contains neurons that connect the cerebrum with lower parts of the brain and spinal cord, occupies only a small region in the brain of humans, but it is relatively larger in lower vertebrates [5]. The cerebral aqueduct separates it into the dorsal *tectum* and the ventral *tegmentum*. The midbrain narrows rostrally into the third ventricle; it is connected to the pons caudally. The *medulla oblongata* is the most caudal part of the brainstem. It is continuous with the spinal cord caudally and the pons rostrally. It lies in the cranial vault, rostral to the *foramen magnum*. In the Wistar rat, it begins about 3 mm rostral to the origin of the first cervical nerve [34], while in the one-humped camel, the level of the first cervical nerve is a convenient landmark for separation of the *medulla oblongata* from the spinal cord [21]. The *medulla oblongata* is the control centre for autonomic functions and a relay centre for impulses between the spinal cord and higher

brain centres. It coordinates autonomic functions such as respiration, blood pressure and heart rate [9].

Gross morphological studies of the *corpora quadrigemina* [11], cerebellum [4, 15] and olfactory bulbs [14] of the African grasscutter are available in extant literature. Conversely, no detailed account of the cerebrum and brainstem is available and the purpose of this article is to provide descriptive information to fill this gap. This study will not only bridge the existing gap in available literature, but, it will also provide a reference for phylogenetic comparison of the rodent brain.

MATERIALS AND METHODS

Experimental animals and management

Nine adult African grasscutters were used for this study. The gender of the animals were not taken into consideration. They were purchased from a grasscutter farm in Elele, Rivers State, Nigeria. Rivers State is on latitude 4.7500° N and longitude 6.8333° E. Prior to purchase, the African grasscutters were physically examined under careful restraint and ascertained to be clinically healthy. They were transported by road, in metal cages, to the Histology/Embryology Laboratory of the Michael Okpara University of Agriculture, Umudike, Abia State, Nigeria, for the study.

The animals were fed twice daily, at 8.00 am and 6.00 pm with fresh guinea grass (*Panicum maximum*), fresh cane grass (*Eragrostis infecunda*) and commercial rodent-pelleted concentrates. Drinking water was provided *ad libitum*. The feeding troughs and drinkers were sterilized daily using Milton®.

Ethical approval

The experimental procedure got the approval of the Research Ethics Committee, College of Veterinary Medicine, Michael Okpara University of Agriculture Umudike, Nigeria. Management of the experimental animals was as stipulated in the Guide for the Care and Use of Laboratory Animals, 8th Edition, National Research Council, USA (National Academic Press, Washington, DC: <http://www.nap.edu>).

Extraction of the brain

Each animal was sedated by intraperitoneal injection of 20 mg.kg⁻¹ thiopental sodium (Rotexmedica, Trittau, Ger-

many) and immediately weighed using a digital electronic balance (Citizen Scales (1) PVT Ltd., South Patel Nagar, New Delhi, sensitivity: 0.01 g). Thereafter, the animal was placed on dorsal recumbency on a dissection table, and perfused, via the left ventricle, with 4 % paraformaldehyde fixative, as described by G a g e et al. [7]. Immediately after the perfusion fixation, each animal was decapitated at the atlanto-axial joint, using a pair of scissors and a knife. The skull was obtained after skinning and stripping off all the facial and cranial muscles. This was followed by brain extraction from the skull, using scalpel blades, thumb forceps and a pair of scissors. The meninges and underlying blood vessels were gently removed to expose the intact brain. A mid-sagittal longitudinal incision was done on 5 brain samples to access the mid-sagittal view of the brain parts for study. The rest of the brain samples were used for the extraction and study of the brainstem.

Extraction of the brainstem from the cerebrum and cerebellum required systematic removal of the cerebral halves, followed by severing of the cerebellum. In order to remove the cerebrum from the rest of the brain, the two cerebral halves were gently pulled apart at the occipital pole to expose the *corpus callosum*. The entire *corpus callosum* together with the *septum pellucidum* and the body and rostral commissure of the fornix were severed in the midline. This completely separated the cerebrum from the brainstem and cerebellum. In order to separate the cerebellum from the brainstem, the flocculi of the cerebellum were manually raised to expose the cerebellar peduncles. These peduncles were then severed on both sides starting with the laterally located *brachium restiformis*, followed by the middle *brachium pontis* and then the *brachium conjunctivum*. Thereafter, the brainstem was freed from the *arachnoidea* and cranial nerves by simple trimming.

Morphological study

The extracted brain samples were studied grossly with the naked eyes and with the aid of a magnifying glass. These included the shape, size, surfaces, borders and angles of existing brain structures. The presence or absence of sulci, gyri, fissures or prominences were evaluated in each of the brain structures. Photographs of the surface of the dorsal and ventral views of the intact brain, the mid-sagittal view of the brain and the dorsal view of the extracted brainstem were obtained using a digital camera (Eastman Kodak® Model 14650, Rochester, New York, USA, 12.5

megapixels). Anatomical structures were defined based on standard rodent anatomy literatures [23, 25, 34]. *Nomina Anatomica Veterinaria* [22] was used for the nomenclature.

RESULTS

Morphology of the cerebrum

On dorsal view of the intact brain, the cerebral cortex was the largest brain part. It was distinctly divided by a longitudinal fissure (Fig. 1. White line arrow) and separated from the cerebellum by a transverse fissure (Fig. 1. Black line arrow). The cerebral cortex was smooth and devoid of prominent gyri and sulci. However, blood vessels on the surface of the cerebral cortex created arterial and venous impressions on the cortex (Fig. 1. White double arrow). The cerebral cortex presented a tapered frontal lobe (Fig. 1. B1) and broad temporal and occipital lobes (Fig. 1. B3 and B4). Thus, the cerebral cortex had an asymmetrically-tapered oval shape. The cerebral cortex presented a notch at the point of expansion of the temporal lobe, which was indicative of the distinctly large temporal lobe relative to the rostrally located frontal lobe (Fig. 1. Black arrowhead). The rostral and caudal colliculi were exposed through the transverse fissure (Fig. 1. C and D).

On the ventral view of the intact brain, the olfactory bulbs existed as rostral outgrowths of the olfactory cortex, with the olfactory tracts connecting the bulbs and the piriform cortex (Fig. 2. A, B1, B2, B3). The olfactory nerve fibres, which were rostral to the olfactory bulbs, could not be accessed due to their position in the cribriform plate of the ethmoid bones. The paired optic nerves (cranial nerve II) united at the optic chiasma and gave off optic tracts that ran on the rostral boarder of the mammillary body (Fig. 2. C1, C2, C3). The *infundibulum*, *cinerium tuber* of the hypothalamus and mammillary bodies were evident (Fig. 2. i, ii, D). The temporal lobe was the largest of the cerebral cortical lobes (Fig. 2. G). It was presented caudal to the piriform lobe (Fig. 2. E). The cerebral peduncles, relaying impulses to and from the cerebral cortex were very visible.

On a mid-sagittal view of the brain (Fig. 3), the absence of cerebral cortical sulci and gyri was further confirmed as no trough was evident on the dorso-ventral extent of the cerebrum. The cerebral lobes were thus, identified by their location, not by the presence of sulci and gyri. The frontal, parietal and occipital lobes were evident on this view

Fig. 1. Dorsal view of the brain of the adult African grasscutter

A—Olfactory bulb; B—Cerebral cortex (B1—Frontal lobe; B2—Parietal lobe; B3—Temporal lobe; B4—Occipital lobe); C—Rostral colliculus; D—Caudal colliculus; E—Paraflocculus; F—Flocculus; G—Vermis; H—*Medulla oblongata*; White line arrow—cerebral longitudinal fissure; Black line arrow—cerebral transverse fissure; White double head arrow—arterial impression on cerebral cortex. Magn. $\times 2.0$

Fig. 2. Ventral view of the brain of the African grasscutter

A—Olfactory bulb; B1—Medial olfactory tracts; B2—Lateral olfactory tracts; B3—Middle olfactory tracts; C1—Optic nerve (CN II); C2—Optic chiasma; C3—Optic tracts; D—Mammillary body; i—Cinerium tuber; ii—Infundibulum; E—Piriform lobe; F1—Oculomotor nerve (CN III); F2—Trigeminal nerves (CN V); F3—Abducence nerve (CN VI); G—Temporal lobe; H—Cerebral peduncle; I—Pons; J—Trapezoid body; K—Pyramid; L—Paraflocculus; M—Olivary body; N—*Medulla oblongata*; O—Point of pyramidal decussation; P—Spinal cord; White line arrow—ventral lateral sulcus; White block arrow—pre-olivary sulcus (CN IX-XI); Black block arrow—post-olivary sulcus (CN XII); Black line arrow—ventral median fissure. Magn. $\times 2.0$

Fig. 3. Mid-sagittal view of the brain of the adult African grasscutter

A—Olfactory bulbs; B—Frontal lobe of cerebrum; C—Parietal lobe of cerebrum; D—Occipital lobe of cerebrum; E—*Corpus callosum* (Genu); F—*Corpus callosum* (Truncus); G—*Corpus callosum* (Splenium); H—Mammillary body; I—Inter-thalamic adhesion; J—Rostral colliculus; K—Caudal colliculus; L—Pituitary gland; M—Pons; N—*Arbor vitae*; O—*Medulla oblongata*; P—Spinal cord; 1—*Lingula*; 1a—*pars rostralis*; 1b—*pars medialis*; 1c—*pars caudalis*; 2—Central lobule; 3—Culmen; 3a—*pars rostralis*; 3b—*pars caudalis*; 4—Declive; 5—Folium; 6—Tuber; 7—Pyramis; 8—Uvula; 9—Nodus; White arrowhead—lateral ventricle; Black arrowhead—primary fissure. Magn. $\times 3.0$

(Fig. 3. B, C, D). Caudal to the occipital lobe were the visible rostral and caudal colliculi, sandwiched between the occipital lobe of the cerebrum and the cerebellum (Fig. 3. J, K). The inner white matter of the cerebrum, the *corpus callosum* lay between the cerebral cortex and the thalamus. The rostro-caudal extent of the *corpus callosum* was from mid-point of the frontal and parietal lobes, up to a point just rostral to the occipital lobe. The genu, truncus and splenium of the *corpus callosum* (Fig. 3. E, F, G), as well as the third ventricles (Fig. 3. white arrow-head) bounded by the *corpus callosum* were very evident.

Morphology of the brainstem

On a dorsal view of the brainstem, the third ventricle was flanked on either side by the thalamus (Fig. 4. i, B). The dorsal surface of the midbrain was characterised by the paired rostral and paired caudal colliculi (Fig. 4. D and F), and their respective geniculate bodies (Fig. 4. C and E). The rostral colliculi were grossly smaller than the caudal colliculi. The pair of rostral colliculi was separated from each other by a longitudinal *intracollicular sulcus* (Fig. 4. ii). The pair of caudal colliculi was also similarly separated. The rostral colliculi were separated from the caudal colliculi by a transverse *intercollicular sulcus* (Fig. 4. iii). Caudal to the midbrain was the open rostral part of the *medulla oblongata* which formed the floor of the fourth ventricle (Fig. 4. H). It was larger than the rostrally placed third ventricle and the lateral ventricles observed in the cerebrum. It was roughly rhomboid in shape. It was bounded rostro-laterally by the *sulcus limitans*, bilaterally by the stumps of the rostral, middle and caudal cerebellar peduncles and caudally by the obex. It was divided into two symmetrical halves by a dorsal median sulcus (Fig. 4. iv). This sulcus extended caudally to also divide the closed caudal part of the *medulla oblongata*. Flanked bilateral to the dorsal median sulcus on the closed caudal part of the *medulla oblongata* was the large *gracile fasciculus* (Fig. 4. J). The *fasciculus* continued rostrally on the ventro-lateral margins of the open part of the *medulla oblongata*. A dorsal intermediate sulcus (Fig. 4. vi) separated the conspicuous *gracile fasciculus* from a laterally placed, faintly visible *cuneate fasciculus*. The dorsal lateral sulcus was not grossly visible. A convex prominence, corresponding to the underlying vestibular nucleus, was evident between the *sulcus limitans* medially and the medial cerebellar peduncles laterally. The hypoglossal trigone and vagal trigone were not visible.

Fig. 4. Dorsal view of the brainstem of the African grasscutter

A—Optic nerve; B—Thalamus; C—Lateral geniculate body; D—Rostral colliculus; E—Medial geniculate body; F—Caudal colliculus; G—*Sulcus limitans*; H—Floor of fourth ventricle; Ia—Rostral cerebellar peduncle; Ib—Middle cerebellar peduncle; Ic—Caudal cerebellar peduncle; J—*Gracile fasciculus*; I—Third ventricle; ii—Longitudinal intracollicular sulcus; iii—Transverse intercollicular sulcus; iv—Dorsal median sulcus; v—obex; vi—Dorsal intermediate sulcus. Magn. $\times 3.0$

On a ventral view of the brainstem, the thalamus marked the most rostral structure. The mammillary body and infundibulum preceded the pons. The oculomotor and trochlear nerves emerged from the ventral midbrain, rostral to the pons (Fig. 2. F1). The pons was exceptionally large, with a bony impression on its middle. It was pre-trigeminal. The trigeminal nerve (Fig. 2. F2) emerged from the pontomedullary junction. It was the largest cranial nerve on the brainstem. The *medulla oblongata* (Fig. 2. N) was symmetrically divided into two by a ventral median fissure (Fig. 2. black line arrow). On either side of the ventral median fissure were conspicuous pyramids (Fig. 2. K). The most rostral structure on each half of the *medulla oblongata* was the trapezoid body (Fig. 2. P). The olivary prominence was situated lateral to each of the pyramids, sandwiched between the pre-olivary and the post-olivary sulci. Nerve rootlets emerged from these sulci. Caudally, the *medulla oblongata* terminated at the prominent fossa, caudal to the pyramidal decussation at the level of the *foramen magnum*.

DISCUSSION

Result of the morphology of the cerebral cortex revealed a smooth cortex, devoid of gyri and sulci, and this finding places the African grasscutter in the lissencephalic group of mammals. Initially, Rakic [28] proposed that gyrification was a phylogenetic trait; so that while lissencephaly was a primitive trait in lower mammals like rodents, gyrencephaly evolved in higher mammals, including primates. Recent molecular analysis has however, objected to this hypothesis [29], and proved that gyrencephaly is more closely related to variability in brain and body sizes in mammals. Thus, while gyrencephaly has been reported in large rodents such as the beaver and capybara [32], lissencephaly has been reported in small primates such as the marmoset monkey [8]. Although the adult African grasscutter is also a large rodent; the fourth largest extant rodent after the crested porcupine, beaver and capybara; the second largest rodent in Africa after the North African crested porcupine [6], there was no observable evidence of gyrification from the present study. One generally acclaimed reason for gyrification is the need to permit more cortical surface areas to be contained in the same volume of cranial vault. It has also been linked to increased neuronal connection and cognitive ability in higher mammals [35]. However, the functional significance of gyrified brain is still in debate, as individuals with severe disruptions of gyrification sequence still survive [33].

The asymmetrically-tapered oval shape of the cerebral cortex, with a tapered frontal lobe, and broad temporal and occipital lobes can be linked to apparently increased neuronal size which was more evident in the temporal and occipital lobes. This shape is different from the spherical cerebral cortex, observed in humans and most mammals. The common assertion is that the cerebral cortex is spherical, thus, each half is referred to as a hemisphere. Studies (including the present study) have revealed that the shape of the cerebral cortex vary in different animals, although spherical in humans. Peng et al. [26] reported that the shape of the cerebral cortex of the African ostrich is an obtuse triangle. Ibe et al. [13] observed a diamond-shaped cerebral cortex in the adult African giant pouched rat. It is pertinent to mention that the terminology hemisphere ought to be restricted to humans and animals with spherical cerebral cortex. The increased size of the auditory cortex (temporal lobe), relative to other cerebral lobes, points to a good auditory ability in the African grasscutter.

Gross observation of the brainstem in our study revealed that the caudal colliculi were bigger than the rostral colliculi. This confers a more acute auditory ability in the African grasscutter. Gross morphometric and histological assessment of these colliculi have been reported by Ibe et al. [11] and Ibe et al. [15], respectively and the results point to a more acute auditory than visual sense in the African grasscutter. The optic lobe (or rostral colliculus in mammals) is present in all vertebrates, but exceptionally large in birds such as the Wild African parrot which rely on visual stimuli for much information about their environment [37]. The rostral colliculus is bigger than the caudal colliculus in the camel [21], rabbit [2], calf [30], donkey [24], pig [31] and dog [17], while the caudal colliculus is bigger than the rostral colliculus in the cetaceans [19] and African giant pouched rat [12].

In our study, the rostral and caudal colliculi were exposed through the transverse fissure separating the cerebrum and the cerebellum. In the African giant pouched rat, only the caudal colliculi were visible through the transverse fissure, with the rostral colliculi occluded by the occipital cerebral lobe [13]. From this disparity, it may be deduced that the caudal colliculi of the African giant pouched rat is relatively bigger than that of the African grasscutter, conferring a better acoustic sense in the African giant pouched rat than the African grasscutter. Voogd and Barmaeh [36] reported that in the platypus (*Ornithorhynchus anatinus*), marsupials and bats, the *tectum* is visible on a dorsal view of the brain; but in larger mammals, it is hidden from view by the cerebral cortex. The disposition of the *tectum* in the Wistar rat is also different from that of the African grasscutter from this study. According to Sukow et al. [34], the *tectum* of the Wistar rat is distinct with the exception of the tips of the caudal colliculi that are covered by the occipital portion of the cerebrum, the pineal body and rostral part of the cerebellum. In the guinea pig, the *tectum* is covered by the cerebrum and cerebellum [27], unlike the observation in our study.

The most rostral part of the *medulla oblongata* in our study was the trapezoid body. It was conspicuous, and this conspicuousness and size may be indicative of the development of the trapezoid nuclei which can be extrapolated to the acuity of the auditory system of the African grasscutter. The medial trapezoid nucleus of the trapezoid body sends ipsilateral auditory sensory impulses to the central nucleus of the caudal colliculus [16]. Marsden

and Rowland [20] opined that the trapezoid body progressively decreases in size relative to the pons in higher primates, so that in humans, it is completely covered by the pons and thus not visible on the ventral surface of the *medulla oblongata*. It is more prominent in our study than was reported in the African giant pouched rat [13].

The exceptionally large size of the pons of the African grasscutter in our study is worthy of note. The pons in the African giant pouched rat, as observed by Ibe et al. [13] was small. The large size of the pons in our study may have some functional significance in the cortico-pontine and striatopontine pathways. The pons of the African grasscutter, from our study is pre-trigeminal, similar to that of the African giant pouched rat [13]. Marsden and Rowland [20] reported that the pons is post-trigeminal in monotremes and pre-trigeminal in marsupials and most species of lower eutherian orders. The pyramids observed in our study were also exceptionally large. This contradicts the report of Vogt and Barman [36] which states that the pyramids are inconspicuous in monotremes, small in insects, rodents, microchiroptera, *Cetacea* and ungulates and prominent in carnivores and primates.

CONCLUSIONS

The morphology of the cerebrum and brainstem of the adult African grasscutter was described. Despite the exceptionally large size of the rodent, there was no observable evidence of gyrification of the cerebral cortex, placing it in the lissencephalic group of mammals. The asymmetrically-tapered oval shape of the cerebral cortex, unlike the spherical shape of the human cerebral cortex, calls for caution in the use of the term “cerebral hemisphere” in animals. The large size of the temporal lobe of the cerebrum and caudal colliculi of the midbrain as well as the presence of a visible trapezoid body all point to a good auditory sense in the rodent. These, and other findings, will be useful in future phylogenetic comparison of rodent brain morphology.

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Received July 6, 2020

Accepted October 31, 2020