Polish Journal of Veterinary Sciences Vol. 29, No. 3 (2026), 473–484

DOI 10.24425/pjvs.2026.3613

Review paper

Advances in the anatomy, histology, and embryology of the dromedary (Camelus dromedarius) brain and spinal cord

M. Salouci

Department of Anatomy, College of Veterinary Medicine, King Faisal University, Al-Ahsa, Saudi Arabia

Correspondence to: M. Salouci, e-mail: msalouci@kfu.edu.sa

Abstract

The dromedary (*Camelus dromedarius*) represents a remarkable model of physiological and anatomical adaptation to extreme environments. While many researchers have focused on its unique metabolic and water-conserving abilities, the neuroscience underlying these adaptations are noticeable unexplored. This study reviews the latest findings in the anatomy, histology, and embryology of the dromedary nervous system. It highlights the gross and comparative neuroanatomy, emphasizing distinctive features of the central, peripheral and autonomic nervous systems, including the complex cerebral vasculature. Histological studies demonstrate a diverse array of neuronal and glial cell types in the caudate nucleus, cerebellum and spinal trigeminal nucleus, reflecting advanced neural processing. Furthermore, embryological investigations trace the development of the nervous system from neurulation and the formation of brain vesicles. Finally, this review connects these neurobiological features to the camel's unique adaptations, such as thermoregulation and pain perception, and discusses the implications of emerging technologies such as nanobody-based therapies derived from camelids for treating neurological disorders. This comprehensive overview underscores the camel as a vital subject for neuroscientific research, offering novel perspectives on neural structure, function and evolution in response to environmental pressures.

Keywords: nervous system, dromedary camel, neuroanatomy, neurophysiology

Introduction

The *Camelini tribe* (Old World camels), which includes the dromedary (one-humped, *Camelus dromedarius*) and the Bactrian camel (two-humped, *Camelus bactrianus*), and the wild camel (*Camelus ferus)*, has attracted the attention of scientists for its ability to adapt to the harshest environments (Jararr 2015, Gebreselassie et al. 2019, Cartiaux et al. 2023). This review will focus primarily on the dromedary. Their physiological adaptations for water conservation (Alim et al. 2019), thermoregulation (Faraz et al. 2025) and efficient digestion (Fesseha et al. 2020) are well-documented. However, the limited data on the neuroanatomy and histology of camels has restricted our understanding of how the brain of this animal and its peripheral nerves are organized to meet its physiological requirements (Metwally et al. 2019, Al-Hussain et al. 2022). Recently, detailed studies have identified a deeper level for studying camel neuroscience. Comparative neuroanatomy, in particular, provides a strong framework for understanding evolutionary adaptations by comparing the neural structures of camels with those of other mammals, including ruminants and humans (Al-Hussain et al. 2021, Almasaad et al. 2025). These studies have demonstrated that the camel brain possesses distinctive features in its overall structure, cellular composition and development (Xie et al. 2006, Al Aiyan et al. 2024).

This review aims to synthesize the latest research on the anatomy, histology, and embryology of the dromedary (*Camelus dromedarius*) nervous system. It will explore the macroscopic and microscopic organization of the central nervous system (CNS) and peripheral nervous systems, detailing the unique diversity of neurons and glial cells in the main brain regions. Furthermore, it examines the developmental processes, from early neural tube formation to the migration of neural crest cells, that lead to the origin of this specialized system. It also discusses how these neurobiological characteristics help explain the camel's remarkable adaptations to its environment, such as its high pain tolerance and sophisticated ability to regulate body temperature (Mensah-Brown et al. 2006, Pastrana et al. 2024). Finally, this review addresses the emerging clinical and therapeutic implications of camel-derived neurobiology, including the development of novel nanobody-based therapies for human neurological disorders (Lafon et al. 2025, Oosterlaken et al. 2025). By integrating this diverse evidence, this review seeks to establish a comprehensive and up-to-date understanding of the camel nervous system, highlighting its importance as a model for evolutionary and adaptive neuroscience.

Gross and comparative neuroanatomy

The anatomical organization of the camel's nervous system provides the structural basis of its unique physiological capabilities. Recent studies using gross anatomy, magnetic resonance imaging (MRI) and diffusion tensor imaging (DTI) have begun to map this complex system, revealing both mammalian conserved features and distinct camelid specializations (Ben Khalifa et al. 2019, Cartiaux et al. 2023). Foundational anatomical texts, such as those by Smuts and Bezuidenhout (1987), have provided the essential baseline for these modern comparative studies.

Central nervous system (CNS): brain and spinal cord

The camel's CNS consists of the brain and spinal cord, surrounded by three layers of connective tissue known as the meninges (Jararr 2015). The cerebral meninges in the dromedary were studied by El-Hagri et al. (1976), who detailed the protective layers of the brain. The brain of the dromedary is characterized by a complexly folded cortical surface, with numerous gyri and sulci which, while similar in general pattern to other ungulates such as horses, exhibit unique features (Xie et al. 2006, Al Aiyan et al. 2024). Recently, detailed studies of the dromedary cerebrum identified specific sulci, such as the caudal rhinal sulcus, not previously reported in camel brain research (Al Aiyan et al. 2024). The cerebrum of the dromedary measures approximately 11.23 cm in length, 8.67 cm in width and 5.77 cm in height (Attaai et al. 2020). The brain's external architecture is most similar to that of horses; however, it displays comparatively less overall folding (Al Aiyan et al. 2024).

Major brain structures such as the cerebellum, responsible for motor control and balance, and the hypothalamus, a vital center for homeostasis, show remarkable specializations. The camel cerebellum has a conserved three-layered cortex (molecular, Purkinje, and granular layers) but it also contains large, atypical neurons such as Lugaro and synaromatic cells (Ghaji 1985, Attaai et al. 2020). The suprachiasmatic nucleus (SCN) of the hypothalamus, the master circadian clock, is unusually large and elongated in the camel, measuring about 9.55 mm, which is significantly longer than in sheep (2.8-3.1 mm) or humans (1.47 mm) (El Allali et al. 2013). This extensive SCN is subdivided into rostral, main and caudal divisions, a complexity that may be related to the camel's need to integrate environmental cues such as temperature and photoperiod in its challenging desert habitat (Jain et al. 2007, El Allali et al. 2013). Furthermore, recent studies by Lin et al. (2022) have elucidated the hypothalamic osmoregulatory con-

trol center of the Arabian dromedary, revealing specialized neural circuits that govern water retention and thirst in response to severe dehydration. The camel's spinal cord is the longest among domesticated animals, extending from the foramen magnum to the level of the second sacral vertebra (Elmonem et al. 2007). Its internal structure consists of gray matter arranged in Rexed laminae and surrounding white matter organized into funiculi, a pattern consistent with other mammals (Waxenbaum et al. 2023). Elmonem et al. (2007) provided extensive histological findings on the lumbar spinal cord, focusing on its cellular organization and developmental progression.

Peripheral nervous system (PNS): cranial and spinal nerves

The peripheral nervous system (PNS) connects the CNS to the limbs and organs. It consists of 12 pairs of cranial nerves originating from the brain and 31 pairs of spinal nerves emerging from the spinal cord segments (Waxenbaum et al. 2023). The cranial nerves in the dromedary follow the general mammalian pattern, with specific nerves dedicated to sensory functions such as the olfactory and optic nerve, motor functions such as the oculomotor and hypoglossal nerve, or mixed functions such as the trigeminal, facial and vagus nerve (Huff et al. 2024). The trigeminal nerve is particularly important, providing sensory innervation to the face and motor control for mastication (Adam et al. 2016). Its branches, such as the ethmoidal, infraorbital, and mental nerves, are crucial for perceiving stimuli from the environment, including the thorny plants that form part of the camel's diet.

A unique structure in dromedaries, known as the "nasal septal island," has been identified, which is innervated by the ethmoidal branch of the trigeminal nerve. This structure is a specialized patch of sensory epithelium located in the nasal septum. While its exact function remains to be definitively established, it is hypothesized to be a nociceptive organ involved in trigeminal chemosensitivity, particularly pain perception (nociception), which may represent adaptations to inhaling dust and irritants (Abo-Ahmed et al. 2021). The facial nerve innervates the muscles of facial expression, including those that allow the camel to voluntarily close their nostrils, a key adaptation to prevent sand inhalation (Abo-Ahmed et al. 2021). Studies on the distal hindlimb of the dromedary have detailed the distribution of the superficial fibular and tibial nerves, providing an anatomical basis for clinical procedures such as nerve blocks (Allouch et al. 2023).

Autonomic nervous system (ANS)

The autonomic nervous system (ANS) regulates involuntary bodily functions and is divided into the sympathetic and parasympathetic systems (Waxenbaum et al. 2023). Detailed anatomical studies by Nourinezhad et al. (2015) have mapped the cranial cervical ganglion in the dromedary, while Abdel-Magied (1995) investigated the fine structure of its nerve endings and junctions at the ultrastructural level. In camels, the ANS is crucial for regulating homeostatic responses to heat stress and dehydration. During heat stress, the sympathetic nervous system is modulated to reduce peripheral blood flow to non-essential organs while maximizing heat dissipation mechanisms. Conversely, during dehydration, sympathetic activation increases renal vascular resistance to minimize water loss, while parasympathetic tone is adjusted to lower the basal metabolic rate, thereby conserving energy and reducing endogenous heat production (Bouâouda et al. 2014). The sympathetic division originates from the thoracic and lumbar spinal cord segments, with fibers projecting to the sympathetic chain ganglia and prevertebral ganglia (such as celiac and mesenteric) to innervate visceral organs (Purves et al. 2001, Nourinezhad et al. 2015). The cranial cervical ganglion (CCG) is a major sympathetic structure in the neck, providing innervation to the head and communicating with cranial and cervical spinal nerves. The parasympathetic division is primarily mediated by the vagus nerve, which provides about 75% of all parasympathetic outflow to the thoracic and abdominal viscera, including the heart, lungs and digestive tract (Al Aiyan et al. 2024). Other cranial nerves (oculomotor, facial and glossopharyngeal nerve) and sacral spinal nerves also contribute to parasympathetic function. The intricate balance between sympathetic and parasympathetic tone allows the camel to precisely regulate heart rate, digestion and other vital functions in response to environmental challenges (Al Aiyan et al. 2024).

Neurovascular anatomy

The brain's high metabolic demand requires a constant and reliable blood supply. In the camel, this is achieved through a complex and unique cerebrovascular architecture. The main arterial supply comes from the carotid and vertebrobasilar systems, which converge at the base of the brain to form the cerebral arterial circle (CAC), or circle of Willis (Elkhawad 1992, Jessen 1998). A distinctive feature in camels, as in many artiodactyls, is the rostral epidural rete mirabile (RERM), a complex network of arteries located at the

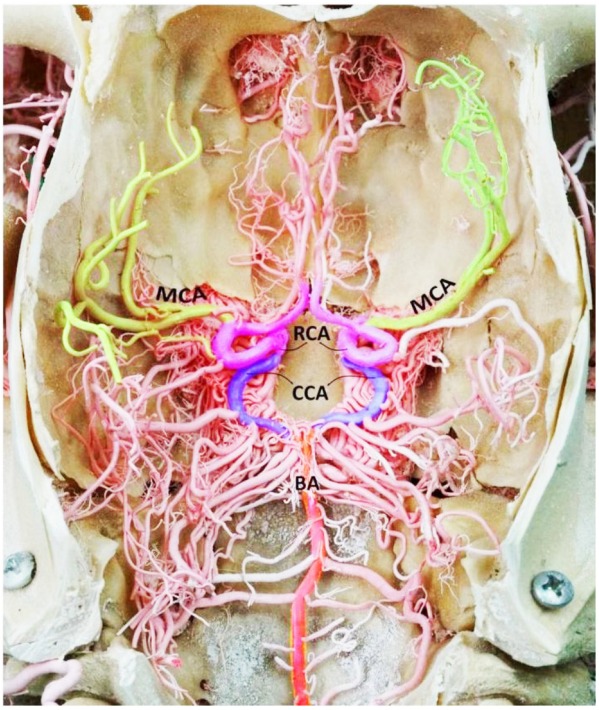

Fig. 1. Dorsal view of the rostral epidural rete mirabile (RERM) with the cerebral arterial circle (CAC) beneath it in the dromedary brain. The CAC is formed by the basilar artery (1), caudal communicating artery (2), rostral cerebral artery (3) and rostral communicating artery (4). Major branches such as the caudal cerebral (5), choroidal (6, 7), and middle cerebral (8) arteries arise from this circle. The RERM (9) is a key structure for cerebral blood supply in camels. Reproduced from Al Aiyan and Balan, Frontiers in Veterinary Science, (2024), licensed under Creative Commons Attribution 4.0 License (CC BY 4.0).

base of the skull. Blood from the carotid system passes through the RERM before entering the CAC (Fig. 1). This structure is believed to play a role in selective brain cooling, a vital mechanism that allows the brain to remain cooler than the body core during hyperthermia, thus protecting it from heat damage (Elkhawad 1992, Jessen 1998, Al Aiyan et al. 2023).

Recent studies using vascular casting and imaging have provided detailed maps of the camel's cerebral arteries. The middle cerebral artery (MCA) in dromedaries is characterized by a number of cortical branches different from that observed in other species, supplying extensive regions of both cerebral hemispheres (Jerbi et al. 2019, Al Aiyan et al. 2023). Additionally, previously unreported branches, including the middle frontal and middle parietal arteries, have also been identified, indicating a more complex vascular network supplying the frontal and parietal lobes. The cerebellum receives its arterial supply from the anterior and posterior cerebellar arteries, which arise from the basilar artery (Jerbi et al. 2019). Such detailed anatomical knowledge is essential for accurate veterinary diagnosis and contributes to a broader understanding of the evolutionary development of cerebral vascular systems in mammals.

Neurohistology and cellular diversity

Using histologic techniques in the camel such as Golgi staining, immunohistochemistry and electron microscopy, a series of studies has characterized the diverse populations of neurons and glial cells in the camel brain, uncovering features that may be linked to its evolutionary specializations (Beheiry 2016, Bataineh 2020, Al-Hussain et al. 2022, El-Dwairi et al. 2023).

Neuronal diversity and morphology

The camel brain exhibits remarkable diversity of neuronal cell types, with distinct morphologies observed across different functional regions. Recent comparative studies, particularly those comparing camels and humans, have identified both distinctive species-specific features and shared organizational patterns (Almasaad et al. 2025).

Caudate nucleus

The caudate nucleus (CN), an important part of the basal ganglia that helps control movement and learning, has been studied across species (Foster et al. 2024, Ramu et al. 2025). In both camels and humans, neurons

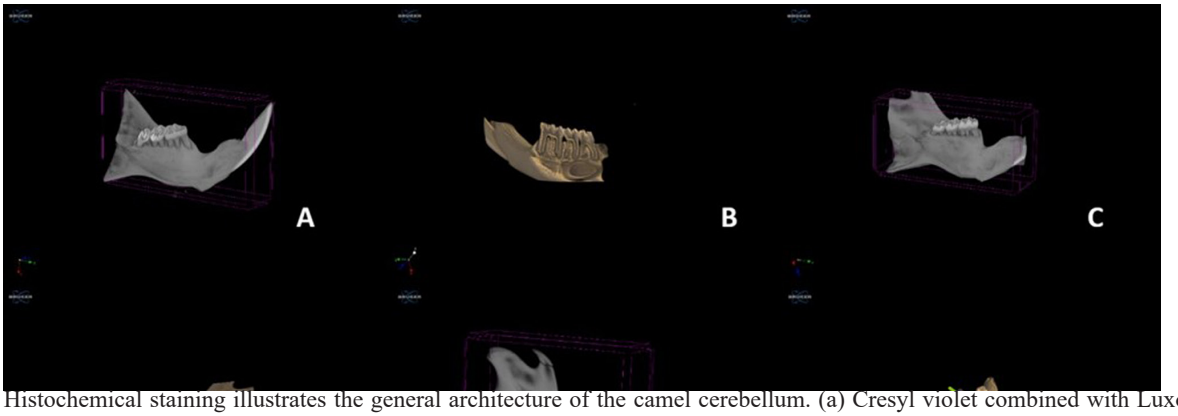

Fig. 2. Histochemical staining illustrates the general architecture of the camel cerebellum. (a) Cresyl violet combined with Luxol fast blue staining. (b) Silver staining demonstrating the cerebellar medullary white matter (W) and the three cortical layers: molecular layer (M), Purkinje cell layer (P), and granular layer (G). Reproduced from Attaai et al., Scientific Reports, (2020), licensed under Creative Commons Attribution 4.0 License (CC BY 4.0).

in the CN fall into three main types based on how densely their dendrites are covered with spines: rich-spiny (Type I), sparsely spiny (Type II) and aspiny (Type III) neurons (Almasaad et al. 2025). However, there are clear differences between the two species. Camel CN neurons tend to have smaller cell bodies and simpler branching of dendrites compared to humans. For example, medium-sized rich-spiny neurons in camels usually have 3-5 main dendrites branching up to four times, while in humans they have 4-8 dendrites branching up to six times. Interestingly, camel neurons have a much higher density of dendritic spines (about 20 spines/10 μm) compared to humans (8.3 spines/10 μm), suggesting that each dendrite in camels may support a more complex network of connections. These differences may reflect how CN has evolved to meet the unique functional needs of each species.

Spinal trigeminal nucleus (STN)

The spinal trigeminal nucleus (STN) is a sensory nucleus in the brainstem that processes pain and temperature information from the face (Patel et al. 2025). In camels, which routinely face harsh environmental challenges such as dust and thorny plants, the STN is particularly relevant from an adaptive neurobiology perspective (El-Dwairi et al. 2023). Golgi staining studies have identified at least twelve distinct morphological types of neurons in the camel STN (Bataineh 2020). These include common types such as stalked, islet, pyramidal and multipolar neurons, but also unique forms described as octopus-like, boat-like and lobulated forms that are different from those reported in other species. A striking feature of many camel STN neurons is the abundance of appendages (spines, grape-like appendages) on both their dendrites and somata, indicating highly complex synaptic activity. Furthermore, some neurons exhibit unique dendritic dilatations, or swellings, particularly at branching points, which may represent areas of low electrical resistance to facilitate signal processing. Together, these features indicate that the camel STN is more than a simple relay station; it is a sophisticated processor of sensory information, particularly noxious stimuli (Bataineh 2020, El-Dwairi et al. 2023).

Cerebellum

The cerebellum plays a central role in coordinating movement and maintaining balance (Kim et al. 2024, Melka et al. 2024). Histological studies of the dromedary cerebellum confirm the conserved three-layered cortical architecture seen in all mammals: an outer molecular layer, a central Purkinje cell layer and an inner granular layer (Attaai et al. 2020). Purkinje cells, the sole output neurons of the cerebellar cortex, are large, pear-shaped cells with expansive, planar dendritic trees (Salouci et al. 2012). In camels, their somata measure between 19.5 and 36.5 μm in diameter (Al-Hussain et al. 2022; Fig. 2). These dendritic arbors extend throughout the molecular layer and are densely covered with spines, receiving input from tens of thousands of parallel fibers (Attaai et al. 2020, Al-Hussain et al. 2022). Immunohistochemical studies have revealed the distribution of calcium-binding proteins (CaBPs) such as calbindin (CB), parvalbumin (PV) and calretinin (CR) in the camel cerebellum. Calbindin is strongly expressed in nearly all Purkinje cells, highlighting their full morphology, but is also present in other cortical neurons, underscoring its broad role in cerebellar function (Attaai et al. 2020). The presence of other interneurons, such as Golgi cells, basket cells and Lugaro cells, further contributes to the complex circuitry that refines motor output (Abdel-Magied et al. 1995, Attaai et al. 2020, Al-Hussain et al. 2022).

Glial cells: astrocytes, oligodendrocytes, and microglia

Glial cells are the most abundant cell type in the CNS, providing essential support to neurons through metabolic regulation, myelination and immune surveillance (Metwally et al. 2019, Busch et al. 2025). Metwally et al. (2019) used immunohistochemistry to characterize the expression of glial cell molecules in the optic nerve, identifying a high density of astrocytes supporting neural transmission. In the camel optic nerve, immunohistochemical studies have identified three major glial subtypes: astrocytes, oligodendrocytes and microglia (Metwally et al. 2019). Astrocytes, identified by the expression of glial fibrillary acidic protein (GFAP), were found to be the most abundant glial cell type, forming a rich network that supports neuronal function (Salouci et al. 2014). In contrast, oligodendrocytes (expressing myelin basic protein, MBP) and microglia (expressing Iba1) were present at lower levels (Ohsawa et al. 2004, Metwally et al. 2019, Floriddia 2022). This differential distribution suggests a coordinated functional organization, with astrocytes playing a central structural and homeostatic role within the visual pathway (Salouci et al. 2016). In the supraoptic nucleus, glial processes form a dense network between magnocellular neurons and capillaries, a relationship that undergoes seasonal plasticity, likely to facilitate hormone synthesis and secretion in response to environmental demands (Baumann et al. 2001).

Myelination and ultrastructural features of neuronal and synaptic cellular components

Myelination, the process by which axons are wrapped in a fatty sheath, is essential for rapid nerve impulse conduction. In the CNS, this role is performed by oligodendrocytes, whereas Schwann cells carry out myelination in the PNS (Stadelmann et al. 2019). Histological studies of the camel optic nerve confirm that axons are aggregated into fascicles and are myelinated, a feature essential for the high-speed transmission of visual information to the brain (El-Zoghby et al. 2010, Metwally et al. 2019). However, not all nerves in the camel are myelinated; for example, the autonomic nerves in the testis and epididymis are predominantly unmyelinated (Saleh et al. 2002).

Ultrastructural studies using electron microscopy have provided even finer details. These finer details include the specific arrangement of synaptic vesicles, the density of mitochondria within presynaptic terminals, and the structural modifications of the synaptic cleft during different seasons. In the supraoptic nucleus, synapses show seasonal changes; the length of synaptic membrane apposition is greater in summer than in winter, indicating increased synaptic activity and remodeling in response to seasonal demand (Baumann et al. 2001, Calligaro et al. 2023). In the retina, six types of neurons have been characterized at the ultrastructural level, with detailed descriptions of their synaptic connections (Hahn et al. 2023). A unique finding in the neuroepithelium of the camel's nasal septal island is the presence of cell-to-cell communication networks featuring spine synapses, supporting its proposed role in complex sensory processing (Abo-Ahmed et al. 2021). These ultrastructural insights are vital for understanding the fine-tuned mechanisms of synaptic transmission and plasticity that underline the camel's neural function.

Embryology and development of the nervous system

The development of the camel's complex nervous system follows a series of highly orchestrated embryological events, from the initial formation of the neural tube to the migration and differentiation of specialized cell populations (Farouk et al. 2019). While comprehensive molecular studies on camelid embryology are still emerging, morphological investigations have clarified the key developmental stages. Embryological development in the dromedary follows conserved vertebrate mechanisms such as neurulation and the formation of the five secondary brain vesicles. However, these processes occur along a specific structural timeline adapted to the species' long gestation period of approximately 13 months (360-440 days), allowing for significant prenatal maturation. Early embryonic development of the lumbar spinal cord was specifically detailed by Elmonem et al. (2007), providing a benchmark for neurodevelopmental studies in camelids. These findings highlight a combination of conserved vertebrate mechanisms and specific structural timelines adapted to the camel's long gestation period.

Neurulation and early brain vesicle formation

The formation of the central nervous system begins with neurulation, a process where the neural plate, a thickened region of the embryonic ectoderm, folds and fuses to form the hollow neural tube (Gong 2014). In vertebrates, this process typically occurs between the third and fourth week of gestation (Singh et al. 2023). In the dromedary, early embryonic observations at the

9-mm crown–vertebral rump length stage reveal a pronounced expansion of the cephalic portion of the neural tube (Farouk et al. 2019). This expansion gives rise to the three primary brain vesicles: the prosencephalon (forebrain), mesencephalon (midbrain), and rhombencephalon (hindbrain). These vesicles are shaped by the formation of key flexures, including the ventral cephalic flexure and the dorsal pontine flexure, which contribute to the overall organization of the developing brain. As development progresses, the primary brain vesicles further subdivide into five secondary vesicles. The prosencephalon differentiates into the telencephalon, which will give rise to the cerebral hemispheres, and the diencephalon. The mesencephalon remains undivided, while the rhombencephalon separates into the metencephalon, forming the pons and cerebellum, and the myelencephalon, which develops into the medulla oblongata. In a camel embryo measuring approximately 3 cm crown – vertebral rump length, proliferation of the alar plate within the metencephalon leads to the formation of the cerebellar plate, the precursor of the cerebellum (Farouk et al. 2019). Throughout this stage, neurons are generated in the ventricular zone lining the neural tube cavities and migrate outward to populate emerging brain regions, ultimately establishing the characteristic layered organization of the cerebral cortex.

Neuroanatomical adaptations to the environment

The camel's nervous system is not simply a product of its evolutionary heritage but is finely adapted to the extreme demands of desert life. During intense heat, prolonged periods of dehydration, navigation across vast and often featureless landscapes, and the consumption of thorny vegetation all require a suite of highly specialized neurobiological adaptations that are essential for survival in such harsh environments (Gebreselassie et al. 2019).

Thermoregulation and the hypothalamus

One of the camel's most well-known adaptations is its ability to tolerate wide fluctuations in body temperature, a strategy termed adaptive heterothermy (Gaughan 2011). By allowing core body temperature to rise to approximately 41°C during the day and fall to around 34°C at night, camels minimize water loss through evaporative cooling and reduce heat gain from the surrounding environment (Grigg et al. 2009). This finely regulated process is controlled by the hypothalamus, the brain's principal center for thermoregulation and homeostatic balance (Mitchell et al. 1987). The hypothalamo-neurohypophyseal system (HNS), which includes supraoptic and paraventricular nuclei (SON), plays a central role in this regulation. Recent investigations by Lin et al. (2022) have further mapped the hypothalamic osmoregulatory control center, demonstrating how specific neural populations integrate thermal and osmotic signals to maintain homeostasis.

These nuclei produce the antidiuretic hormone arginine vasopressin (AVP), which is critical for water reabsorption in the kidneys (Dimicco et al. 2007, Alim et al. 2019). In camels, the HNS exhibits pronounced seasonal plasticity. During the hot, arid summer months, the system shifts into an "activated" state in anticipation of dehydration. Ultrastructural studies have demonstrated increased synaptic contacts and modifications in capillary architecture within the SON during summer, changes that enhance the efficiency of hormone synthesis and release (Mitchell et al. 1987). These structural adaptations are supported by transcriptomic and peptidomic findings showing elevated AVP mRNA levels in summer, along with seasonal modulation of other neuropeptides such as pro-melanin-concentrating hormone (PMCH) and secretogranin-2 (SCG2) (Wu et al. 1990). Together, this proactive seasonal remodeling of the hypothalamus highlights a remarkable neuroadaptive strategy that enables camels to survive in extreme desert conditions (Gebreselassie et al. 2019). Furthermore, camels possess a rostral epidural rete mirabile (RERM), a specialized vascular network located at the base of the brain that functions as an efficient heat exchanger. Through a mechanism known as selective brain cooling, the RERM enables the brain to be maintained at a lower temperature than the rest of the body during periods of hyperthermia, thereby protecting sensitive neural tissue from thermal damage (Strauss et al. 2017).

Sensory processing and pain perception

Life in the desert exposes camels to constant physical challenges, from abrasive sand to a diet of thorny plants. This has likely driven adaptations in their sensory and pain processing pathways. The spinal trigeminal nucleus (STN), which processes facial sensation, shows remarkable neuronal complexity in camels (El-Dwairi et al. 2023). At least twelve distinct neuronal types have been identified, including unique octopus-like and boat-like cells, alongside an abundance of somatic and dendritic spines (Bataineh 2020). These features suggest that the STN functions as a major center for sophisticated sensory integration, rather than merely serving

as a simple relay station. These features may represent an evolutionary adaptation to better process and perhaps modulate the painful stimuli frequently encountered in their environment (Bataineh 2020, El-Dwairi et al. 2023).

Further evidence for a specialized pain-modulation system comes from the superior colliculus, a midbrain structure involved in orienting movements (Gharaei et al. 2020). In camels, this region contains a substantial population of neurons immunoreactive for methionine-enkephalin (met-enk), an endogenous opioid peptide critical for pain suppression (Mensah-Brown et al. 2006). These met-enk projections are thought to form the initial components of a descending pain-inhibitory pathway, providing an analgesic system that likely allows camels to endure injury and discomfort while navigating their extreme environment. Camel sensory systems are also finely tuned for navigation and social communication. The nasal cavity is anatomically complex, enhancing olfactory sensitivity, a vital adaptation for locating scarce resources and facilitating social interactions (Ben Khalifa et al. 2019). Notably, the discovery of the "nasal septal island," a specialized neuroepithelium innervated by the trigeminal nerve, suggests potential integration of olfactory and trigeminal (somatosensory) inputs (Abo-Ahmed et al. 2021). This multisensory processing could provide camels with an enhanced perception of their environment, improving both survival and social behavior.

Future directions and emerging technologies

The study of camel neurobiology is a rapidly advancing field, with emerging technologies providing unprecedented opportunities to investigate the relationships between genes, neural circuits and behavior. Despite considerable progress, many aspects of camelid neural biology remain unexplored, and their unique physiological and anatomical traits are proving to be a valuable source of innovative biomedical tools (Al Aiyan et al. 2019, Oosterlaken et al. 2025).

Genomics and neurodegenerative diseases

The sequencing of the dromedary and Bactrian camel genomes (Jirimutu et al. 2012, Wu et al. 2014, Elbers et al. 2019, Lado et al. 2020, Ming et al. 2020) has provided a powerful resource for understanding the genetic basis of their specialized features (Almathen et al. 2025, Bahbahani et al. 2025). Future research should focus on linking genomic data to specific phenotypic traits of the nervous system. This involves creating comprehensive databases that integrate genomic information with detailed anatomical, histological and physiological data, an effort that could be advanced through international collaborations such as the Functional Annotation of Animal Genomes (FAANG) consortium (Almathen et al. 2025).

Camels are also emerging as a model for studying neurodegenerative diseases. A novel prion disease, Camel Prion Disease (CPrD), was identified in dromedaries in Algeria (Babelhadj et al. 2018). Affected animals show neurological signs such as nervousness and aggression, with histopathological analysis revealing spongiform changes, gliosis, and neuronal loss in the brain, particularly in subcortical areas such as the striatum and thalamus (Babelhadj et al. 2018). The prion protein (PrPSc) deposits show unique molecular characteristics compared to scrapie in sheep or BSE in cattle, suggesting a distinct prion strain (Wright et al. 2024). Additionally, another neurological condition, "Dubduba syndrome", characterized by non-suppurative meningoencephalomyelitis, has been reported, though its viral etiology remains unidentified (Al-Dubaib et al. 2008, Al-Ghamdi et al. 2009). Studying these naturally occurring neurodegenerative diseases in camels offers a valuable opportunity to advance our understanding of prion biology and other neuropathological processes.

Advanced imaging and tractography

Non-invasive imaging techniques are revolutionizing neuroanatomical research. Magnetic Resonance Imaging (MRI) and Computed Tomography (CT) have been used to visualize the gross anatomy of the camel brain (Arencibia et al. 2004, Ben Khalifa et al. 2019). More recently, Diffusion Tensor Imaging (DTI) tractography has been applied to the camel brain to reconstruct major white matter tracts, such as the corpus callosum, cingulum and internal capsule (Cartiaux et al. 2023). This approach allows for the virtual dissection of neural pathways, providing insights into the brain's structural connectivity.

Camelid-derived nanobodies for neurological therapy

One of the most promising frontiers in biomedical research is the development of therapeutic agents derived from camelids. Camels, llamas and alpacas produce unique single-domain antibodies, known as nanobodies (VHHs), which are small, highly stable and remarkably specific (Lafon et al. 2025, Oosterlaken et al. 2025). These properties give nanobodies distinct

advantages over conventional antibodies, particularly in overcoming the blood–brain barrier (BBB) a major obstacle in treating central nervous system disorders, as most large molecules cannot reach their targets in the brain (Al-Numair et al. 2022, Zheng et al. 2022). Studies demonstrate that engineered nanobodies can cross the BBB and effectively modulate brain receptors (Oosterlaken et al. 2025). This study demonstrated that a bivalent nanobody targeting the metabotropic glutamate receptor 2 (mGlu2), when administered peripherally to mice, reached the brain and corrected cognitive deficits in models of NMDA receptor hypofunction, which is relevant to schizophrenia. This landmark proof-of-concept highlights the potential of nanobody-based therapies for a wide range of neurological and psychiatric disorders, from schizophrenia to Alzheimer's disease (Zheng et al. 2022, Oosterlaken et al. 2025).

Conclusion

The camel's nervous system is remarkably well-adapted to the harsh challenges of the desert. It is unique among ungulates in its anatomy, cellular architecture and developmental pathways. The camel brain is highly folded, with specialized vascular structures such as the rete mirabile that cool the brain, and a large suprachiasmatic nucleus that likely helps the animal keep time with the extreme arid cycles of the desert. Microscopically, its neurons are very diverse, with unusual shapes and dense, complex connections in areas responsible for sensing and processing the environment, allowing camels to detect, interpret and respond to pain, heat and other challenges with remarkable precision. Developmentally, comparisons with humans and other mammals reveal both shared evolutionary patterns and innovations unique to camelids. Today, advances in genomics, imaging, and molecular tools are opening new windows into this remarkable system. Nanobody-based therapies, derived from camelid antibodies and capable of crossing the blood – brain barrier, are just one example of how studying the camel nervous system could lead to treatments for human neurological disorders.

Acknowledgements

The author would like to thank the support of the Deanship of Scientific Research, Vice Presidency for Graduate Studies and Scientific Research, King Faisal University, Saudi Arabia (Grant Number: KFU260286) for financial support for this publication.

Author Declarations

Ethics approval

Not applicable.

Use of generative artificial intelligence

The authors declare that no Generative AI was used in the creation of this manuscript.

Conflict of interest

The authors declare that there is no conflict of interest.

References

Abdel-Magied EM **(1995)** Fine structure of nerve endings and junctions in the superior cervical ganglion of the camel (Camelus Dromedarius). Anat Histol Embryol 24:135-140.

Abo-Ahmed AI, Eshrah EA, Latifi F **(2021)** Unique nasal septal island in dromedary camels may play a role in pain perception: Microscopic studies. Saudi J Biol Sci 28: 3806- 3815.

Adam ZA, Awaad AS, Tawfiek MG, Ibrahim A **(2016)** Gross anatomy of the narial and labial musculatures of one humped camel (Camelus Dromedarius). J Morphol Sci 33: 171-178.

Al-Dubaib M, Al-Swailem A, Al-Ghamdi G, Alyamani E, Al-Naeem AA, Al-Mejali AM, Shehata MM, Hashad M, El-Lithy DA, Mahmoud O **(2008)** Dubduba Syndrome: An Emerging Neurological Disease of Camels with a Possible Viral Etiologic Agent. J Camel Pract Res 15: 147-152.

Al-Ghamdi GM, Al-Naeem AA, Wuenschmann A, Wernery U, Al-Dubaib M, Al-Swailem AM, Hamouda M,Al-Yamani E, Shehata M, El-Lithy O, Mahmoud A, Al-Mujali M **(2009)** Dubduba Syndrome: Non-suppurative meningoencephalomyelitis in dromedary camels in Saudi Arabia. J Camel Pract Res 16: 19-23.

Al-Hussain SM, Albostanji SA, Mustafa AG, Zaqout S **(2021)** Neuronal cell types in the anterior ventral thalamic nucleus of the camel. Anat Rec 304: 2044-2049.

Al-Hussain SM, Yousuf MS, Hani AB, Zaqout S, Djouhri L, Mustafa AG **(2022)** A Golgi study of neurons in the camel cerebellum (Camelus Dromedarius). Anat Rec 305: 1264-1276.

Al-Numair NS, Theyab A, Alzahrani F, Shams AM, Al-Anazi IO, Oyouni AAA, Al-Amer OM, Mavromatis C, Saadeldin IM, Abdali WA, Hawsawi YM **(2022)** Camels' biological fluids contained nanobodies: Promising Avenue in cancer therapy. Cancer Cell Int 22: 279.

Al Aiyan A, Balan R **(2023)** Mapping the branching pattern of the middle cerebral artery in the camel (Camelus Dromedarius): A Comprehensive Anatomical Analysis. Front Vet Sci 10: 1224197.

Al Aiyan A, Balan R **(2024)** Comprehensive Analysis of the rostral and caudal cerebral artery branching patterns in the dromedary camel (Camelus Dromedarius). Front Vet Sci 11: 1426372.

Al Aiyan A, Balan R, Gebreigziabiher S, Zerom S, Mihreteab Y, Ghebrehiwot E, Aldarwich A, Willingham AL, Kishore U **(2024)** Comprehensive mapping of the exterior architecture of the dromedary camel brain. Sci Rep 14: 2971.

Al Aiyan A, Menon P, Aldarwich A, Almuhairi F, Alnuaimi S, Bulshawareb A, Qablan M, Shehab S **(2019)** Descriptive analysis of cerebral arterial vascular architecture in dromedary camel (Camelus Dromedarius). Front Neuroanat 13: 67.

Alim FZD, Romanova EV, Tay YL, Abdul Rahman AYB, Chan KG, Hong KW, Rogers M, Southey BR, Greenwood MP, Mecawi AS, Mustafa MR, Mahy N, Campbell C, Antunes-Rodrigues J, Sweedler JV, Murphy D, Hindmarch CCT **(2019)** Seasonal adaptations of the hypothalamo-neurohypophyseal system of the dromedary camel. PLoS One 14: e0216679.

Allouch GM, Alshanbari FA **(2023)** Anatomical study of the nerve supply of the dromedary camel (Camelus Dromedarius) in the distal hindlimb with a special reference to the cutaneous innervation. Vet Sci 10: 305.

Almasaad JM, Bataineh ZM, Zaqout S **(2025)** Neuronal diversity in the caudate nucleus: a comparative study between camel and human brains. Anat Rec 308: 1410- 1424.

Almathen F, Salim B **(2025)** Time to link camel genomics and traits by bridging the phenotypic gap. Front Genet 16: 1627229.

Arencibia A, Rivero MA, Ramírez JA, Gil F, Gutierrez C, Oros J **(2004)** Magnetic resonance imaging of the normal brain in a newborn dromedary camel. Vet J 168: 353- 357.

Attaai AH, Noreldin AE, Abdel-Maksoud FM, Hussein MT **(2020)** An updated investigation on the dromedary camel cerebellum (Camelus Dromedarius) with special insight into the distribution of calcium-binding proteins. Sci Rep 10: 21157.

Babelhadj B, Di Bari MA, Pirisinu L, Chiappini B, Gaouar SBS, Riccardi G, Marcon S, Agrimi U, Nanno R, Vaccari G **(2018)** Prion disease in dromedary camels, Algeria. Emerg Infect Dis 24: 1029-1036.

Bahbahani H, Mohammad Z, Alfoudari A, Al Abri M **(2025)** Genomic insights into racing camels: Inbreeding levels and positive selection linked to athletic traits. Animal 19: 101467.

Bataineh ZM **(2020)** Types of Neurons in the spinal trigeminal nucleus of the camel brain: Golgi Study. FASEB J 34: 1-1.

Baumann N, Pham-Dinh D **(2001)** Biology of oligodendrocyte and myelin in the mammalian central nervous system. Physiol Rev 81: 871-927.

Beheiry RR **(2016)** Histological, immunohistochemical and scanning electron microscopic studies on the cerebellum of dromedary camel (Camelus Dromedarius). J Vet Anat 9: 25- 38.

Ben Khalifa A, Belkhiria J, Hamdi H, Dakhli B, Chandoul W, Mattoussi A **(2019)** Computed tomography and magnetic resonance imaging of the brain and associated structures of the one humped camel (Camelus Dromedarius): A comparative study. J New Sci 68: 4221-4231.

Bouâouda H, Tali A, Chahboun M, El Allali K, Achaâban MR **(2014)** Adaptive heterothermy and selective brain cooling in the dromedary camel. In: The dromedary camel: A model for health and disease. BSP: 113-125.

Busch SE, Bosman C, Chadderton P, Apps R, De Zeeuw CI, Reeber SL **(2025)** Human purkinje cells are larger and more complex than mouse, with an expanded capacity for input integration. eLife 14: e105013.

Calligaro H, Shoghi A, Chen X, Kim K-Y, Yu HL, Khov B, Finander B, Le H, Ellisman MH, Panda S **(2023)** Ultrastructure of synaptic connectivity within subregions of the suprachiasmatic nucleus revealed by a genetically encoded tag and serial blockface electron microscopy. eNeuro 10: 0227-0223.

Cartiaux B, Amara A, Pailloux N, Paumier R, Malek A, Elmehatli K, Kachout S, Bensmida B, Montel C, Arribaratr G, Mogicato G **(2023)** Diffusion tensor imaging tractography in the one-humped camel (Camelus Dromedarius) Brain. Front Vet Sci 10: 1231421.

Dimicco JA, Zaretsky DV **(2007)** The dorsomedial hypothalamus: A new player in thermoregulation. Am J Physiol Regul Integr Comp Physiol 292: R47-R63.

El-Dwairi QA, Al-Hussain SM, Banihani AS, Bataineh ZM, Djouhri L, Mustafa AG, Zaqout S **(2023)** Neuronal cell types in the spinal trigeminal nucleus of the camel brain. Brain Sci 13.

El-Zoghby I, Osman DI **(2010)** Comparative study on the optic nerve of the donkey and camel. J Camel Pract Res 17: 211-215.

El Allali K, Achaâban MR, Bothorel B, Piro M, Bouâouda H, El Allouchi M, Ouassat M, Malan A, Pevet P **(2013)** Entrainment of the circadian clock by daily ambient temperature cycles in the camel (Camelus Dromedarius). Am J Physiol Regul Integr Comp Physiol 304: 1044-1052.

El Allali K, Achaâban MR, Piro M, Ouassat M, Challet E, Errami M, Lakhdar-Ghazal N, Calas A, Pevet P **(2017)** The suprachiasmatic nucleus of the dromedary camel (Camelus Dromedarius): Cytoarchitecture and Neurochemical Anatomy. Front Neuroanat 11: 103.

Elbers JP, Rogers MF, Perelman PL, Proskuryakova AA, Serdyukova NA, Johnson WE, Horin P, Corander J, Murphy D, Burger PA **(2019)** Improving illumina assemblies with hi-c and long reads: an example with the north african dromedary. Molecular Ecology Resources 19: 1015-1026.

Elkhawad AO **(1992)** Selective brain cooling in desert animals: The camel (Camelus Dromedarius). Comp Biochem Physiol 101: 345-347.

Elmonem ME, Mohamed SA, Aly KH **(2007)** Early embryonic development of the camel lumbar spinal cord segment. Anat Histol Embryol 36: 43-46.

Faraz A, Masebo NT, Hussain SM, Waheed A, Ishaq HM, Tauqir NA, Abbasi AR, Saleem F, Padalino B **(2025)** Association of environmental temperature and relative humidity with ocular and flank temperatures in dromedary camels. Animals 15: 309.

Farouk SM, Hassan SA, Elsayed AK, Abdo M **(2019)** Vesicles stage of camel brain development. Int J Morphol 37: 498-503.

Fesseha H, Desta W **(2020)** Dromedary camel and its adaptation mechanisms to desert environment: A Review. Int j zool stud 5: 23-28.

Floriddia E **(2022)** New myelin for old oligodendrocytes. Nat Neurosci 25: 404-404.

Foster M, Dwibhashyam S, Patel D, Gupta K, Matz O, Billings BK, Bitterman K, Bertelson M, Tang CY, Mars RB, Raghanti MA, Hof PR, Sherwood CC, Manger PR, Spocter MA **(2024)** Comparative anatomy of the caudate nucleus in canids and felids: Associations with brain size, curvature, cross-sectional properties and behavioral ecology. J Comp Neurol 532: e25618.

Ganapathy MK, Reddy V, Tadi P **(2024)** Neuroanatomy, spinal cord morphology. StatPearls Publishing.

Gaughan J **(2011)** Which physiological adaptation allows

camels to tolerate high heat load and what more can we learn? J Camelid Sci 4.

Gebreselassie M, Assen AM **(2019)** Adaptation mechanisms of camels (Camelus Dromedarius) for desert environment: A Review. J Vet Sci Technol 10: 486.

Ghaji, A **(1985)** The cerebellum of the one-humped camel. Anat Histol Embryol 14: 54-65.

Gharaei S, Honnuraiah S, Arabzadeh E, Stuart GJ **(2020)** superior colliculus modulates cortical coding of somatosensory information. Nat Commun 11: 1693.

Gong S-G **(2014)** Cranial neural crest: Migratory cell behavior and regulatory networks. Exp Cell Res 325: 90-95.

Grigg G, Beard L, Dörges B, Heucke J, Coventry J, Coppock A, Blomberg S **(2009)** Strategic (Adaptive) hypothermia in bull dromedary camels during rut; could it increase reproductive success? Biol Lett 5: 853-856.

Hahn J, Monavarfeshani A, Qiao M, Kao AH, Kölsch Y, Kumar A, Kunze VP, Rasys AM, Richardson R, Wekselblatt JB, Bair H, Lucas RJ, Li W, Meiter M, Trachtenberg JT, Yan W, Peng Y, Sanes JR, Shekhar K **(2023)** Evolution of neuronal cell classes and types in the vertebrate retina. Nature 624: 415-424.

Huff T, Weisbrod LJ, Daly DT **(2024)** Neuroanatomy, cranial nerve 5 (Trigeminal). StatPearls Publishing.

Jain RK, Gupta AN **(2007)** Gross anatomical studies on the spinal cord of camel (Camelus Dromedarius). Indian J Anim Sci 77: 55.

Jararr B **(2015)** Normal Pattern of the Ccmel histology. FAO Publications, Riyadh.

Jerbi H, Vazquez N, Pérez W **(2019)** Morphological configuration and topography of the brain arterial supply of the one-humped camel (Camelus Dromedarius, Linnaeus 1758). Int J Morphol 37: 1095-1100.

Jessen C **(1998)** Selective brain cooling in mammals and birds. Physiol 13: 281-286.

Jirimutu, Wang Z, Ding G, Chen G, Sun Y, Sun Z, Zhang H, Wang L, Hasi S, Zhang Y, Li J, Shi Y, Xu Z, He C, Yu S, Li S, Zhang W, Batmunkh M, Ts B, Narenbatu, Unierhu, Bat-Ireedui S, Gao H, Baysgalan B, Li Q, Jia Z, Turigenbayila, Subudenggerile, Dabxilt, Erdemet, Altansha, Altansukh, Liu T, Cao M, Aruuntsever, Bayart, Hosblig, He F, Zha-ti A, Zheng G, Qiu F, Sun Z, Zhao L, Zhao W, Liu B, Li C, Chen Y, Tang X, Guo C, Liu W, Ming L, Temuulen, Cui A, Li Y, Gao J, Li J, Wurentaodi, Niu S, Sun T, Zhai Z, Zhang M, Chen C, Baldan T, Bayaer T, Li Y, Meng H **(2012)** Genome sequences of wild and domestic bactrian camels. Nat Commun 3: 1202.

Kim LH, Heck DH, Sillitoe RV **(2024)** Cerebellar functions beyond movement and learning. Annu Rev Neurosci 47: 145-166.

Lado S, Elbers JP, Rogers MF, Melo-Ferreira J, Yadamsuren A, Corander J, Horin P, Burger PA **(2020)** nucleotide diversity of functionally different groups of immune response genes in old world camels based on newly annotated and reference-guided assemblies. BMC Genomics 21: 606.

Lafon PA, Prézeau L, Pin JP, Rondard P **(2025)** Nanobodies: A new paradigm for brain disorder therapies. Trends Pharmacol Sci 46: 1049-1051.

Lin P, Al-Hussain SM, Mustafa AG, Zaqout S, Djouhri L et al. **(2022)** The hypothalamic osmoregulatory control centre of the Arabian dromedary camel. Commun Biol 5: 904.

Melka N, Pszczolinska A, Klejbor I, Moryś J **(2024)** the cerebellum: The 'little' brain and its big role. Folia Morphologica 83: 497-508.

Mensah-Brown EPK, Garey LJ **(2006)** The lamination of the superior colliculus of the camel, Camelus Dromedarius: A neuron-specific nuclear protein and neuropeptidergic immunohistochemical study. J Anat 209: 351-366.

Metwally E, Farouk SM, Hossain MS, Raihan O **(2019)** Expression of glial cells molecules in the optic nerve of adult dromedary camel (Camelus Dromedarius): A histological and immunohistochemical analysis. Anat Histol Embryol 48: 74-86.

Ming L, Wang Z, Yi L, Batmunkh M, Liu T, Siren D, He J, Jurmat N, Jambl T, Li Y, Jirimutu **(2020)** Chromosome-level assembly of wild bactrian camel genome reveals organization of immune gene Loci. Mol Ecol Resour 20:3.

Mitchell D, Laburn HP, Nijland MIM, Zurovsky Y, Mitchell G **(1987)** Selective brain cooling and survival. S Afr J Sci 83: 598-604.

Nourinezhad J, Mazaheri Y, Biglari Z **(2015)** Detailed anatomy of the cranial cervical ganglion in the dromedary camel (Camelus Dromedarius). Anat Rec (Hoboken) 298: 1479- 1491.

Ohsawa K, Imai Y, Sasaki Y, Kohsaka S **(2004)** Microglia/ /Macrophage-specific protein iba1 binds to fimbrin and enhances its actin-bundling activity. J Neurochem 88: 844-856.

Oosterlaken M, Rogliardo A, Lipina T, Lafon PA, Tsitokana ME, Keck M, Cahuzac H, Prieu-Serandon P, Diem S, Derieux C, Camberlin C, Lafont C, Meyer D, Chames P, Vandermoere F, Marin P, Prezeau L, Servent D, Salahpour A, Ramsey A, Becamel C, Pin JP, Kniazeff J, Rondard P **(2025)** Nanobody therapy rescues behavioural deficits of nmda receptor hypofunction. Nature 645: 262-270.

Pastrana CI, Busch SE, Reidenberg JS, Raghunathan G, Hof PR, Manger PR **(2024)** Negative reinforcement and sensory cues boost camel proactivity. Behav 161: 781-807.

Patel NM, Jozsa F, Das JM **(2025)** Neuroanatomy, spinal trigeminal nucleus statpearls. StatPearls Publishing: Treasure Island (FL).

Purves D, Augustine GJ, Fitzpatrick D **(2001)** The sympathetic division of the visceral motor system. Sunderland (MA).

Ramu K, Kumaravel A, Selvaraju T, Iniyah K, Kathirvel S **(2025)** Histological architecture of the caudate nucleus in adult goat brain. Int J Vet Sci Anim Husb 10: 395- 397.

Saleh AM, Alameldin MA, Abdelmoniem ME, Hassouna EM, Wrobel KH **(2002)** Immunohistochemical investigations of the autonomous nerve distribution in the testis of the camel (Camelus Dromedarius). Ann Anat 184: 209-220.

Salouci M, Antoine N, Shikh Al Sook MK, Piret J, Mignon Y, Kirschvink N, Gabriel A **(2014)** Developmental profiles of GFAP-positive astrocytes in sheep cerebellum. Vet Res Commun 38: 279-285.

Salouci M, Engelen V, Gyan M, Antoine N, Jacqmot O, Mignon Y, Kirschvink N, Gabriel A **(2012)** Development of Purkinje cells in the ovine brain. Anat Histol Embryol 41: 227-232.

Salouci M, Gabriel A **(2016)** Focus Sur Les Astrocytes: Cellules De La Glie Aux Rôles Multiples Et Importants Dans Le Snc. Le Mouton Est-Il Un Excellent Modèle Animal ? Rev Med Vet 167: 176-191.

Singh R, Munakomi S **(2023)** Embryology, Neural Tube. StatPearls Publications.

Smuts MMS, Bezuidenhout AJ **(1987)** Anatomy of the dromedary. illustrations and photographs by David Mazierski. Oxford University Press.

Stadelmann C, Timmler S, Barrantes-Freer A, Simons M **(2019)** Myelin in the central nervous system: Structure, function, and pathology. Physiol Rev 99: 1381-1431.

Strauss WM, Hetem RS, Mitchell D, Maloney SK, O'brien HD, Meyer LCR, Fuller A **(2017)** Body water conservation through selective brain cooling by the carotid rete: A physiological feature for surviving climate change? Conserv Physiol 5: cow078.

Waxenbaum JA, Reddy V, Futterman B **(2023)** Anatomy, cranial nerves. StatPearls Publications.

Wright EA, Reddock MB, Roberts EK, Legesse YW, Perry G, Bradley RD **(2024)** Genetic characterization of the prion protein gene in camels (camelus) with comments on the evolutionary history of prion disease in Cetartiodactyla. PeerJ 12: e17552.

Wu H, Guang X, Al-Fageeh MB, Cao J, Pan S, Zhou H, Zhang L, Abutarboush MH, Xing Y, Xie Z, Alshanqeeti AS, Zhang Y, Yao Q, Al-Shomrani BM, Zhang D, Li J, Manee MM, Yang Z, Yang L, liu Y, Zhang J, Altammami MA, Wang S, Yu L, Zhang W, Liu S, Ba L, Liu C, Yang X, Meng F, Wang F, Wang S, Li L, Li E, Li X, Wu K, Zhang S, Wang J, Yin Y, Yang H, Al-Swailem AM, Wang J **(2014)** Camelid genomes reveal evolution and adaptation to desert environments. Nat Commun 5: 5188.

Wu P, Childs GV **(1990)** Cold and novel environment stress affects AVP mRNA in the paraventricular nucleus, but not the supraoptic nucleus: An in-situ hybridization study. Mol Cell Neurosci 1: 233-249.

Xie ZH, Li HY, Wang JL **(2006)** Morphological study on the cerebrum of bactrian camel (Camelus Bactrians) with particular reference to sulci. J Camel Pract Res 13: 61-66.

Zheng F, Pang Y, Li L, Pang Y, Zhang J, Wang X, Raes G **(2022)** Applications of nanobodies in brain diseases. Front Immunol 13: 978513.