At the Edge: Neuroethological Approaches to Reptilian Mechanoreception

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The neural circuitry directing behavior is one of the fundamental questions of neurobiology. Historically, studies of ethology have been descriptive in nature; however, by adopting a comparative biological perspective, patterns of animal behavior and corresponding neural substrates can be examined systematically. Although they are morphologically similar to early tetrapod ancestors, modern crocodilians have adapted distinct sensory abilities that have made them impressive predators in both terrestrial and aquatic environments. Characterization of the activity of peripheral nervous system adaptations, central nervous system organization, and accompanying behaviors remain open questions suited to comparative neuroethological strategies.

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THE NEUROETHOLOGICAL PERSPECTIVE

Insights into the organization and function of the nervous system have arisen through assimilation of a variety of experimental approaches ranging from molecular and cellular techniques to behavioral analyses. Similarly, neuroethology represents a field at the crossroads, fostering interdisciplinary research with methods familiar to zoology, physiology, evolutionary biology, and neurobiology[1]. These efforts are unified in their foundations in understanding animal behavior and its underlying neural processes. However, given the complexity of nervous systems within highly developed animals, broader questions of the neural basis of behavior are explored through a comparative approach. Fundamental to these ideas is an appreciation for the "ethology" – that is, the behaviors observable both in animals' natural habitats – balanced with the rigorous control of stimuli to elicit these patterns[2]. Pioneering work from animal behaviorists Lorenz[3], von Frisch[4], and Tinbergen[5] in the past century have provided a framework for investigation, as outlined in Tinbergen's classification of four explanations for behavior[6], which are equally relevant in approaching neuroethology. Rather than broadly grouping proximate and ultimate explanations for behavior, Tinbergen argued that physiological and mechanistic bases, development or ontogeny, functional contributions to survival and reproduction, and evolutionary history or phylogeny provide a structure for addressing questions of ethology[6,7].

Within the realm of sensory biology, comparative neuroethological approaches have proven effective. For example, the circuits underlying electroreception and the "jam avoidance response" in afferents from gymnotiform fish *Eigenmannia* have been identified in detail[8-10]. This weakly electric fish discharges its electric organ in order to "electrolocate" or sense perturbations in the electric field of the surrounding environment. In order to accommodate the presence of other actively electrolocating fish which could potentially mask the reception of subtle electric field variations from prey, *Eigenmannia* and other species of gymnotiforms can alter the frequency of the discharge of the electric generating organ, thereby increasing the frequency difference relative to the neighboring fish. As electroreception is widespread among vertebrates with examples in all classes of fish, some amphibians[11,12], and potentially mammals[13,14], this "exotic" sensory modality has evolved multiple times through non-homologous receptor and neural circuits over the course of vertebrate evolution[15].

Neuroethology and comparative studies of nervous systems integrate information from two different levels. Even distantly related organisms can show similarities in motor patterns and sensory processing (indeed these functional and structural homologies contribute to the utility of commonly used animal models in studying human neurobiology). Comparative analysis using organisms of varying phylogenetic relationships provides a framework for understanding nervous system organization that takes historical forces and evolutionary pressures into account in the shaping of the final architecture of neural circuits. Through a comparative approach, information on the uniqueness of a particular behavior or sensory processing mechanism is revealed. One example of the benefit of this combined perspective can be seen in studies of somatosensory processing among members of the mammalian order *Insectivora*[16-18]. Included in this group are shrews and moles - animals that have been used in examinations of mammalian nervous system evolution as they have retained morphological traits

similar to those found in fossils of small-bodied eutherian ancestors. Through comparisons of nervous system organization among these related animals, as well as their behaviors, the uniqueness of certain species becomes apparent. The star-nosed mole (*Condylura cristata*) has a specialized symmetrical star array of 22 appendages, covered in more than 25,000 highly-innervated Eimer's organ mechanoreceptors[19,20] and a somatosensory cortical organization dominated by the star's representation with the most densely-innervated appendages occupying the most cortical space[21]. Using its star appendages to minimize prey searching and handling latencies, the star-nosed mole is the fastest mammalian forager[22]. The unusual anatomical and neural circuits underlying distinct sensory processing abilities is revealed through integration of behavioral and comparative perspectives.

This review discusses unique mechanosensory structures found among some of the most phylogenetically ancient tetrapods: extant members of the order *Crocodilia*. Respecting Tinbergen's ethological considerations, as well as integrating a comparative neuroanatomical perspective, we describe the evolution and ecological pressures faced by these species. Lastly, we present the current understanding of receptor physiology and corresponding neural circuitry.

THE EVOLUTION OF TETRAPODS AND CROCODILIANS

About 370 million years ago, a large lobe-finned fish emerged from the water, having evolved into a giant-salamander-like "labyrinthodont" amphibian[23]. The evolution of this amphibian in the Upper Devonian period of the Paleozoic era marked a transition among vertebrates from an aquatic fish-like lifestyle to terrestrial life, and consequently, heralded unique physiological and morphological changes[24]. Among these adaptations was the development of four paired limbs, replacing four paired fins, giving rise to a new group of vertebrate organisms: the tetrapods, a group with modern amphibian, reptile, bird, and mammal representatives. Approximately 320 million years ago, with the advent of fluid-filled amniotic membranes and yolk sacs to prevent dehydration of eggs and embryos among the synapsids (mammals and "proto-mammals") and sauropsids (dinosaurs, reptiles, and birds), the transition to terrestrial life was complete[25,26]. Some tetrapods became amphibious and continued to occupy the transitional water-to-land habitats. Living in these environments at the water-to-land matrix, these organisms evolved distinct sensory systems that allowed them to face the series of challenges presented in aquatic and terrestrial environments[27]. This semi-aquatic tetrapod lifestyle is seen today in some species of modern mammals, birds, reptiles, and amphibians, including members of the order *Crocodilia*.

Extant members of the order *Crocodilia* (referred to collectively as "crocodilians") are represented in twenty-three species, occupying semi-aquatic habitats throughout North and South America, Africa, Asia, and Australia. Furthermore, crocodilians are generally regarded as a sister group and the closest modern relatives to birds, based on morphological and genomic comparisons[28]. The order is divided into three families – Crocodylidae, Alligatoridae, and Gavialidae. All modern crocodilians are descendants of archosaurian ancestors[29,30]. Furthermore, modern crocodilians occupy a range of aquatic environments and vary in the amount of time spent in the water. The most aquatic species include the gharials (*Gavialis*) which have large, narrow snouts adapted to their primarily piscivorous diets[31]. Many species, including the saltwater crocodile (*Crocodylus porosus*), Nile crocodile (*C. niloticus*), and the American crocodile (*C. acutus*), can accommodate both freshwater and marine environments to differing degrees as they swim from coastal areas into the ocean[32]. Evidence from phylogenetic and physiological studies suggests transoceanic migrations might have occurred among crocodilian lineages.

Modern crocodilian tolerance to a variety of external chemical[33] and environmental conditions, even among areas developed by humans[34], are reflected in their archosaurian ancestors' survival through both the Triassic-Jurassic and Cretaceous-Tertiary mass extinction events[35]. Crocodilian fossils have retained the general skeletal and morphological features of extant crocodilians since the late Triassic/early Jurassic period, 180-200 MYA[36], underscoring the great degree of conservation in the evolution of their body plans. Under periods of prolonged development and a growth rate similar to juvenile extant crocodilians, extinct species such as the so-called *Deinosuchus* "terror-crocodile" of the Late Cretaceous period attained dinosaur-like lengths of 8 to 10 meters and masses between 2,500 and 5,000 kg, growing into broad-snouted crocodilians similar in appearance to modern alligators[37].

Although crocodilian populations have become vulnerable to declines in population even within the recent past[38], crocodilians have shown a remarkable degree of resilience when sufficient habitats are recovered[39]. In fact, no crocodilian species have been driven to extinction during recorded human history despite considerable economic incentives to hunt and kill them[40,41]. These reptiles inspire both fear and fascination as successful large-bodied, long-lived ectotherms thriving among a world of endotherms, having survived extinction events to remain the closest living reptilian relatives to the Dinosauria, comprising one branch of its extant phylogenetic
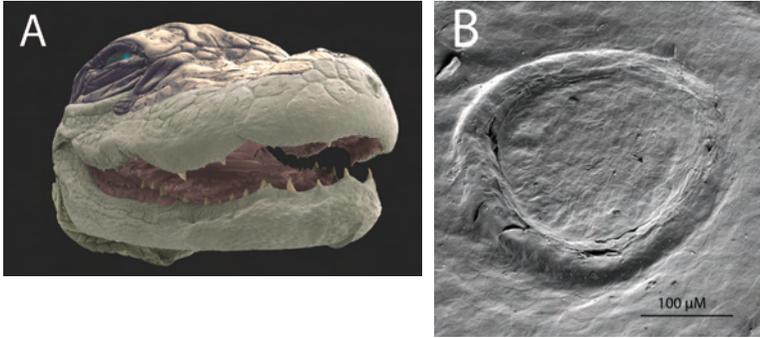
Figure 1 | **Mechanoreception in *A. mississippiensis*. a |** Pseudo-colored scanning electron micrograph of head of juvenile *A. mississippiensis*. Epidermal touch papillae appear over upper and lower jaw regions (paler scales). The head is 4.5 cm in length. **b |** Scanning electron micrograph of single epidermal touch papilla from the upper jaw. These dome-like structures are innervated by many mechanoreceptors. The scale bar is 100 μM.

bracket[42,43]. Beyond their armored osteoderm-plated bodies and their abilities to tolerate and adapt to a variety of environmental conditions, crocodilians have distinct sensory specializations, enabling them to rapidly process stimuli to determine the presence of potential prey, making them apex[44] predators and survivors.

MECHANORECEPTION IN CROCODILIANS

In the evolution of a sensitive mechanosensory system balanced with the development of a protected body surface, all orders of reptiles developed arrays of touch papillae that vary in morphology, function, and distribution among taxa. Initial studies using the American alligator (*Alligator mississippiensis*) identified myelinated afferents for rapidly adapting fibers responsive to transient "on" and "off" stimuli and afferents for slowly adapting fibers[45,46]. Considering their semi-aquatic habitats which include murky bodies of water with poor illumination, it is likely that mechanoreception plays a significant role in prey localization over other sensory modalities[47]. This is not to say that their visual[48,49], chemosensory[50], and auditory[51-53] systems are poorly represented, and in fact, several anatomical[54] and functional[51,55-57] studies, primarily in *A. mississippiensis* and the caiman (*C. crocodilus*), have examined these modalities. However, comprehensive discussion of these sensory systems is beyond the scope of this review.

As first characterized by von Düring, arrays of sensory organs in the form of spot-like touch papillae cover crocodilians[58,59]. These dense arrangements of darkly pigmented pits, also called "follicle pits," "follicle glands," or "integumentary sense organs," have been used in the identification of crocodilian skin[60]. Among species in the alligatorid family (including alligators and caimans), these touch papillae are found on cranial scales surrounding the face of the animal (**Figure 1a**), whereas they are distributed post-cranially on ventral integumentary scales in members of the crocodylid family. Despite speculation on their possible function as secretory pores[61] or their osmoreceptive properties[62-64], these touch papillae are dome-like structures (**Figure 1b**), lacking pore or hair follicles, and externally resemble specialized mechanoreceptors such as the push rod organs on the hairless bills of monotremes[13] and the Eimer's organs on the rhinarium of moles[19,65,66]. Noting the pronounced thinning of the keratin and stratum corneum epidermal layers, the complex organization of discoid receptors through the stratum spinosum, the Merkel cell neurite columns and complexes in the dermis and epidermis, and the presence of encapsulated and unencapsulated lamellated receptors, von Düring proposed that these papillae were "particularly complex" sensory structures, especially when compared to tactile structures identified in other reptiles[59].

Using *A. mississippiensis*, which have these specialized touch papillae on only the cranial scales, Soares demonstrated that partially submerged alligators could orient themselves to water surface disturbances created by a single drop of water in complete darkness[67]. This behavior was abolished when the animals were completely submerged, had their heads completely out of the water, or had their touch papillae covered by a thin plastic elastomer. In recording from the trigeminal ganglion, neurons produced single spikes phase-locked to water surface wave stimuli, with increasing wave amplitude producing increased spike firing probability. Based on these examinations, Soares coined a new term for these sensory organs, calling them "dome pressure receptors;" however, this nomenclature has led to some confusion by grouping together post-cranial receptors and von Düring's "touch papillae," a categorization that has yet to be confirmed functionally or physiologically[62].

NEURAL TARGETS FOR UNIQUE SENSORY ORGANS

One aspect of touch papillae-mediated orientation not yet understood is the neuroanatomical representation of water surface movements. Forming the majority of the reptilian midbrain roof is the optic tectum (the homolog to the mammalian superior colliculus), the single largest visual center in reptiles. Examined in great detail for patterns in cytoarchitecture and afferent and efferent connections[68,69], the optic tectum (or tecta mesencephali) is notable for its concentric laminated structure, consisting of 14 layers, divided into periventricular, central, and superficial zones[70] (Alternatively, different nomenclatures have been proposed which group together some laminae[71]). Of

the tectal organization patterns observed in reptiles, the so-called lacertid pattern shows relatively poorly developed superficial layers and more prominent periventricular layers, as noted in crocodilians, turtles, and several families of lizards[72]. As the layers of the superficial zone, characterized by horizontal cells and vertically-arranged fusiform cells, are the primary target for retinal ganglion axons, this atrophy of lamination in the lacertid pattern suggests a lessened degree of dependence on visual processing, especially compared to the clearly defined laminae of highly visual *Iguanidae* and *Chamaeloeonidae* lizards.

The contralateral retina provides the single largest source of afferents to the optic tectum in most reptiles, and precise retinotopic projections on the tectum have been established for a variety of reptiles[73-76]. With the exception of the *Iguana iguana*, in all examined reptiles the nasotemporal visual axis is oriented along the tectum's rostrocaudal axis, and the dorsoventral visual axis is oriented along the tectum's mediolateral axis. Despite having receptive fields significantly smaller in size, the central 10º of the visual field is expanded in representation and occupies approximately 20% of the tectal surface, thus allowing a degree of magnified foveal representation, similar to that noted in other tetrapods[76,77].

Similar to other vertebrates, the reptilian optic tectum receives non-visual afferents, particularly in deeper layers where overlap of visual, auditory, and tactile modalities occurs, via unimodal and multimodal neurons. Based on HRP and fast blue retrograde experiments, a number of non-visual diencephalic structures were found to project to the optic tectum in reptiles[78,79]. Hartline and colleagues demonstrated that specialized infrared receptors known as "pit organs," found in *Boidae* and *Viperidae* snakes, project to the central layers of the contralateral optic tectum via the lateral descending trigeminal tract, thereby providing the snake with cues in guiding orientation towards warm-blood prey[75,80,81]. As observed in rattlesnakes, the upper and lower regions of the infrared fields are mapped onto the medial and lateral tectal areas, with infrared and visual units responding to stimuli in roughly the same spatial region of the tectum. Through tectobulbar projections, the optic tectum has indirect control of spinal cord activity via the brainstem reticular formation[82,83]. In *Iguana*, somatotopic receptive fields responsive to tactile stimulation of the contralateral body surface have been detected in deeper layers of the tectum[76]. These studies found somatosensory receptive fields for the face to be roughly in register with the iguana's visual fields, with the smallest fields corresponding to stimulation of face regions. For somatosensation, the horizontal body axis (head to tail) is oriented along the tectum's lateromedial axis, and the vertical body axis (dorsal to ventral skin surface) is oriented along the tectum's rostrocaudal axis. In light of Stein and Gaither's somatotopic organization found within the contralateral optic tectum, it is evident that the tectum is receiving input via both spinotectal and dorsal column projections, and the crossing of these pathways has been seen in a variety of reptiles[84-86].

As opportunistic, ambush predators, crocodilians are successful in localizing stimuli and rapidly orienting towards prey both in aquatic and terrestrial environments. With specialized epidermal receptors covering either the facial regions or the entire integument as in alligators and crocodiles respectively, it is likely that mechanoreception of water movements contributes to unique sensory processing and thus, their formidable predatory behaviors. However, it remains to be seen how activity from these receptors is represented and how this might vary between different species of crocodiles. Is there a "computational" map, integrating combinations of action potentials from specific receptors thereby guiding orientation[87-90]? Is distance from the stimuli encoded through mechanoreception? Is this map in spatial registration with receptive fields for other sensory modalities? Although impressive bodies of literature exist delineating tectal laminar patterns, cell morphology, and general patterns of tectal efferents and afferents among vertebrates, the behavioral output of these neural circuits are open question amenable to neuroethological strategies.

SUMMARY

Research in neuroethology seeks to determine the neural mechanisms underlying patterns of animal behavior. In adopting a comparative approach, distinct behavioral and physiological mechanisms that have evolved in response to ecological constraints can be identified. As relatives to early tetrapods and having retained similar morphological traits for more than 180 million years, modern crocodilians present a unique opportunity in the study of nervous system organization and evolution. With body surfaces covered by arrays of specialized touch papillae, crocodilians can detect minute movements on the water surface. Investigations into the neural circuitry of these sensations and their influence on crocodilian behavior can yield insight into the evolution and organization of vertebrate nervous systems.

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FURTHER INFORMATION

Kenneth Catania's Lab:
http://www.vanderbilt.edu/exploration/stories/starnosedmole.html