Neuronal Classes in Different Vertebrates

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Abstract: Brain, an essential organ serves to play a pivotal role in the nervous system of all vertebrates and is known to exert centralized control over the other body organs. Brain in all species is primarily composed of two broad classes of cells: neurons and glial cells, where former are usually considered the most important cells. The property that makes neurons unique is their ability to send signals to specific target cells over long distances. The present review showcases the different neuronal classes or types studied in different vertebrates.

Keywords: Brain, Neuronal classes, Vertebrates.

Introduction:
Nervous system and more precisely the brain, has always been point of interest in field of research and investigation. Brain being an essential organ has always fascinated the scientific world towards itself. The six fundamental brain sub-divisions studied are cerebellum, diencephalon, optic tectum, tegmentum, optic tract and telencephalon. It is still quite interesting to establish a phylogenetic sequence of the brain among different vertebrates. Evolution favoured a process of building expansions and additions in cerebral cortex due to their effectiveness for meeting certain fundamental needs. Cerebral cortex, a structure that constitutes the outermost layer of the cerebrum is anatomically divided into neocortex (isocortex) and allocortex. Former is six layered structure and constitutes 95.6% of the cerebral cortex whereas allocortex is divided into paleocortex and archicortex. Archicortex has also been referred as hippocampus (Schwerdtfeger, 1984).

Research on cerebral cortex started back in the eighteenth century, but the early efforts made to study the anatomical organization of the cortex were not successful due to the lack of suitable staining techniques. Later in 1873, Golgi discovered the silver stain; and with the help of it in his first study (1874), he studied the cerebral cortex and spinal cord. By 1883, Golgi described pyramidal and stellate cells and made clear distinctions between axons and dendrites (Golgi, 1883). In the early 1900s, a detailed morphological description was kept forward about the anatomical organization of cerebral cortex (Cajal, 1911). The dedication and scientific approach of Camillo Golgi and Santiago Ramon Y Cajal on their work related to the study of nervous system earned them Nobel Prize in 1906.

Fishes:
Fish's telencephalon has been reported as mainly specialized for olfaction purpose (Herrick, 1924). It has been reported that different sensory modalities in dorsalis telencephali of fishes reach different pallial regions (Yamamoto et al., 2007) such as visual information reaches dorsal pars lateralis mediated by nucleus prethalamicus (Ito and Vanegas, 1983); somatosensory information reaches pars medialis, pars centralis and pars lateralis mediated by ventromedial thalamic nuclei (Ito et al., 1986); and gustatory information reaches mainly pars medialis mediated by preglomerular complex or its homologue. Telencephalon in teleost is made up of two solid hemispheres separated by a T-shaped ventricle (covered with tela choroidea) and it comprises of nuclear masses (Ito and Yamamoto, 2009) indicating that in teleost fishes telencephalic nuclear mass evolved as pallium instead of laminar cortex. Despite the differences in pallial structure between mammals and fishes, afferent, efferent and intrinsic connections of teleost telencephalon are comparable with that of mammalian neocortex (Ito and Yamamoto, 2009). Eversion evolved in embryos of ray-finned fishes because of small telencephalon which could not evaginate rather got narrower in the cranium leading to reduction in the pial surface area on the wall of pallium (Strieder and Northcutt, 2006). Area dorsalis telencephali and area ventralis telencephali in fishes have been considered homologous to pallium and subpallium of other vertebrates, respectively (Alunni et al., 2004; Kage et al., 2004).

Neuronal classes reported in fishes:
Non-laminar cortex in fishes has been studied and it was observed that the neurons in pars centralis show resemblance with those reported in layer V of mammalian cortex. Similarly neurons from pars lateralis and pars medialis resemble with those in layer VI, as both posses short descending fibres running towards the diencephalon (Ito and Yamamoto 2009). Many studies reported the presence of ruffled cells in the olfactory bulb of catfish and sea eel (Kosaka and Hama, 1980); and goldfish (Kosaka and Hama, 1979a, b; 1982-83; Kosaka, 1980). Alonso et al., (1987) applied Golgi-Colonnier (Colonnier, 1964) and Golgi-Meyer (Meyer, 1982) techniques to study neuronal types within the olfactory bulb of freshwater teleosts. They reported relatively large ruffled cells in olfactory bulb of Barbus meridionalis, Carassius carassius, Chondrostoma polylepis, Cyprinus carpio, Tinca tinca and Salmo
gairdneri with generalized pattern with slight qualitative as well as quantitative differences across different species. Characteristically they could be identified by oval to spherical soma with thick, branched, intermingled and varicose ramifications of dendrites. Ruffled cells in fishes could be easily differentiated from other bulbous neurons in fishes by the presence of axon which originated from soma in most of the cases and formed a field with ovoid contour often referred to as ‘the ruff’ (Ito and Yamamoto, 2009).

Amphibia:

 Morphologically brain varies among the vertebrates in terms of sub-divisions, differentiation, presence of distinct nuclei, numbers of different cell types and neuronal connectivity. Morphological organization/complexity of brain in frogs and salamanders have been studied and it has been observed that frogs exhibit more complex morphology within the tectum mesencephali (Roth et al., 1994). Tectum mesencephali has been proposed as the main visual centre in anamnios (Kuhlenbeck, 1975). Roth et al. (1994) opined that the structure of brain arises independent of real demands, the increase in genome size results in simplification of brain morphology. Tectum opticum (Székely and Lázár, 1976), various diencephalic nuclei (Neary and Northcutt, 1983) and torus semicircularis (Potter, 1969) in frogs exhibits alternation of cellular and fibrous layers. In salamanders, compact periventricular gray matter i.e. cellular layers and superficial white matter (fibrous layer) have been reported (Roth et al., 1994). On comparing tectum mesencephali of salamanders with that of frogs it was observed that they exhibited similarities except that tectal cells in former showed juvenile morphology and number of migrated cells was nearly 10 times higher in frogs which points towards the simplification of brain structures due to the phenomenon of paedomorphosis (Roth et al., 1990).

Neuronal classes reported in Amphibians:

The tectum in 11 species of salamanders have been studied with the help of Golgi technique and the study reported three types of neuronal cells namely Type 1, Type 2 and Type 3 (Roth et al., 1990). The classification criteria used for differentiation of tectal neurons were based on position and shape of soma, angle of dendritic ramification with respect to their origination point on the main dendritem and site as well as structure of dendritic tree pattern.

Type 1 neurons had round or oval soma and very broad dendritic tree with angle of dendritic ramification to be around 130-180° that extended within layers 4-5 comprising of efferent fibres. Type 2 appeared to be heterogenous group of neurons with variable soma shape and angle of dendritic ramification whereas Type 3 neurons were narrower and made an angle of 25-60° with fine branches extending almost parallel to tectal surface. Apart from these three types a few migrated neurons were also observed in salamanders with a difference to type 1 neurons that the primary dendrite in migratory neurons were inverted with 180° orienting towards the periventricular cellular layers (Roth et al., 1990).

Székely and Lázár (1976) identified four types of neurons in tectum opticum of frog, Rana esculenta viz., Large and Small piriform cells, Pyramidal cells and Large ganglionic cells. Large piriform cell with round or oval perikary were reported to be prominent in layer 2, 4 and 6; whereas small piriform cells with smaller perikary and fine dendrites were found in layer 8 and 9. Pyramidal cells spotted mainly in layer 6 had pyramidal to oval soma with thick main dendrite diverging into 2-4 secondary branches within layer 7. Except for trigeminal cells in frog, large ganglionic cells were reported to be largest neuronal type with boat shaped or spindle shaped soma, two to several thick dendrites extending towards surface and wide dendritic arborization (Székely and Lázár, 1976; Lázár, 1984).

Reptiles:

Reptiles representing an interesting class of vertebrates exhibit the highest degree of diversification because of being first to inhabit terrestrial lifestyle which led to varied physiological, morphological and behavioral changes imposing its impact on brain. Reptilian brain has been documented by several investigators (Goldby and Gamble, 1957; Northcutt, 1967; Ulinski, 1974; Cruce, 1974; Cruce and Nieuwenhuys, 1974; Prasada and Subedar, 1977; Prasada et al., 1981; Smeets et al., 1986; Dwivedi and Prasada, 1992). Cerebral cortex of reptiles is represented by a laminar structure with grouped neuronal cell bodies forming a principal cell layer sandwiched between inner and outer plexiform layers (Ulinski, 1974; Luis de la Iglesia and Lopez-Garcia, 1997a, b; Lopez-Garcia et al., 2002; Srivastava and Srivastava, 2006; Molnar et al., 2006; Srivastava et al., 2007b). Inner plexiform layer separated from lateral ventricle by a thin layer of ependymal cells is known to retain neurogenic capabilities during the time of adulthood (Lopez Garcia et al., 1988).

Different investigators have proposed the homology between reptilian cortical areas and mammalian brain structures. Some of them are:

a) The dentate gyrus and reptilian medial cortex share homology in many respect as it displays a similar laminar organization and neuronal population (Luis de la Iglesia and Lopez-Garcia, 1997a, b; Berbel et al., 1981; Luis de la Iglesia, et al., 1994; Ramirez-Castillejo, 2002; Maurya and Srivastava, 2006); prominent glutamate and zinc-enriched axonal projection have been observed which are comparable with the hippocampal mossy fibers (Lopez-Garcia and Martinez-Guijarro, 1988) and, the presence of delayed postnatal neurogenesis (Marchioro, 2005).

b) The lateral cortex may be considered homologous to the mammalian olfactory cortex as it also receives majority of projections from the principal olfactory bulb (Ramirez-Castillejo et al., 2002; Martinez-Garcia, 1986; Hoogland and Vermeulen, 1995).
c) The dorsomedial cortex is considered to be homologous to CA3 area of the hippocampus because of its commissural-contralateral projection (Ramirez-Castillejo et al., 2002; Martinez-Guijarro, 1990) and receiving zinc-positive “lizard mossy fibers” from the medial cortex (Martinez-Guijarro et al., 1984).

Goldby and Gamble (1957) presented a detailed description of the reptilian cerebral hemispheres in the lizard, *Lacerta viridis*, where a preliminary survey of the distribution of the perikarya of neurons and topography of the main fiber systems was carried out. Northcutt (1967) studied telencephalon of *I. iguana* and made a comparative study on the forebrain of various species of reptiles. He proposed that the turtles and the mammals belong to the same major line of telencephalic evolution.

**Neuronal classes reported in reptiles:**

Golgi method has been widely used to study the neuronal population of the cerebral cortex of reptiles (Luis de la Iglesia and Lopez-Garcia, 1997a, b; Lopez-Garcia et al., 2002; Srivastava and Srivastava, 2006; Molnar et al., 2006; Srivastava et al., 2007b; Luis de la Iglesia et al., 1994; Ramirez-Castillejo, 2002; Maurya and Srivastava, 2006; Ulinski, 1990; Bernabeu et al., 1994). In reptiles, the pallium has developed into a three-layered cortical structure which is divided into four cytoarchitecture areas: medial, dorsomedial, dorsal and lateral cortices (Luis de la Iglesia and Lopez-Garcia, 1997a, b; Srivastava et al., 2007a; Ulinski, 1990). The studies report different number of the neuronal types in all the four cortical areas within different reptilian species.

Neuronal sub-types reported in lacertilians are: pyramidal (inverted and bipyramidal), multipolar, monotufted, bitufted, stellate neurons, candelabra like monotufted, monotufted monopolar, monotufted bipolar neurons. Neurons are further classified on the basis of the presence or absence of spines as spinous and aspinous respectively. Different methodologies have been applied to reveal the morphology of the neurons and neuropil within the cerebral cortex of reptiles (Ulinski, 1974; Luis de la Iglesia and Lopez-Garcia, 1997a, b; Lopez-Garcia et al., 2002; Srivastava and Srivastava, 2006; Molnar et al., 2006; Srivastava et al., 2007b; Maurya and Srivastava, 2006; Martinez-Guijarro et al., 1984, Ulinski, 1977; Wouterlood, 1981; Srivastava et al., 2009).

Ulinski (1977) reported only one type of neurons from the medial cortex in *Natrix* and *Boa*, five types of neurons have been reported in the lizard *L. pipyonsensis* (Berbel et al., 1987), *P. hispanica* (Luis de la Iglesia and Lopez-Garcia, 1997a) and *M. carinata* (Srivastava, 2007b). Maurya and Srivastava (2006) observed seven types of neurons in *H. flaviviridis*.

In dorsomedial cortex of *A. agama* one type of neurons (Wouterlood, 1981) whereas three types of neurons in each layer of snake’s dorsomedial cortex (Ulinski, 1979) have been reported. Four types of neurons have been reported in the dorsal cortex of lizard *P. algirus* (Guirado et al., 1987), and five types in *M. carinata* (Srivastava, 2007b).

In lateral cortex of snakes, four types of neurons have been reported in all the three layers (Ulinski and Rainey, 1980), whereas only three types in the *M. carinata* (Srivastava, 2007) and four types *H. flaviviridis* (Srivastava and Maurya, 2009) were observed.

Differences in neuronal distribution among reptilian brain have led to selection of reptiles as an important model system for studying the organization of brain of lower and higher vertebrates. Since, there exists a wide variation in the composition of different parts of brain in different reptilian orders and also among various species of lizards due to behavioral and environmental factors.

Spinous bipyramidal neurons have been reported to be the main neuronal type found in dorsomedial cerebral cortex of the lizards *Agama agama* (Wouterlood, 1981), *Lacerta* (Berbel, 1988) and snakes (Ulinski, 1979). The soma of these spinous bipolar neurons formed the granular layer whereas their dendrites extended into the outer and inner plexiform layers (Ulinski, 1979; Wouterlood, 1981; Garcia Verdugo et al., 1983; Martinez-Guijarro et al., 1984, Berbel, 1988).

Srivastava et al., (2009) reported six types of projection neurons within the dorsomedial cortex of *H. flaviviridis* namely: bitufted, pyramidal, inverted pyramidal, bipyramidal, multipolar and candelabra like monotufted neuron. The dendrites of these neurons were entirely covered with spines and their thickness extended throughout the cortex thereby representing intra-cortical connections. The projections of these neurons showed resemblance to the two systems reported in *Gecko* with one arising from the dorsal part of the medial cortex and terminating on the proximal parts of the apical and basal dendrites whereas the second system originating in the ventral part of medial cortex and ending mainly on the more distal parts of both the apical and basal dendrites of the dorsomedial cortex neurons (Bruce and Butler, 1984; Hoogland and Vermeulen-Van, 1993).

The difference noticed in the neuronal types across the reptilian species may be due to the technique used: Golgi procedure which may impregnate neuronal types at random and number of experiments may also have its effect. On the other hand the dendritic morphology may also be affected by the location of neurons. And most importantly, certain difference in the neuronal types between the different species can be attributed to considerable variation in behavioral patterns between them.

**Birds:**

Hippocampus (Hippocampal complex)/Dorsomedial forebrain of birds is a strip of tissue lying on dorsomedial surface of avian telencephalon. It is separated from rest of the hemisphere by a lateral ventricle (Montagnese et al., 1996; Tömböl et al., 2000). Hippocampal complex can be
subdivided into a dorsal parahippocampal area and a ventral hippocampus, and is widest dorsally at the junction with the parahippocampal area and it tapers ventrally with the septum (Montagnese et al., 1996; Tömölő et al., 2000; Srivastava et al., 2007a; 2012). On the basis of the presence of different neuronal types, it has been divided into five different fields: medial (HCM) and lateral (HCL) hippocampus, parahippocampal area (APH), central field of parahippocampus (PHC) and crescent field (CF) (Srivastava et al., 2007a; 2012; Singh et al., 2015). According to phylogenetic development study, hippocampus developed from a simple cortical plate in amphibians into complex three dimensional convoluted structures in mammals (Srivastava et al., 2011). The region adjacent to hippocampus is referred to as corticoid complex (CC), which occupies the dorsolateral surface of telencephalic pallium in Taeniopygia guttata (Montagnese et al., 1996) and Estrilda amandava (Srivastava et al., 2007a). Corticoid complex is divided into two subfields: an intermediate corticoid area (CD) and a dorsolateral corticoid area (CDL). Hippocampus in birds have been reported to be involved in learning (Bingman and Able, 2002; Vargas et al., 2004), memory and foodstoring behavior (Hampton and Shettleworth, 1996; Volman et al., 1997), spatial cognition (Bingman et al., 2003; Jacobs, 2003; Bingman et al., 2005), spatial navigation (Tömölő et al., 2000; El Falougy and Benuska, 2006), and sexual behavior (Atoji and Wild, 2006).

Hippocampus plasticity in birds have been studied in respect with various kinds of sensory inputs like experience (learning) and hormonal influences (Cramer, 1988; Clayton and Krebs, 1994); migration (Healy et al., 1996) and navigational experience in homing pigeons (Cnotka et al., 2008) which led to enlargement of hippocampus. Previous studies show that the hippocampus is proportionally larger in food storing birds than in non-storing birds (Krebs et al., 1989; Sherry et al., 1989) since; food-storing birds need to perform better than non-storing birds, which in turn is dependent on the hippocampal functioning (Krebs, 1990; Shettleworth et al., 1995).

Avian brain plasticity is also proposed to be controlled by photoperiod, and such variations in the day length are sufficient to induce male and female birds into breeding stage (Smulders et al., 1995). They reported that hippocampus varies across the season with increase in level of about 40% during October in Black-capped Chickadees, which was correlated with increase in demand/use of the hippocampus to relocate the stored food. Seasonal variation in food-storing birds is accompanied by seasonal recruitment of new neurons within the hippocampus, which results in an increase in hippocampal volume (Barnea and Nottebohm, 1991; Smulders et al., 2000; Hosshooley and Sherry, 2004). Brood parasitic nature of birds has been also reported to be related to the hippocampus (Sherry et al., 1993; Rebecorda et al., 1996; Singh et al., 2015). Singh and Srivastava (2013) reported significant increase in neuronal spacing within the hippocampus of the Psittacula krameri during the breeding period of the bird and related it with an increase in the dendritic field of neurons providing long-range connections during the breeding period. Oscillations in neuronal size and spacing within area of the avian song control system in wild adult male Song Sparrows (Melospiza melodia) have also been explored (Thompson and Brenowitz, 2005). De Groof et al., (2009) reported decrease in volume of the telencephalon in Starlings (Sturnus vulgaris L., 1758) between breeding and nonbreeding conditions. Srivastava et al. (2012), Srivastava and Singh (2012) and Singh et al. (2015) in their study on avian hippocampus observed seasonal variations in the parameters of neurons (dendritic thickness, spine density and spine morphology) across the season. They reported increase in the neuronal parameters during breeding time of bird suggesting that changes in season not only affects the volume of hippocampus but leaves it’s impact over the neuronal classes. Similarly in 2013, Srivastava and Gaur reported neuronal plasticity in the visual wulst of male Baya Weavers (Ploceus philippinus (L., 1766)) during the breeding and non-breeding periods and reported increase in dendritic thickness, spine density, and morphology in breeding birds.

**Neuronal classes reported in birds**

On the basis of Golgi study, the neurons of hippocampus of birds have been classified into two main groups. The predominant cell types were projection neurons with spinous dendrites and local circuit neurons having sparsely spinous and aspinous dendrites. In HCM area pyramidal, multipolar, bitufted, monufotted; in PHC and CF region multipolar neurons have been observed. The neurons of the corticoid complex are classified into three main cell groups: predominant projection neurons, local circuit neurons and stellate neurons. These neurons are sub classified into pyramidal neurons (located only in CI) and multipolar neurons (located both in CI and CDL). The stellate neurons of the CI have a small round or ovoid cell body that extends 4–6 long thin dendrites. The spines on the dendrites are moderately distributed. The axon of these neurons originates either from cell body or from a dendrite, and ramifies locally. The above mentioned neuronal types and their projections have been completely described in strawberry finch, Estrilda amandava by Srivastava et al. (2007a).

Golgi-impregnation method has been employed by different workers to study the neuronal types in the wulst of different bird species. In Japanese quail (Coturnix coturnix japonica), Watanabe et al. (1983) observed that most of the neurons present in wulst were stellate which have been observed in the HA of zebra finch (Montagnese et al., 1996). Tömölő and Maglóczky (1990) reported four types of projection neurons in chicken on the basis of dendritic tree and spine density. Tömölő (1995) reported projection neurons, interneurons and stellate neurons within the chicken wulst observed throughout the laminae of the wulst. Chand (2009) on the basis of soma shape, dendritic...
ramification and distribution of spines on dendrite classified neurons into four main cell types: projection neurons, local circuit neurons, stellate neurons, and granule cells in *Estrilda amandava*.

Srivastava *et al.* (2012) reported four types of neurons (Multipolar, Pyramidal and Bipolar neurons) in the parahippocampal area of female *E. scolopacea* during breeding phase whereas only three types of neurons (Multipolar, Pyramidal and Bipolar neurons) were spotted during non-breeding cycle of bird. Seasonal variations in neuronal classes of hippocampus in birds have been also reported with the help of Golgi-Colonnier and Nissl staining techniques (Srivastava *et al.*, 2012; Srivastava and Singh, 2012; Singh and Srivastava, 2013; Singh *et al.*, 2015). The studies proposed significant increase in dendritic thickness, spine density, spine head diameter, spine neck length and neuronal spacing during breeding time of the bird.

**Mammals:**

Ever since the first mammals appeared more than 200 million years ago, the cerebral cortex has assumed greater and greater importance compared with the brain’s other, older structures. Mammalian telencephalon comprises of a six-layered pallium or neocortex or isocortex which differs from the three-layered telencephalic laminar structures such as the hippocampal formation, olfactory and the reptilian cortices (Super *et al.*, 1998). Mammalian telencephalon has undergone an enormous expansion in the tangential domain (Rakic, 1988).

The neocortex is divided into frontal, parietal, occipital, and temporal lobes, which perform different functions. Occipital lobe contains the primary visual cortex whereas the temporal lobe contains the primary auditory cortex. In humans, frontal lobe comprises of areas that devoted to abilities such as complex language processing localized to the ventro-lateral prefrontal cortex and known as Broca’s area (Noback *et al.*, 2005) while the temporal lobe is associated with perception and recognition of auditory stimuli, memory, and speech. The mammalian cortex plays a pivotal role in sleep, memory and learning processes. Not only the morphological feature of neurons, but the spines present on the dendrites of the neurons have also been studied and it was noticed that they also differ in different cortical layers as well as among the species. Interlaminar variations in spine density of pyramidal neurons have been reported in parietal region of bat (Srivastava and Pathak, 2010); parietal region in squirrel (Srivastava and Srivastava, 2011) and within all the four regions and different layers of mongoose isocortex (Srivastava *et al.*, 2013) and distribution of non-pyramidal neurons within the frontal lobe of mongoose (Singh *et al.*, 2016).

Morphological features of pyramidal neurons have been studied in layer V of rat neocortex (Chagnac-Amitai *et al.*, 1990). Several other studies reported, cell type in auditory cortex of mustached bat (Fitzpatrick and Henson, 1994); dendritogenesis in pyramidal cell of ferret (Zervas and Walkley, 1999); variation in dendritic arborization of pyramidal neurons within the visual areas of marmoset monkeys (Elston *et al.*, 1999); and pyramidal cell morphology in cortex of owl monkey (Elston, 2003); neuroarchitectural and auditory cortex in horseshoe bat (Radtke-Schuller, 2001); neuronal distribution in the isocortex of echidna (Hassiottis and Ashwell, 2003); morphological variations in pyramidal neurons within parietal lobe of mongoose (Srivastava and Chauhan, 2010); heterogeneity of pyramidal neurons’ spine density within the isocortex of mongoose (Srivastava *et al.*, 2013) and distribution of non-pyramidal neurons within the frontal lobe of mongoose (Singh *et al.*, 2016).

Neuronal distribution within mammalian cortex exhibits a differential distribution among different cortical layers and regions and even among species (Hof *et al.*, 1999) as reported in mustached bat auditory cortex, where the distribution of cell types and laminar arrangement were different from those observed in primary sensory cortex of other species (Fitzpatrick and Henson, 1994). Similarly, dendritic tree pattern of pyramidal neurons present in layer II/III within secondary somatosensory, lateral secondary motor, lateral secondary visual and association temporal cortex was observed to significantly differ in characteristics within rat (Benavides-Piccione *et al.*, 2006).

The study of neuronal classes in fishes, amphibians, reptiles, ammals and mammals highlights following points:

1. With evolution of brain from fishes to mammals, the evolution/modification of neurons also took place.
2. The diversity of neuronal classes increased in reptiles, birds and mammals in comparison to fishes and amphibians.
3. These modifications in higher vertebrates may be attributed to complex brain activity in them, leading to modification and diversification of neurons.

References


