Evolution, Homology, Cell Classification, and Parallel Processing for Vision FREE

W. Martin Usrey, Professor and Chair of Neurobiology, Physiology and Behavior, University of California, Davis and S. Murray Sherman, University of Chicago

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Summary

A first step in analyzing complex systems is a classification of component elements. This applies to retinal organization as well as to other circuit components in the visual system. There is great variety in the types of retinal ganglion cells and the targets of their axonal projections. Thus, a prerequisite to any deep understanding of the early visual system is developing a proper classification of its elements. How many distinct classes of retinal ganglion cells are there? Can the main classes be broken down into subclasses? What sort of functional correlates can be established for each class? Can homologous relationships between apparently similar classes between species be established? Can a common nomenclature based on homologous cell and circuit classes be developed?

Keywords: vision, thalamus, retina, retinal ganglion cell, lateral geniculate nucleus, cat, monkey

Subjects: Sensory Systems

Dedication

We dedicate this article to the memory of Vivien Casagrande, a great friend and colleague and a pioneer on the very subject of this article: parallel pathways and their homology among mammals.

Introduction

Understanding of the functional organization of the visual system has benefited tremendously from research examining a diversity of species. Taken together, these studies reveal an amazing scope of strategies used by the visual system to take in and process information under a variety of environmental conditions. They also provide important information about conserved and core aspects of vision that are maintained across species. For mammals, the pathway from retina to thalamus to cortex is essential for conscious vision. This pathway is further organized into parallel processing streams that involve distinct classes of retinal ganglion cells that differ in their morphological and functional properties and, together, broaden the range of signals sent to cortex. This article explores the concepts of homology and analogy in the context of evolution and applies these concepts to current understanding of parallel processing streams in the retino-geniculo-cortical pathway in different mammalian model organisms.

Homology Versus Analogy

Endeavors to identify and compare common organizational features between species usually involve one of two approaches: homology or analogy. *Homology* refers to features believed to be similar in related species due to their inheritance from a common ancestral species. The arms and hands of humans, the wings of birds and bats, and the flippers of whales are examples of homologous structures (Figure 1). Although they are closely related in evolutionary terms and occupy similar locations on the body, they look quite different and have very different functions: grasping versus flying versus swimming. In contrast, *analogy* refers to features that evolved to perform a similar function even though they are not closely related to each other in evolutionary terms. The fins of fishes and the flippers of whales are an example of an analogous structure (see Figure 1). These structures did not emerge from a recent common ancestor, although they did evolve for a similar purpose—swimming—from different structures in more distantly related species. Analogous features are often referred to as products of convergent evolution.

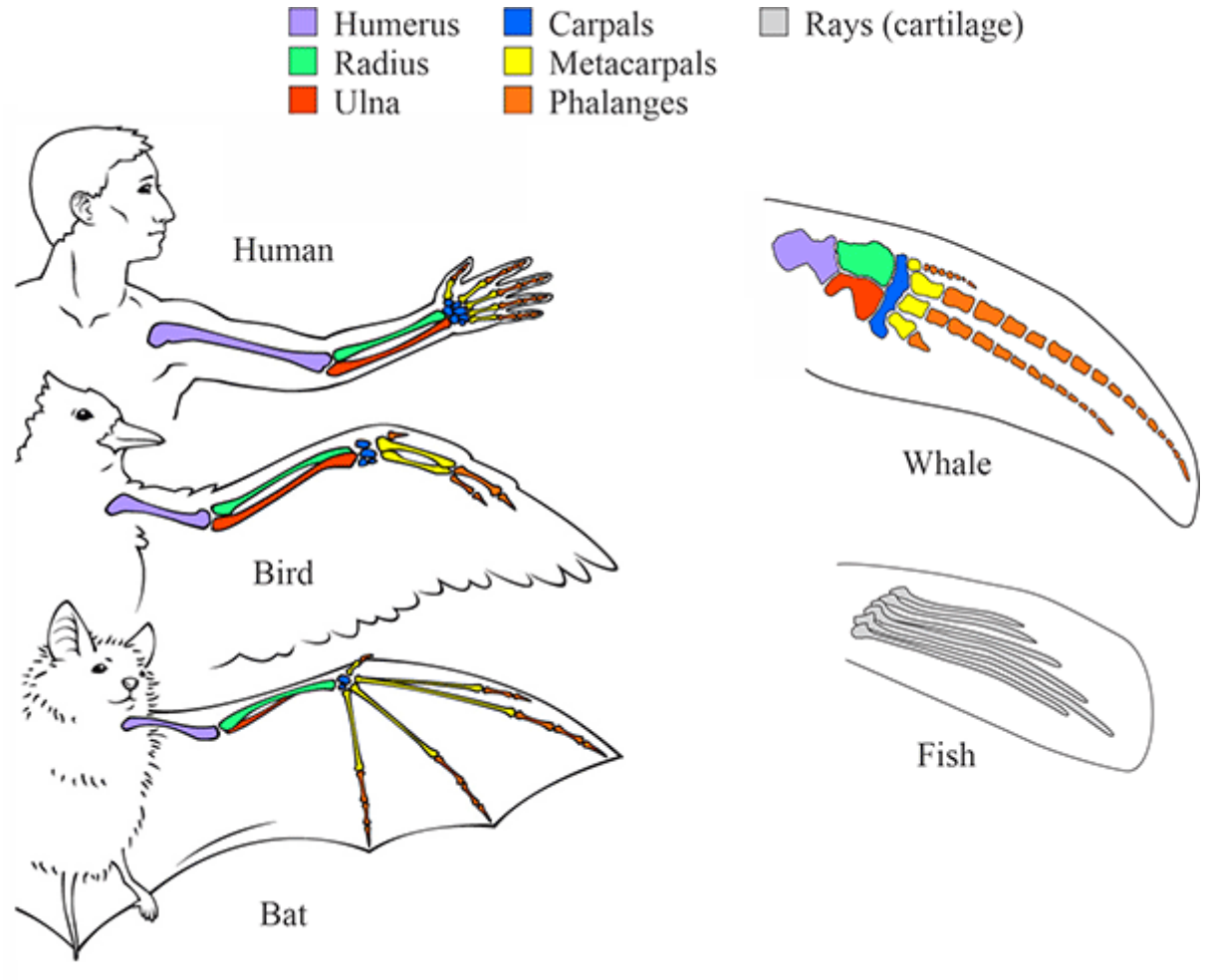

Figure 1. The organization of bones in the human arm, bird wing, bat wing, and whale. Although these appendages are used for very different purposes, the tremendous similarity in their organization indicates they are homologous structures. Also shown is the fin of a fish. Although it serves the same function as the whale flipper, its cartilaginous structure shows little resemblance to the bone structure of the whale flipper. Consequently, these structures are considered analogous, rather than homologous.

Source: Adapted from Arizona State University, "Human, Bird, and Bat Bone Comparison <*https://askabiologist.asu.edu/human-bird-and-bat-bone-comparison*>."

It is important to understand the distinction between homology and analogy because establishing homologous features between species is the "gold standard" for providing meaningful insight into core relationships between biological structures. Establishing homologous relationships for parallel streams of visual processing across mammalian species is therefore key for understanding the underlying mammalian design.

For structures such as bones and teeth, the fossil record can be quite useful in establishing homologies. Unfortunately, soft tissues such as brains do not fossilize, and so the fossil record provides limited information for neuroscientists attempting to establish homologies. As a consequence, there has been much controversy and too little certainty in homologies that have been suggested. Thus, the following discussion should be regarded with healthy skepticism.

Homology of Thalamic Nuclei

Early anatomists were eager to name brain structures, and most thalamic nuclei were named in multiple mammalian species by the late 19th and early 20th centuries. Many of these anatomists were aware of the general principle of homology and used neuroanatomical criteria, such as location within the thalamus and connectivity, to identify homologous structures in different species. Accordingly, the lateral geniculate nucleus was identified in many species as a homologous structure based on its location within the thalamus, its innervation by the retina, and its innervation of posterior cortical areas identified as visual. The homology identified and terminology given by the early anatomists are generally accepted because it is believed that they mostly got things correct. Examples are the main sensory thalamic relays (e.g., the lateral geniculate nucleus for vision, the medial geniculate nucleus for audition, and the ventral posterior nuclei for somatosensation), the main motor thalamic relays (e.g., the ventral anterior and posterior complex), and the medial dorsal nucleus.

There are also examples in which the naming accuracy is open to question, and the terminology used should be reconsidered. For instance, the pulvinar is generally recognized as present in most mammals but, curiously, not in rodents. The pulvinar is the largest visual thalamic relay (much larger than the lateral geniculate nucleus). Consequently, its "absence" in rodents has been used as an argument to support views that mice are a poor model to study vision. With that in mind, rodents, including mice, do have a thalamic relay, the lateral posterior nucleus, named as such by early neuroanatomists. Important for this discussion, recent evidence of connectivity makes a

convincing case that the lateral posterior nucleus is indeed homologous to the pulvinar seen in other mammals (Zhou et al., 2017); thus, rodents do not appear to be an exception to the general mammalian plan in this respect.

The posterior medial nucleus is another example of a naming problem. It is located near the ventral posterior nucleus in rodents and carnivores, but its identity in primates is unclear. Primates do have a thalamic structure called the posterior nuclear complex that includes a medial region, but this region does not appear to have the same relationship to the ventral posterior nucleus that is seen in other mammalian species. Instead, a better candidate for homology with other species may be the anterior region of the primate pulvinar (Harting et al., 1972; Jones et al., 1979; Pons & Kaas, 1985). In this example, the putative naming problem has part of a thalamic structure, the pulvinar, normally associated with vision that in terms of function is really more properly associated with somatosensation.

It is noteworthy that the two examples described previously for possible misidentification regarding homology, the pulvinar and posterior medial nucleus, are higher order relays that appear to play an important role in cortico-thalamo-cortical communication rather than relaying peripheral sensory signals to cortex. The early neuroanatomists got the nomenclature correct for the first-order sensory relays because they understood what inputs were being relayed (e.g., the retina for the lateral geniculate nucleus). However, the source of the main input to be relayed for higher order relays, namely signals from layer 5 of cortex, was not understood and appreciated until relatively recently. Without this knowledge, it is understandable that misguided homologous relationships were created. Moreover, it seems likely that there may be other examples of improperly named thalamic nuclei (and implied homologies), particularly among the higher order nuclei. A reconsideration of terminology for thalamic nuclei based on the current understanding of relevant data would therefore be of great benefit to the understanding of homologous structures in the thalamus and the determination of common core structures in the mammalian plan. Similar terminological issues regarding the avian brain were addressed by a group of experts that convened to form a new consensus on the topic (Ebert, 2005; Reiner et al., 2004), and perhaps a similar strategy is needed for naming of thalamic nuclei of mammals.

Criteria for Establishing Homology Among Cell Types

Key questions to ask when comparing cell types are What parameters should be used for establishing homology? How do these rank in terms of usefulness to identify homology? For a visual neuron in two species, there are several parameters to consider, including receptive field properties, internal membrane properties, somadendritic morphological features, connections with other structures, neurotransmitters, molecular markers, etc.

Answers to these questions are far from clear, but a consideration of the process of evolution provides some limited guidance. Genetic mutations and natural selection underlie the process of evolution. Genetic mutations are random and occur all the time, with some helping an animal line survive and others hindering survival. With time, the function of a structure in a “parent” organism can change as new closely related “offspring” organisms arise. A homologous structure

in closely related species might, therefore, have quite different functions, as with the hands of humans and the wings of birds and bats. This suggests that searching for functional criteria to establish homology might be misleading, as with the fins of fish and flippers of whales.

Given possible concerns about using functional criteria for assessing homology, which criteria are better? Although there is not a definitive answer to this question, if the example of hands, wings, and flippers is again considered, the similarity between them in terms of underlying structure is striking. Likewise, the basic structure of neurons and their connections may be a more useful parameter to evaluate for potential homology between cell types compared to functional attributes (Krahe et al., 2011). Molecular markers may also be less susceptible to evolutionary changes, and even if such changes occur, if they are small, they may still be identified by the same antibodies and therefore be useful candidates for assessing homologous cell types in the brain (Felch & Van Hooser, 2012; Piscopo et al., 2013).

Most previous studies of vision and visual processing were not conducted in an effort to understand evolution and, consequently, just a few animal models have been the focus of scientific attention. Arguably, most is known about visual processing in the cat, mainly because of historical reasons: Sherrington's (1906) influential work focused on the cat, making that animal a major model for neuroscience research for the ensuing decades. Also, there were practical and scientific reasons for studying the cat: their availability; ease of care; tolerance for numerous experimental protocols; and features they share with primates, such as forward-facing eyes and heavy reliance on vision. Monkeys have also been popular models for studies of vision for the obvious reason that they are closely related to humans. In the following sections, fundamental properties of the retino-geniculo-cortical pathway are presented for cats and monkeys. These properties are then assessed in an effort to understand homology between cell types in the two species, as well as to provide guidance for determining homology with other animal models, including rodents, which are more closely related to primates than cats and are increasingly being used for studies examining the neural mechanisms for vision.

Cell Classification and Parallel Processing in the Cat

Retinal ganglion cells are the only cells in the retina with axons that leave the eye to send visual signals to the brain. In cats, most retinal ganglion cells have receptive fields with a stereotypical center–surround organization, a feature first described by Stephen Kuffler (Kuffler, 1952, 1953) and later reported in essentially every mammalian species examined. Kuffler described two types of cells. The first type, "on-center cells," are maximally excited by small spots of light surrounded by darkness, whereas the second type, "off-center cells," are maximally excited by small spots of darkness surround by light (Figure 2). These two cell types tile the retina, indicating there are at least two complete, but different, representations of the visual world that travel together (i.e., "in parallel") in the axons that leave the eye to innervate the rest of the brain. Following Kuffler's report, the idea of separate and complete representations of visual space expanded rapidly as other investigators identified additional cell types within the on-center and off-center categories. For instance, Enroth-Cugell and Robson (1966) provided compelling evidence that within both the on-center and off-cent classes of retinal ganglion cells,

there are two additional cell categories: X and Y (also known as tonic/sustained and phasic/transient cells). These two cell types differed in how they summated their excitatory and inhibitory inputs. The visual responses of X cells could be described by simple summation of their inputs, referred to as linear summation, whereas the responses of Y cells were more complex and included response components that showed nonlinear summation. Although this distinction may seem somewhat abstract, the X and Y cells identified by means of their summation properties were later found to be distinct from each other in several other respects. Compared to retinal Y cells (also called alpha cells), the X cells (also called beta cells) have smaller dendritic fields, smaller receptive fields, longer visual response latencies, slower axonal conduction velocities, respond in a sustained fashion to stationary stimuli, and prefer stimuli with lower temporal and higher spatial frequencies (Table 1; reviewed in Lennie, 1980; Sherman, 1985; Sherman & Guillery, 2006; Sherman & Spear, 1982; Stone, 1983; Usrey & Alitto, 2015). These cell types also differ in their central projections as described later. It is worth noting that many of the attributes that distinguish the X and Y cell types in the cat retina also distinguish cell types in other sensory modalities. For instance, differences in cell morphology, receptive field size, sustained versus transient responses, and preferences for stimulus temporal frequency (flutter vs. vibration) are used to identify and distinguish tactile receptors in the skin (e.g., Pacinian corpuscles, Meissner corpuscles, Ruffini endings, and Merkle discs) and their postsynaptic targets in the ventral posterior nucleus.

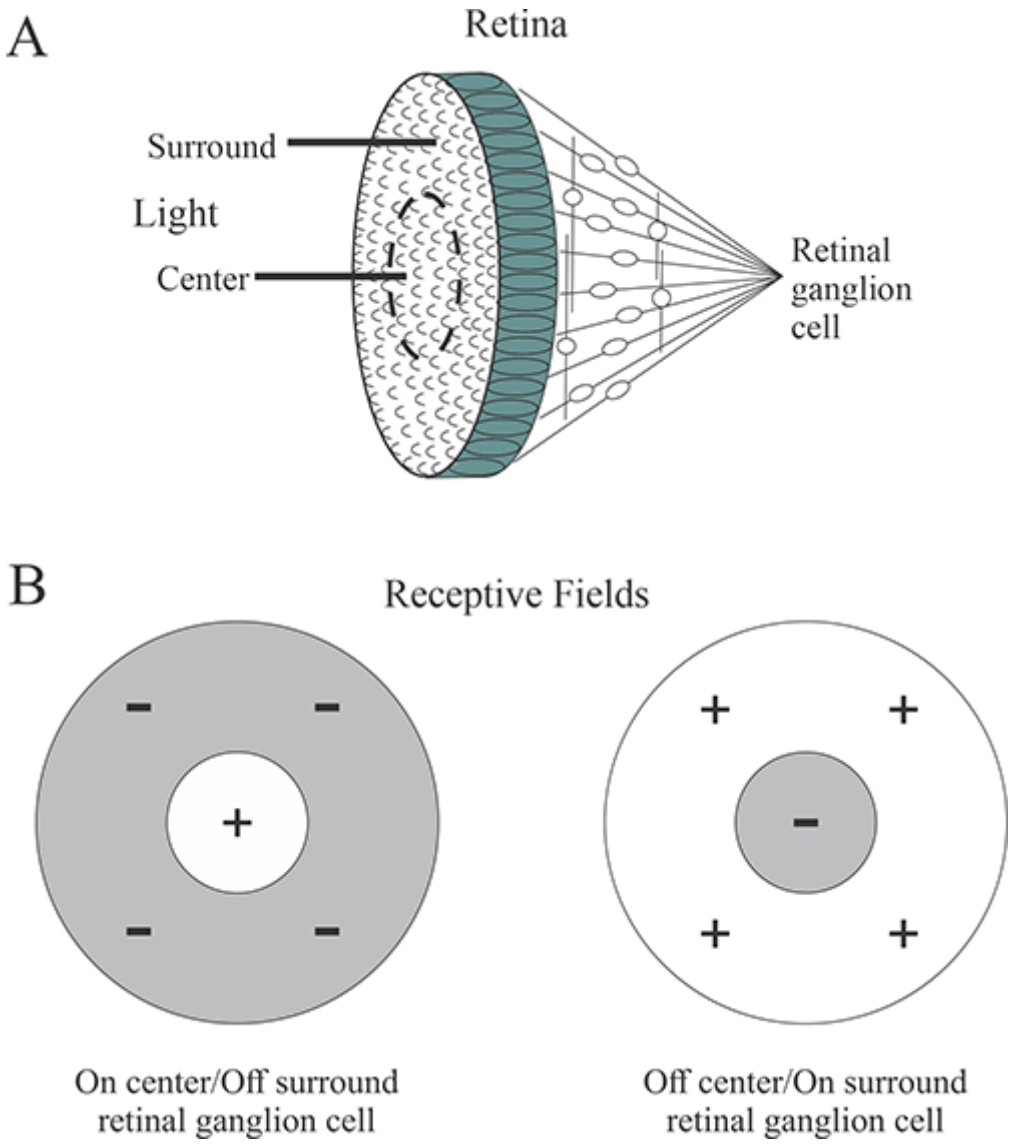

Figure 2. The circuitry in the retinal establishes two major classes of retinal ganglion cells—those with on-center/off-surround receptive fields and others with off-center/on-surround receptive fields. (A) Schematic diagram illustrating the field of photoreceptors that supply the center and surround of retinal ganglion cell receptive fields, shown in B.

Table 1. Comparison of the Morphological and Physiological Properties of X and Y Cells in the Cat and Their Relationship to the Parvocellular and Magnocellular Neurons in the Monkey

Property	X cells (Cat) Parvo cells (monkey)	Y cells (Cat) Magno cells (Monkey)
Center/surround organization	Yes	Yes
Cell/receptive field size	Smaller	Larger
Spatial summation	Linear	Y cells—nonlinear

Property	X cells (Cat) Parvo cells (monkey)	Y cells (Cat) Magno cells (Monkey)
		Magno cells—linear*
Response time course	Sustained	Transient
Axonal velocity	Slower	Faster
Axon diameter	Smaller	Larger
Response latency	Longer	Shorter
Sensitivity to low-contrast stimuli	Poor	Very good
Sensitivity to fast-moving stimuli	Poor	Very good
Laminar input to VI	Lower layer 4—cat Lower layer 4C—monkey	Upper layer 4—cat Upper layer 4C—monkey
Chromatic organization of receptive field	Broadband—cat Color opponent (red/green)—monkey*	Broadband—cat Broadband—monkey

Note: With just a few exceptions, indicated with asterisks, X cells are similar to parvocellular neurons and Y cells are similar to magnocellular neurons. Not included in the table are the W cells (cat) and koniocellular neurons (monkey), each of which has a diversity of cell types.

In addition to the X and Y cells in the cat retina, there is a third group of cells, the W cells (also called gamma cells). Initially, retinal ganglion cells were placed into this group when their anatomy and physiology did not fit neatly within the X and Y cell categories. With further studies, it is now recognized that W cells, as a group, are made up of several unique cell classes, with each class believed to form a complete mosaic across the retina. Compared to the X and Y cells, however, much less is known about W cells, except that some have center/surround receptive fields, like X and Y cells; others have overlapping on- and off-responses within their receptive fields and/or direction selectivity; and some have chromatic selectivity for blue versus yellow, a property not present in X or Y cells in the cat and one that depends on the organization of the two types of cone photoreceptors—short- and medium-wavelength cones—that establish their receptive fields.

Relay cells in the lateral geniculate nucleus receive direct input from retinal ganglion cells and have axons that innervate neurons mostly in primary visual cortex, thus playing an essential role in conveying visual information from retina to cortex. Similar to the retina, there are three broad categories of relay cells in the cat lateral geniculate nucleus—X cells, Y cells, and W cells (note that the alpha, beta, and gamma nomenclature is not used outside of the retina)—that differ in their morphology (Figure 3) and, as might be expected, these cell classes receive input fairly

exclusively from their respective retinal counterparts (Cleland et al., 1971; Hamos et al., 1987; Usrey et al., 1999). As with retinal X cells, geniculate X cells come in two types, on-center and off-center, and both have linear center–surround receptive fields (Stone, 1983). Geniculate X cells are somewhat distinct from their retinal inputs; however, because they are generally not as linear in their responses, they often display a degree of contrast gain control (i.e., response amplification for low-contrast stimuli and response saturation for high-contrast stimuli), and they have somewhat stronger extraclassical suppression (i.e., suppressed responses for stimuli that extend beyond the classical receptive field) (Alitto & Usrey, 2004; Jones et al., 2000). Likewise, geniculate Y cells in the cat have responses closely resembling their retinal inputs but also demonstrate stronger contrast gain control and more robust extraclassical suppression (Alitto et al., 2019; Fisher et al., 2017). Similar to their sources of input from the retina, the receptive fields of geniculate Y cells are larger than those of their X cell counterparts at similar eccentricities (Linsenmeier et al., 1982; Usrey et al., 1999). Also, compared to geniculate X cells, Y cells also have shorter visual response latencies, faster conducting axons, more transient responses to visual stimuli, and prefer lower spatial frequencies and higher temporal frequencies (see Table 1; Cleland et al., 1971; Fukada, 1971; Hoffmann et al., 1972; Ikeda & Wright, 1972; Usrey et al., 1999). As with the retina, less is known about W cells in the cat lateral geniculate nucleus, except that there is diversity in the cell types classified as W cells; also, as in the retina, geniculate W cells tend to have larger receptive fields and longer response latencies than either the X or Y cell types, and some have chromatic (blue vs. yellow) selectivity (Wilson et al., 1976).

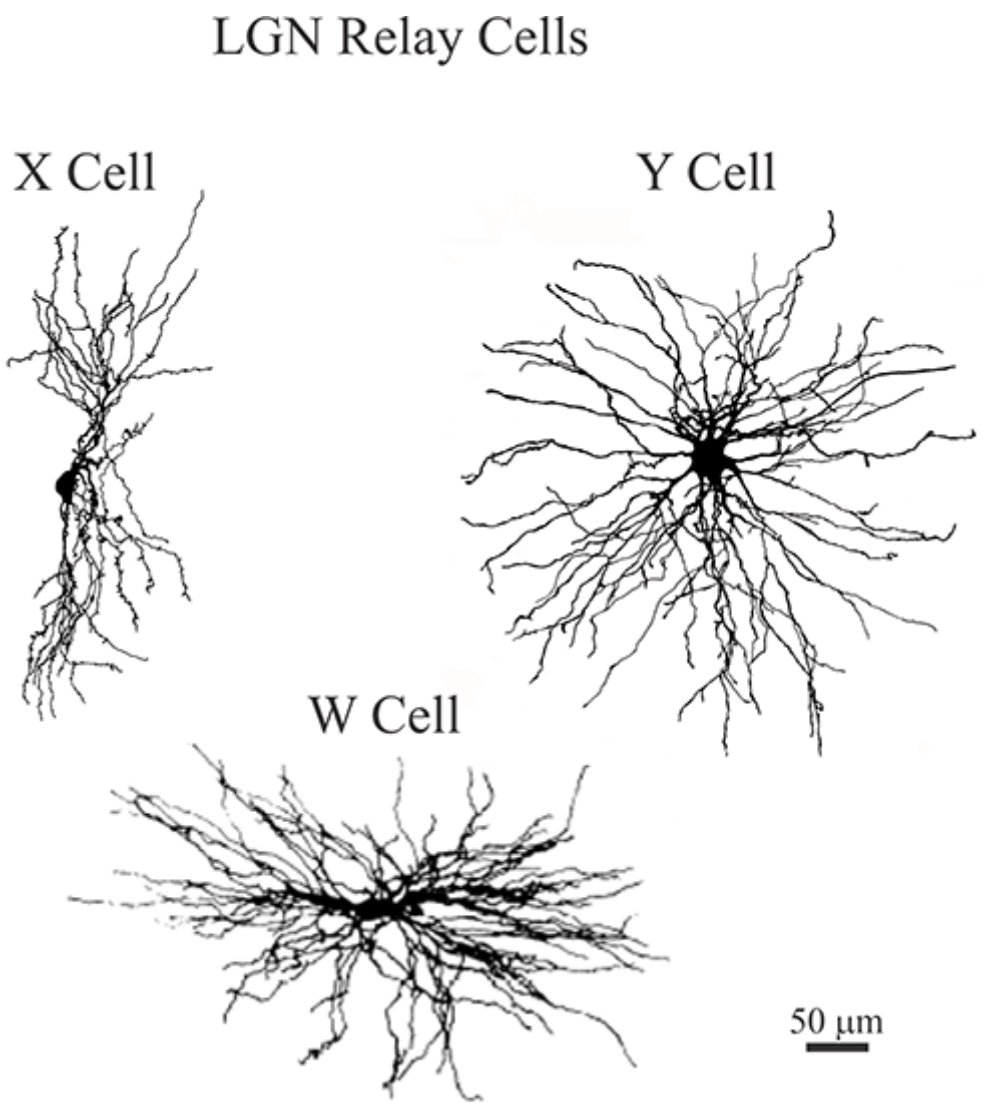

Figure 3. Cell types in the cat's lateral geniculate nucleus (LGN). Camera lucida reconstructions of three geniculate neurons (X, Y, and W types) labeled with intracellular injection of horseradish peroxidase. Each cell type receives input from a different class of retinal ganglion cells, and each projects to distinct laminar targets in primary visual cortex. Typical of these cell types, the dendritic arbor of the X cell is tufted and is oriented perpendicular to the plane of the layers, the W cell arbor is oriented parallel to the layers, whereas the arbor of the Y cell is more spherical.

Sources: Data from Friedlander et al. (1981); Hamos et al. (1985); Stanford et al. (1981, 1983); and Uhlrich et al. (1991).

The X, Y, and W relay cells all project to primary visual cortex, and their projections suggest there is both stream mixing and stream segregation in the geniculocortical pathway (Alonso et al., 1996, 2001). In particular, although the axons of geniculate Y cells arborize in the upper half of layer 4, whereas the axons of geniculate X cells arborize in the lower half of layer 4 (Figure 4), the dendrites of some layer 4 neurons span both the upper and lower divisions of layer 4 (Hirsch et al., 1998), providing a possible substrate for stream mixing. In contrast, the axons of geniculate W cells pass through layer 4 and arborize more superficially in layers 1–3 (see Figure 4).

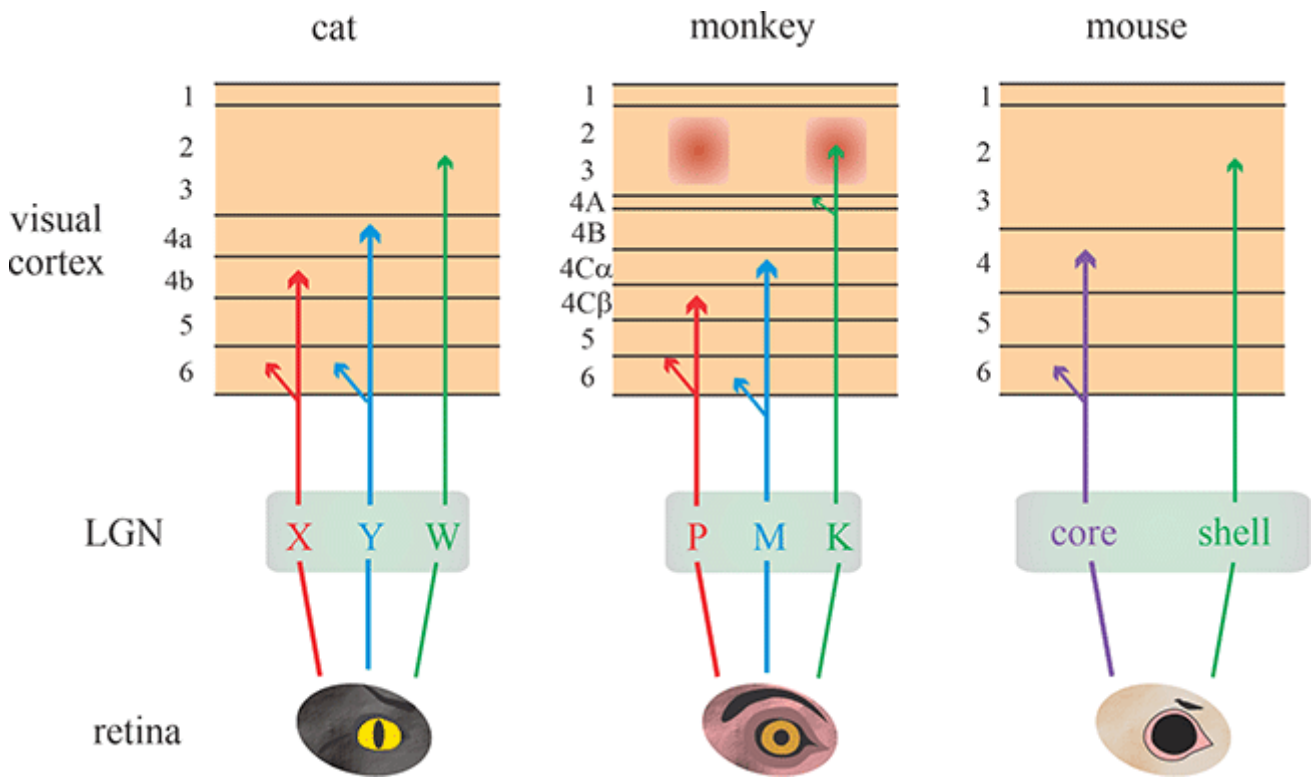

Figure 4. Diagram illustrating the organization of the retino-geniculo-cortical pathway in the cat, monkey, and mouse. In the cat, there are three major parallel pathways to cortex: the X-cell pathway terminates primarily in layer 4b, the Y-cell pathway terminates primarily in layer 4a, and the W-cell pathway terminates in layers 1–3. There are also three parallel pathways in the primate: the parvocellular (P) pathway terminates in layer 4Cα, the magnocellular (M) pathway terminates in layer 4Cβ, and the koniocellular (K) pathway terminates in the layer 1–3 blobs. In mice, the lateral geniculate nucleus (LGN) is divided into core and shell regions. Relay cells in the core project primarily to cortical layer 4, whereas relay cells in the shell project primarily to the overlying superficial layers.

Source: Adapted from Rathbun & Usrey (2009).

Cell Classification and Parallel Processing in the Monkey

Similar to the cat retina, the monkey retina contains a rich diversity of retinal ganglion cell types that differ in their anatomy and physiology. This diversity is perhaps better understood in the monkey, compared to the cat, with results from several studies collectively providing a fairly complete catalog of the cell types in the macaque retina, where approximately 20 cell classes comprise an estimated 96.5% of all retinal ganglion cells (Table 2; Crook, Packer, & Dacey, 2014; Crook, Packer, Troy, et al., 2014; Crook et al., 2009; Dacey, 1999, 2000, 1993; Dacey & Lee, 1994; Dacey et al., 2003; Martin et al., 2001; Masland, 2011, 2012; Wässle, 2004; Wässle et al., 1989; Watanabe & Rodieck, 1989). Many of these cell classes project to the lateral geniculate nucleus and therefore are the source of parallel streams of information to cortex. Among these, the on- and off-center midget ganglion cells comprise approximately 58% of all retinal ganglion cells and have axons that innervate the parvocellular layers of the lateral geniculate nucleus, and the

on- and off-center parasol ganglion cells comprise another 16% of all retinal ganglion cells and have axons that innervate the magnocellular geniculate layers. Several additional retinal ganglion cell subtypes also project to the lateral geniculate nucleus, and their axons innervate neurons in the geniculate koniocellular layers (described below). Altogether, there are at least 13 parallel streams of information flow from the retina to the lateral geniculate nucleus in the macaque monkey, and these streams arise from an estimated 84% of all retinal ganglion cells.

Table 2. Diversity of Retinal Ganglion Cell Types in the Macaque Monkey

Ganglion cell Morphological Type	% of Ganglion Cell Population	Central Projections	Physiological Properties
Midget (on-center)	27.0	LGN parvo layers	L vs. M cone opponent; on- and off-center–surround; sustained
Midget (off-center)	31.0		
Parasol (on-center)	8.0	LGN magno layers; SC; pretectum	
Parasol (off-center)	7.8		Achromatic; L vs. M cone non-opponent; on- and off-center–surround; transient
Small bistratified	6.1	LGN konio layers	S ON, L + M OFF opponent; small and coextensive receptive field
Recursive monostratified (3 populations)	1.4	LGN; pretectal areas	Possible correlate of nonprimate ON-direction selective cells
	1.4		
	1.4		
Narrow thorny (on-center)	1.5	LGN; SC; pretectum	Transient; achromatic
Narrow thorny (off-center)	1.5		

Ganglion cell Morphological Type	% of Ganglion Cell Population	Central Projections	Physiological Properties
Smooth (on-center)	1.3	Achromatic L + M cone input	
Smooth (off-center)	1.3	LGN; SC	
Sparse (on-center)	0.9	LGN; SC	L + M ON, S OFF opponent; details unknown for sparse outer cells
Sparse (off-center)	0.9		
Recursive bistratified (ON–OFF)	1.5	LGN; SC	Possible correlate of rabbit ON–OFF direction selective cells
Large bistratified (ON–OFF)	1.5	LGN; SC	S ON vs. L + M OFF opponent; large receptive field
Broad thorny (ON–OFF)	1.3	LGN; SC; pretectum	Possible correlate of mouse and rabbit “local edge detector”; ON–OFF
Melanopsin (on-center)	0.5	LGN; SC; pretectal area; PON; SCN	Intrinsically photosensitive; sustained; intraretinal axon collaterals
Melanopsin (off-center)	0.6		

Notes: Nineteen classes of retinal ganglion cells make up 96.5% of all ganglion cells. These cell classes differ in their morphology, physiological properties, and central targets. Approximately 84% of known retinal ganglion cells have axons that innervate the lateral geniculate nucleus (many also innervate other central structures). LGN, lateral geniculate nucleus; PON, pretectal olivary nucleus; SC, superior colliculus; SCN, suprachiasmatic nucleus.

Source: Adapted from personal communication with Dennis Dacey.

The lateral geniculate nucleus in primates, including monkeys, contains three major neuronal classes that reside in three types of layers—the magnocellular, parvocellular, and koniocellular layers. Although all primates have koniocellular layers, these layers are more clearly visible in some species, such as galagos (Figure 5; (Irvin et al., 1986), than they are in others. Across all primates, neurons in each of these layers receive selective input from specific classes of retinal ganglion cells, with the midget cells innervating neurons in the parvocellular layers, the parasol cells innervating neurons in the magnocellular layers, and the remaining retinal cell types projecting to the geniculate neurons in the koniocellular layers. Thus, similar to the cat, there are multiple and segregated parallel streams of information flow from the retina to the lateral geniculate nucleus.

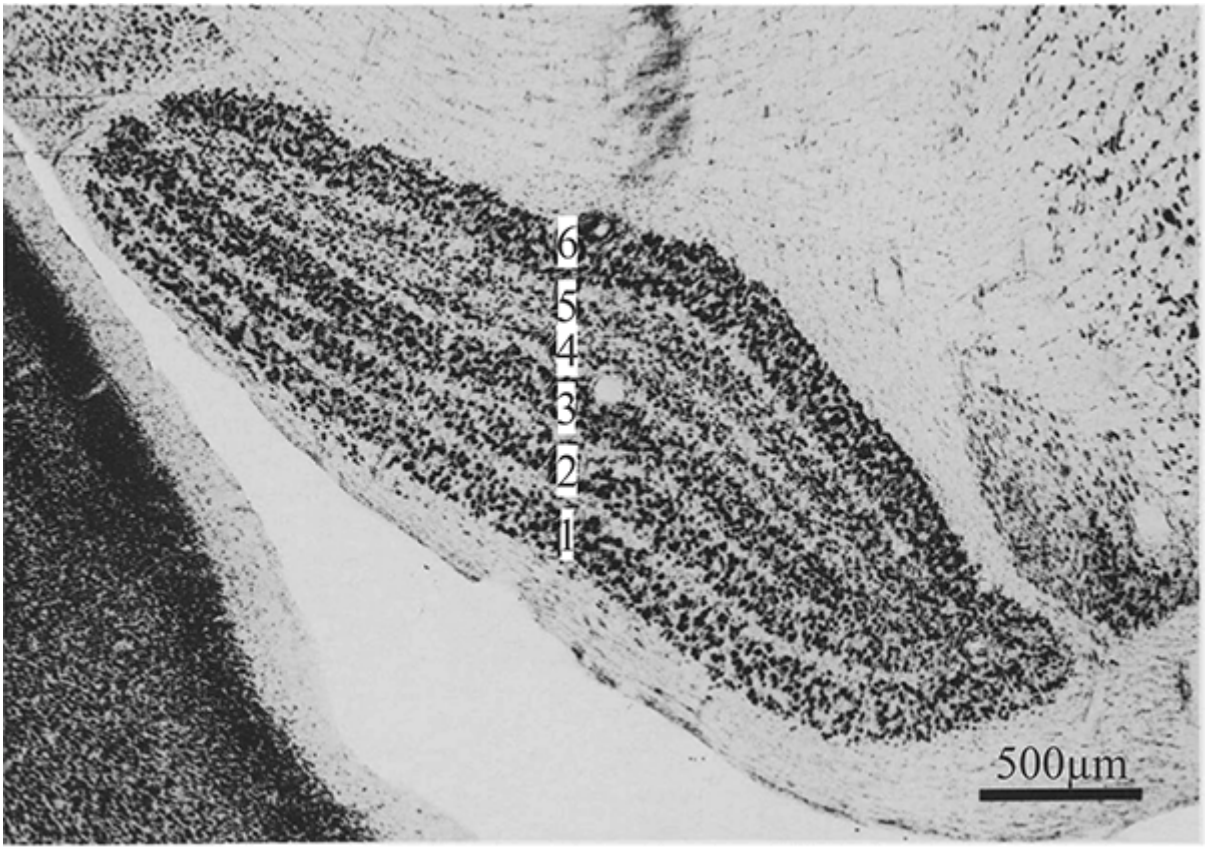

Figure 5. Parasagittal Nissl-stained section of the galago lateral geniculate nucleus. Layers 1 and 2 are the magnocellular layers, layers 3 and 6 are the parvocellular layers, and layers 4 and 5 are the koniocellular layers.

Source: Adapted from (Irvin et al., 1986).

Neurons in the magnocellular, parvocellular, and koniocellular layers also have distinct morphological and physiological properties (see Table 1; reviewed in Casagrande, 1994; Casagrande & Kaas, 1994; Hendry & Reid, 2000; Lee, 1996; Merigan & Maunsell, 1993; Nassi & Callaway, 2009; Schiller & Logothetis, 1990). Similar to the situation in cats, more is known about the response properties of cells involved in the parvocellular and magnocellular streams than in the koniocellular stream.[1] Compared to parvocellular neurons (or midget ganglion cells),

magnocellular neurons (or parasol ganglion cells) have larger cell bodies, larger receptive fields, faster and more transient responses to visual stimuli, faster conducting axons, shorter response latencies, greater response gain, and prefer lower spatial and higher temporal frequencies. Magnocellular neurons have achromatic receptive fields (i.e., they are not wavelength selective), whereas parvocellular neurons, at least in Old World monkeys and some New World monkeys, have receptive fields that are chromatically selective. In particular, the receptive fields of parvocellular neurons are red/green color opponent, a feature that follows the spatial organization of the long- and medium-wavelength cones that establish their center–surround receptive fields (Reid & Shapley, 1992).

Magnocellular and parvocellular neurons project to distinct subdivisions of layer 4 in primary visual cortex (see Figure 4). Magnocellular axons arborize in the upper division of layer 4C, known as 4Cα, whereas parvocellular axons arborize in the lower division of layer 4C, known as 4Cβ. Because the dendrites of stellate cells within these subdivisions of layer 4C are restricted to either layer 4Cα or 4Cβ, these cortical cell targets receive stream-specific input. However, there are opportunities for the mixing of magno- and parvocellular stream input to cortex because layer 5 and 6 pyramidal cells have apical dendrites that extend through layers 4Cα and 4Cβ, and these apical dendrites might receive thalamic inputs, as in the cat (da Costa & Martin, 2009).

Similar to cat W cells, relay cells in the koniocellular layers of the lateral geniculate nucleus have axons that pass through cortical layers 4Cα and 4Cβ to arborize instead within layers 1–3 of primary visual cortex (Casagrande et al., 2007; Fitzpatrick et al., 1983). Also similar to W cells in the cat, neurons in the koniocellular layers are a diverse group, containing multiple subclasses of cells that receive input from distinct classes of retinal ganglion cells. The classes of retinal ganglion cells that innervate neurons in the koniocellular layers include the small and large bistratified cells, the recursive monostratified and bistratified cells, the smooth and sparse inner cells, and the narrow and broad thorny cells (reviewed in Crook, Packer, Troy, et al., 2014; Dacey & Packer, 2003; Masland, 2011, 2012; Wässle, 2004). Unlike magnocellular and parvocellular geniculate neurons, which have strictly monocular responses, some koniocellular neurons have binocular responses (Cheong et al., 2013), suggesting that these koniocellular neurons combine retinal inputs either directly or through polysynaptic circuits. Similar to the cat, some koniocellular neurons also have chromatically selective (blue/yellow) receptive fields that come about from an organization of cone inputs where the short-wavelength sensitive cones are antagonistic to mixed input from the medium- and long-wavelength sensitive cones (Dacey & Lee, 1994; Hendry & Reid, 2000).

Importantly, as with felines, the distinct visual physiology of primate geniculate magnocellular, parvocellular, and koniocellular neurons is mostly the result of differences in the physiology of their retinal inputs. Moreover, most of the features that distinguish the magnocellular and parvocellular streams in the primate are similar to those that distinguish the Y cell and X cell streams, respectively, in the cat (see Table 1), suggesting these neuronal classes share a common evolutionary history.

Homology and the Parallel Retinogeniculate Pathways in Cats and Monkeys

Past efforts to establish homologies between the parallel visual processing streams from retina to cortex in cats (the W, X, and Y streams) and monkeys (the koniocellular, parvocellular, and magnocellular streams) have often placed heavy reliance on the receptive field. For example, the presence or absence of chromatic selectivity has been used to contend that cat W cells are homologous with monkey parvocellular neurons (Shapley & Perry, 1986). Likewise, the presence or absence of nonlinear subunits in the receptive fields of cat X and Y cells, respectively, has been used to find X and Y homologs in the magnocellular layers of the monkey (Kaplan & Shapley, 1982) and in the retina of the rat (Heine & Passaglia, 2011).

With respect to chromatic selectivity, it seems plausible that evolution could result in a parvocellular homolog that has wavelength sensitivity in one species but not another by mutations affecting how the cones supply retinal circuitry. Clearly, parvocellular cells across monkey species are homologous. Yet parvocellular neurons in macaque monkeys and female squirrel monkeys show wavelength sensitivity, whereas those in male squirrel monkeys and all owl monkeys do not (Carvalho et al., 2017; Jacobs et al., 1993; Levenson et al., 2007; Mundy et al., 2016; Tan & Li, 1999), which illustrates how homologous neurons in monkey species can have such different functional (e.g., receptive field) properties. Likewise, it seems plausible that the nonlinear subunits that are characteristic of Y cells in cats could be eliminated during evolution, resulting in homologous cells that lack these subunits. This would explain why magnocellular neurons in monkeys that seem homologous to Y cells in cats generally lack nonlinear subunits (Derrington & Lennie, 1984; Levitt et al., 2001).

Cats and monkeys belong to two different orders, carnivores and primates, having shared a common ancestor approximately 65–80 million years ago. Since that time, their evolutionary paths have led to many species-specific differences. Given their history, it is rather remarkable how similar the distinctions between cat geniculate X and Y cells are with those of monkey parvocellular and magnocellular neurons (reviewed in Cleland, 1986; Merigan & Maunsell, 1993; Schiller & Logothetis, 1990; Shapley, 1992; Sherman, 1985; Stone, 1983). Compared to cat Y cells and monkey magnocellular neurons, cat X cells and monkey parvocellular neurons have smaller cell bodies, smaller dendritic fields, and slower conducting axons (Friedlander et al., 1981; Headon et al., 1985; Maunsell et al., 1999; Schiller & Malpeli, 1978; Sherman et al., 1976). The axons of cat X cells and monkey parvocellular neurons make synapses with cortical neurons in deeper regions of layer 4 than do those of Y cells and magnocellular axons Figure 4 (Blasdel & Lund, 1983; Diamond et al., 1985; Freund et al., 1985; Hendrickson et al., 1978; Humphrey et al., 1985a, 1985b). Physiologically, cat X cells and monkey parvocellular neurons have smaller receptive fields, slower visual responses, more sustained visual responses, and prefer stimuli with lower temporal and higher spatial frequencies than do their parallel Y or magnocellular stream counterparts (Croner & Kaplan, 1995; Levitt et al., 2001; Maunsell et al., 1999; Saul & Humphrey, 1990; So & Shapley, 1979; Troy & Lennie, 1987; Usrey & Reid, 2000; Usrey et al., 1999). Last, the same molecular markers that are selective for X cells versus Y cells are also selective for

parvocellular versus magnocellular neurons (Hendry et al., 1984; Hockfield & Sur, 1990; Iwai et al., 2013). Taken together, the anatomy, physiology, and molecular markers provide evidence for a compelling case of homology between cat X cells and monkey parvocellular neurons as well as for cat Y cells and monkey magnocellular neurons.

The W cell/koniocellular pathway to cortex appears to be evolutionarily older than the X/Y and magnocellular/parvocellular pathways, and it terminates in the superficial layers of visual cortex, rather than in layer 4 (see Figure 4). Across a broad range of species, including cats, ferrets, minks, monkeys, galagos, mice, rats, and tree shrews, the differences between the cell types projecting to the superficial layers of cortex versus layer 4 are striking, supporting the view that these two routes to cortex have been distinct for much of mammalian evolution. Geniculate relay cells projecting to the superficial layers of cortex are typically small and pale staining, and they receive input from fine-caliber retinal fibers and from neurons located in the superficial layers of the superior colliculus, the latter being a source of input not directed to X and Y cells or to magnocellular and parvocellular neurons (Diamond et al., 1985; Fitzpatrick et al., 1983; LeVay & Gilbert, 1976; Usrey et al., 1992; Weber et al., 1983). Finally, included in the great diversity of relay cells with projections to the superficial layers of cortex are cells with the largest receptive fields and slowest visual responses found in the lateral geniculate nucleus (Cleland et al., 1976; Stanford et al., 1983; Sur & Sherman, 1982; Wilson & Sherman, 1976). Given their similarities with each other and their marked differences with relay cells that target layer 4, an argument can be made that the geniculostriate streams projecting to the superficial layers in cats and monkeys are in some sense homologous, but until a proper classification of this heterogeneous cell group is completed, homological relationships must remain superficial.

If homology exists between the different classes of relay cells in cats and monkeys, as described previously, then it may seem surprising that the lateral geniculate nucleus appears so different between the two species, in terms of its shape, size, and lamination patterns (Figure 6). Indeed, there is tremendous variation in the morphology of the lateral geniculate nucleus across mammals. For instance, in some species (e.g., minks, ferrets, and tree shrews), the lateral geniculate nucleus has separate layers for cells with on-center versus off-center receptive fields, whereas in others (e.g., cats, which are closely related to minks and ferrets), the lateral geniculate nucleus combines these cell types within the same layers. Among monkeys, the lateral geniculate nucleus has six layers in some species (e.g., macaque monkey; (Le Gros Clark, 1941) and four layers in others (e.g., owl monkey; (Diamond et al., 1985). More remarkably, the number of layers in an individual monkey and human lateral geniculate nucleus varies across the nucleus from four to eight as layers divide and consolidate (Hickey & Guillery, 1979). Moreover, lamination is difficult to discern in rats and mice. Given the tremendous diversity in geniculate organization and layering that exists between species, it is noteworthy that the visual cortex is relatively more consistent in terms of its thickness and layering. Although speculative, it seems entirely plausible that the invariance in cortical morphology compared to that of the geniculate reflects precise developmental constraints needed to establish the much greater number of intrinsic and extrinsic circuits that are present in the cortex compared to the lateral geniculate nucleus.

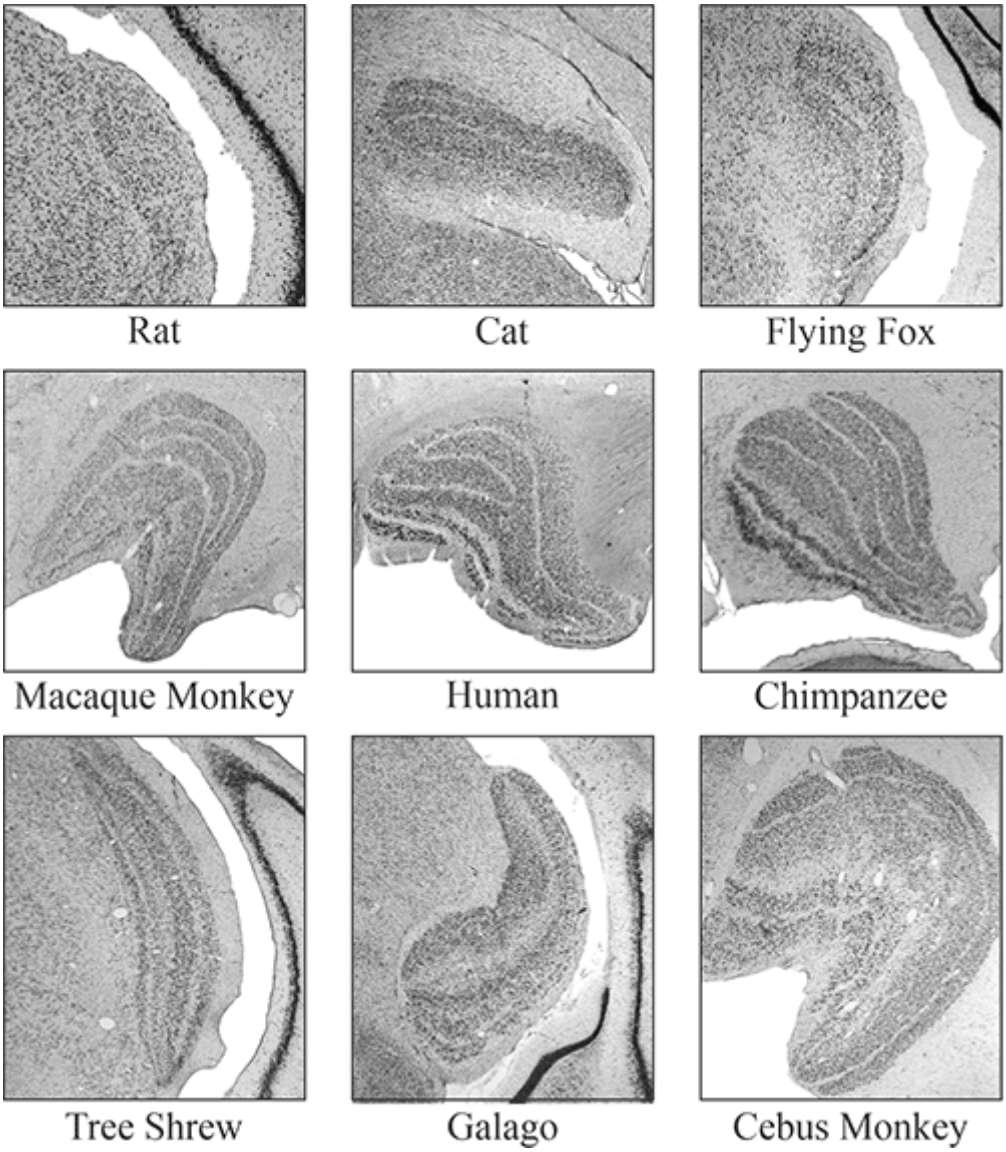

Figure 6. Nissl-stained sections of the lateral geniculate nucleus from nine different species illustrating a diversity of shapes and lamination patterns. *Top row*: rat, cat, and flying fox; *middle row*: macaque monkey, human, and chimpanzee; *bottom row*: tree shrew, galago (bush baby), and cebus monkey.

Source: Adapted from Usrey and Alitto (2015).

Mice—Homologous Cell Types with Cats and Monkeys?

Mice have recently become a popular animal model for studies investigating visual processing. Much of this popularity is due to new and powerful molecular methods for manipulating and assessing their visual circuits and responses. A major goal of the use of mice is to identify neural mechanisms for vision that are more difficult to ascertain in other species, such as cats and monkeys (reviewed in Seabrook, Dhande, et al., 2017). With this goal in mind, it is therefore important to know which cell types are homologous. Similar to cats and other nonprimate mammals, the rodent retina contains two major classes of cone photoreceptors—one maximally

sensitive to short-wavelength (blue) light and the other maximally sensitive to medium-wavelength (green) light. The density and distribution of the two cone classes are not uniform across the retina (Szel & Rohlich, 1992) but, rather, have an inverse dorsal–ventral gradient that serves to optimize the detection of visual features in the sky versus on the ground (Applebury et al., 2000; Baden et al., 2016; Haverkamp et al., 2005; Szel & Rohlich, 1992; reviewed in (Heukamp et al., 2020; Wernet et al., 2014). Similar to cats and monkeys, there is a diversity of retinal ganglion cell types in rodents (Heukamp et al., 2020; Masland, 2012; Seabrook, Burbridge, et al., 2017). Current evidence supports the existence of approximately 33 different types of retinal ganglion cells that tile the retina in mice (Baden et al., 2016) that collectively project to approximately 40 different targets in the brain. As with all mammals, the lateral geniculate nucleus serves as a relay for retinal signals destined for cortex, and the diversity of retinal ganglion cell types that provide synaptic input to the geniculate may be as large as, if not larger than, that for the primate. However, unlike the primate, in which the density of parvocellular and magnocellular projecting retinal ganglion cells is far greater than the density of koniocellular projecting neurons, the density of different classes of retinal ganglion cells projecting to the lateral geniculate nucleus is more balanced in the mouse, which has important implications for the utility of the mouse in finding and studying the ganglion cell types that are rare and more difficult to find in cats and primates. With these distinctions in mind, among the retinal ganglion cells that project to the mouse lateral geniculate nucleus, many with a wide variety of receptive field types project to the shell region, and some with on-center or off-center receptive fields terminate in the core region (reviewed in Seabrook, Burbridge, et al., 2017). Neurons in the shell also receive input from the superficial layers of the superior colliculus (Bickford et al., 2015; Okigawa et al., 2021), similar to koniocellular neurons in the monkey and W cells in the cat, which strengthens the argument that these neurons are homologous to W (cat) and koniocellular (primate) cells. Although it is tempting to speculate that the core region of the mouse lateral geniculate nucleus includes neurons that are homologous to X and/or Y cells in cats (or magnocellular and/or parvocellular cells in monkeys) (Guido, 2018), one cannot rule out that the retinal ganglion cells innervating the core region are a subtype of W cells.

Results from electrophysiological and optical recordings indicate there is at least as much diversity among the cell types and response properties of neurons in the lateral geniculate nucleus of mice as there is in cats and monkeys. In mice, this diversity includes cells with response properties generally considered more typical of cortical neurons in cats and monkeys, such as orientation selectivity and direction selectivity, and cells with response properties considered unique from those of cats and monkeys, such as cells that encode the absence of contrast or axis of motion selectivity (Huberman et al., 2009; Marshel et al., 2012; Piscopo et al., 2013; Scholl et al., 2013); see also (Barlow et al., 1964). Keeping in mind the current paucity of knowledge about cell diversity in the cat W pathway and the primate koniocellular pathway, it may turn out that the cell types identified considered unique in the mouse have a counterpart in other model organisms, including cats and monkeys. In support of this possibility, it is generally agreed that there is a much greater diversity of retinal ganglion cells in the primates with projections to koniocellular layers compared to those with projections to the parvocellular and magnocellular layers (reviewed in Crook, Packer, Troy, et al., 2014; Dacey & Packer, 2003; Masland, 2011, 2012; Wässle, 2004). Thus, results from the mouse may provide insight into the

broader range of possible processing strategies utilized across mammals, and tools developed for identifying and studying these cell types in mice may be effective for shedding light on the breadth of homologous cell types across species.

Conclusion and Perspective on Nomenclature

It has been said that anatomists would prefer sharing each other's toothbrushes over sharing their nomenclature, and at some point while reading this article, the reader has likely reached a similar conclusion for vision scientists. The diversity of nomenclature used for cell types between species and even within a species can seem daunting. For instance, in cats, the terms X cells, beta cells, and sustained (or tonic) cells are commonly used when describing one class of retinal ganglion cells, and the terms Y cells, alpha cells, and transient (or phasic) cells are used when describing another class of cells. As a result, different studies frequently use different nomenclature when referring to the same cell type. The nomenclature is even more diverse when including other species. In primates, additional terms for the two classes of retinal ganglion cells mentioned previously include midget cells and parasol cells. Adding even more confusion, these two cell classes are sometimes referred to as M cells and P cells, respectively, but the cells distinguished with these abbreviations are reversed depending on whether the M is short for midget or for magnocellular projecting and, likewise, whether the P is short for parasol or for parvocellular projecting, because the midget cells project to the parvocellular layers of the lateral geniculate nucleus and the parasol cells project to the magnocellular layers.

An understanding of homology may provide a means to simplify and standardize the nomenclature. If there are indeed homologous cell types in the cat and monkey, as has been argued in this article, then perhaps these cell types should share a singular common name, as is the case with the bones that make up the hand of a human, the wing of a bat, and the flipper of a whale (see Figure 1). If this is an agreed upon view, then the difficult question is which names should be used? Fortunately, there is guidance available on this topic (Edgecombe, 2008; Hughes, 1979; Rowe & Stone, 1977). In general, nomenclature should avoid the use of descriptive labels or role-indicating names. The problem with these descriptive names is that they are essence-indicating and imply a particular operation as being the primary function of a cell. Some terminologies seem inherently limited: For instance, "sustained" and "transient" would seem to allow only two classes, and it is now know that many more ganglion cell types exist. Moreover, as described previously, the same cell class may appear functionally distinct between species if only a singular criterion is applied (e.g., color selectivity). That is, function is a feature that evolution works to change in homologous elements. Instead of concentrating on functional features, a collection of cellular attributes—including the morphology, neurochemistry, connections, and physiology—should be considered for purposes of classification.

Regarding terminology, it is argued here, in agreement with Edgecombe (2008), that it is best to avoid terms that imply function that may not apply across species. Thus, terms such as "tonic," "phasic," "local edge detectors," "directionally selective," and many others should be avoided. "Beta," "alpha," and "gamma," while implying no special function, are specifically applicable just to the cat retina. Likewise, "parasol" and "midget" are limited to the monkey retina. The

"parvocellular," "magnocellular," and "koniocellular" terms apply just to primates. That leaves "W," "X," and "Y" as the one commonly used set of terms for these parallel pathways that implies no special function and can be generally used across species.

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Notes

1. For terminological simplicity, these visual neurons are hereafter referred to as parvocellular, magnocellular, or koniocellular, even including retinal ganglion cells. Thus, midget ganglion cells are referred to as parvocellular.

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