Title:
A comparative approach to parallel geniculocortical pathways

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Abstract

The dorsal lateral geniculate nucleus of the thalamus (LGN) occupies a central locus in both the passage of visual signals from retina to cortex and in the development of theories for vision. Six decades of research, in several mammalian species, allows deep empirical understanding of the structure, connections, and functional properties of the LGN. This work supports the idea that LGN is organised into compartments with different afferent inputs, projections, and functional properties. That is, signals are conveyed from retina to cortex through parallel channels. The aim of this chapter is to develop a comparative, historical overview of this work, and to help the reader understand some of the key debates.

1. Anatomical and functional evidence for parallel pathways

Our understanding of parallel pathways has been driven by distinct stages of research, each dominated by different species (particularly domestic cat, non-human primate and human, and laboratory mouse), and it is helpful to understand the evolution of understanding by presenting this work in partially chronological order. The primary literature here is extensive and this short chapter cannot do it all justice, so the reader is encouraged to explore excellent reviews, which are indicated where they are available.

Initial studies

Anatomical work had already shown the importance of the dorsal lateral geniculate nucleus (LGN) in connecting retina to primary visual cortex (V1), and clear segregation of nerve cell bodies within LGN (e.g. le Gros Clark, 1941; Walls, 1953), before techniques for recording from single neurons in central brain areas were established. Physiological measurements in retina and cortex were already providing important insights, and initial measurements in cat LGN (Hubel and Wiesel, 1961) therefore aimed to establish if visual responses of LGN resembled their retinal afferents or cortical targets. This work found presence of ON- and OFF receptive fields with centre-surround receptive field organisation like that already described for retinal ganglion cells (RGCs) (Barlow, 1953; Kuffler, 1953). Comparison of response properties between dorsal (A, A1) layers and ventral (C) layers of cat LGN hinted at functional segregation, with larger receptive fields in layer C accompanied by weaker responses and longer visual latency. Contemporaneous measurements from monkey LGN also showed receptive fields with centre-surround organisation, and additional presence of colour-sensitive (cone-opponent) responses (De Valois et al., 1958; De Valois et al., 1966; Wiesel and Hubel, 1966). This work also hinted at functional segregation, with stronger cone-opponency in dorsal (parvocellular, P) layers and weaker cone-opponency in ventral (magnocellular, M) layers.

X,Y and W pathways in cat

Techniques for tracing of brain pathways were still in their infancy, so early progress was driven by physiological measurements, particularly from cat RGCs. Several attempts were made to derive classification schemes to explain these functional properties (why this is important is discussed in Rowe and Stone, 1977; Hughes, 1979; Rodieck and Brening, 1982), but the scheme that gained most traction was the identification of two dominant subclasses of cat RGC (X and Y) with further subdivision into ON and OFF cells within each class (Enroth-Cugell and Robson, 1966). The functional properties of X- and Y-cells are respectively: linear or non-linear spatial summation, smaller or larger receptive fields, sustained or transient light response, and slower or faster conduction velocity. This scheme became particularly attractive when the functional classes were shown to correspond to morphologically distinct classes of RGC (**Figure 1a**; beta, alpha; (Boycott and Wassle, 1974). X and Y RGCs had different central projections: X-cells projected to layers A/A1 of LGN; Y-cells also projected to A/A1, but had collaterals including LGN layer C and superior colliculus (Hoffmann, 1973; Bowling and Michael, 1980; Tamamaki et al., 1995). Other RGCs, with diverse morphology and diverse receptive field properties were grouped into a third class ('W'; Stone and Hoffmann, 1972), the projections of which included layer C of LGN as well as other central brain areas (Fukuda and Stone, 1974). Measurements from cat LGN showed that the functional distinctions between X-, Y- and W-like RGCs were largely preserved in thalamocortical cells, and further, that the morphology of X,Y and W

thalamocortical cells was different, even when they were in the same LGN layer (Sherman and Spear, 1982; Stanford et al., 1983). The emerging picture of parallel retino-geniculo-cortical pathways was reinforced when the axons of X,Y and W LGN cells were found to project onto different layers of V1 (Ferster and LeVay, 1978; Gilbert and Wiesel, 1979; Leventhal, 1979); for simplicity here we refer to area 17 as V1), and by the discovery that while LGN X-cells projected only to V1, LGN Y- and W-cells had additional cortical targets (Stone and Dreher, 1973).

P, M and K pathways in primates

Rapidly improving techniques for tracing brain pathways showed that P-layers of the monkey LGN were targeted by a small and numerous class of RGC (midget; **Figure 1b**), while M-layers were targeted by a larger and less numerous class (parasol; (Leventhal et al., 1981; Perry et al., 1984; Rodieck and Watanabe, 1993), and that LGN P- and M-cells projected to different sub-laminae of layer 4C in V1 (Hubel and Wiesel, 1972; Hendrickson et al., 1978). Analysis of visual responses showed that neurons in the P-layers had sustained visual responses, small receptive fields and stronger cone-opponency, while those in the M-layers had transient responses, larger receptive fields and little cone-opponency (Dreher et al., 1976; Sherman et al., 1976; Schiller and Malpeli, 1978; Shapley et al., 1981; Derrington and Lennie, 1984; Blakemore and Vital-Durand, 1986; Spear et al., 1994; Usrey and Reid, 2000; White et al., 2001; Xu et al., 2001). Further, P- and M- cells had overlapping but distinct responses to achromatic stimuli: M-cells responded better to low contrast stimuli (Kaplan and Shapley, 1982, 1986), and they responded to higher rates of temporal flicker ((Dreher et al., 1976; Derrington and Lennie, 1984); but see Levitt et al., 2001). The high sampling density of P-cells, and presence of cone-opponency, suggested they were important for high spatial acuity and colour vision; the high contrast sensitivity and fast temporal response of M-cells suggested they were important for motion vision. Subsequent behavioural studies in experimentally lesioned monkeys provided broadly consistent evidence (Merigan, 1989; Merigan and Maunsell, 1990; Schiller et al., 1990), though the contribution of P- and M-cells to cortical processing and hence perception has been the subject of extensive debate (see for example: (DeYoe and Van Essen, 1988; Livingstone and Hubel, 1988; Shapley, 1990; Merigan and Maunsell, 1993).

Overall anatomical and functional similarity between the two major retino-geniculo-cortical pathways in cat (X/Y) and monkey (P/M) encouraged attempts to assimilate them (Stone and Dreher, 1982). Attempts to align X/P and M/Y were, however, challenged particularly by the observation that only some M-cells showed the non-linear spatial summation found in all Y-cells (Shapley and Perry, 1986). Whether non-linear M-cells are a distinct subset, or the extreme of a continuous distribution remains unclear. Additional challenges, however, remained in the fact that both X- and Y cells in cat showed presence of ‘contrast gain controls’, such that response latency decreased at high contrast, response amplitude saturated at high visual contrast, and response often depended on spatial and temporal context within which a stimulus was viewed (Shapley and Victor, 1978; Shapley and Victor, 1979). These gain controls were present in M-cells in monkey, but largely absent from P-cells (Kaplan and Shapley, 1986; Benardete et al., 1992; Solomon et al., 2002; Solomon et al., 2004; Solomon et al., 2006; Alitto and Usrey, 2008).

Absent from most early work on parallel pathways in monkey was consideration of the other, non-standard receptive fields and their anatomical correlates (Casagrande, 1994). However the projection to monkey LGN was known to include a variety of morphologically distinct RGCs (Leventhal et al., 1981; Rodieck and Watanabe, 1993; Dacey et al., 2003; Szmajda et

al., 2008), RGCs with non-standard receptive field properties were known to be present (de Monasterio, 1978), and anatomical work had shown that neurons intercalated between the P and M LGN layers ('K cells'; Kaas et al., 1978) expressed distinct neurochemicals that are also expressed by neurons in neighbouring inferior pulvinar (Hendry and Yoshioka, 1994; Huo et al., 2019; Bakken et al., 2021), showed distinct projection to superficial layers of V1 (Livingstone and Hubel, 1982; Fitzpatrick et al., 1983), and included neurons with direct projections to extrastriate visual cortex, bypassing V1 (Benevento and Yoshida, 1981; Sincich et al., 2004; Schmid et al., 2010; Warner et al., 2010; Bridge et al., 2019). Evidence that these non-standard pathways might be important for vision was provided by recordings from one of the non-P-non-M RGC types that projected to LGN ('small bistratified cells'), which showed a distinct type of cone-opponent receptive field ('blue-ON'; (Dacey and Lee, 1994). Subsequent measurements from LGN of New- (Martin et al., 1997) and Old-World monkeys (Roy et al., 2009) showed that blue-ON responses could be localised to K-layers, and measurements of thalamocortical activity in V1 (Chatterjee and Callaway, 2003) showed projection of blue-ON responses onto superficial layers, where many K-pathway LGN cells project, distinct from deeper P- and M-like thalamocortical inputs. Other work has shown additional, diverse visual response properties among K-cells in LGN, at least in New World marmoset monkey, including non-linear spatial summation, 'blue-ON' and 'blue-OFF' cone-opponent receptive fields, orientation selectivity, 'suppressed-by-contrast' responses, and binocular response (White et al., 2001; Tailby et al., 2007; Tailby et al., 2008b; Solomon et al., 2010; Cheong et al., 2013; Zeater et al., 2015). K-cell pathways are therefore functionally and anatomically distinct to those of P- and M-cells. Whether and how this collection of pathways can be likened to the similarly broad collection of 'W-cells' in cat remains unclear, though it is useful to note here that 'blue-ON' colour response is localised to layer C in cat LGN, and therefore part of the W-pathway (Buzas et al., 2013).

The lamination pattern of human LGN resembles that of non-human primates and the organisation of retino-geniculo-cortical pathways in human visual system is likely similar to non-human primates (Hickey and Guillery, 1979). The connectivity between RGCs and central brain areas is not established, but morphological classes of resembling P- and M-pathway monkey RGCs, as well as other RGC types, are now clear (Dacey and Petersen, 1992; Grunert and Martin, 2020; Masri et al., 2020). Recordings from donated human retina have shown that the visual response of putative P- and M-pathway RGCs are similar to monkey (Soto et al., 2020; Reinhard and Munch, 2021). Functional MRI of LGN in human has shown presence of voxels that may prefer achromatic or red-green chromatic modulation (Schneider et al., 2004; Denison et al., 2014; Zhang et al., 2015), and the positioning of these voxels is consistent with M- and P-layers respectively. Anatomical MRI has also shown white matter pathways linking LGN and V1, and revealed additional pathways linking LGN to extrastriate visual cortex (Ajina et al., 2015). These data are broadly consistent with the connectivity of P,M and K pathways in monkey, though the resolution of the techniques is not yet sufficient to specify exact sources and targets.

Core- and shell pathways in mouse

Availability of expanding genetic toolkits and resultant ability to image functional activity in genetically defined cell classes increased interest in mouse retino-geniculo-cortical pathways. Mouse LGN appears homogenous in the Nissl stains that reveal cellular layers in cat and primate LGN, however analysis of projections from retina and other brain regions reveals 'hidden' lamination. Mouse LGN is therefore usually subdivided into a thin dorsal 'shell' and larger ventral 'core' regions, as in rat (**Figure 1c**; Reese, 1988; Grubb and Thompson, 2004; Kerschensteiner and Guido, 2017). The shell receives retinal input predominantly from

contralateral eye, while the core comprises a larger contralateral projection surrounding a smaller ipsilateral projection. Morphologically, most thalamocortical neurons in shell resemble W-type thalamocortical neurons in cat, while those in core resemble X- or Y-type with some regional variation (Krahe et al., 2011; Bickford et al., 2015; Guido, 2018). Retrograde tracing from V1 suggests thalamocortical neurons in shell project to superficial layers of V1 while those in core project to deeper layers of V1 (Cruz-Martin et al., 2014), but further characterisations are surprisingly spare. Large scale surveys indicated two types of LGN axons in middle-upper layers of V1, and a third type in lower layers (Peng et al., 2021); there was little evidence for thalamocortical projection outside V1, though a small projection from, for example, shell, may yet to be discovered.

LGN is a target of about one-third of mouse RGCs, including ~30 of the ~40 RGC classes that can be identified by various quantitative methods (mouse RGCs are less morphologically distinct than cat or primate RGCs; (Morin and Studholme, 2014; Martersteck et al., 2017; Bae et al., 2018; Roman Roson et al., 2019). Many or all of these RGCs send collaterals to superior colliculus, the major projection of the mouse retina (Ellis et al., 2016). LGN core receives relatively strong projections from 'alpha-like' RGCs, while LGN shell receives relatively strong projections from direction-selective RGCs (Huberman et al., 2008; Huberman et al., 2009; Kay et al., 2011; Rivlin-Etzion et al., 2011; Hong et al., 2019; Okigawa et al., 2021; Jiang et al., 2022) (see (Liang and Chen, 2020; Kerschensteiner, 2022). There is also extensive influence of non-canonical photoreception, derived from intrinsically-photosensitive RGCs (Brown et al., 2010).

Early recordings from mouse LGN found presence of sustained and transient responses and centre-surround receptive fields (Grubb and Thompson, 2003). Later work found that these were complemented by orientation- or direction selective, and 'suppressed-by-contrast' responses consistent with retinal projections (Piscopo et al., 2013; Aydin et al., 2018; Roman Roson et al., 2019). Many cells (especially in awake animals) showed non-linear spatial summation, but it is not clear they form a discrete class (Denman and Contreras, 2016; Durand et al., 2016; Aydin et al., 2018). Centre-surround receptive fields are relatively more prevalent in core, while non-standard receptive fields including direction- and orientation selectivity are relatively more prevalent in shell (Piscopo et al., 2013; Suresh et al., 2016). Consistently, imaging of LGN afferents in V1 has found evidence for orientation and direction-selective input to superficial and middle-layers (Kondo and Ohki, 2016; Sun et al., 2016; Zhuang et al., 2021). Increased prevalence of orientation tuning in LGN over retina may suggest recombination of direction-selective RGC responses into orientation-selective LGN responses (Marshel et al., 2012; Scholl et al., 2013; Zhao et al., 2013).

2. How parallel are parallel pathways?

A central concern is whether and how processing within LGN alters the signals provided by RGCs. The question here is whether there is convergence of multiple RGC classes onto a single LGN cell, convergence within RGC classes, or convergence of non-retinal inputs, that may alter the nature of the signals that parallel pathways convey. The answer to these questions may be species- and pathway dependent. In cat, there are at least twice as many LGN neurons (~510,000) as retinal afferents (~151,000) (Chalupa et al., 1984; Williams et al., 1993). Anatomical measurements have consistently implied convergence and divergence of RGC signals in LGN (Guillery, 1966; Hamos et al., 1987). Several lines of evidence have suggested convergence of a small number (~1-4) of RGC inputs to each LGN cell, including recordings from connected pairs of RGC and LGN neurons (Cleland et al., 1971; Usrey et al., 1999), simultaneous measurement of slow ('S') potential (synaptic activity of an RGC) and

spiking activity within LGN (Hubel and Wiesel, 1961; Kaplan and Shapley, 1984; Kaplan et al., 1987), and intracellular measurements from X-like LGN cells (Martinez et al., 2014). Convergence may be higher within Y-pathway (Robson, 1993; Weyand, 2016), but the visual preferences of retinal inputs are usually the same as that of their target LGN cell, suggesting limited convergence across RGC classes (Cleland et al., 1971; Mastronarde, 1987; Usrey et al., 1999). Functional measurements from LGN cells of the same class have also shown precisely correlated spiking activity, indicating divergent output from the same RGC (e.g. (Yeh et al., 2003). The picture in cat LGN is therefore one of resampling and interpolation across RGC inputs, potentially enhancing signal propagation without substantially disturbing parallel functional organisation (Alonso et al., 2006; Martinez et al., 2014; Rathbun et al., 2016).

In primate, LGN neurons (~1.28M) are about as numerous as RGC afferents, suggesting neither divergence nor convergence is necessary (Spear et al., 1996). As with cat, the different functional properties of P- and M-cells appear to be built in retina, and the major functional properties of LGN cells are not readily distinguished from RGC afferents (Kaplan and Shapley, 1984). There is less direct evidence, but simultaneous measurement of S-potential and LGN spiking activity has also suggested limited functional convergence (Lee et al., 1983; Carandini et al., 2007). There is limited binocular interactions, but at least in New World monkey a small number of LGN K-cells show strong binocular input (Zeater et al., 2015) (see (Dougherty et al., 2019). Simultaneous recordings have not shown precisely correlated firing in nearby LGN cells, suggesting little divergence of RGC outputs to multiple LGN neurons (Cheong et al., 2011).

There are fewer LGN neurons (~17,000) than RGC (~45,000) in mouse (Jeon et al., 1998; Seecharan et al., 2003), but what fraction of RGCs project to the LGN is not precisely known, and what convergence there is remains a matter of debate. It appears likely that there are a limited number (~2-5) of strong RGC inputs to each LGN cell, and a larger number of weak inputs (Morgan et al., 2016; Litvina and Chen, 2017; Rompani et al., 2017; Roman Roson et al., 2019). Functional work in shell suggested that some cells receive strong input from a single RGC class, but that most cells probably derived weak input from multiple RGC types (Marshel et al., 2012; Liang et al., 2018; Jiang et al., 2022). Additional work has shown that most LGN cells are driven by a single eye (Bauer et al., 2021), even though anatomical connections can be less discriminating (Rompani et al., 2017), so the functional consequence of weak connections remain mysterious.

LGN is a target of several non-retinal brain areas. These inputs could dilute pathway segregation, but many appear pathway specific. Inputs from superior colliculus primarily target C-layers in cat LGN, K-layers in primate, and shell – with parallel projection to core - in mouse (Harting et al., 1991b; Baldwin and Bourne, 2020; Okigawa et al., 2021). Similarly, inputs from parabigeminal nucleus, which have quite different organisation in the three species, nevertheless target the C-, K- and shell layers respectively (Harting et al., 1991a; Bickford et al., 2000; Okigawa et al., 2021). 'Feedback' signals from layer 6 of visual cortex, a major synaptic input to LGN, may also show pathway specificity, at least in primate (Briggs, 2020). The P-, M-, and K-layers of primate LGN receive input from distinct groups of corticothalamic neurons in V1 (Fitzpatrick et al., 1994; Usrey and Fitzpatrick, 1996; Ichida and Casagrande, 2002; Ichida et al., 2014), and perhaps V2 (Briggs et al., 2016). Remarkably, these corticothalamic neurons show distinct functional properties that resemble those of the layers they project to (Briggs and Usrey, 2009). The functional consequences of these pathway-specific non-retinal influences remain unclear, but presumably explain why

infra-slow oscillations are prominent in K-layers but not in P- or M-layers (Cheong et al., 2011).

3. Importance of colour vision

Psychophysical work showed long ago that the capacity for colour vision in humans relied on receptoral and post-receptoral mechanisms. First, typical human colour vision requires three types of broadly-tuned cone photoreceptor, each sensitive to overlapping but different parts of the visible spectrum (short, S, medium, M, or long, L, wavelengths). Second, colour vision requires post-receptoral mechanisms that compare the activity of these receptors ('cone opponency'). As most mammals are dichromatic, with only S- and M-cones, the properties of the cone-opponent pathways have been explored most extensively in trichromatic non-human primates where L-cones are also present. The details have been reviewed extensively elsewhere (e.g. Solomon and Lennie, 2007) but some points are particularly relevant to concepts of parallel processing.

Early measurements from trichromatic primates revealed presence of cone-opponent receptive fields in retina and LGN, but were less certain about how these receptive fields were arranged. This changed when human psychophysical work established stimuli that could isolate the activity of each cone photoreceptor, and specified the importance of two cone-opponent mechanisms (MacLeod and Boynton, 1979; Estevez and Spekreijse, 1982; Krauskopf et al., 1982). One mechanism compared the activity of L- and M-cones (L-M, 'red-green'), and the other compared S-cones to the sum of L- and M-cones (S-(L+M), 'blue-yellow'). Concomitant computational and theoretical work showed that cone-opponent channels with similar structure allowed efficient encoding of chromatic information (Buchsbaum and Gottschalk, 1983). Application to recordings in and around P-layers of monkey LGN showed presence of two distinct functional clusters (Derrington et al., 1984), with patterns of cone-inputs similar to those implied by human psychophysics and theory. In addition, M-cells generally respond as if they summed the signals of L- and M-cone photoreceptors (L+M, 'luminance'; Lennie et al., 1993). These measurements supported a tight link between theory, perception and physiology, and they also hinted that there might be distinct substrates for blue-yellow signals (components of which, were subsequently described as detailed above). Evolution of our understanding of colour vision therefore illustrates the importance of precise control of visual stimulation, and alignment of theory, perceptual and neuroscientific work.

While it is now generally accepted that blue-yellow chromatic signals are conveyed to cortex by K-pathways, there remain competing proposals for the analysis of other chromatic dimensions. One debate is whether red-green signals are carried by midget RGCs and LGN P-cells, or by other pathways, yet to be defined, but likely analogous to the blue-yellow K-pathways (Rodieck, 1991; Patterson et al., 2019). The second debate is whether the receptive fields of P-cells are specialised for analysing red-green colour information, or for analysing achromatic spatial information (Kaplan et al., 1990; Lennie et al., 1991). Comparison of dichromatic and trichromatic individuals among New World monkeys has not yet revealed structural differences in retina, LGN or cortex (Solomon, 2002), and the achromatic visual response properties of P-cells in LGN of dichromatic animals are indistinguishable from those in trichromatic animals (Blessing et al., 2004). The third debate is which aspects of achromatic spatial vision are supported by P- or M-cells (Shapley, 1990); for a related discussion in cat, see (Sherman, 1985). Note that while the receptive fields of P-cells are generally smaller than those of M-cells at the same location in the visual field, this does not imply that only P-cells could signal the location of an object. This is partly because M-cells

have greater contrast sensitivity than P-cells, and are therefore better able to distinguish the position of stimuli within their receptive field.

Central to all these debates is the question of whether P-cells 'multiplex' signals for both red-green (L-M) and luminance (L+M) vision in trichromatic animals. P-cells certainly respond to appropriate luminance and chromatic stimuli, but unfortunately that observation does not answer the question. This is because the receptive fields of P-cells are very small, particularly those near the centre of gaze (ie. in or near the fovea), where their excitatory receptive field centre is dominated by a single cone photoreceptor (i.e. an L-cone or an M-cone; (McMahon et al., 2000; Godat et al., 2022)). Even if P-cells were not specialised for red-green colour vision, the larger receptive field surround would be driven by a mix of L- and M-cones and have different spectral sensitivity to that of the receptive field centre (the 'random-wiring' hypothesis; (Ingling and Martinez-Uriegas, 1983; Lennie et al., 1991). The receptive fields of P-cells near the centre of gaze must therefore be cone-opponent, even if not specialised to be so. Finely controlled measurements have addressed crucial elements of these debates (Martin et al., 2001; Lee et al., 2012; Wool et al., 2018), but the broader questions remain unresolved, and we are left with the uncomfortable reminder that observing that a class of neurons responds to a particular stimulus is not sufficient to specify its role (cf. 'linking hypotheses'; (Brindley, 1960)).

4. Why have parallel pathways?

The short history above makes clear that there is a great deal of knowledge about the organisation and functional properties of parallel retino-geniculo-cortical pathways, but we have much less idea as to *why* they are as they are, *why* the details of their structural and functional organisation vary as they do among species, or even *how* these organisations influence subsequent analysis.

There are two major perspectives on the purpose of early visual processing. One, anchored by the observation of centre-surround, circularly symmetric receptive fields in ON- and OFF-retinal ganglion cells, is that the purpose of RGCs is to efficiently transmit a version of the retinal image to the brain through the bottleneck of the optic nerve, along channels with limited dynamic range (Barlow, 1961). This perspective is fairly agnostic (and therefore flexible) to the visual preferences of different parallel pathways, as long as together they sample the retinal image appropriately. The other, anchored by Lettvin et al.'s (Lettvin et al., 1959) survey of RGCs in the frog, observing responses selective for object motion or curvature, is that the purpose of an RGC is to measure "how much there is in a stimulus of that quality which excites [it] maximally, naming that quality" (ibid, pp. 1959; see also (Barlow, 1972). Different researchers have explored and named different features (a brief list: local edge detector, suppressed-by-contrast, loom-detector, convexity detector, object-motion selective; or even simply orientation- or direction selective, and sustained or transient).

The retina could therefore either efficiently transmit information about the retinal image to subsequent brain areas, or provide estimates of the probability of features in that image. Said another way, the retina could either defer decisions about the content of the visible world to subsequent stages of processing (akin to making the "least commitment"; (Marr, 1982) p106), or make decisions and communicate the results of those decisions to guide action. These perspectives have different implications for understanding the organisation of parallel pathways.

If the purpose of the retino-geniculo-cortical pathway were to transmit a representation of the retinal image to cortex, then further parcellation into multiple sub-pathways should mainly reflect optimisations that improve encoding of the retinal image or extend the range of vision. For example, it might be impossible for a single neural code to support requisite fine spatial resolution and fine temporal resolution. In this case, one pathway may be optimised to transmit highest spatial resolution, and another may be optimised to transmit highest temporal resolution. Many have suggested that this is what is accomplished by the subdivision of the primate visual pathway into P- and M pathways, or the subdivision of the cat visual pathway into X- and Y classes (Merigan and Maunsell, 1993; Schiller, 1993; Silveira and De Mello Jr., 1998; Casagrande et al., 2009). Similarly, presence of ON- and OFF channels within each of the subdivisions, or presence of parallel 'red-green' and 'blue-yellow' cone-opponent pathways, like the presence of centre-surround receptive fields, may reflect solutions that reduce the redundancy of retinal signals, or overcome the limited dynamic range of real neurons (Attneave, 1954; Barlow, 1961, 1986) and improve transmission of the retinal image to cortex. This perspective appears to require relatively complete coverage ('tiling') of the retinal image by each representation, and may also require quasi-linear processing, to enable subsequent recombination and extraction of relevant information (Kaplan, 2003).

If the purpose of the retino-geniculo-cortical pathway were instead to indicate the presence of features to guide action, then parcellation into parallel pathways should mainly reflect the nature of the features that it is important for the organism to represent ["we have been tempted, for example, to call the convexity detectors "bug perceivers"" ((Lettvin et al., 1959), pp. 1959]. The space of potential features (e.g. convexity) is however very large, and the fitness they provide is hard to define. We can gain some traction by supposing that if a ganglion cell is attempting to signal the presence of a particular feature, then it might be insensitive to otherwise irrelevant variations in the local retinal image (Barlow, 1972). For example, a neuron whose task is to signal the presence of a small object may respond regardless of the precise location or intensity (brighter, or darker than its background) of that small object within its receptive field, much like a Y-cell in retina, or complex cell in cortex (Roska and Meister, 2014). Similarly, a neuron whose task is to signal the presence of a 'blue' (or more precisely, a short-wavelength reflecting) object may respond regardless of the intensity of light reflected from that object. This approach would have risks – changes in viewpoint or lighting for example can dramatically alter the image of an object or feature on the retina. Generating feature selectivity often also requires non-linear processing, which may be an impediment to subsequent recombination.

Recent computational work exploring deep convolutional networks with structure similar to the visual pathway suggests these two perspectives may be considered as variations (Ocko et al., 2018; Lindsey et al., 2019). Imposing an energy budget produced two classes of quasi-linear receptive field (each with ON- and OFF subtypes): one with smaller receptive fields and more sustained visual response, another with larger receptive fields and more transient visual response (Ocko et al., 2018). Further, centre-surround receptive fields are favoured when there was a bottleneck (e.g. the optic nerve), or when complex subsequent processing needed to be supported, because such organisation retained more information about the retinal image. Relaxation of the bottleneck or simplification of subsequent processing allowed spatially richer, non-linear retinal receptive fields to emerge (Lindsey et al., 2019). It is useful to note here that there are about 475,000 cells in mouse V1 (Herculano-Houzel et al., 2013), about 32M in cat (Peters and Yilmaz, 1993), and in monkey estimates vary between 140M and 416M (Vanni et al., 2020). Thus, there is between 110 and 325 V1 cells for every LGN cell in monkey, and in mouse there is 30, suggesting that the retino-geniculo-

cortical pathway may be a more problematic functional bottleneck for monkey than for mouse. What might drive relatively larger, and more involved cortical processing is not known, though species with greater visual cortical expansion usually have more frontally placed eyes, greater binocular overlap, and a fovea or area centralis (Kremkow and Alonso, 2018).

Better understanding of why these parallel retino-geniculo-cortical pathways are as they are requires better understanding of how their signals interact (if they do) in cortex (**Figure 2**). For example, convergence of quasi-linear signals provided by P-cells and K-cells can explain chromatic responses in monkey cortex (Tailby et al., 2008a); similar operations would also allow demultiplexing of luminance and chromatic signals from P-cells (**Figure 2b;** Lennie and D'Zmura, 1988). Convergence of more non-linear signals may be more difficult to achieve, and if instead the signals of parallel pathways were kept largely separate in cortex they may play quite distinct roles. For example, the signals of P- and M-cells may make distinct contributions to subsequent cortical processing (Livingstone and Hubel, 1988). Or, M-cell signals may instead be thought of as gating the progression of signals from P-cells, and similarly for Y- and X-cells (**Figure 2d;** Lennie, 1980; Shapley, 1992). Or, because much of the visual information needed for behaviour can be extracted without fine spatial sampling of the retinal image, X-cells may only be needed where fine-grained texture is required (Sherman and Spear, 1982) (Sherman, 1985). Others have likened the W-pathways to 'ambient' vision, with X- and Y-pathways providing 'focal' vision (Trevarthan, 1968) (Stone et al., 1979); likened P- and M-pathways to 'epicritic' and 'protopathic' (Mollon, 1990); or proposed that K-pathways form a matrix, with similarity to pulvinar and widespread connections to cortical areas, that coordinates and modulates the signals provided by neurons in core P- and M-pathways (Jones, 2001). There is likely to be some truth in all these explanations – a single explanation for the role of parallel retino-geniculo-cortical pathways in an individual animal, or the diversity of organisation seen across species, may not be possible or even desirable.

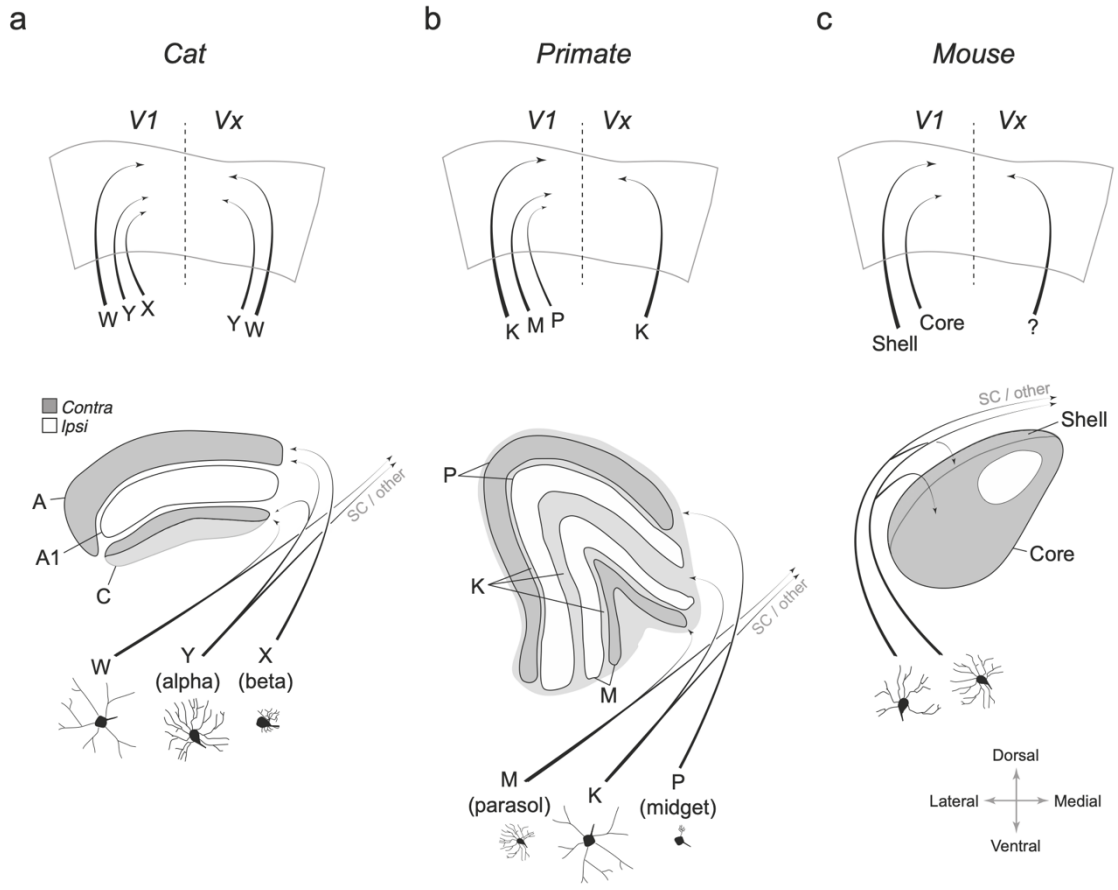

Figure 1. Overview of retino-geniculo-cortical pathways in cat, primate and mouse. Top panels provide schematic overview of dorsal lateral geniculate nucleus (LGN) input to primary visual cortex (V1) and other visual cortical areas (Vx). Bottom panels show the overall structure of the LGN in each case. Layers receiving dominant input from the ipsilateral eye are indicated by unfilled regions; layers receiving dominant input from the contralateral eye are indicated by filled regions, and some of the retinal ganglion cell (RGC) input from the contralateral eye is indicated by the cartoons below. A. Cat. LGN can be subdivided into A, A1 and C layers. Layers A/A1 receive major input from Y (alpha) RGCs and X (beta) RGCs, while layer C receives mainly W-pathway RGC inputs, comprising diverse classes. Y- and W-pathway RGCs in particular also project to other brain regions, including superior colliculus (SC). B. Primate. Schematic is based on the slightly simpler organisation found in New World (marmoset) monkey. LGN can be subdivided into P, M, and K subdivisions. P layers receive major input from midget RGCs, M layers receive major input from parasol RGCs, K-layers from a diverse set of RGCs. M- and K-pathway RGCs often also project to other brain regions. C. Mouse. LGN can be subdivided into core and shell regions. RGC classes in mouse are less morphologically distinguishable. Most RGCs also project to SC.

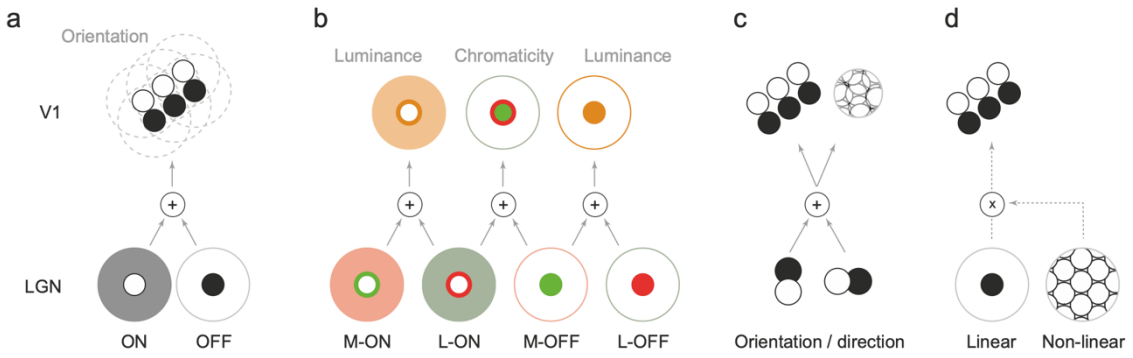

Figure 2. Some of the major functional properties of cells in LGN, and potential contribution to cortical receptive fields. A. Most cells in LGN of cat and primate, and many in mouse, show centre-surround receptive field organisation. Some are ON-centre, others are OFF-centre. Orientation selectivity in visual cortex is often explained by summation of LGN afferents with appropriate spatial location and polarity (ON, OFF). B. Many cells in P-layers of primate LGN show centre-surround organisation, with one cone photoreceptor (L-cone, or M-cone) dominating the receptive field centre. Appropriate summation over these LGN cells can produce cortical receptive fields sensitive to luminance, or chromaticity. C. Many cells in LGN of cat and primate show weak receptive fields with some orientation sensitivity; some LGN cells in primate, and many cells in mouse, show evidence of stronger orientation selectivity. Summation over LGN cells may contribute to cortical orientation selectivity (top, left), but may also result in more complicated receptive field organisation (top, right), particularly when strong non-linearities are required to build orientation sensitivity in LGN receptive fields. D. Other interactions between LGN pathways are possible. For example, the output of pathways with largely linear receptive fields may be gated by the activity in more non-linear pathways.

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