European Journal of Neuroscience

WILEY | FENS Federation of European Neuroscience Societies

OPINION

A Reconsideration of Parallel Processing in Vision: Importance of Lower Spatial Frequencies to Form Vision

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Received: 1 September 2025 | **Revised:** 21 October 2025 | **Accepted:** 23 October 2025

Associate Editor: John Foxe

Funding: This work was supported by the National Eye Institute (EY012576, EY036242, and P50MH132642), National Institute of Neurological Disorders and Stroke (R01 NS094184).

Keywords: acuity | magnocellular and parvocellular cells | spatial frequency | vision | X and Y cells

ABSTRACT

The appreciation of parallel visual pathways from retina to cortex in mammalian vision has greatly advanced our understanding of sensory processing. While these anatomical pathways are well-characterized, their specific functional roles remain incompletely understood, particularly in terms of parsing natural scenes. Here, we start with a re-evaluation of the functional contributions of parallel X and Y pathways in the cat, emphasizing the underappreciated role of Y cells in spatial vision. Contrary to the traditional view that prioritizes the importance of high acuity for visual function and thus the role of X cells, because they support high acuity vision, we argue that lower spatial frequencies are more important for visual function. For instance, these lower frequencies dominate natural visual scenes, and Y cells are much more responsive to these than X cells are. We provide further anatomical and behavioral evidence that the Y pathway plays the dominant role in basic spatial vision, particularly during active vision. These findings challenge the adequacy of visual acuity and the X pathway as a proxy for visual function and underscore the need to consider functioning in response to natural scenes in models of visual processing. Implications for primate and rodent vision are discussed, including the need for comparative and integrative research and the importance of understanding similarities and differences across species.

The discovery of parallel X and Y[1] retino-geniculo-cortical pathways in the cat, later extended to the W pathway and to the monkey visual system (Enroth-Cugell and Robson 1966; Sherman 1985a; Sherman 1985b: Casagrande and Xu 2004; Sherman and Guillery 2013; Usrey and Sherman 2022), transformed thinking about the functional organization of sensory pathways. Whereas this arrangement is well-documented, the question of the functional significance of these pathways remains enigmatic. For instance, what distinct functional differences are involved in the processing of these parallel pathways?

1 | Function of X and Y Pathways in the Cat

The X and Y pathways in the cat have been extensively classified as two unique and clearly defined neuronal circuits (Sherman 1985a; Sherman and Guillery 2013; Usrey and Sherman 2022). In contrast, the W cell stream is poorly understood and remains to be properly classified. It appears to include a number of separate types with variable properties and is often simply regarded as "neither X nor Y". For these reasons, the W cell projections remain functionally enigmatic and are not

further considered in detail here. On the other hand, specific hypotheses for the functioning of X and Y pathways have been advanced and are done so here as an update to earlier hypotheses (Sherman 1985a; Sherman 1985b).

Details of the functional properties and organization of these pathways can be found elsewhere (Stone 1983; Casagrande and Xu 2004; Sherman and Guillery 2013; Usrey and Sherman 2021; Usrey and Sherman 2022), and some are considered below. Figure 1 shows a cartoon view of the geniculocortical projection patterns of these parallel pathways in the cat, as well as in the monkey and mouse. In the cat (Figure 1A), geniculate X cells primarily innervate visual cortex (V1) in the bottom half of Layer 4 with a smaller projection to Layer 6, whereas Y cells innervate the upper half of Layer 4 and Layer 6.

1.1 | Responses of X and Y Cells

Most early suggestions for the functions of these parallel retino-geniculocortical pathways derive from the response properties of retinal ganglion and lateral geniculate cells. Particularly important in this regard are their responses to spatial and temporal stimuli. Figure 2A,B shows these features for average cat geniculate cell responsiveness. Shown is neuronal contrast sensitivity as a function of the spatial (Figure 2A) or temporal (Figure 2B) frequency of sinusoidal grating stimuli. Contrast sensitivity is defined as the inverse of the lowest contrast that evokes a response, and the more sensitive, the greater the neuronal response to that frequency. X cells show better responses to finer gratings (higher spatial frequencies), indicating better spatial resolution or acuity, whereas Y cells are more responsive to lower spatial frequencies and to all temporal frequencies. This has led to a common hypothesis: "Cat X cells handle fine detail and are important for pattern discrimination while Y cells signal change and movement" (Shapley and Perry 1986).

1.2 | Importance of Low Spatial Frequencies for Vision

This idea of the X cell importance in spatial vision is likely related to the conventional view of acuity in determining the quality of spatial vision. For instance, clinical eye exams for vision quality typically test how small an object one can discriminate, such as a letter or a small gap in a line segment. Normal vision is "20/20," which translates to being able to discriminate an object at a distance of 20 ft, but not further, that a normal observer can discriminate at 20 ft; 20/40 vision is poorer, meaning that one can discriminate an object at 20 ft that a normal observer can discriminate at 40, and 20/10 vision is better than average, because the observer can discriminate an object at 20 ft that a normal observer can only discriminate at 10 ft or nearer. In general, one with visual acuity of 20/200 or less is considered legally blind[2]. As noted below, this measure of visual quality, while useful, is severely limited and often misleading.

A major criticism of the idea that X cells are the primary basis for spatial vision involves the importance of low spatial frequencies for vision. Y cells are far more responsive to these lower frequencies than X cells (Figure 2A), which is of interest, because the spatial analysis of natural scenes in which visual systems evolved to operate indicates that these are dominated by lower spatial frequencies, and the falloff toward higher frequencies is rather steep (Figure 2C) (Tolhurst

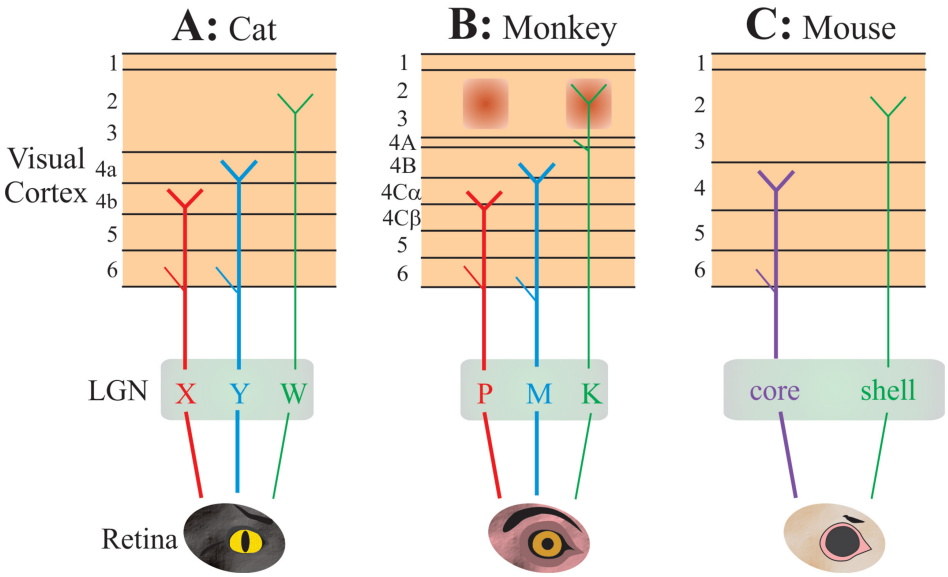

FIGURE 1 | Cartoon illustrating the organization of the retino-geniculo-cortical pathway in the cat (A), monkey (B), and mouse (C). In the cat, there are three major parallel pathways to cortex—the X cell pathway terminates primarily in layer 4b, the Y cell pathway terminates primarily in layer 4a, and 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 4Cβ, the magnocellular (M) pathway terminates in layer 4Cα, and the koniocellular (K) pathway terminates in the Layer 1–3 blobs. In mice, the 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. From Usrey and Sherman (2022).

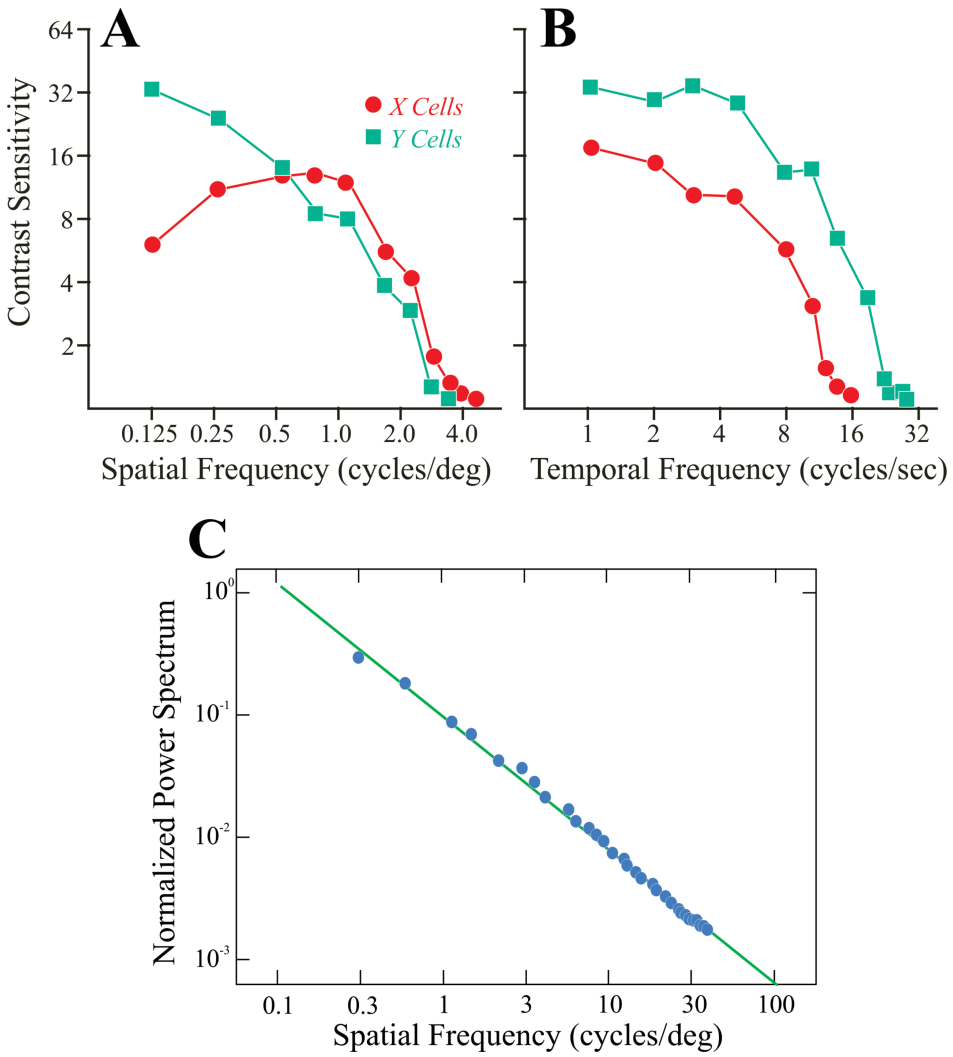

FIGURE 2 | Response functions of X and Y pathways. (A) Spatial contrast sensitivity functions for geniculate X and Y cells in the cat. (B) Temporal contrast sensitivity functions. (C) Representation of spatial frequencies in natural scenes. (B and A) redrawn from Lehmkuhle et al. (1980). (C) redrawn from Roberts et al. (2022).

et al. 1992; van der Schaaf and van Hateren 1996; Roberts et al. 2022). This relationship is roughly as follows: The power represented by each spatial frequency is proportional to the inverse of its value (Tolhurst et al. 1992; van der Schaaf and van Hateren 1996; Roberts et al. 2022). Figure 3 illustrates the importance of lower spatial frequencies in our ability to interpret visual scenes. When only the lowest 10% (Figure 3B) of the image is seen after low pass filtering, there is little difficulty in properly interpreting the image even with the resultant blurring (see insets enlarged from Figure 3A,B). However, with high pass filtering, when the upper 90% (Figure 3D) of spatial frequencies are available, the interpretation of the image is much less certain.

One point that might be derived from Figures 2C and 3 is that measures of acuity alone are insufficient to evaluate vision, given the importance to vision of low spatial frequencies that are ignored in acuity measurements. Indeed, there is a vast literature on the contribution of different spatial frequency ranges to various aspects of visual processing (De Valois and De Valois 1980; Graham 1981; Kauffmann et al. 2014; Groen et al. 2017; Schütt and Wichmann 2017), including the highly specialized field of face recognition (e.g., Collin et al. (2006); Gao and Maurer (2011); Jeantet et al. (2017); Lacroix et al. (2022). However, consideration of this in detail is beyond the scope of this Opinion piece. Here, we aim to focus on the relatively unappreciated importance to general visual performance of low spatial frequencies and what this suggests for the functional significance of parallel visual processing.

One might conclude from Figures 2C and 3 that a measure of spatial acuity alone for vision is rather limited, and a test of the ability to respond to lower spatial frequencies would be far more revealing. Relative to the X system, the superior performance of the Y system in these lower spatial frequencies suggests its importance in processing spatial vision.

1.3 | Anatomical Features

A consideration of the central pathways of the X and Y streams to cortex also supports the importance of the Y pathway for basic spatial vision.

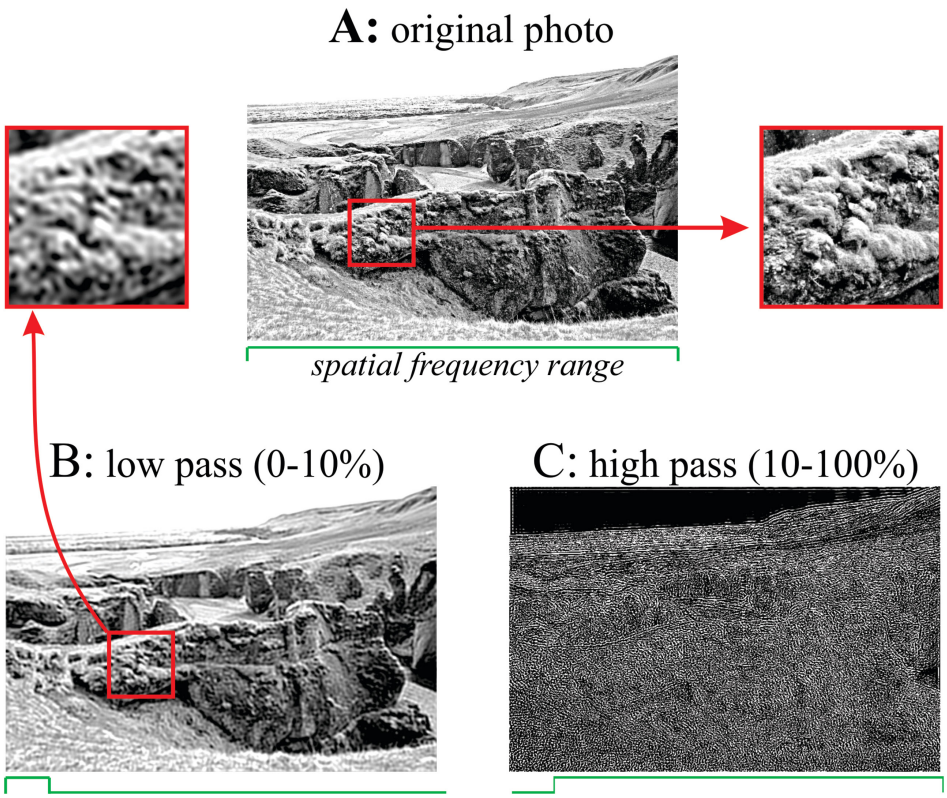

FIGURE 3 | Effect of Fourier filtering of photographic image of a landscape. (A) Original, in focus image. (B) Low pass filtered image so that only the lowest 10% of spatial frequencies are included. The insets (via red arrows) show the blurring effect of the low pass filtering. (C) High pass filtered image so that the highest 90% of spatial frequencies are included. This is the opposite filtering of that in (B) Fourier filtering achieved with ImageJ (https://imagej.net/ij/).

1.3.1 | Organization of X and Y Retinal Ganglion Cells

In order to subserve spatial vision, any parallel pathway from the retina must start with the participating ganglion cells completely tiling the retina. This means that their receptive fields fully cover the entire retina. In a classic pair of papers, Wässle, Boycott, and Illing (1981); Wässle, Peichl, and Boycott (1981) showed that this indeed occurs. A summary of their results is shown in Figure 4. Two points are emphasized here. First, the receptive field size covered by each cell roughly corresponds to the extent of their dendritic arbor, and thus, the area covered by each Y receptive field is roughly 10 times larger than that for X receptive fields (Figure 4A). This size difference is consistent with the contrast sensitivity functions shown in Figure 2A, because the better responsiveness of X cells to finer gratings, implying greater spatial acuity, requires denser tiling of the retina and smaller receptive fields. Second, each X and Y system completely tiles the retina in a roughly hexagonal array (Figure 4B). Shown is a schematic version of the tiling for on center cells; the off center arrays would be similar but slightly and randomly offset from those of the on center cells.

However, because Y cell receptive fields are roughly 10 times larger in area than those of X cells, the X to Y cell ratio among ganglion cells is roughly 10–1 (Stone 1978; Stein et al. 1996). This factor alone, namely, that X cells relative to Y cells seem to dominate retinal circuitry, led some to conclude that X cells are the major substrate for vision. As we shall see, this is akin to (mis)judging a book by its cover.

1.3.2 | Organization of X and Y Geniculate Cells

The X to Y cell ratio among geniculate relay cells is vastly different from the retinal ratios: The geniculate ratio is estimated at roughly 1 to 1 (Friedlander et al. 1981). This transformation is achieved mainly through the difference in retinogeniculate circuitry: Compared to retinal X axons, Y axons produce many more synaptic inputs over a larger region of the lateral geniculate nucleus (Sur et al. 1987), resulting in the innervation by each of roughly an order of magnitude more relay cells (Figure 5).

1.3.3 | Organization of X and Y Geniculocortical Axons

A similar relative expansion of the Y pathway compared to the X is seen in their projections to visual cortex. As is the case for retinogeniculate axon arbors, Y geniculocortical arbors produce more synapses, which happen to extend over a larger volume, than do X arbors (Humphrey et al. 1985a; Humphrey et al. 1985b). This is true not only for the terminations in V1, but, in addition, many Y axons branch to innervate V2 as well, whereas X axons only innervate V1. It is difficult to extend this to a quantitative estimate of how much cortical circuitry is controlled by either pathway, but at least for the first synapse into cortex, it appears that the Y system dominates by a ratio of something like 5 to 1 (Humphrey et al. 1985a); Humphrey et al. 1985b.

This analysis indicates that the relative importance of the two pathways as far as cortex is concerned appears to be a reversal

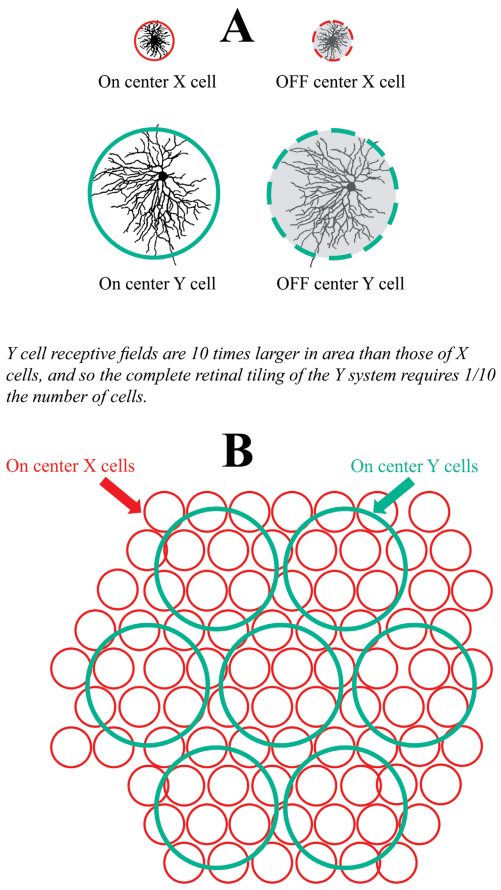

FIGURE 4 | Tiling of cat's retina. (A) Area covered by each X and Y ganglion cell roughly equivalent to area covered by each dendritic arbor. Note that the Y cell arbor coverage is roughly 10 times larger in area than that of the X cell. (B) Tiling basically takes the form of hexagonal arrays. Because of the size difference of each units coverage, there are roughly 10 times more X cells required than is the case for Y cells. Redrawn from Wässle, Boycott, and Illing (1981); Wässle, Peichl, and Boycott (1981).

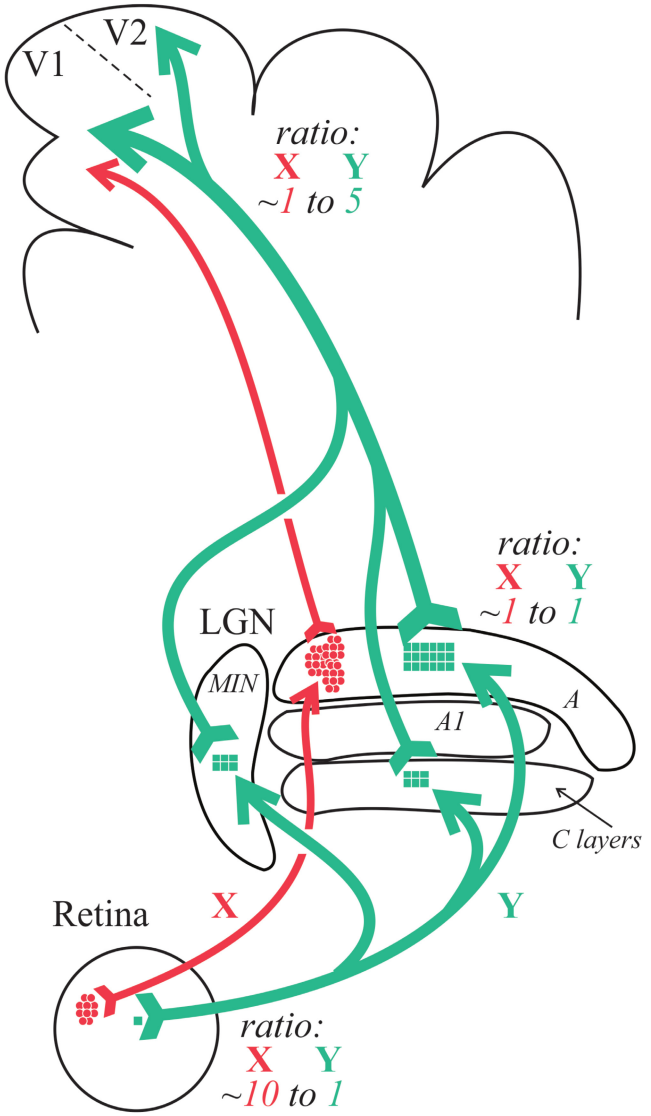

FIGURE 5 | Relative sizes of X and Y pathways from retina to cortex in the cat. See text for details.

of the appearance in the retina. As noted, the ratios in the retina are dictated by the need to tile the retina, meaning that the system (X) with smaller receptive fields requires more units for complete tiling. This, in itself, does not say much more about relative importance or functioning except for support of spatial acuity. Furthermore, the cortex has roughly 10^8 neurons and 10^{12} synapses compared to 10^5 and 10^8 for the retina, and thus, the cortex would appear to be a more relevant site to determine relative functional significance.

1.4 | Behavioral Correlates

Finally, there are some behavioral data consistent with the relative importance of the Y pathway for basic spatial vision. Psychophysical contrast sensitivity functions in cats show that an ablation of V1, which eliminates all X cell representation in the cortex but preserves some Y cell input (e.g., to V2), seems only to reduce the spatial acuity of the cat with other aspects of spatial vision preserved (Figure 6) (Berkley and Sprague 1978, 1979; Lehmkuhle et al. 1982).

1.5 | Hypotheses Regarding the Importance of the Y Pathway for Basic Spatial Vision

There are several general conclusions that may be drawn from this analysis.

1.5.1 | Cats Are Not Blind

Humans are able to resolve gratings as fine as 60 cycles/degree, which reflects 20/20 vision. The cat can only resolve about 6 cycles/degree, meaning that they have 20/200 vision. As indicated above, this is the legal definition of blindness. But anyone who has observed cats appreciates that their vision is quite good. Recall that cats have excellent sensitivity to low spatial frequencies (Figure 6B) and that lower frequencies dominate natural scenes (Figures 2C and 3). It is this, and not high spatial acuity,

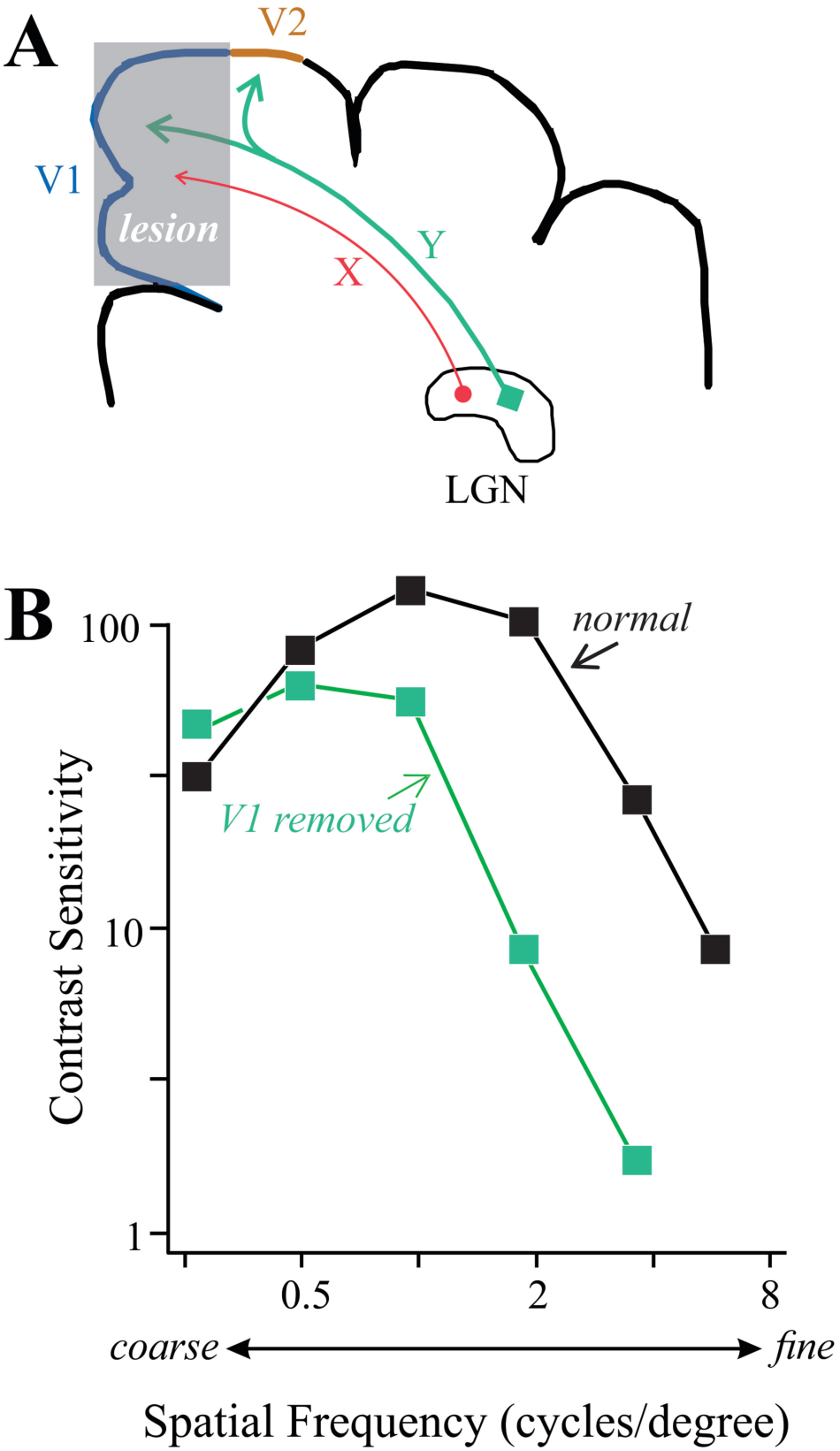

FIGURE 6 | Psychometric behavioral data for different cats. (A) Geniculate X cells innervate only V1, whereas Y cells innervate both V1 and V2. Thus, a lesion to V1 effectively abolishes the X pathway to cortex but leaves much of the Y pathway to V2 intact. (B) Contrast sensitivity functions for normal cats and those with V1 lesions (A). Redrawn from Lehmkuhle et al. (1982).

that confers excellent vision for cats and emphasizes the limitation of defining vision based solely on visual acuity.

1.5.2 | Y Cells Provide Basic Spatial Vision for the Cat

Several factors point to the relative importance of the Y versus the X system for basic spatial vision:

- Anatomical data indicate that Y geniculocortical synaptic inputs far outnumber those from the X pathway.
- Psychophysical evidence also supports the relative importance of the Y system.
- Y cells are far more responsive than are X cells to lower spatial frequencies, and it is these lower frequencies that dominate natural visual scenes.

What, then, is the functional significance of the X system? Its main advantage over the Y system seems to be as a substrate for improved acuity. It may be that a primary analysis of visual scenes is carried out by the Y system, and the X, where possible, mainly adds spatial resolution to the mix. Consider that the best acuity can only be achieved when the eyes are in proper focus. However, when the object of interest requires refocusing of the eyes, it takes 0.5 to 1 s or more to do so in order to maintain best acuity (Mordi and Ciuffreda 2004). Imagine a cat racing through the underbrush in pursuit of a mouse: There is not time for its eyes to accommodate to the shifting visual environment as objects change in relative distance to the active cat. This means that the images on the retinas are blurred, which in turn means that high spatial frequencies are lost and the cat is operating mostly via lower frequencies supported by the Y system. The X system thus may not be of much use when the animal is actively moving through the environment, times that often involve life-or-death scenarios. Instead, the X system is most useful when the cat is relatively inactive and has time to properly focus its eyes.

Finally, it must be strongly emphasized that this hypothesis for the primacy of the Y system for basic spatial vision represents an unproved hypothesis that is highly speculative. An important proviso regards our ignorance of functional features of the W system. For instance, evidence for the importance of the Y pathway is seen in its better responsiveness to lower spatial frequencies (Figure 2A) and also in the visual abilities of cats after removal from the cortex of the X pathway (Figure 5B). However, it is logically possible that the W system also supports low spatial frequency vision and can support spatial vision in the absence of the X pathway. In any case, the goal here is not necessarily to convince the reader to accept these ideas but rather to think about these issues in perhaps a new light.

2 | Relevance to Vision in Monkeys and Mice

Analysis of retino-geniculo-cortical pathways in monkeys and mice lags far behind that in cats. Thus, hypotheses regarding the significance of parallel processing in these species are relatively poorly developed. Nonetheless, in the context of the above consideration of vision in cats, certain points are worth emphasizing and exploring further.

2.1 | Application to Monkey Vision

How does any of this relate to the differential functioning of the parvocellular and magnocellular pathways in humans and monkeys? For monkeys, the case is made that appropriate homologies exist with cats: Cat X and Y pathways are homologous, respectively, to the primate parvocellular and magnocellular pathways (Casagrande and Xu 2004; Usrey and Sherman 2022).[3] Figure 1A,B shows some of the evidence for this homology: X cells and parvocellular cells innervate Layer 4 ventral to that of Y cells and magnocellular cells, and both W cells and koniocellular cells primarily innervate Layers 2/3. Additionally, molecular markers unique to the X and Y pathways also highlight the parvocellular and magnocellular pathways, respectively (Hendry et al. 1984; Hockfield and Sur 1990; Iwai et al. 2013). However, homology does not necessarily mean equivalent function, since evolution often works to produce different functional properties for homologous structures. An example is our arms and hands versus the wings of birds and bats; these are homologous but evolved to produce very different functions. Unfortunately, the relevant data to parse functional properties in the primate pathways, such as a detailed anatomical evaluation available for cat X and Y pathways, are generally lacking for the parvocellular and magnocellular streams.

One important difference between cat and monkey is that the relative expansion of the Y to X representation in retinogeniculate circuitry is not seen in the monkey in terms of a similar expansion of the magnocellular pathway: In the monkey, the parvocellular to magnocellular cell ratio is roughly 10 to 1 in both the retina and lateral geniculate nucleus (Perry et al. 1984; Ahmad and Spear 1993; Hendry and Reid 2000). However, there is a relative expansion of the magnocellular pathway in the geniculocortical projection (Blasdel and Lund 1983). Clearly, we need to understand more regarding the relative dominance of either pathway in cortical processing.

An intriguing hint to the separate functioning of these pathways in monkeys may be derived from studies of how parvocellular and magnocellular cells respond to visual stimuli. Figure 7 shows how these cells in the lateral geniculate nucleus of monkeys respond to different spatial and temporal frequencies. Compared to parvocellular cells, magnocellular cells are considerably more responsive at all temporal frequencies, but regarding spatial vision, they are more responsive at lower spatial frequencies and less so at higher ones (Derrington and Lennie 1984; Movshon et al. 2005; Alitto et al. 2011; Usrey and Alitto 2015). Thus, like cat Y cells, monkey magnocellular cells provide more responsiveness to these lower frequencies. An important behavioral correlation has been described: Lesions of magnocellular geniculate neurons affect discrimination of drifting gratings at lower spatial and higher temporal frequencies (Merigan and Maunsell 1990), and lesions of parvocellular geniculate cells affect discrimination at higher spatial and lower temporal frequencies (Merigan et al. 1991).

Recall that lower spatial frequencies in natural scenes are more prominent than higher ones (Figures 2C and 3). Perhaps the cat Y and primate magnocellular pathways are both homologous and serve a similar function as a basic substrate for spatial vision. As noted above, an animal moving rapidly through its environment cannot achieve optical focus fast

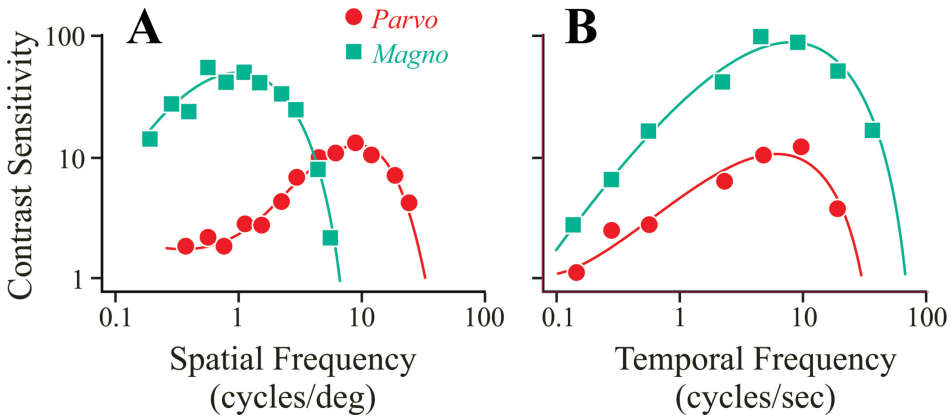

FIGURE 7 | Response functions of geniculate parvocellular and magnocellular cells in the monkey. (A) Spatial functions. (B) Temporal functions. Redrawn from Movshon et al. (2005).

enough to maintain its best visual acuity. This would apply, for instance, for a monkey swinging through the trees, which is consistent with the idea that the magnocellular system is more important for the monkey's vision during periods of activity. In this regard, just as the cat X system adds improved acuity, the monkey parvocellular system adds acuity and color sensitivity, properties that are particularly emphasized in the fovea but are available mainly during periods of inactivity when proper focus can be maintained. Unfortunately, much more data are needed to parse functional properties in the primate pathways, but this remains an important issue that needs further study.

Finally, some studies in humans, whose visual systems have magnocellular and parvocellular parallel pathways much like those in monkeys, provide data that emphasize the importance of low spatial frequencies and the magnocellular stream for spatial vision. Behavioral and functional magnetic resonance imaging studies show that visual object recognition is initiated by processing of low spatial frequencies suggested to be the result of processing by the magnocellular stream (Cheng et al. 2004; Bar et al. 2006).

2.2 | Application to Mouse Vision

Compared to our understanding of the components of retino-geniculo-cortical processing in cats and monkeys, such knowledge in mice is especially lacking. Limited evidence for homology exists related to the organization of the mouse lateral geniculate nucleus into core and shell regions. There are two relevant observations (Casagrande and Xu 2004; Sherman and Guillery 2013; Usrey and Sherman 2021; Usrey and Sherman 2022): like cat W cells and monkey koniocellular cells, the shell projection to cortex primarily targets layers 2/3; and there is a large projection from the superior colliculus to the lateral geniculate nucleus that primarily targets cat W cells, monkey koniocellular cells, and the shell region in the mouse (Harting et al. 1978; Torrealba et al. 1981; Harting et al. 1991; Bickford et al. 2015; Kerschensteiner and Guido 2017). What is lacking is a firm understanding of the relationship between mouse geniculate cells and the X and Y cells or magnocellular and parvocellular cells in cats and monkeys, respectively; such data are much needed. Without a proper classification of these pathways in mice, it is impractical to attempt any detailed homology of these circuits with those of cats and monkeys. However, the mouse visual system has become an important neuroscientific model, and there are a few possibly interesting points that can be made about their visual capabilities.

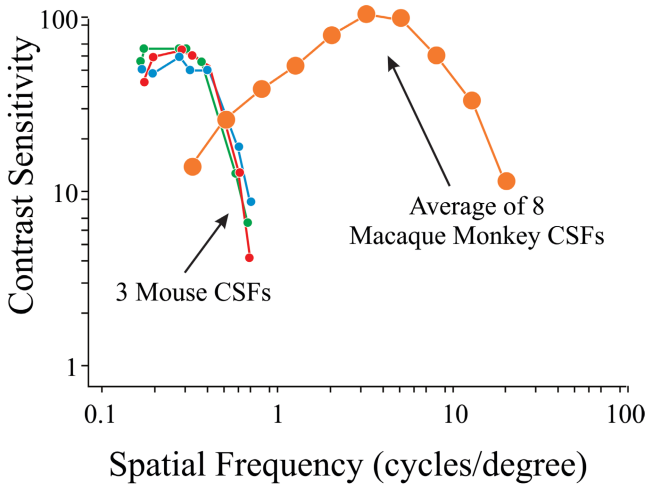

FIGURE 8 | Spatial contrast sensitivity functions for mice and macaque monkeys. Data from three mice redrawn from Histed et al. (2012). Data averaged from eight monkeys redrawn from Ridder et al. (2019).

One knock on the mouse model is that mice have extremely poor spatial vision. Figure 8 shows spatial contrast sensitivity functions for three mice. Clearly, they have very poor acuity. Peaking at perhaps 0.6 cycles/degree, this would mean 20/2000 vision. It seems that such poor acuity is a major reason for the "blind mice" label. However, it might be relevant to compare sensitivity across the visual spectrum between mice and monkeys, also shown in Figure 8. Based on these examples, mice have better sensitivity to very low spatial frequencies (e.g., <0.1 cycles/degree), and the importance to vision of these low frequencies has been repeatedly stressed. Indeed, under certain conditions, mice show visual capabilities far better than might be expected from data such as shown in Figure 8 (Hoy et al. 2016; Dyballa et al. 2018).

3 | Conclusions

We suggest several conclusions and useful hypotheses that may be tested and can be drawn from the ideas presented here.

We argue that Figures 2C and 3 strongly make the case that good spatial vision in natural settings relies much more on lower rather than higher spatial frequencies. Yet, the visual capability of animals, including humans in clinical settings, is typically assessed from a determination of spatial acuity, which measures the visibility of higher spatial frequencies. We suggest that this can often be quite misleading. For instance, it supports the notion that cats are blind because of their relatively poor acuity,

Indeed, if we compare the spatial functions shown in Figures 6 and 8, we see that cats have better sensitivity at the low spatial frequency of 1 cycle/degree than do monkeys, and mice are better than monkeys at 0.1 cycles degree. It would be a gross misrepresentation of our argument here that mice and cats see better than monkeys, but the better vision of monkeys may be largely attributed to the much larger regions of the brain devoted to visual processing. The point we wish to make is that acuity itself is an uncertain measure of overall visual performance and that the capabilities of animals such as cats and mice with relatively poor acuity have been underappreciated.

Regarding how all of this relates to understanding parallel processing in the retino-geniculo-cortical pathways, we have suggested the following. For a variety of reasons, including neuronal responsiveness, behavioral data, and anatomical analysis of the parallel pathways, we have suggested that, for cats, the Y system provides basic spatial analysis, and that the X system adds to it improved acuity under relatively calm conditions during which proper ocular focusing can be achieved. Relevant data from the monkey are much scarcer, but they are consistent with the idea that the magnocellular system is both homologous and functionally equivalent to the cat Y system, thereby providing for basic spatial vision, whereas the parvocellular system (homologous to the cat X system) provides for better acuity and color vision. We emphasize that this last point about the monkey pathways is extremely speculative. Unfortunately, for the mouse, we simply lack relevant data to identify, and much less analyze, the separate parallel visual pathways.

We stress again that a major proviso to these arguments is our general ignorance of the classification and functioning of the W (cat) and koniocellular (monkey) pathways.

Finally, we reiterate that the ideas expressed here are ideas to be challenged. Our goal is not to convince the reader that these hypotheses are correct but rather that they are worth pursuing.

Author Contributions

S. Murray Sherman: conceptualization, writing – original draft, writing – review and editing. **W. Martin Usrey:** conceptualization, writing – original draft, writing – review and editing.

Acknowledgments

We thank Marlene Cohen for helpful comments regarding the manuscript and Narayanan Kasthuri for help with the graphics. S.M.S. is supported by grants from the NINDS (R01 NS094184). W.M.U. is supported by grants from the NEI (P50MH132642 and P30 EY012576). Both are supported by a grant from the NEI (R01 EY036242).

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ejn.70313.

Endnotes

[1] Terminology can be confusing. X and Y cells have at times been referred to respectively as "sustained" and "transient", "linear" and "nonlinear", and "beta" and "alpha" (for the morphology of their respective retinal ganglion cells). We stick here to "X" and "Y".

[2] See statement from the American Optometric Association: https://www.aoa.org/news/clinical-eye-care/diseases-and-conditions/legal-blindness-in-america.

[3] A general relationship also exists for cat W and monkey koniocellular pathways. However, in both cases, these pathways seem to be an as yet unclassified mixture of different types with poorly understood properties. As is the case for the cat W pathway, the monkey koniocellular pathway is not further considered here in any detail.

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