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CHAPTER 1

Retinogeniculate connections: a balancing act between connection specificity and receptive field diversity

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Abstract: Retinogeniculate connections are one of the most striking examples of connection specificity within the visual pathway. In almost every connection there is one dominant afferent cell per geniculate cell, and both afferent and geniculate cells have very similar receptive fields. The remarkable specificity and strength of retinogeniculate connections have inspired comparisons of the lateral geniculate nucleus (LGN) with a simple relay that connects the retina with the visual cortex. However, because each retinal ganglion cell diverges to innervate multiple cells in the LGN, most geniculate cells must receive additional inputs from other retinal afferents that are not the dominant ones. These additional afferents make weaker connections and their receptive fields are not as perfectly matched with the geniculate target as the dominant afferent. We argue that these 'match imperfections' are important to create receptive field diversity among the cells that represent each point of visual space in the LGN. We propose that the convergence of dominant and weak retinal afferents in the LGN multiplexes the array of retinal ganglion cells by creating receptive fields that have a richer range of positions, sizes and response time courses than those available at the ganglion cell layer of the retina.

Keywords: thalamus; thalamocortical; visual cortex; V1; Y cell; X cell; response latency; simultaneous recording

The cat eye has 160,800 retinal ganglion cells that fit within a retinal area of 450 mm^2 (Illing and Wassle, 1981). One-half of these cells (53–57%) has small receptive fields and is classified as X and a much smaller proportion (2–4%) has larger receptive fields and is classified as Y (Enroth-Cugell and Robson, 1966; Friedlander et al., 1979; Illing and Wassle, 1981). X and Y retinal ganglion cells are the origin of two major functional channels within the cat visual pathway that remain relatively well segregated within the lateral geniculate nucleus (LGN) (Cleland et al., 1971a, b; Mastronarde, 1992; Usrey et al., 1999). These two major channels have pronounced anatomical differences. For example, the X retinal afferents have very restricted axon terminals (~100 μm diameter) that are confined to a single layer of LGN and connect small geniculate cells. In contrast, the Y axon terminals are twice as large, usually diverge into two different LGN layers (Sur and Sherman, 1982; Sur et al., 1987) and connect geniculate cells with large dendritic trees that tend to cross layer boundaries (Friedlander et al., 1979; Fig. 1).

X and Y retinal ganglion cells diverge at the level of the LGN to connect up to 20 geniculate cells per

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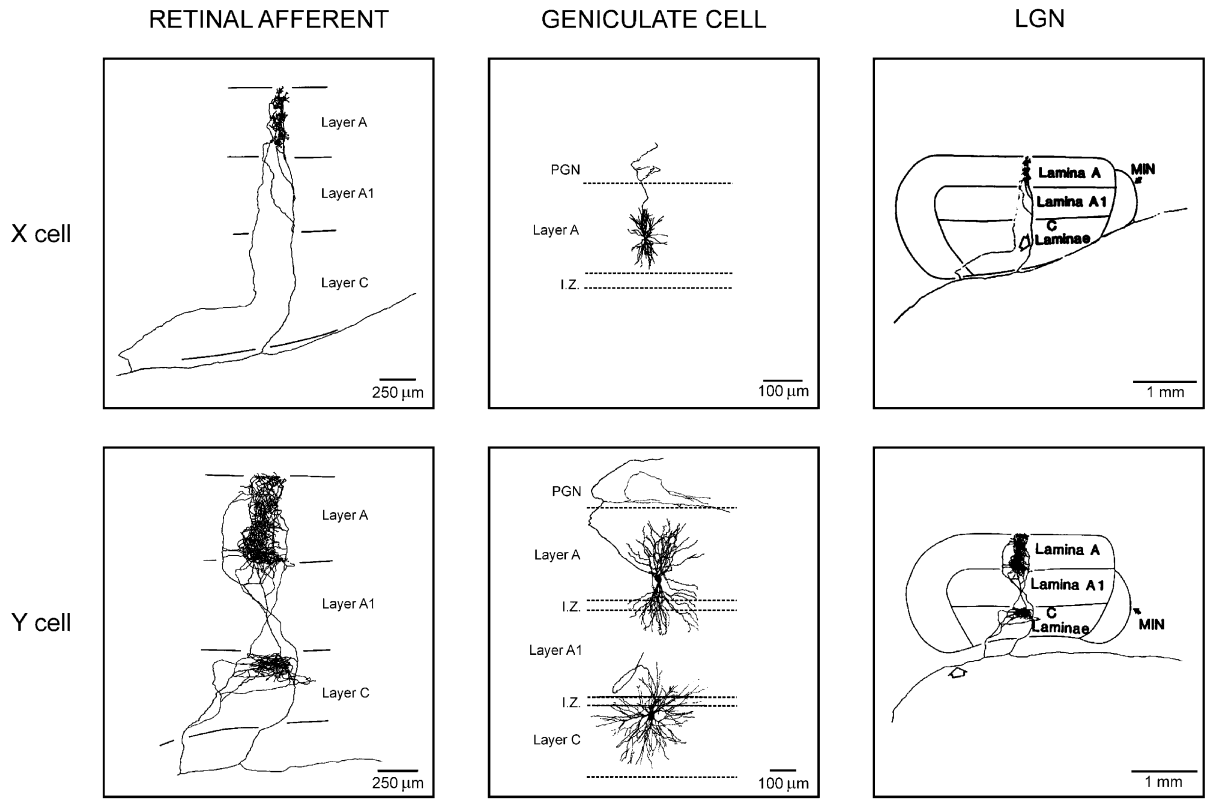

Fig. 1. Retinal afferents and geniculate cells. Left: axon terminals from X and Y retinal afferents in LGN. X retinal axons project into a single LGN layer and they are very restricted. Y retinal axons can project into two different LGN layers and are wider. Middle: X and Y geniculate cells. X cells have small dendritic trees that are restricted to a single LGN layer. Y cells have larger dendritic trees that frequently cross layers. Right: the same axon terminals on the left of the figure are shown at a different scale. Reprinted with permission from Sur and Sherman (1982); Copyright 1982 AAAS; left and right: Sur (1988); middle: Friedlander et al. (1981). MIN: medial interlaminar nucleus; PGN: perigeniculate nucleus; I.Z.: interlaminar zone.

retinal afferent (Hamos et al., 1987). This divergence could do much more than just copying the properties of each retinal ganglion cell into the geniculate neurons; it could diversify the spatial and temporal properties of the receptive fields that represent each point of visual space. This receptive field diversity could then be used at the cortical level to maximize the spatiotemporal resolution needed to process visual stimuli. In this review, we illustrate this idea with two different examples. In the first example, we show evidence that a single class of Y retinal afferent can be used to build two different types of Y receptive fields within the LGN. In the second example, we show that geniculate neurons representing the same point of visual space have a rich variety of receptive field sizes and response latencies that emerge as a consequence of retinogeniculate divergence/convergence.

Retinogeniculate divergence in the Y visual pathway of the cat

Y retinal ganglion cells are a conspicuous minority within the cat retina (2–4%), which is greatly amplified at subsequent stages of the visual pathway. While X retinal ganglion cells diverge, on average, into 1.5 geniculate cells, Y retinal ganglion cells diverge into 9 geniculate cells (X geniculate cells/retinal cells: 120,000/89,000; Y geniculate cells/retinal cells: 60,000/6700; and the Y cells from layer C are not included in this estimate (LeVay

and Ferster, 1979; Illing and Wassle, 1981; Peters and Payne, 1993)).

The huge amplification of the Y pathway in the cat is reminiscent of the magnocellular pathway in the primate. In the rhesus monkey, there is little retinogeniculate divergence, probably because there is a limit on how many retinogeniculate connections can be accommodated within the LGN (the primate retina has 1,120,000 parvocellular cells and 128,000 magnocellular cells (see Masland, 2001, for review)). However, as in the cat, magnocellular cells are a minority within the primate retina (~8% of all retinal ganglion cells) and, by connecting to magnocellular geniculate cells, they are able to reach a remarkably large number of cortical neurons — at the cortical representation of the fovea in layer 4C, magnocellular geniculate cells connect about 29 times more cortical cells than parvocellular geniculate cells (Connolly and Van Essen, 1984). Interestingly, neuronal divergence seems to be delayed by one synapse in primate with respect to the cat, as is also the case for the construction of simple receptive fields (Hubel and Wiesel, 2005).

The cat LGN is an excellent model to study the functional consequences of the Y pathway divergence. Unlike the primate, the cat LGN has two main layers that receive Y contralateral input (A and C; A1 receives ipsilateral input) and the retinotopic map of each layer is not excessively folded, making it easier to record from multiple cells with overlapping receptive fields across the different LGN layers. Fig. 2 illustrates the retinotopic map of cat LGN (Fig. 2A) and the response properties of four cells that were simultaneously recorded from different layers. The four cells had on-center receptive fields with slightly different positions and receptive field sizes (Fig. 2B, left). Their response time courses, represented as impulse responses, were also different (receptive fields and impulse responses were obtained with white noise stimuli by reverse correlation (Reid et al., 1997; Yeh et al., 2003)).

As shown in the figure, the Y cells had the largest receptive fields and fastest response time courses within the group. Moreover, the receptive field was larger and the response latency faster for the Y cell from layer C (Y_C, shown in green) than the Y cell from layer A (Y_A, shown in orange). Simultaneous recordings, like the one shown in Fig. 2, allowed us to compare the response properties from the neighboring Y_A and Y_C cells that had overlapping receptive fields. These measurements demonstrated that, on average, the receptive fields from Y_C cells are 1.8 times larger than those from Y_A cells and the response latencies are 2.5 ms faster ($p < 0.001$, Wilcoxon test).

The differences in receptive field size and response latency between Y cells located in different layers were sometimes as pronounced as the differences between X and Y cells located within the same layer. To quantify these differences, we did simultaneous triplet recordings from the neighboring Y_A, Y_C and X_A cells[1]. Fig. 3, top, shows an example of a triplet recording from three off-center geniculate cells of different types (X_A, Y_A and Y_C). The Y_C cell had the largest receptive field and the fastest response latency and the X cell the smallest receptive field and the slowest response latency. For each cell triplet recorded, we calculated a similarity ratio to compare the differences between the Y_A and Y_C cells with the differences between the Y_A and X_A cells. A ratio higher than 1 indicates that the Y_C cell differed from the Y_A cell more than the Y_A cell differed from the X_A cell. As shown in the histograms at the bottom of Fig. 3, in many cell triplets, the similarity ratio for receptive field size and response latency was higher than 1. Moreover, the mean difference in receptive field size was significantly higher for the Y_C–Y_A cells than that for the Y_A–X_A cells ($p < 0.001$, Wilcoxon test). Y_C and Y_A cells also differed significantly in other properties such as spatial linearity, response transience and contrast sensitivity (Frascella and Lehmkuhle, 1984; Lee et al., 1992; Yeh et al., 2003), and are not illustrated here. These results indicate that Y retinal afferents connect to two

[1]The precise retinotopy of LGN and the interelectrode distances used in our experiments strongly suggest that all our recordings came from cells (and not axons) that were located within a cylinder of $<300\,\mu m$ in diameter (Sanderson, 1971). Recordings from axons, which were extremely rare in our experiments, had a characteristic spike waveform (Bishop et al., 1962), and could not be maintained for the long periods of time needed for our measurements.

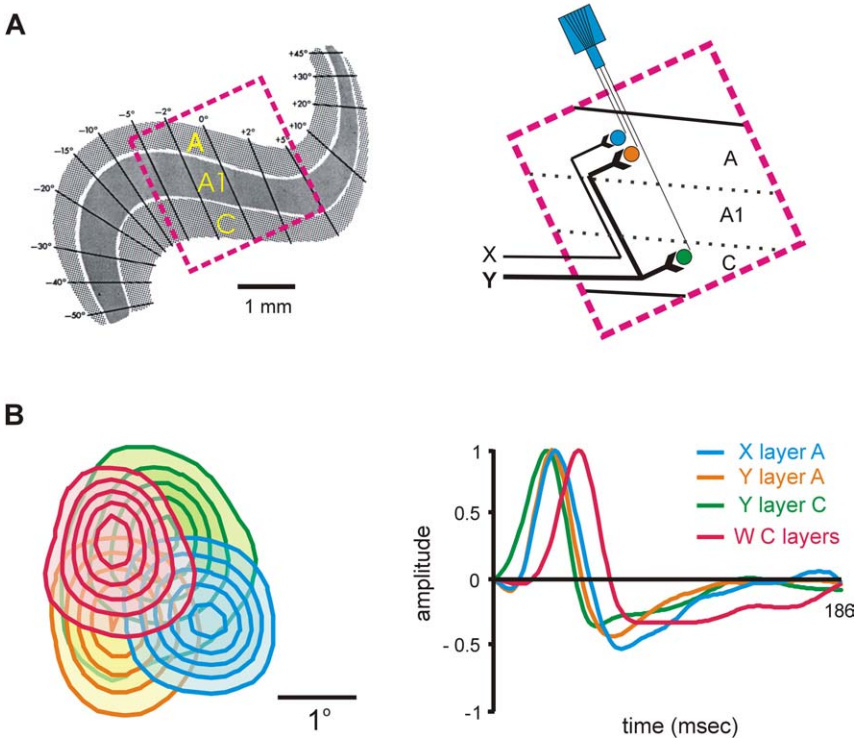

Fig. 2. Simultaneous recordings from four geniculate cells recorded at different layers in the cat LGN. (A) Left: retinotopic map of cat LGN (adapted from Sanderson, 1971). Right: schematic representation of the simultaneous recordings. (B) Left: receptive fields of the four simultaneously recorded geniculate cells mapped with white noise by reverse correlation. The contour lines show responses at 20–100% of the maximum response. Right: impulse responses of the four cells obtained by reverse correlation; the impulse response represents the time course of the receptive field pixel that generated the strongest response. The different cell types are represented in different colors (X cell from layer A, X_A, in blue; Y cell from layer A, Y_A, in orange; Y cell from layer C, Y_C, in green and W cell from the deep C layers in pink). Throughout this review, on-center receptive fields are represented as continuous lines and off-center receptive fields as discontinuous lines. Reprinted with permission from Yeh et al. (2003).

types of Y geniculate cells with significantly different response properties, Y_C and Y_A.

At first sight, this conclusion seems at odds with the idea that retinogeniculate connections are highly specific. If the receptive field of each geniculate neuron resembles very closely the receptive field of the dominant retinal afferent (Cleland et al., 1971a, b; Mastronarde, 1983; Cleland and Lee, 1985; Usrey et al., 1999), it should not be possible to construct two types of Y receptive fields with one type of Y retinal afferent. Certainly, there is no evidence for two types of Y retinal afferents that could match the properties of Y_A and Y_C geniculate receptive fields and almost every Y retinal afferent has been found to diverge in the two layers of the LGN (Sur and Sherman, 1982; Sur et al., 1987).

A better understanding of how Y_A and Y_C receptive fields are generated requires a precise comparison of the response properties from Y_A and Y_C cells that share input from the same retinal afferent. Geniculate neurons that share a common retinal input can be readily identified with cross-correlation analysis because they fire in precise synchrony — their correlogram has a narrow peak of <1 ms width centered at zero (Alonso et al., 1996; Usrey et al., 1998; Yeh et al., 2003). Fig. 4 shows an example of a pair recording from a Y_C cell and a Y_A cell that were tightly correlated (see narrow peak centered at zero in the correlogram, Fig. 4A, bottom). As expected from cells that share a retinal afferent, the receptive fields of the Y_A and Y_C cells were similar in many respects.

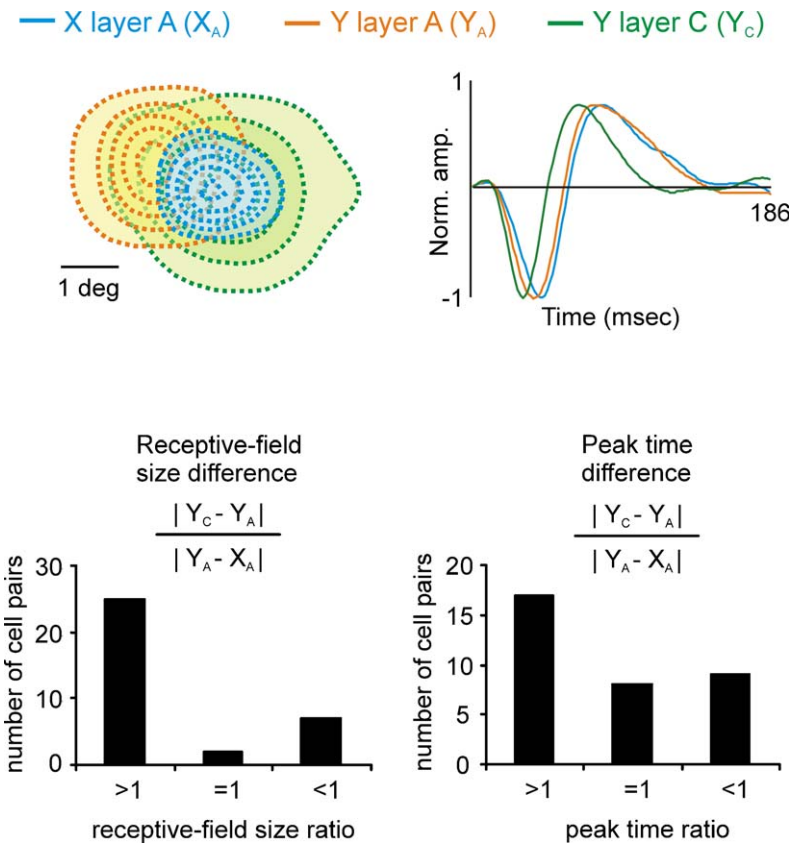

Fig. 3. Comparisons of receptive field size and response latency obtained from triplet recordings of Y_A, Y_C and X_A cells. Top: an example of a triplet recording from three cells with off-center receptive fields. Receptive fields are shown on the left and impulse responses on the right. Bottom: comparisons of receptive field size (left) and response latency (right). An index higher than 1 indicates that the differences between Y_C and Y_A were higher than the differences between Y_A and X_A. An index lower than 1 indicates the opposite. Note that the differences between Y_C and Y_A were frequently higher than those between Y_A and X_A. Reprinted with permission from Yeh et al. (2003).

They were both off-center and they had similar positions in visual space (Fig. 4A, left). On the other hand, the receptive fields showed substantial differences that were reminiscent of the differences between Y_A and Y_C cells described above. For example, the receptive field was larger and the response latency faster for the Y_C cell than those for the Y_A cell (Fig. 4A, top). A similar finding was obtained in recordings from other Y_C–Y_A cell pairs. Y_A and Y_C cells sharing a retinal afferent always had receptive fields of the same sign (e.g., off-center superimposed with off-center) that were highly overlapped (>80%). However, they differed frequently in receptive field size and response latency, probably owing to the inputs from other retinal afferents that were not shared.

Interestingly, cell synchrony across layers was weaker and more frequently found than cell synchrony within the same layer (when considering only cell pairs with >80% receptive field overlap). These findings point to a possible mechanism that could allow two types of Y geniculate receptive fields to be constructed with one type of Y retinal afferent. The weaker and more frequent synchrony across layers could be due to a higher divergence of Y retinal afferents within layer C than within layer A. As a consequence of this higher divergence,

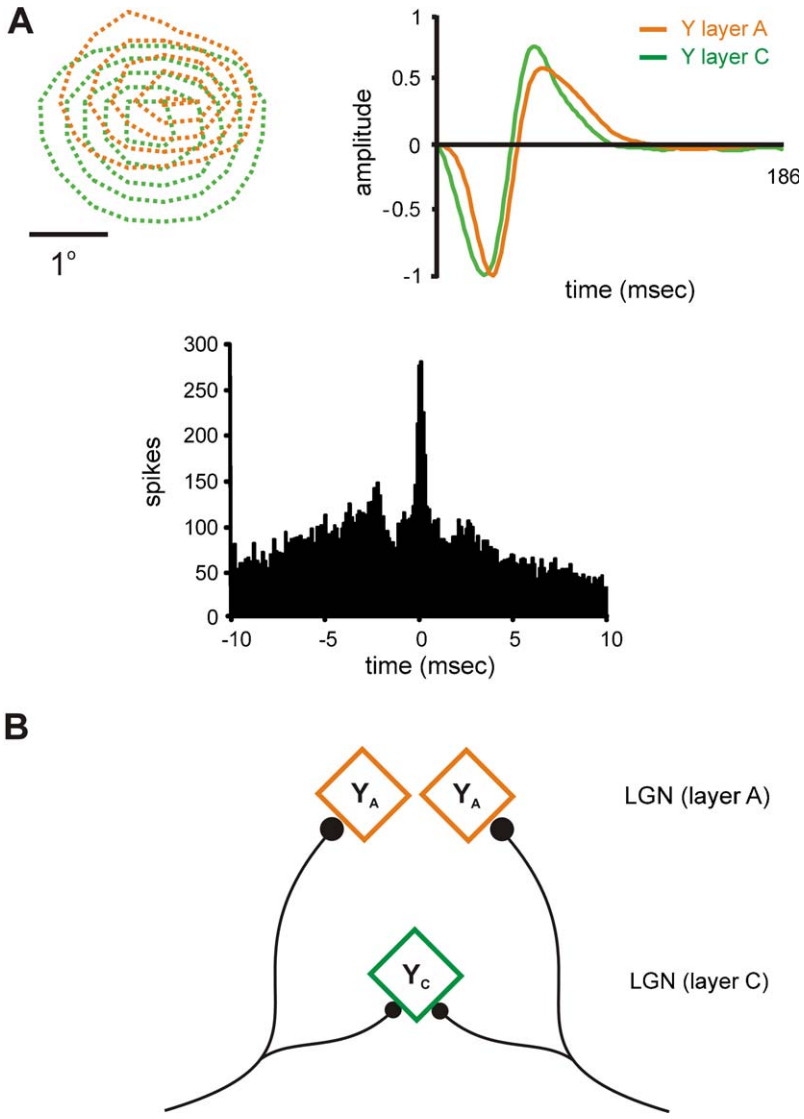

Fig. 4. Different types of Y receptive fields (Y_A and Y_C) are constructed in the LGN with one type of Y retinal afferent. (A) Example of a pair of Y_A and Y_C cells that shared input from the same retinal afferent. The two cells had off-center receptive fields that were well overlapped (top, left). However, the Y_C cell had a slightly larger receptive field and faster response latency (top, right) than the Y_A cell. The correlogram shows, a narrow peak centered at zero indicating that both cells fired in precise synchrony, as is characteristic of cells that share a retinal afferent. (B) Cartoon of a possible neural mechanism to construct two different types of Y receptive fields with a single type of Y retinal afferent. Reprinted with permission from Yeh et al. (2003).

the Y_C geniculate cells would receive input from more retinal afferents than would the Y_A cells (Fig. 4B), and owing to this higher convergence, Y_C cells would have larger receptive fields and faster response latencies than Y_A cells (Fig. 4B; Yeh et al., 2003).

Receptive field properties of geniculate neurons representing the same point of visual space

The differences in the response properties of Y_A and Y_C cells could be an extreme case of a common phenomenon in the LGN: geniculate cells

that share input from a common retinal afferent may have substantially different receptive fields owing to weak retinal inputs that are not shared.

The ganglion cell layer of the retina is a thin structure (<100 μm thickness) that can only accommodate a limited number of retinal ganglion cells to cover each point of visual space (~30 X cells and 5 Y cells in central retina; Peichl and Wassle, 1979). Reaching such coverage factors is particularly challenging at the area centralis, where receptive fields are the smallest and therefore, cell density has to be the highest (6500 X cells/mm^2 and 200 Y cells/mm^2 at the area centralis compared with 80 X cells/mm^2 and 3 Y cells/mm^2 at the far periphery; Peichl and Wassle, 1979). The limited space to fit all these retinal ganglion cells has functional consequences: the receptive fields of neighboring cells of a given type (e.g., X or Y) have to be separated by at least half a receptive field center within most of the retina (Wassle et al., 1981a, b; Mastronarde, 1983; Meister et al., 1995).

In the cat, the limitation in physical space is somewhat alleviated once the retinal ganglion cells leave the eye. Fig. 5A shows the receptive fields of four neighboring geniculate cells that were simultaneously recorded within layer A of the LGN. The four cells had well-overlapped receptive fields of the same sign (off-center). Furthermore, unlike the retina, the receptive field overlap was almost complete among three cells of the same type (Y cell). Moreover, although the three Y cells showed precise synchronous firing indicating that they shared input from the same retinal afferent, their receptive field sizes (Fig. 5A) and response latencies (Fig. 5B) were substantially different. Interestingly, there was a correlation between the receptive field size and response latency (Fig. 5C), suggesting that both properties may be generated by a common

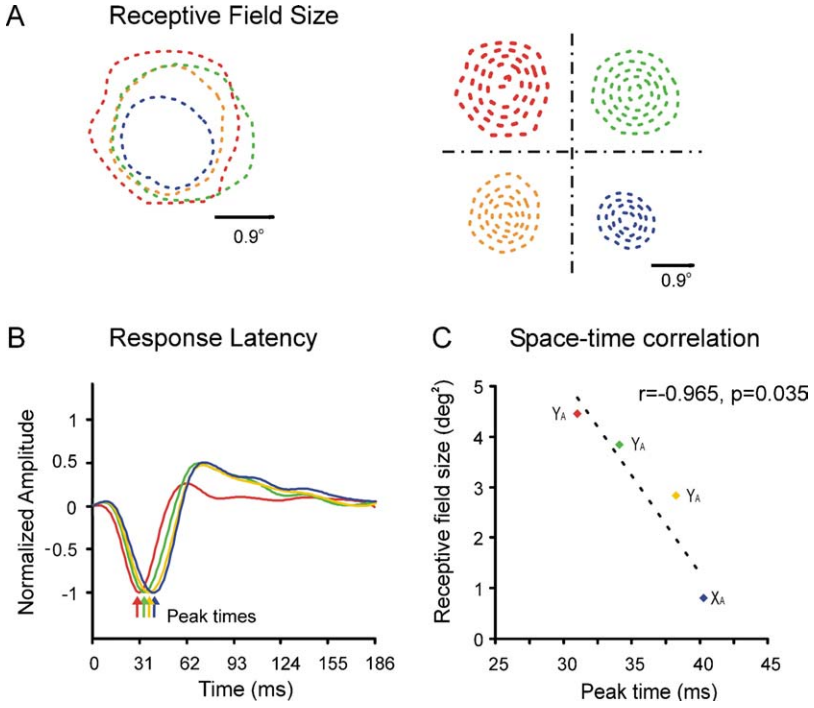

Fig. 5. Receptive field properties of neighboring geniculate neurons that represent the same point of visual space. (A) Receptive fields from four off-center geniculate cells that were simultaneously recorded. The receptive fields of the four neurons have very similar positions, but they differed substantially in size. The receptive fields are shown as contour plots on the right and superimposed on the left (only the 20% contour is shown on the left for clarity). (B) The four neurons also differed in their response latencies, as illustrated by the impulse responses obtained by reverse correlation. (C) There was a strong correlation between receptive field size and response latency: the larger the receptive field, the faster the response to visual stimuli. Reprinted with permission from Weng et al. (2005).

mechanism. Receptive field size and response latency could both be determined by the number of retinal afferents that converge onto a given geniculate cell — more convergent afferents will lead to larger receptive fields and faster responses.

Recordings like the one shown in Fig. 5 demonstrate a surprising diversity of receptive field positions, sizes and response latencies among neighboring neurons within the LGN. This receptive field diversity could provide the cortex with a richer representation of space and time than the one available at the retina.

Multiplexing the receptive field properties of the retinal ganglion cells

The connections from the retina to the LGN are among the strongest and the most specific connections within the visual pathway. One retinal axon can provide more than 100 synapses to the same geniculate cell (Hamos et al., 1987; Chen and Regehr, 2000), a number which is at least 10 times larger than the number of synapses provided by a geniculate axon to a cortical cell (Freund et al., 1985). Moreover, each geniculate cell receives highly specific input from one dominant afferent, whose receptive field is very similar to the geniculate receptive field (Cleland et al., 1971a, b; Cleland and Lee, 1985; Mastronarde, 1992; Usrey et al., 1999).

In addition to the dominant afferent, there are other weak retinal inputs that converge at the same geniculate cell, but whose receptive fields are not a 'near-perfect match' as is the case with the dominant afferent (Cleland et al., 1971a; Mastronarde, 1992; Usrey et al., 1999). The functional significance of these weaker inputs remains unclear. A reasonable possibility is that the weak inputs are remnants of the pruning process during development (Sur et al., 1984; Hamos et al., 1987; Chen and Regehr, 2000). These developmental mistakes (Garraghty et al., 1985) could explain the existence of a few geniculate cells that receive mixed X and Y inputs and have intermediate X/Y properties (Cleland et al., 1971b; Mastronarde, 1992; Usrey et al., 1999). The idea of a developmental error is attractive since most retinogeniculate cells are known to be highly specific of cell type: most X retinal ganglion cells connect to X geniculate cells and most Y retinal ganglion cells connect to Y geniculate cells (Cleland et al., 1971a, b; Cleland and Lee, 1985; Mastronarde, 1992; Usrey et al., 1999). However, our simultaneous recordings from neighboring geniculate cells suggest an alternative interpretation. The weak retinal inputs could be important to interpolate the spatiotemporal receptive fields of the retinal ganglion cells into a more continuous representation of visual space and time (see also Mastronarde, 1992, for a similar idea). Fig. 6 illustrates this idea with a cartoon. Representative examples of receptive fields from neighboring neurons recorded within the cat retina (taken from Mastronarde, 1983) and cat LGN (taken from Weng et al., 2005) are shown at the top, and a possible mechanism for the coverage transformation at the bottom. The bottom-left of the cartoon shows the receptive fields of three retinal ganglion cells, illustrated as Gaussian curves (shown in red, green, and blue) and the bottom-right, the geniculate receptive fields that result from combining the retinal inputs. The LGN Gaussian at

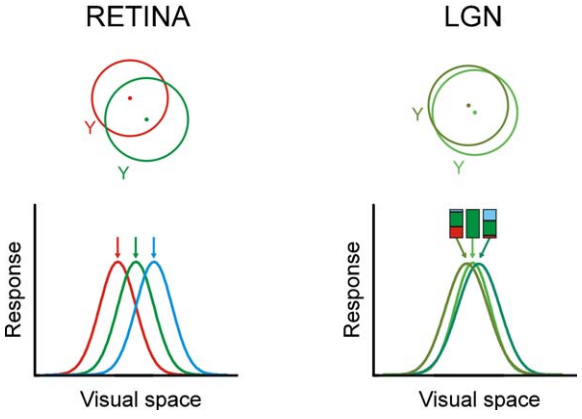

Fig. 6. Multiplexing the receptive field positions of retinal inputs in the LGN. Top: the cartoon illustrates the receptive fields of two neighboring Y cells in the cat retina (based on Mastronarde, 1983) and two neighboring Y cells in the cat LGN (based on Weng et al., 2005). Bottom left: the receptive fields of three Y cells in the retina are represented as Gaussian curves in three different colors. Bottom right: the combination of the three retinal inputs yields LGN receptive fields that can sample stimuli at a finer spatial resolution than in the retina. The bar graphs on the top illustrate the relative weights of the retinal inputs that were used to generate the LGN Gaussians.

the center is an exact copy of the green retinal Gaussian; it represents a geniculate cell that receives only one retinal input. The LGN Gaussians on the sides are obtained from a weighted sum of the green retinal afferent (that contribute 52% of the total input) and the weaker red and blue afferents (that contribute 40% and 8%). The input percentages used in the cartoon are consistent with the synaptic weights estimated from counts of retinogeniculate synapses (Hamos et al., 1987) and retinogeniculate correlations measured in pair recordings from retinal and geniculate cells (Cleland et al., 1971a, b; Mastronarde, 1992; Usrey et al., 1999). The weaker the additional retinal inputs, the closer the receptive field positions within the LGN.

It is estimated that 8–50% of geniculate cells receives input from just one retinal afferent (Cleland et al., 1971a; Cleland and Lee, 1985; Hamos et al., 1987; Mastronarde, 1992). These one-input geniculate cells could be the carriers of a nearly exact copy of the retinal receptive field array (position, size, and response time-course) to the cortex. The rest of the geniculate cells are dominated by one retinal input, but they also receive input from additional afferents (Cleland et al., 1971a, b; Hamos et al., 1987; Mastronarde, 1992; Usrey et al., 1999). These multiple-input geniculate cells could carry spatiotemporal interpolations that are heavily based on the receptive field of each dominant afferent. Notice that although the cartoon (Fig. 6) shows retinal and geniculate Gaussians with identical widths, the geniculate Gaussians should be narrower (Cleland et al., 1971a; Cleland and Lee, 1985) because center–surround interactions are stronger in the LGN than in the retina (Hubel and Wiesel, 1961; Singer and Creutzfeldt, 1970; Levick et al., 1972; Singer et al., 1972; Usrey et al., 1999). This increase in surround strength in the LGN could be important to reduce the overlap among the geniculate Gaussians shown in Fig. 6.

Multiplexing retinal inputs could increase the range of receptive field positions in the LGN, and also the sizes and response latencies. A continuous representation of response latencies in the LGN could be obtained by a weighted sum of the impulse responses from the retinal afferents equivalent to the one illustrated in Fig. 6 for visual space. Impulse responses are slower at the borders than at the middle of the retinal receptive field center. Therefore, the combined inputs from dominant afferents (retinal center superimposed with geniculate center) and weak afferents (retinal border superimposed with geniculate center) could provide the basis to generate a continuous range of response latencies within the LGN (see Mastronarde (1992) for good examples of the receptive field relation of a geniculate cell with their multiple retinal inputs).

The idea of using interpolation to improve spatial acuity has been proposed decades ago (Barlow, 1979; Crick et al., 1981; Fahle and Poggio, 1981) and is usually associated with some type of cortical computation (however, see Barlow, 1979). However, the properties of retinogeniculate divergence (Sur and Sherman, 1982; Hamos et al., 1987; Sur et al., 1987; Alonso et al., 1996; Yeh et al., 2003) strongly suggest that spatiotemporal interpolation could already be taking place at the level of the LGN, at least in the cat. In that sense, the LGN could serve an important function: to multiplex the receptive field array of retinal ganglion cells and create, by interpolation, a diverse representation of space and time that can be used by the cortex to process visual stimuli more precisely.

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References

Alonso, J.M., Usrey, W.M. and Reid, R.C. (1996) Precisely correlated firing in cells of the lateral geniculate nucleus. Nature, 383: 815–819.

Barlow, H.B. (1979) Reconstructing the visual image in space and time. Nature, 279: 189–190.

Bishop, P.O., Burke, W. and Davis, R. (1962) The interpretation of the extracellular response of single lateral geniculate cells. J. Physiol. (Paris), 162: 451–472.

Chen, C. and Regehr, W.G. (2000) Developmental remodeling of the retinogeniculate synapse. Neuron, 28: 955–966.

Cleland, B.G., Dubin, M.W. and Levick, W.R. (1971a) Simultaneous recording of input and output of lateral geniculate neurons. Nat. New Biol., 231: 191–192.

Cleland, B.G., Dubin, M.W. and Levick, W.R. (1971b) Sustained and transient neurons in the cat's retina and lateral geniculate nucleus. J. Physiol., 217: 473–496.

Cleland, B.G. and Lee, B.B. (1985) A comparison of visual responses of cat lateral geniculate nucleus neurons with those of ganglion cells afferent to them. J. Physiol., 369: 249–268.

Connolly, M. and Van Essen, D. (1984) The representation of the visual field in parvicellular and magnocellular layers of the lateral geniculate nucleus in the macaque monkey. J. Comp. Neurol., 226: 544–564.

Crick, F.H.C., Marr, D.C. and Poggio, T. (1981) An information-processing approach to understanding the visual cortex. In: Francis, O.S., Frederic, W., George, A. and Stephen, G.D. (Eds.), The Organization of the Cerebral Cortex. MIT Press, Cambridge, MA.

Enroth-Cugell, C. and Robson, J.G. (1966) The contrast sensitivity of retinal ganglion cells of the cat. J. Physiol. (London), 187: 517–552.

Fahle, M. and Poggio, T. (1981) Visual hyperacuity:spatiotemporal interpolation in human vision. Proc. R. Soc. Lond. B Biol. Sci., 213: 451–477.

Frascella, J. and Lehmkuhle, S. (1984) A comparison between Y-cells in A-laminae and lamina C of cat dorsal lateral geniculate nucleus. J. Neurophysiol., 52: 911–920.

Freund, T.F., Martin, K.A., Somogyi, P. and Whitteridge, D. (1985) Innervation of cat visual areas 17 and 18 by physiologically identified X- and Y- type thalamic afferents, II. Identification of postsynaptic targets by GABA immunocytochemistry and Golgi impregnation. J. Comp. Neurol., 242: 275–291.

Friedlander, M.J., Lin, C.S. and Sherman, S.M. (1979) Structure of physiologically identified X and Y cells in the cat's lateral geniculate nucleus. Science, 204: 1114–1117.

Friedlander, M.J., Lin, C.S., Stanford, L.R. and Sherman, S.M. (1981) Morphology of functionally identified neurons in lateral geniculate nucleus of the cat. J. Neurophysiol., 46: 80–129.

Garraghty, P.E., Salinger, W.L. and Macavoy, M.G. (1985) The development of cell size in the dorsal lateral geniculate nucleus of monocularly paralyzed cats. Brain Res., 353: 99–106.

Hamos, J.E., Van Horn, S.C., Raczkowski, D. and Sherman, S.M. (1987) Synaptic circuits involving an individual retinogeniculate axon in the cat. J. Comp. Neurol., 259: 165–192.

Hubel, D.H. and Wiesel, T.N. (1961) Integrative action in the cat's lateral geniculate body. J. Physiol., 155: 385–398.

Hubel, D.H. and Wiesel, T.N. (2005) Brain and Visual Perception. Oxford University Press, New York.

Illing, R.B. and Wassle, H. (1981) The retinal projection to the thalamus in the cat: a quantitative investigation and a comparison with the retinotectal pathway. J. Comp. Neurol., 202: 265–285.

Lee, D., Lee, C. and Malpeli, J.G. (1992) Acuity-sensitivity trade-offs of X and Y cells in the cat lateral geniculate complex: role of the medial interlaminar nucleus in scotopic vision. J. Neurophysiol., 68: 1235–1247.

LeVay, S. and Ferster, D. (1979) Proportion of interneurons in the cat's lateral geniculate nucleus. Brain Res., 164: 304–308.

Levick, W.R., Cleland, B.G. and Dubin, M.W. (1972) Lateral geniculate neurons of cat: retinal inputs and physiology. Invest. Ophthalmol., 11: 302–311.

Masland, R.H. (2001) The fundamental plan of the retina. Nat. Neurosci., 4: 877–886.

Mastronarde, D.N. (1983) Correlated firing of cat retinal ganglion cells, I. Spontaneously active inputs to X- and Y-cells. J. Neurophysiol., 49: 303–324.

Mastronarde, D.N. (1992) Nonlagged relay cells and interneurons in the cat lateral geniculate nucleus: receptive-field properties and retinal inputs. Vis. Neurosci., 8: 407–441.

Meister, M., Lagnado, L. and Baylor, D.A. (1995) Concerted signaling by retinal ganglion cells. Science, 270: 1207–1210.

Peichl, L. and Wassle, H. (1979) Size, scatter and coverage of ganglion cell receptive field centres in the cat retina. J. Physiol, 291: 117–141.

Peters, A. and Payne, B.R. (1993) Numerical relationships between geniculocortical afferents and pyramidal cell modules in cat primary visual cortex. Cereb. Cortex, 3: 69–78.

Reid, R.C., Victor, J.D. and Shapley, R.M. (1997) The use of m-sequences in the analysis of visual neurons: linear receptive field properties. Vis. Neurosci., 14: 1015–1027.

Sanderson, K.J. (1971) The projection of the visual field to the lateral geniculate and medial interlaminar nuclei in the cat. J. Comp. Neurol., 143: 101–108.

Singer, W. and Creutzfeldt, O.D. (1970) Reciprocal lateral inhibition of on- and off-center neurons in the lateral geniculate body of the cat. Exp. Brain Res., 10: 311–330.

Singer, W., Poppel, E. and Creutzfeldt, O. (1972) Inhibitory interaction in the cat's lateral geniculate nucleus. Exp. Brain Res., 14: 210–226.

Sur, M. (1988) Development and plasticity of retinal X and Y axon terminations in the cat's lateral geniculate nucleus. Brain Behav. Evol., 31: 243–251.

Sur, M., Esguerra, M., Garraghty, P.E., Kritzer, M.F. and Sherman, S.M. (1987) Morphology of physiologically identified retinogeniculate X- and Y-axons in the cat. J. Neurophysiol., 58: 1–32.

Sur, M. and Sherman, S.M. (1982) Retinogeniculate terminations in cats: morphological differences between X and Y cell axons. Science, 218: 389.

Sur, M., Weller, R.E. and Sherman, S.M. (1984) Development of X- and Y-cell retinogeniculate terminations in kittens. Nature, 310: 246–249.

Usrey, W.M., Reppas, J.B. and Reid, R.C. (1998) Paired-spike interactions and synaptic efficacy of retinal inputs to the thalamus. Nature, 395: 384–387.

Usrey, W.M., Reppas, J.B. and Reid, R.C. (1999) Specificity and strength of retinogeniculate connections. J. Neurophysiol., 82: 3527–3540.

Wassle, H., Boycott, B.B. and Illing, R.B. (1981a) Morphology and mosaic of on- and off-beta cells in the cat retina and some functional considerations. Proc. R. Soc. Lond. B Biol. Sci., 212: 177–195.

Wassle, H., Peichl, L. and Boycott, B.B. (1981b) Morphology and topography of on- and off-alpha cells in the cat retina. Proc. R. Soc. Lond. B Biol. Sci., 212: 157–175.

Weng, C., Yeh, C.I., Stoelzel, C.R. and Alonso, J.M. (2005) Receptive field size and response latency are correlated within the cat visual thalamus. J. Neurophysiol., 93: 3537–3547.

Yeh, C.I., Stoelzel, C.R. and Alonso, J.M. (2003) Two different types of Y cells in the cat lateral geniculate nucleus. J. Neurophysiol., 90: 1852–1864.