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 per geniculate cell, and both afferent and geniculate cell 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 visual cortex. However, because each retinal ganglion cell diverges to innervate multiple cells in LGN, most geniculate cells must receive additional inputs from other retinal afferents that are not the dominant one. 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 LGN. We propose that the convergence of dominant and weak retinal afferents in 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

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The cat eye has 160,800 retinal ganglion cells that fit within a retinal area of 450 mm^2 (Illing & Wassle, 1981). Half of these cells (53–57%) have small receptive fields and are classified as X and a much smaller proportion (2–4%) have larger receptive fields and are classified as Y (Enroth-Cugell & Robson, 1966; Friedlander *et al.*, 1979; Illing & 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 LGN (Cleland *et al.*, 1971b, a; 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 microns 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 & 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 retinal afferent (Hamos et al., 1987). This divergence could do much more than just

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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 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 emerges 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: 60,000/6,700; the Y cells from layer C are not included in this estimate (LeVay & Ferster, 1979; Illing & Wassle, 1981; Peters & 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 LGN (the primate retina has 1,120,000 parvocellular cells and 128,000 magnocellular cells (see Masland, 2001 for review)). However, like 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 & Van Essen, 1984). Interestingly, neuronal divergence seems to be delayed one synapse in primate with respect to the cat as is also the case for the construction of simple receptive fields (Hubel & 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 different LGN layers. Figure 2 illustrates the retinotopic map of cat LGN (Fig. 2A) and the response properties of 4 cells that were simultaneously recorded from different layers. The 4 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 this 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 figure 2 allowed us to compare the response properties from 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 neighboring Y_A, Y_C and X_A cells1[1]. The top of figure 3 shows an example of a triplet recording from three off-center geniculate cells of different type (X_Y, Y_A, Y_C). The Y_C cell had the largest receptive field and fastest response latency and the X cell the smallest receptive field and slowest response latency. For each cell triplet recorded, we calculated a similarity ratio to compare the differences between the Y_A-Y_C cells with the differences between the Y_A-X_A cells. A ratio larger 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 figure 3, in many cell triplets the similarity ratio for receptive field size and response latency was larger than 1. Moreover, the mean difference in receptive field size was significantly larger for Y_C-Y_A than Y_A-X_A (p<0.001, Wilconxon test). Y_C and Y_A cells also differed significantly in other properties that are not illustrated here such as spatial linearity, response transience and contrast sensitivity (Frascella & Lehmkuhle, 1984;Lee *et al*., 1992;Yeh *et al*., 2003). These results indicate that Y retinal afferents connect to two 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*., 1971b, a; Mastronarde, 1983; Cleland & 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 LGN (Sur & 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 less than 1 ms width centered at zero (Alonso *et al*., 1996; Usrey *et al*., 1998; Yeh *et al*., 2003). Figure 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. 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 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 frequently differed in receptive field size and response latency, probably due 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 a more frequent synchrony across layers could be due to a higher divergence of Y retinal afferents

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[1]The precise retinotopy of LGN and the interelectrode distances used in our experiments strongly suggests that all our recordings came from cells (and not axons) that were located within a cylinder of less than 300 microns of 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.

within layer C than layer A. As a consequence of this higher divergence, Y_C geniculate cells would receive input from more retinal afferents than Y_A cells (Fig. 4B), and due 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 of a common phenomenon in LGN: geniculate cells that share input from a common retinal afferent may have substantially different receptive fields due to weak retinal inputs that are not shared.

The ganglion cell layer of the retina is a thin structure (< 100 micron 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 & Wassle, 1979). Reaching such coverage factors is particularly challenging at the area centralis where receptive fields are smallest and therefore, cell density has to be 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 & 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; Wassle *et al.*, 1981b; 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. Figure 5A shows the receptive fields of 4 neighboring geniculate cells that were simultaneously recorded within layer A of LGN. The 4 cells had well-overlapped receptive fields of the same sign (off-center). And 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, receptive field size and response latency were correlated (Fig. 5C) suggesting that both properties may be generated by a common 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 figure 5 demonstrate a surprising diversity of receptive field positions, sizes and response latencies among neighboring neurons within LGN. This receptive field diversity could provide the cortex with a richer representation of space and time that the one available at the retina.

Multiplexing the receptive field properties of the retinal ganglion cells

The connections from the retina to LGN are among the strongest and 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 & 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.*, 1971b, a; Cleland & 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 & 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*., 1971b, a; Cleland & 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). Figure 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 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 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*., 1971b, a; 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 receive input from just one retinal afferent (Cleland *et al*., 1971a; Cleland & 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, 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*., 1971b, a; 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 shows retinal and geniculate gaussians with identical widths, the geniculate gaussians should be narrower (Cleland *et al*., 1971a; Cleland & Lee, 1985) because center-surround interactions are stronger in LGN than in the retina (Hubel & Wiesel, 1961; Singer & Creutzfeldt, 1970; Levick *et al*., 1972; Singer *et al*., 1972; Usrey *et al*., 1999). This increase in surround strength in LGN could be important to reduce the overlap among the geniculate gaussians shown in Figure 6.

Multiplexing the retinal inputs not only could increase the range of receptive field positions but also the receptive field sizes and response latencies within LGN. A continuous representation of response latencies in LGN could be obtained by a weighted sum of the impulse responses from the retinal afferents equivalent to the one illustrated in Figure 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 LGN (see Mastronarde, 1992 for beautiful 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 & Poggio, 1981) and is usually associated with some type of cortical computation (although see Barlow, 1979). However, the properties of retinogeniculate divergence (Sur & 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 taken 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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RETINAL AFFERENT   GENICULATE CELL   LGN
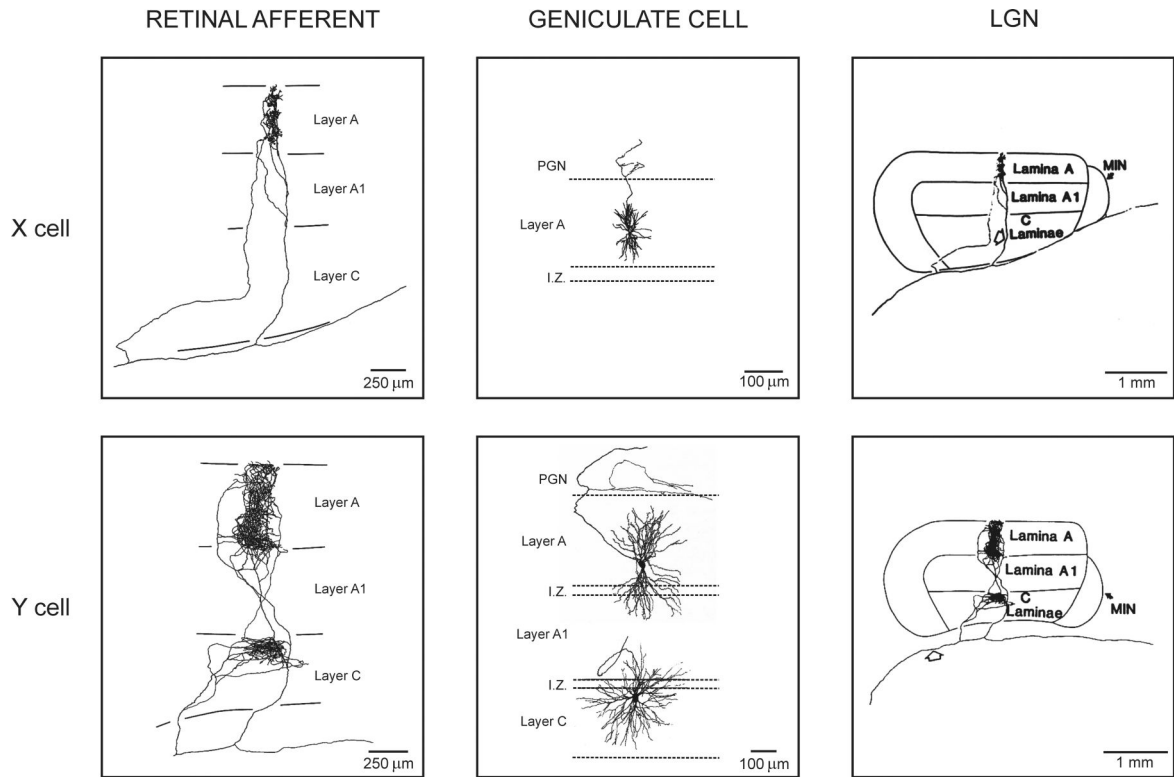

Figure 1. Retinal afferents and geniculate cells
Left. Axon terminals from X and Y retinal afferents in LGN. X retinal axons project into a single LGN layer and they are very restricted. Y retinal axons can project into two different LGN layers and are wider. **Middle.** X and Y geniculate cells. X cells 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 from the left of the figure shown at a different scale. Reprinted with permission from (Sur & Sherman, 1982, Copyright 1982 AAAS; Sur, 1988) (left and right) and (Friedlander *et al.*, 1981) (middle).
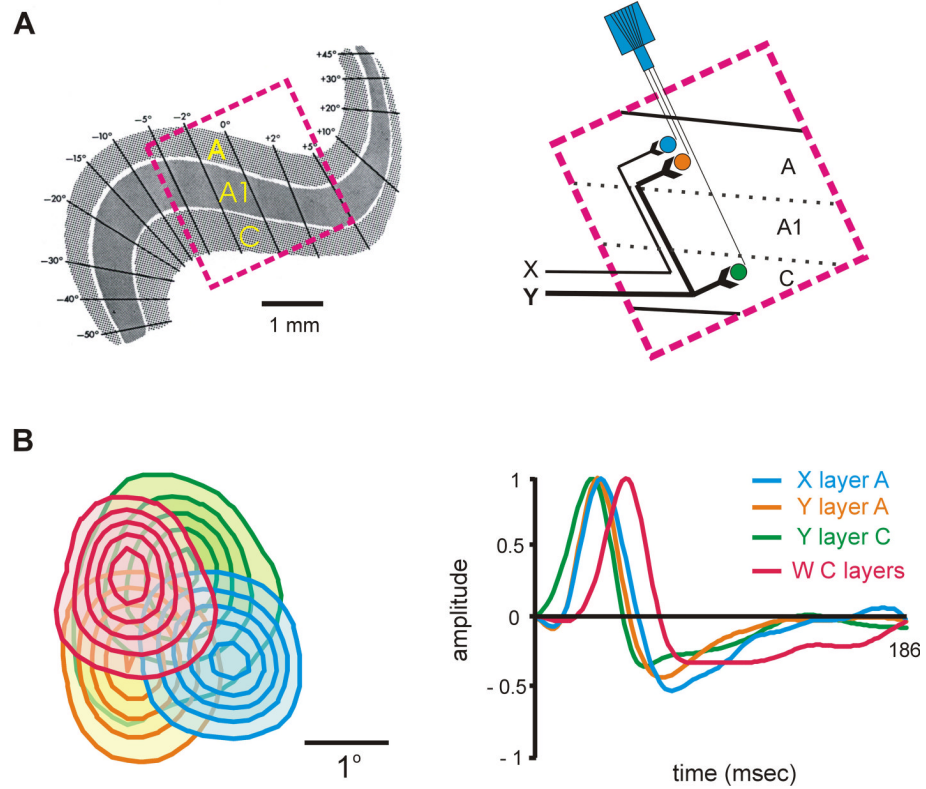
Figure 2. Simultaneous recordings from 4 geniculate cells recorded at different layers in the cat LGN
A. Left. Retinotopic map of cat LGN adapted from (Sanderson, 1971). Right. Schematic representation of the simultaneous recordings. **B.** Left. Receptive fields of the 4 simultaneously recorded geniculate 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 4 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. The figure was reprinted with permission from (Yeh et al., 2003).
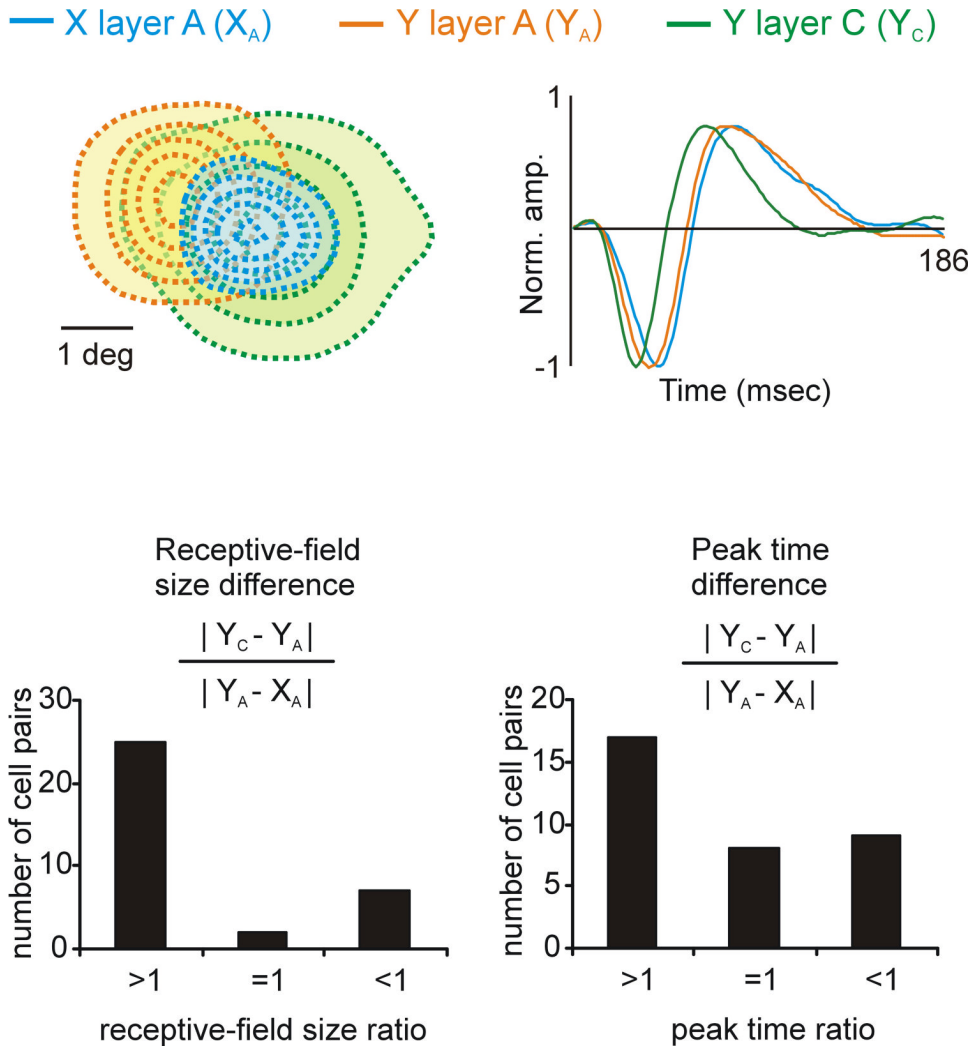
Figure 3. Comparisons of receptive field size and response latency obtained from triplet recordings of Y_A, Y_C and X_A cells

Top. An example of a triplet recording from 3 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 larger than 1 indicates that the differences between Y_C-Y_A were larger than the differences between Y_A-X_A. An index smaller than one indicate the opposite. Note that the differences between Y_C-Y_A were frequently larger than the differences between Y_A-X_A. The figure was reprinted with permission from (Yeh *et al.*, 2003).

A

B
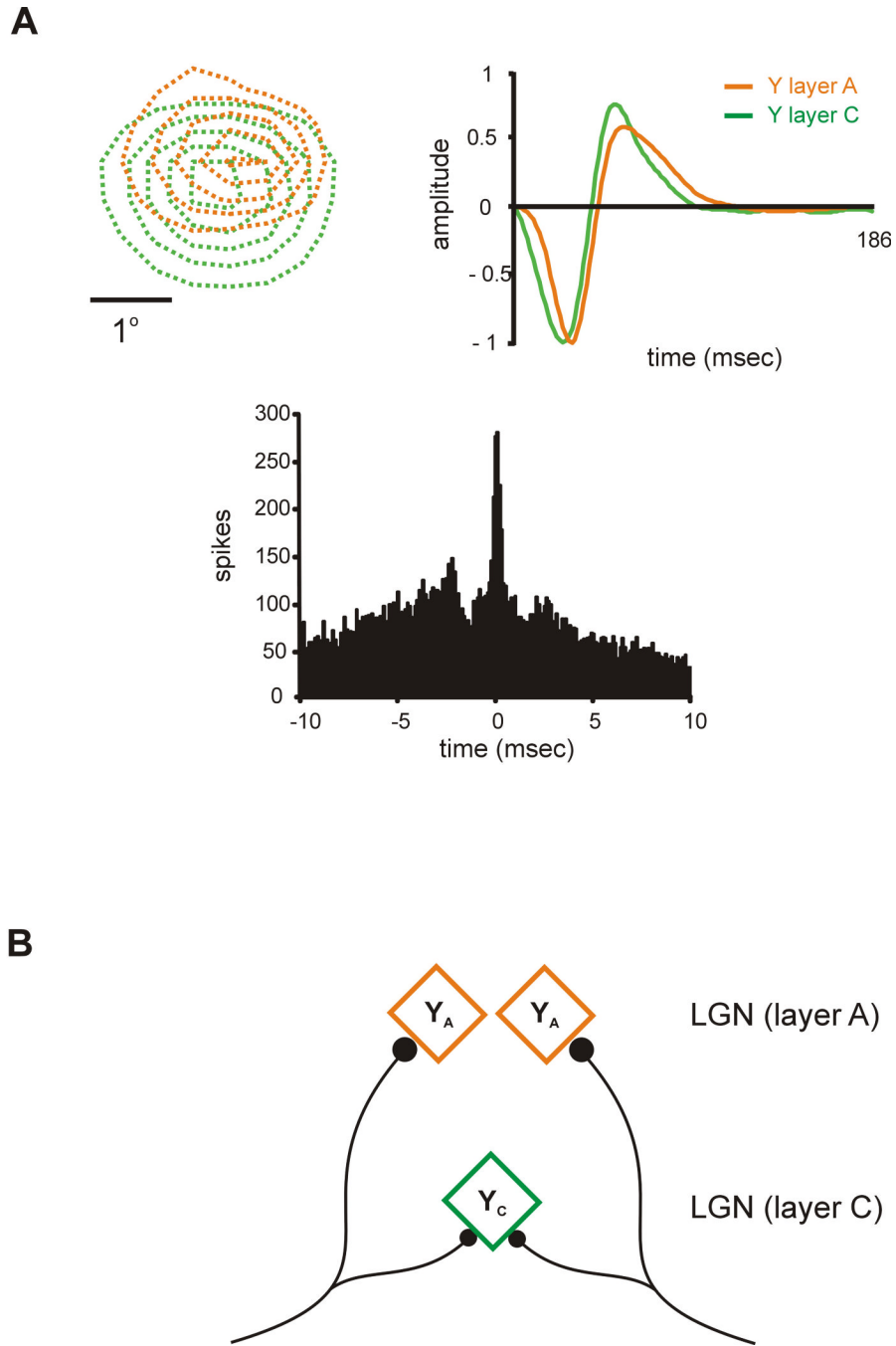
Figure 4. Different types of Y receptive fields (Y_A and Y_C) are constructed in LGN with one type of Y retinal afferent

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 correlograms show 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 field with a single type of Y retinal afferent. The figure was reprinted with permission from (Yeh *et al.*, 2003).
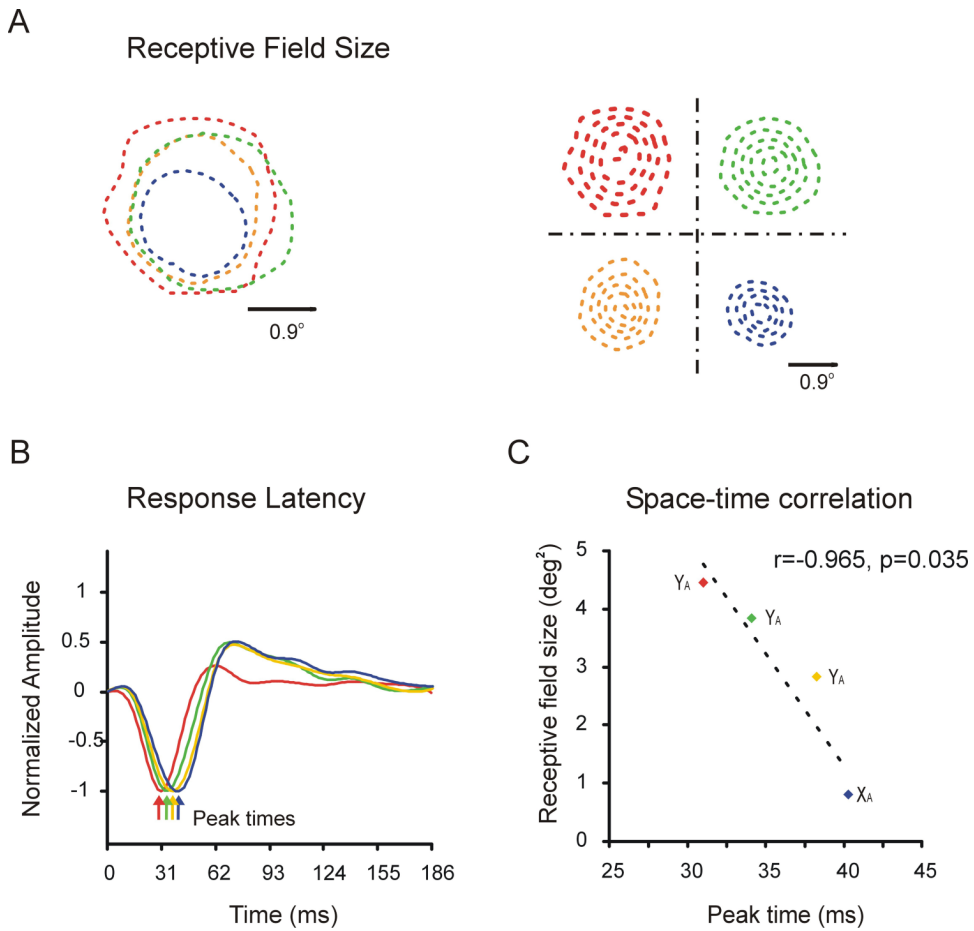
Figure 5. Receptive field properties of neighboring geniculate neurons that represent the same point of visual space

A. Receptive fields from 4 off-center geniculate cells that were simultaneously recorded. The receptive fields of the 4 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 4 neurons also differed in their response latencies, as illustrated by the by 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. The figure was reprinted with permission from (Weng *et al.*, 2005).
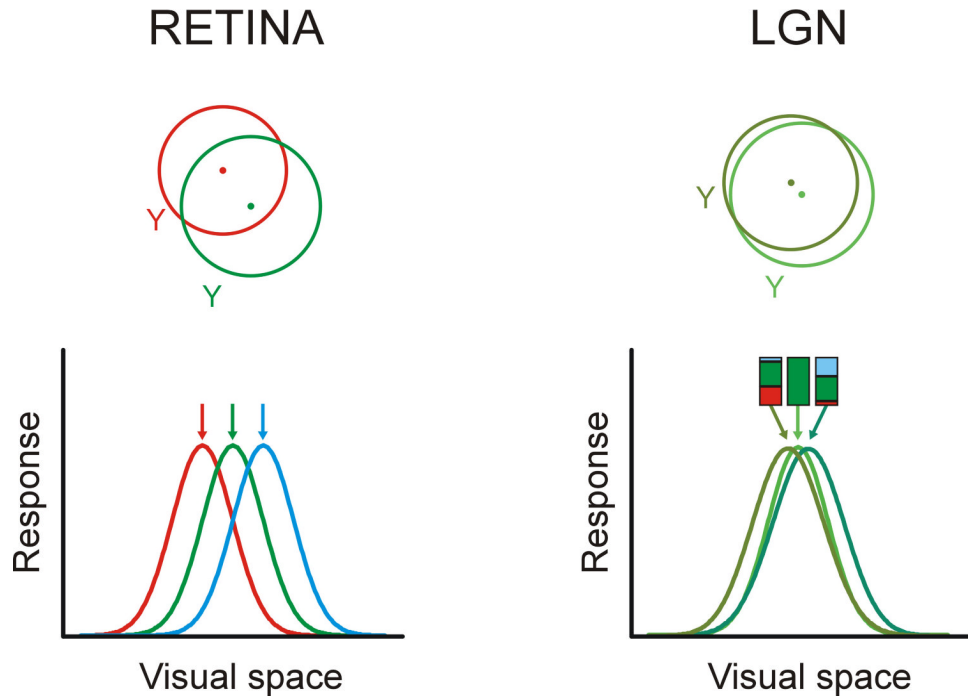
Figure 6. Multiplexing the receptive field positions of retinal inputs in LGN
Top. The cartoon illustrates the receptive fields of two neighboring Y cells in the cat retina (based on Mastronarde, 1983) and two neighboring Y cells in cat LGN (based on Weng *et al.*, 2005). **Bottom left.** The receptive 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 at the top illustrate the relative weights of the retinal inputs that were used to generate the LGN gaussians.