Receptive Field Size and Response Latency Are Correlated Within the Cat Visual Thalamus

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Weng, Chong, Chun-I Yeh, Carl R. Stoelzel, and Jose-Manuel Alonso. Receptive field size and response latency are correlated within the cat visual thalamus. J Neurophysiol 93: 3537–3547, 2005; doi:10.1152/jn.00847.2004. Each point in visual space is encoded at the level of the thalamus by a group of neighboring cells with overlapping receptive fields. Here we show that the receptive fields of these cells differ in size and response latency but not at random. We have found that in the cat lateral geniculate nucleus (LGN) the receptive field size and response latency of neighboring neurons are significantly correlated: the larger the receptive field, the faster the response to visual stimuli. This correlation is widespread in LGN. It is found in groups of cells belonging to the same type (e.g., Y cells), and of different types (i.e., X and Y), within a specific layer or across different layers. These results indicate that the inputs from the multiple geniculate afferents that converge onto a cortical cell (approximately 30) are likely to arrive in a sequence determined by the receptive field size of the geniculate afferents. Recent studies have shown that the peak of the spatial frequency tuning of a cortical cell shifts toward higher frequencies as the response progresses in time. Our results are consistent with the idea that these shifts in spatial frequency tuning arise from differences in the response time course of the thalamic inputs.

INTRODUCTION

The cat lateral geniculate nucleus (LGN) is organized into channels of information processing that have different temporal and spatial properties. On average, Y geniculate cells respond faster to visual stimuli and have larger receptive fields than X geniculate cells at the same eccentricity (Saul and Humphrey 1990; Sestokas and Lehmkuhle 1986; So and Shapley 1979; Troy and Lennie 1987; Yeh et al. 2003), and the same is true for Magnocellular and Parvocellular cells in primate (Croner and Kaplan 1995; Levitt et al. 2001; Maunsell et al. 1999; Usrey and Reid 2000; Xue et al. 2001). However, the differences in response latency between X and Y cells (or Magno and Parvo cells) are far from being clear-cut. For example, Troy and Lennie (1987) found that, although the average Y geniculate cell had a shorter latency (36.6 ms) than that of the average X geniculate cell (37.8 ms), the latency range within each category was very large (about 25 ms). Similarly, Maunsell et al. (1999) found that the distribution of response latencies for Parvocellular and Magnocellular neurons in primate overlapped extensively.

The differences in receptive field size between X and Y cells are more pronounced than the differences in response latency. So and Shapley (1979) indicated that, at a given eccentricity, it was almost always possible to categorize a cell as X or Y based on the size of its receptive field center (although the best categorization method was the linearity test; Shapley and Hochstein 1975). Specifically, the highest spatial frequency of a drifting grating that can effectively drive an X cell (modulate the first Fourier harmonic) was shown to be 2–3 times higher than the one that drives a Y cell (So and Shapley 1979), and the frequency ranges did not overlap much, at least within 5 deg of the area centralis [X cells: 0.3–1.8 cycles/deg; Y cells: 0.1–0.5 cycles/deg (Derrington and Fuchs 1979)]. It should be noticed, however, that X and Y cells have the same spatial resolution when measured with contrast reverse gratings (comparing resolution of first Fourier harmonic in X cells to second Fourier harmonic of Y cells; So and Shapley 1979) because the X cell center size and the Y cell subunit size are both determined by the spatial resolution of the bipolar cell (Demb et al. 2001). Hand-plotting measurements also indicate that the receptive field sizes of Y cells are 1.5–2 times larger than those of X cells [see Sherman and Spear 1982 for review; Saul and Humphrey (1990) estimated that the average receptive field diameter is 0.7 deg for an X cell (0.2–2.0 deg) and 1.58 deg for a Y cell (0.3–3.5 deg) within 35 deg of the area centralis]. Most measurements of receptive field size and response latency are somewhat limited by the fact that cells are usually recorded at different times, under different conditions, and in different animals. The level of anesthesia/arousal, eccentricity, individual variations like age, and the properties of the stimulus projected on the retina could affect the measurements (Cleland et al. 1979; Kremers et al. 2001; Maunsell et al. 1999; Swadlow and Weyand 1985; Worogorot et al. 1998). This variability is not trivial and has been demonstrated by some careful studies in the past. For example, by recording from 42 on-center retinal ganglion cells in a single animal, Cleland et al. (1979) demonstrated that the variability in receptive field size was much smaller than previously thought. Similarly, Maunsell et al. (1999) showed that response latencies in LGN could significantly vary across individuals in relation with age and size (see also Maunsell and Gibson 1992 for V1 cells).

The variability in measuring conditions can be greatly diminished by comparing the response properties of pairs of X and Y geniculate cells that are simultaneously recorded and have overlapping receptive fields. Measurements of these X–Y cell pairs demonstrate that the average Y geniculate cell has a response latency 3.9 ms faster and a receptive field center 1.6

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times larger than that of the average neighboring X geniculate cell (Yeh et al. 2003). However, even neighboring cells that are simultaneously recorded show great variation in receptive field size and response latency. What could be the reason for such variability? If the variability in receptive field size and response latency were correlated (i.e., the larger the receptive field, the faster the response), the cortex would receive initially a fast, low-resolution image that would become increasingly sharper over time. In this scenario, the variability in receptive field size and timing could help to smooth the transition from low to high spatial-resolution images. The results presented here are consistent with this hypothesis and also support recent findings showing that the peak of the spatial frequency tuning of a cortical cell shifts toward higher frequencies as the response progresses in time (Bredfeldt and Ringach 2002; Frazor et al. 2004; see also Mazer et al. 2002). Recently Frazor et al. (2004) modeled this shift in spatial frequency with a feedforward circuit in which X and Y cells (in cats) or Parvocellular and Magnocellular cells (in primates) converge simultaneously into the LGN (Eckhorn and Thomas 1993). The electrophysiological recordings and data acquisition

**Surgery and preparation**

Cats were initially anesthetized with ketamine (10 mg/kg, intramuscular) followed by thiopental sodium [20 mg/kg, intravenous (iv), supplemented as needed during surgery; and at a continuous rate of 1–2 mg kg\(^{-1}\) h\(^{-1}\), iv, during recording]. Lidocaine was administered topically or injected subcutaneously at all incisions or points of pain and pressure. The animal was then intubated and placed in a stereotaxic apparatus. We monitored the following vital signs: electrocardiogram, electroencephalogram, oxygen in blood (measured by pulse oximetry), expired carbon dioxide, heart rate, blood pressure (measured with a pressure cuff), and rectal temperature. A craniotomy and durotomy were made to introduce recording electrodes into LGN (anterior, 5.5; lateral, 10.5). Animals were paralyzed with Norcuron (0.2 mg kg\(^{-1}\) h\(^{-1}\), iv) to minimize eye movements and artificially ventilated to keep the expired CO\(_2\) between 28 and 33 mmHg. Pupils were dilated with atropine sulfate (1%) and nictitating membranes retracted with Neo-Synephrine (2.5%). The eyes were covered with contact lenses to protect the corneas. The optic disk and the area centralis were projected onto a tangent screen located 114 cm from the cat (Pettigrew et al. 1979). All surgical and experimental procedures were performed in accordance with U.S. Department of Agriculture guidelines and were approved by the Institutional Animal Care and Use Committee at the University of Connecticut and at the State University of New York, State College of Optometry.

**Electrophysiological recordings and data acquisition**

A matrix of 7 independently moveable electrodes arranged circularly was introduced into the LGN (Eckhorn and Thomas 1993). The electrodes were very thin (80 μm rod; 25 μm at the shaft) and had impedances of 3–6 MΩ (System Eckhorn Thomas Recordings, Marburg, Germany). A glass guide tube with an inner diameter of about 300 μm at the tip was attached to the shaft probe of the multielectrode to reduce the interelectrode distances to about 80–300 μm. The matrix of electrodes was then lowered into the brain, leaving the tip of the guide tube about 3 mm above the LGN. Each electrode was moved independently within the LGN and positioned either within layer A or layer C. The angle of the multielectrode was adjusted precisely for each experiment (about 25–30° anterior–posterior; about 2–5° lateral–central) to simultaneously record from cells with spatially overlapping receptive fields in both layers. All cells were recorded within 5–10° of the area centralis. Recorded voltage signals from all 7 electrodes were conventionally amplified, filtered, and passed to a computer running the Discovery software package (Datawave System, Longmont, CO). For each cell, spike waveforms were identified initially during the experiment and verified carefully off-line by spike-sorting analysis (Datawave System). Visual stimuli were generated with an AT-vista graphics card (Truevision, Indianapolis, IN) and shown on a 20-in. monitor (Nokia 445Xpro, Salo, Finland; frame rate: 128 Hz).

**Receptive field mapping**

Geniculate receptive fields were mapped by reverse correlation with white noise. The white-noise stimulus was derived from a binary m-sequence (Reid et al. 1997; Sutter 1987), and spatially consisted of a 16 × 10 grid of black or white squares (pixels). Each pixel in the white-noise stimulus was 0.81 deg\(^2\) in size (0.9° × 0.9°) and each frame was presented for 15.5 ms (the entire white-noise sequence lasted about 508 s). From all the frames presented, we selected those that preceded a spike within a specific time delay. Then the selected frames were averaged and represented as a contour plot smoothed with a cubic spline, each contour line showing from center to periphery 100 to 20% of the maximum response (Matlab, The MathWorks, Natick, MA). The receptive field size was quantified as the number of contiguous pixels within the 20% contour line at the time delay that contained the maximum response (≥15 ms earlier than the latency of the surround response). The 20% contour line was used because it defines quite precisely the size of the geniculate center (measurements <20% are less accurate because they include responses from the surround and background noise). It should be emphasized that the receptive field size in this study refers exclusively to the receptive field center and not the surround. In all figures, on-center receptive fields are shown as continuous lines and off-center receptive fields as discontinuous lines.

**Time course of the visual response**

The time course of the visual response was also calculated from responses to white-noise stimuli by reverse correlation. The impulse response was defined as the time course of the response evoked by the most effective stimulus pixel within the receptive field center (the pixel that generated the maximum response). This pixel is ideal for our measurements because it is located at the middle of the receptive field center and its response is least contaminated by surround inhibition. Impulse responses were normalized and smoothed with a cubic spline to compare timing differences between simultaneously recorded cells (Alonso et al. 2001; Yeh et al. 2003). A not-a-knot end condition was chosen to interpolate bins of 15.5 ms, from the −46.5-ms bin [−61 ms, −46.5 ms] to the 186-ms bin [170.5 ms, 186 ms] (spline function, Matlab). With respect to the figures shown herein, impulse responses are shown from the 0-ms bin [−15.5 ms, 0 ms] to the 186-ms bin [170.5 ms, 186 ms]. Most impulse responses were biphase. For example, the impulse response of an on-center geniculate cell had a positive first phase followed by a negative second phase. By convention, the first phase is positive for on-center cells and negative for off-center cells. The peak time (maximum of the first phase) was measured from the smoothed impulse response. This method gave a reliable estimate of the response latency for each cell (i.e., latency of the cell’s maximum response). We estimated the error in the measurements of peak time by calculating the impulse responses of 10 cells in 3 consecutive repetitions of white-noise stimulation. In 6 of these cells the values of peak time were identical in the 3 repetitions. In 4 other cells there was a difference of 1.55 ms between 2 of the repetitions. This measurement error is consistent.
with previous results from our laboratory. Yeh et al. (2003) was able to demonstrate that the average peak time of Y cells recorded from layer C is 2.5 ms faster than the average peak time of Y cells recorded from layer A. This 2.5-ms difference in peak time was highly significant ($P < 0.001,$ Wilcoxon test).

**Rank-order analysis**

We used a rank-order analysis to measure the correlation between receptive field size and response latency for the entire population of X and Y cells recorded in this study. This analysis aimed to minimize the variability in receptive field size and response latency caused by the different experimental conditions in which the cells were recorded (i.e., different eccentricities and different animals). In this analysis, each cell within a simultaneously recorded group was assigned a rank value based on its receptive field size (the rank values ranged from 1 to $n$, where $n$ is the number of simultaneously recorded cells). The cell with the largest receptive field was assigned a rank value of 1 and the cell with the smallest receptive field a rank value of $n$. Cells with the same receptive field sizes were treated as follows. First, they were assigned temporary numbers as if they had different sizes (e.g., 1 and 2 for two cells with the same receptive field size that was the largest in a group). They were then given a rank value obtained from the average of the temporary numbers (e.g., 1.5 and 1.5 for two cells with the same receptive field size that was the largest in a group). Because the value of $n$ varies (e.g., some groups have 4 cells and others have 9 cells), we normalized the ranks by subtracting the mean rank value $[(n + 1)/2]$ from each group. For example, a group with the rank values 1, 2, 3, 4, and 5 would be normalized as $-2, -1, 0, 1,$ and 2, respectively.

Similarly, each cell within a simultaneously recorded group was assigned a rank value based on the peak time of the impulse response, which was 1 for the cell with the fastest response. For example, in a group of 3 cells, the cell with the shortest peak time had a rank of 1, the one with the longest peak time a rank of 3, and the one with the intermediate peak time a rank of 2. When 2 cells had impulse responses with the same peak times, we used the zero-crossing values to determine the rank (zero-crossing: zero value between first and second phases of impulse response). If the zero-crossing values were also the same, we used the rebound times (rebound: maximum of the second phase of the impulse response in absolute value), and if all these values were the same we used the same method described above for receptive field size. As for receptive field size, the ranks were normalized by subtracting the mean rank value.

Monte Carlo simulations were done to estimate the significance of the correlations obtained with the normalized rank-ordered data. As a first approach, we ran 1,000 simulations using a bootstrap method. In each bootstrap simulation, we took the entire sample of cells (e.g., 144 Y cells) and replaced random paired values of peak time/receptive field size with other paired values already present in the data sample. As a second approach, we ran 1,000 Monte Carlo simulations by randomly choosing $n$ values in each simulation from the entire sample of cells recorded ($n = 150$ for all cells, $n = 100$ for Y cells, $n = 60$ for X cells). The correlation coefficients between peak time and receptive field size were calculated for each simulation.

**Regression analysis**

The strength of the correlation between peak time and receptive field size was measured by linear regression analysis. Statistical significance was assessed with a Pearson test in all cases except for the rank-order analysis in which we used a Spearman test. Multiple regression analysis was used to estimate the possible contribution from other variables to the correlations between peak time and receptive field size. The multiple regression analysis was done as follows. First, we selected all cell groups in which we were able to demonstrate a correlation between peak time and receptive field size and treated each as if it was independently recorded. Then, we used the following model ($y = b_1 x_1 + b_2 x_2 + \text{error}$) to estimate whether the value of peak time ($y$) could be predicted by taking into account both the receptive field size ($x_1$) and another additional variable ($x_2$). The additional variables tested were: amplitude of the first phase of the impulse response, mean firing rate under white-noise stimulation, layer location of the cell recorded, contrast polarity of the receptive field (ON- or OFF-center), and cell type (X or Y). We also did multiple regression analysis in each of the 10 cell groups that showed the strongest correlations between peak time and receptive field size (average $r: 0.95$).

**Classification of geniculate cells**

All geniculate cells recorded from layers A and C were classified as X or Y based on the linearity of spatial summation (Enroth-Cugell and Robson 1966; Hochstein and Shapley 1976; Shapley and Hochstein 1975). The linearity of spatial summation was measured with contrast reverse sinusoidal gratings. We used at least 2 different spatial frequencies that were higher than the optimal, usually 0.55 and 1.1 cycle/deg. Because some Y cells can generate linear responses when tested with very low spatial frequencies, high spatial frequencies were used to unambiguously classify groups of X and Y geniculate cells that were simultaneously recorded (Hochstein and Shapley 1976; So and Shapley 1979). Each spatial frequency was tested at 8 different phases. The gratings were presented at 0.4 Hz and repeated $\geq 8$ times at each spatial phase. The Y/X identification was always made from the response to the highest spatial frequency that generated a significant response ($\geq 5$ spikes/50-ms bin). Cells that responded poorly ($<5$ spikes/50-ms bin) were labeled as unclassified. This study includes cells recorded in layer A and the first few hundred microns of layer C. A few cells recorded deep in layer C (>500 microns below the transition A1–C) had impulse responses with very long latencies and were not included in this study (Stanford et al. 1983; Sur and Sherman 1982; Wilson et al. 1976). Overall, we recorded from a total of 248 cells from layer A (104 XA, 87 YA) and layer C (57 YC). Our matrix of 7 independently movable electrodes (Eckhorn and Thomas 1993) allowed us to record from clusters of 4–9 cells. These clusters were divided in groups based on cell type (X, Y) and layer location of the cells recorded (layer A or C). For example, a simultaneous recording from 4 XA, 4 YA cells, and 1 YC cell yielded 4 groups: one XA group ($n = 4$ cells), one YA group ($n = 4$ cells), one XAYA group ($n = 8$ cells), and one all-cells group ($n = 9$ cells).
Note that the contour plots represent the total receptive field center and not the Y cell subunit size (So and Shapley 1979).

The reverse-correlation method was also used to measure the response time course of the cells to the most effective white-noise pixel within the receptive field center (impulse response). Each impulse response was sampled at the stimulus refresh rate (bin size = 15.5 ms) and then smoothed with a cubic spline. The impulse responses of the 4 cells are shown on the right.

FIG. 1. Receptive field size and response latency are correlated. A, left: receptive fields of 4 neighboring cells recorded within layer A of lateral geniculate nucleus (LGN): an X cell (in blue) and 3 Y cells (in red, green, and orange). For clarity, only the most external contour lines (20% of maximum response) are represented when showing superimposed receptive fields. All cells had off-center receptive fields (in all figures, off-center receptive fields are shown in discontinuous lines and on-center receptive fields in continuous lines). Right: receptive fields are shown separately for each cell. Y cell in red had the largest receptive field size and the X cell the smallest one. B: impulse responses of the 4 cells had different peak times (indicated by arrows). Y cell in red had the fastest response latency and the X cell in blue the slowest one. Left: superimposed impulse responses. Right: impulse response of each cell is shown separately both as binned data (bin size = 15.5 ms) and as a cubic spline. C: peak time and receptive field sizes of these 4 cells were strongly correlated ($r = 0.965$, $P = 0.035$). XA: X cell recorded from layer A. YA: Y cell recorded from layer A. YC: Y cell recorded from layer C.

FIG. 2. Space–time correlations are found among cells of the same type and of different types, within the same LGN layer (layer A), or across different layers. A, left: example from 5 XA cells with overlapping receptive fields that were simultaneously recorded. Each cell is represented in a different color. Five cells had overlapping receptive fields of different sizes. Continuous lines represent on-center geniculate cells; discontinuous lines represent off-center geniculate cells. Middle: 5 cells had impulse responses with different peak times. First phase of the impulse response is positive for on-center geniculate cells and negative for off-center cells (see METHODS). Right: receptive field size and response latency were strongly correlated ($r = -0.948$, $P = 0.014$). B: example from 5 YA cells. C: example from 7 cells of different type (XA, YA, YC) simultaneously recorded in different geniculate layers. D: example from 6 Y cells simultaneously recorded from layer C. No significant correlation was found between receptive field size and response latency in this example ($r = 0$, $P = 1$). XA: X cell recorded from layer A. YA: Y cell recorded from layer A. YC: Y cell recorded from layer C.
separately for each cell (binned data and cubic spline) and superimposed on the left (cubic spline). The 4 impulse responses had clearly different peak times (peak time: time at the first phase of the impulse response; by convention, the first phase is negative in off-center cells and positive in on-center cells). The values of the peak times indicated that the 4 cells responded to white noise in a temporal sequence that was precisely the reverse given above for receptive field size (in our color code: red → green → orange → blue; Fig. 1B). As illustrated in Fig. 1C, peak time and receptive field size were strongly correlated: the larger the receptive field, the faster the response to visual stimuli. As illustrated in Fig. 2, similar space–time correlations were found in groups of X cells (A), groups of Y cells (B), and groups of different cell types recorded within the same layer or different layers (C). These correlations were usually not found in simultaneous recordings from Y cells in layer C (D) because Y cells in this layer tend to have very similar response time courses.

Although the correlations between receptive field size and response latency were strong (average $r = 0.8$), significance was found in only a small percentage of simultaneously recorded groups (18%, $n = 34/192$). This modest percentage does not indicate that the population of space–time correlated cells is small; most likely, it reflects the difficulty in obtaining a significant correlation with a relatively small number (4–9) of simultaneously recorded cells. Increasing the number of simultaneously recorded cells did not reduce the probability of finding such correlations (Fig. 3A). Moreover, the probabilities for groups of 4 cells (6%) and 5 cells (16%) were reduced by half if we calculated all possible 4- and 5-cell subgroups obtained from groups of 9 cells (the probabilities obtained with this method were 3% for groups of 4 cells and 6% for groups of 5 cells). The likelihood of finding a significant correlation between peak time and receptive field size also depended on the range of receptive field sizes sampled at each position of visual space; when the range was low, some cells had the same value of receptive field size, reducing the effective sample size (Fig. 3B; the probability also depended on the LGN layer; inset). These results are consistent with the idea that space–time correlations are not uncommon in LGN.

Such a concept is further supported by correlation measurements across the entire population of X and Y cells recorded. When each of the 248 sampled cells (104 X cells and 144 Y cells) was treated as if it was recorded independently, the space–time correlations were absent for X cells ($r = -0.013$, $P = 0.899$) and for Y cells ($r = -0.113$, $P = 0.179$) and present only when X and Y cells were lumped together ($r = -0.251$, $P < 0.001$). However, when some of this variability was removed by using a rank-order analysis we found significant correlations in the 3 cell populations. The ideal approach to remove the variability in the experimental conditions would be to record simultaneously with closely spaced electrodes from all 248 cells. Here, we simulated this scenario by using data from the simultaneous recordings to normalize the receptive field size and peak time of the 248 sampled cells. The rank-order analysis is explained in Fig. 4A using an example of three simultaneously recorded cells: green (X cell), black (Y cell) and blue (Y cell). In this example, each cell is order ranked by receptive field size (1 for the largest and 3 for the smallest) and response time course (1 for the fastest and 3 for the slowest) and then the rank values are normalized by subtracting the mean rank (see methods for detail). The bubble graphs in Fig. 4B are obtained by plotting the normalized rank values for all the cells recorded. The size of the circle indicates the number of cells that fall on the same point on the graph. These graphs demonstrate significant space–time correlations for all cells ($r = 0.36, P < 0.001$), Y cells ($r = 0.3, P < 0.001$) and X cells ($r = 0.26, P < 0.01$). The significance of these correlations was confirmed by running bootstrap and Monte Carlo simulations (see methods). Figure 5 shows the results from 1,000 Monte Carlo simulations (the results from boot-
The average correlation coefficients obtained were 0.359 for all cells together, 0.293 for Y cells, and 0.285 for X cells (100% of the correlation coefficients obtained were positive).

Although the rank-order analysis minimized some of the measurement variability, the correlation values obtained with this method ($r \approx 0.3$) were about 3 times weaker than the correlations measured in individual groups of simultaneously recorded cells. A similarly weak correlation was obtained if we selected all cell groups that showed significant space–time correlations and treated each cell as if it was independently recorded. Clearly, there are several factors that contribute to the variability in response latency other than the receptive field size. In the selected sample of space–time correlated cells, the response latency and receptive field size were correlated with cell type (X or Y), layer location (A or C), and mean firing rate (Yeh et al. 2003) and there was also a correlation between the size and the contrast polarity of the receptive field (Table 1).

Moreover, the cell type (X or Y) was correlated with the mean firing rate and other parameters (Table 2). We wondered whether these correlations contributed to the space–time correlations reported here. To test this possibility we did multiple regression analysis with the entire sample of cells that showed significant space–time correlations, treating each cell as if it was independently recorded. In addition, we did multiple regression analysis for each of the 10 cell groups that showed the strongest correlations ($r > 0.92$; we reasoned that the contribution from other parameters may be easier to detect in the groups that are most strongly correlated). We used the model ($y = b_1 x_1 + b_2 x_2 + \text{error}$) to estimate whether the value of peak time ($y$) could be predicted by the receptive field size ($x_1$) in combination with another parameter ($x_2$: response amplitude, mean firing rate, layer location, contrast polarity, or cell type). The results from the multiple regression analysis were not significant. In other words, we could not find a condition in which the peak time could be predicted by a

**FIG. 4.** Space–time correlations can be demonstrated in large populations of X and Y cells by using data from simultaneous recordings. A: each cell in one simultaneously recorded group was rank-ordered according to its receptive field size and response latency. In each simultaneously recorded group, the cell with the biggest receptive field was ranked as 1 in “receptive field size” (top) and the cell with shortest response latency was ranked as 1 in “peak time” (middle). Rank values were normalized by subtracting the mean rank and then represented in a scatter plot (bottom). See METHODS for detail. B: when the entire cell population was rank-ordered by receptive field size and response latency, significant correlations were found within and across cell types. Circles of different sizes are used to represent the number of the cells with the same rank values. RF, receptive field.
combination of receptive field size and one of the other parameters tested. In the 10 groups with the strongest correlations, the best predictor of the peak time was consistently the receptive field size (average $b_1 = 0.94$).

Finally, we found that the strength of the correlations between receptive field size and response latency was relatively independent of the stimulus contrast. Although changes in stimulus contrast had a pronounced effect on the response time course of the geniculate neurons and on the variability of the response latencies, the correlation coefficients remained strong under different contrasts. Figure 6A shows an example of 5 X and 4 Y cells recorded simultaneously from layer A. A significant space–time correlation could be obtained at 98, 45, and 22% white-noise contrast. The strongest correlation was sometimes found at the lowest contrast (as in this example) and other times at the middle and highest contrasts. However, on average the correlation strength was very similar ($r = 0.8$) for all contrasts tested (Fig. 6).

DISCUSSION

We have demonstrated that X and Y neighboring cells within the main layers of cat LGN follow a general principle: the larger the receptive field size, the faster the response to the visual stimuli. The correlation between receptive field size and response time course is relatively independent of cell type (X, Y) and layer except for Y cells in layer C, which have very similar response time courses. The correlations between receptive field size and response latency are strong (average $r = 0.8$) when measured in groups of cells that are simultaneously recorded and can sometimes explain around 20–30 ms of variability in response latency (Fig. 6). The possible functional significance and the mechanisms that could be responsible for these space–time correlations are discussed in the following text.

Why were space–time correlations not reported before?

The receptive field size and response time course of LGN cells have been measured in the past with several methods, although no study did a systematic comparison between both parameters (for review see Sherman and Spear 1982; Stone et al. 1979; Van Hooser et al. 2003). Previous studies emphasized
the high variability of the spatial and temporal properties of LGN cells and the importance of using similar measuring conditions to reduce such variability (Cleland et al. 1979; So and Shapley 1979). The use of simultaneous recordings greatly minimizes this variability and, in addition, allows a direct comparison of neighboring geniculate cells. For example, simultaneous recordings from 2 cells with the same electrode showed that a Y retinal cell could respond 10–15 ms faster to visual stimuli than its neighboring X retinal cell (Bolz et al. 1982). Similarly, simultaneous recordings within the LGN demonstrated that a Y geniculate cell could respond 10–20 ms faster than the neighboring X geniculate cell (Yeh et al. 2003).

It is well accepted that Y geniculate cells have, on average, larger receptive fields and respond faster to visual stimuli than X geniculate cells (Saul and Humphrey 1990; Sestokas and Lehmkuhle 1986; So and Shapley 1979; Troy and Lennie 1987; Yeh et al. 2003). However, this fact could reflect either differences between cell types (i.e., X, Y) or a more general correlation between receptive field size and response latency. Our results provide support for the second possibility. In other words, if 2 neighboring cells have different receptive field sizes, the one with the larger receptive field is more likely to respond faster to visual stimuli than the one with the smaller receptive field, even if the 2 cells are of the same type (i.e., Y cells).

Possible mechanisms

What could be the mechanism responsible for the space–time correlations described here? It is possible that the mecha-
anism that makes receptive fields larger is closely related to the mechanism that makes responses faster. An interesting possibility is that both parameters depend on the number of convergent inputs that a cell receives (from the photoreceptor to the LGN). Increasing the number of convergent inputs should make geniculate receptive fields larger (more cones per geniculate cell) and visual responses faster [more synapses being simultaneously activated lead to a larger compound synaptic potential that reaches threshold faster (e.g., Andreasen and Lambert 1998)]. Data on X and Y geniculate cells provide support for this "convergence hypothesis." Y geniculate cells have larger receptive fields than X geniculate cells because they receive input from more cones (for review see Sterling 2004), and possibly from more retinal inputs (Yeh et al. 2003). In addition, Y geniculate cells respond faster to visual stimuli than X cells because they may receive input from larger and more numerous synaptic boutons (Sur et al. 1987) [thicker axons may be necessary to maintain the higher metabolic demand of a larger volume of synaptic boutons (Sterling 2004)]. Summing a larger number of inputs also improves the signal-to-noise ratio and the contrast sensitivity. A low-contrast stimulus generates the fastest responses in cells with the highest contrast sensitivity, which usually have the largest receptive fields (Shapley and Victor 1978). Therefore cells with large receptive fields should generate faster responses than other cells because they have higher contrast gain. This mechanism clearly influences the space–time correlations reported here (particularly when using low-contrast stimuli). Although the strength of the correlation does not depend on the stimulus contrast (Fig. 6), the range of response latencies is reduced when the contrast increases.

The space–time correlations could also be a consequence of a common developmental mechanism of receptive field size and response latency. Just before eye opening, a geniculate cell receives weak synaptic contacts from many retinal ganglion cells; however, as the LGN matures most of the multiple inputs are eliminated (Chen and Regehr 2000; Mason 1982; Sretavan and Shatz 1986; Sur et al. 1984). The elimination of multiple retinal inputs could lead to both a reduction in receptive field size and a faster synaptic integration (because the remaining inputs become much stronger and therefore reach threshold faster).

Functional significance

Because of their space–time correlations, X and Y geniculate cells should provide the cortex with images whose spatial resolution becomes sharper over time. This finding is consistent with evidence indicating that low spatial frequencies generate faster visual responses than high spatial frequencies in cortical cells (Frazor et al. 2004; Mazer et al. 2002). It is also consistent with results in macaque showing that the peak of the spatial frequency tuning in visual cortical cells shifts toward higher frequencies as the response progresses in time (Bredfeldt and Ringach 2002; Frazor et al. 2004). Recently Frazor et al. (2004) modeled these spatial frequency shifts using convergent feedforward inputs. As indicated in their paper, the model applies to different types of thalamic neurons: Magnocellular and Parvocellular in the primate, X and Y in the cat, or any thalamic inputs with latencies that covary with spatial frequency. Here, we demonstrate that LGN inputs in the cat show space–time covarations that are independent of cell type. Therefore our results indicate that the shifts in the peak of the spatial frequency tuning of a cortical cell can be explained by the convergence of feedforward thalamic inputs—in both cortical cells that receive one type of input (X or Y) and those that receive mixed input.

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