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Neural Connections and Receptive Field Properties in the Primary Visual Cortex

JOSE-MANUEL ALONSO
Department of Psychology
University of Connecticut
Storrs, Connecticut

A cubic millimeter of primary visual cortex contains about 100,000 neurons that are heavily interconnected by intrinsic and extrinsic afferents. The effort of many neuroanatomists over the past has revealed the general outline of these connections; however, their function remains a mystery. Recently, combined physiological and anatomical approaches are beginning to reveal the role of these connections in the generation of cortical receptive fields. A common theme emerges from all these studies: cortical connections are remarkably specific and this specificity is determined in great extent by the type of connection and the neuronal response properties. Feedforward connections follow relatively rigid rules of wiring selectively targeting neurons with receptive fields matched in position and contrast polarity (thalamus → cortical layer 4) or position and orientation selectivity (layer 4 → layers 2 + 3). In contrast, horizontal connections follow more flexible rules connecting distant cells that are not retinotopically aligned and neighboring cells with different orientation preferences. These differences in connectivity may give a hint on how visual stimuli are processed in the primary visual cortex. An attractive hypothesis is that local stimuli use the highly selective feedforward inputs to reliably drive cortical neurons while background stimuli modulate their activity through more flexible horizontal (and feedback) connections. NEUROSCIENTIST 8(5):443–456, 2002. DOI: 10.1177/107385802236967

KEY WORDS Lateral geniculate nucleus, Intracortical, Thalamocortical, Cortical circuitry

With the aid of a small microscope and the Golgi staining method, Santiago Ramón y Cajal drew the first general outline of neural connections within the primary visual cortex (Cajal 1899). The Golgi staining yielded a complete view of neuronal bodies and dendrites; however, a full reconstruction of the cortical circuitry would have to wait for future generations and more modern techniques—the Golgi staining did not adequately impregnate myelinated axons. With the use of anatomical tracers and single cell labeling, axons were better reconstructed and a more complete scheme of the cortical circuitry became available. As Cajal found, the cortices of different species shared many features in common. These similarities motivated the study of a large variety of circuits, from mice to primates, to learn lessons about connectivity and neural processing. Of all the species studied, the cat has been by far the most intensively investigated. As Payne and Peters recently stated, "the cat primary visual cortex is probably one of the best studied areas in the brain of any species" (Payne and Peters 2002).

A systematic study of neural connections in the primary visual cortex is leading to more accurate hypotheses about the role of specific circuits in visual processing. This review focuses on connections that are likely to be involved in the construction of two types of cortical receptive fields: layer 4 simple cells and layers 2+3 complex cells. The study of cortical circuitry has benefited enormously from technical tools such as anatomical tracers and electron microscopy. However, these approaches fell short of answering important questions at the single cell level, as they could not reveal the synaptic strength of the connections and the neuronal response properties. With the advent of additional techniques, a more complete picture is emerging. Intracellular recordings in vitro made it possible to simultaneously record from two or more connected neurons and measure the connection strength. In addition, simultaneous extracellular recordings from multiple neurons and intracellular recordings in vivo allowed us to study the response properties of connected neurons. Also, studies using optical imaging and 2-deoxyglucose revealed the several maps in which cortical circuits are embedded.

This review is centered on the cat primary visual cortex but refers to other species frequently as certain circuits are better understood in primates or rodents. It focuses on connections that are likely to be involved in the generation of response properties as opposed to connections that diffusely modulate excitability (e.g., brain stem afferents). There are several thousand references...
about the circuitry of the cat primary visual cortex, so obviously many important ones must be omitted to present a concise review. In general, this review covers in most detail circuits that have been studied by the author (e.g., feedforward connections are discussed more extensively than horizontal connections). The primary visual cortex receives many different names in the literature (e.g., striate cortex, V-1, area 17). Here, I use area 17 for cats and V-1 for other species including primates.

**Feedforward Inputs from Subcortical Structures**

**General Characteristics**

The main thalamic input to the primary visual cortex originates in the lateral geniculate nucleus (LGN). In the cat, the primary visual cortex receives geniculate input from at least three different pathways: X, Y, and W. These pathways differ in several response properties such as conduction velocity, receptive field size, and linearity of spatial summation within the receptive field. Y cells have the fastest conduction velocities, largest receptive field sizes, and nonlinear spatial summation. X cells have intermediate conduction velocities, small receptive field sizes, and linear spatial summation. Finally, the W cells are a diverse group of neurons with very slow conduction velocities, large receptive field sizes, and linear or nonlinear spatial summation (for review, see Orban 1984; Sherman and Guillery 2001).

The LGN of the cat is organized in three main layers, two contralateral (A and C) and one ipsilateral (A1). Whereas layer C has almost exclusively Y cells, the A layers have a mixture of X and Y cells with a bias toward X cells (particularly near the area centralis; LeVay and Ferster 1977). Below layer C, the cat LGN also has three smaller parvocellular layers, two contralateral (C1, C3) and one ipsilateral (C2), that contain mostly W cells (Fig. 1, top). X, Y, and W cells differ not only in their laminar location within the LGN but also in their projection patterns within the cortex. X cells project almost exclusively to area 17, Y cells project to area 17 and area 18, and W cells project to many areas but predominantly to area 19 (Stone and others 1979; Kawano 1998). Within area 17, X and Y cells project, respectively, to the bottom and top of layer 4 (Ferster and LeVay 1978; Gilbert and Wiesel 1979; Humphrey and others 1985), whereas W cells project to the borders of this layer embracing the X/Y projection (LeVay and Gilbert 1976). In addition, there are weaker projections to layer 6 (X, Y) and layer 1 (W), and some X cells project through the entire layer 4 (Humphrey and others 1985). In summary, the projection from three different pathways in the cat visual cortex—X, Y, and W—is partially segregated across cortical areas (areas 17, 18, and 19) and across layers within area 17 (Fig. 2, top).

Similar to the cat, the monkey visual system has three main pathways—the magnocellular (M), parvocellular (P), and koniocellular (K) pathways—that are segregat-ed in different layers at the level of the LGN (Fig. 1, bottom). The M, P, and K pathways, respectively, target cortical layers 4Cm, 4C, and the cytochrome oxidase-rich blobs in the superficial layers (Hubel and Wiesel 1972; Fitzpatrick and others 1983). In addition, there are some weaker projections to layer 6 (M and P pathways), layer 4A (P pathway), and layer 1 (K pathway) (Fig. 2, bottom). The projections from the M, P, and K pathways in the monkey share certain resemblances to the projections from the X, Y, and W pathways in the cat (Florence and Casagrande 1987). However, the parvocellular pathway in the monkey may be considered as a "totally new pathway" owing to its color selectivity, and the magnocellular pathway is sometimes subdivided into Mx and My based on the linearity of spatial summation like X and Y cells in the cat (Kaplan and Shapley 1982).

An important difference between the visual pathways of cats and primates is the extent in which the LGN pro-
Feedforward geniculocortical pathways

Fig. 2. Feedforward geniculocortical pathways to the primary visual cortex. Top. Three different geniculocortical pathways project to the cat primary visual cortex (X in red, Y in black, and W in blue). The cartoon illustrates the laminar targets, the lateral spread, and the cluster organization of the strongest axonal projections from each pathway based on data obtained from single axon labeling (Ferster and LeVay 1978; Humphrey and others 1985). For simplicity, the cartoon does not illustrate the projection of some X cells through the entire layer 4 and differences in projection strength (e.g., the X projection is 9 times stronger in layer 4 than in layer 6). Also, it should be noticed that the illustration for the W cell projection is based on relatively sparse data (Ferster and LeVay 1978). Bottom. Three different geniculocortical pathways project to the macaque primary visual cortex (Parvocellular in red, Magnocellular in black, and Koniocellular in blue). The cartoon illustrates the laminar targets, the lateral spread, and the cluster organization of the strongest axonal projections from each pathway based on data obtained from single axon labeling in the macaque (Blasdel and Lund 1983). The cartoon illustrates the targets of two different types of thin axons (in dark blue and light blue) labeled by Blasdel and Lund (1983).

Lack of knowledge about their circuitry. A more detailed knowledge of this circuitry will eventually lead to more precise comparisons and let us benefit from the large amount of data gathered in both species over the past.

In addition to the main geniculate layers, cat area 17 receives a scant projection from the MIN (medial interlaminar nucleus of the thalamus), a nucleus that is only present in carnivores. The MIN contains mostly Y cells and W cells (Humphrey and Murthy 1999); Y cells project to the top of layer 4 and W cells to layer 1 (LeVenthal 1979). Finally, another source of subcortical input that should not be neglected is the claustrum. The caudal end of this nucleus contains visually driven cells, and it is retinotopically organized. The claustrum receives input from layer 6 of area 17 and projects back to area 17 terminating predominantly within layers 4 and 6 (LeVay and Sherk 1981).

Topography and Clustering of Synaptic Terminals

The geniculocortical pathway has an exquisite retinotopic organization. Each axonal arbor is restricted to a very small portion of the cortex (Fig. 2, top). X axons are the most restrictive ones and cover an area of 0.6 to 0.9 square millimeters, with most of the boutons concentrated in layer 4 and a smaller proportion in layer 6 (layer 6 receives 10% of all boutons; Humphrey and others 1985). Y axons cover a cortical area twice as large as X axons and make several clusters that align with the ocular dominance columns (1–1.8 square millimeters with gaps of 500 microns; Ferster and LeVay 1978; Gilbert and Wiesel 1983; Humphrey and others 1985). On average, Y axons have twice as many synaptic boutons as X axons (Y: 4280; X: 2620) and give a significantly larger number of boutons to layer 6 (~14% of all boutons; Humphrey and others 1985). Moreover, Y cells make more synaptic contacts per neuron (n = 3–6) than X cells (n = 2–3) and tend to target cortical cells with larger somata (Freund and others 1985).

We know little about the span of W axons in the cortex and the number of synapses per axon. Ferster and LeVay (1978) filled some very thin axons after injecting HRP in the optic radiations that are likely to belong to W cells. Based on this study, W axons make clusters separated by 500-micron gaps and cover distances of up to 3.8 mm mainly within layer 1 (twice as large as the Y axons). The W axons, some very thin axons in the monkey (probably from the K pathway) can span distances of 2 mm within layer 1, making clusters separated by 300-micron gaps (Fig. 2, bottom). Magnocellular axons make clusters with the same periodicity (~300-micron gaps), but they only span 1 mm laterally. Finally, the parvocellular axons in monkeys can be restricted to a single terminal field of 200 microns (Blasdel and Lund 1983). On average, the cortical area covered by a geniculate axon is larger in the cat than in the monkey. Consequently, the cortical area containing cells with overlapping receptive fields is also larger in the cat (cat: 5 mm² [Albus 1975]; monkey: 3.1 mm² [Hubel and Wiesel 1974]).
Response Properties

The specificity of the geniculocortical pathway goes further than a precise retinotopic organization. Based only on the size of the axonal arbor in the cat visual cortex, an X cell could potentially contact 15,000 cortical cells (Peters and Payne 1993); however, bouton counts suggest that this number is much lower. For example, if a Y cell makes 3600 synapses within layer 4 (Humphrey and others 1985) and makes 5 contacts per cortical neuron (Freund and others 1985), then each Y axon would contact 720 neurons.

The idea that each geniculate axon targets a small number of cortical neurons is very consistent with physiological studies (Reid and Alonso 1995; Alonso and others 2001; see also Tanaka 1983). The connections between geniculate cells and layer 4 neurons are strongly determined by the cells’ receptive field properties. In the cat, the receptive fields of geniculate cells and layer 4 cells have very different geometry (Fig. 3a). Whereas geniculate receptive fields are roughly circular and have a center-surround organization (e.g., on-center/off-surround), most layer 4 cells have simple receptive fields made of separate and elongated subregions (e.g., on-subregion flanked by off-subregions). As would be expected from the anatomy, geniculocortical connections link cells that are retinotopically aligned—in almost every connection the receptive field center of the geniculate cell precisely overlaps the receptive field of the layer-4 neuron. In addition, geniculocortical connections are strongly determined by a precise match in other response properties. The probability of finding a monosynaptic connection between a geniculate cell and a layer 4 simple cell is highest when 1) the geniculate center is superimposed with a simple cell subregion of the same sign (e.g., on-center superimposed with on-subregion), 2) the geniculate center and the overlapped simple cell subregion generate responses with similar time courses, 3) the geniculate center overlaps the strongest subregion of the simple cell, and 4) the diameter of the geniculate center equals (or is slightly larger) than the width of the simple cell subregion (Alonso and others 2001). Figure 3a shows the receptive fields of a geniculate cell and a layer 4 simple-cell that follow all these rules of connectivity (receptive field position, sign, timing, subregion strength and size).

The remarkable precision of the geniculocortical connections has important implications for models of receptive field generation. For many years, two general models attempted to explain how orientation selectivity was generated in the visual cortex. In the Hubel and Wiesel model, the orientation selectivity of simple cells originated from the convergence of geniculate inputs with receptive fields aligned in visual space. In cross-orientation models, orientation selectivity emerged as a result of inhibitory connections between cells with different orientation preferences (see Ferster and Koch 1987 for review). Recent studies have provided strong support for the original Hubel and Wiesel model (Hubel and Wiesel 1962). First, the receptive fields of the geniculate inputs to a simple cell are aligned in visual space (Reid and Alonso 1995; Alonso and others 2001; also see Chapman and others 1991). Second, the synaptic potentials of simple cells maintain their orientation selectivity even if most cortical inputs are inactivated (Chung and Ferster 1998; Ferster and others 1996). And third, orientation selectivity can be modeled by combining convergent geniculate inputs with a push-pull mechanism in a circuit that is very consistent with the Hubel and Wiesel model (Troyer and others 1998; but see Somers and others 1995 as an example of an alternative model).

Feedback Inputs from Other Cortical Areas

General Characteristics

The primary visual cortex also receives feedback input from other cortical areas. In monkeys, V-1 is clearly the lowest area in a cortical hierarchy because it is by far the main recipient of geniculate input. In the cat, however, hierarchies and feedback are more difficult to establish because geniculate connections target several cortical areas with similar strength. In fact, areas 17 and 18 in the cat share more connections in common than any other combination of cat visual areas (Symonds and Rosenquist 1984), and both should be probably considered as part of the primary visual cortex (Bullier and others 1984; Payne and Peters 2002).

In the monkey, feedback connections to V-1 originate in several cortical areas including V-2, V-3, V-4, MT, and the inferotemporal cortex (see Salin and Bullier 1995 for review). Connections from higher areas originate mainly in infragranular layers, whereas those from lower areas originate in both supragranular and infragranular layers. The connections from the highest areas target almost exclusively layer 1, whereas those from lower areas target a large variety of layers including 1-3, 4B, and 5-6 (Rockland and Pandya 1979; see Fig. 4, bottom). In some cases, a cortical area sends feedback to the layers of V-1 that give origin to the feedback input for that area. For example, layer 4B of V-1 both receives and sends input to MT. However, although there is some evidence for bidirectional feedforward–feedback circuits in the rat (Johnson and Burkhalter 1997), these closed loops are not a general rule in feedback connections. For example, MT sends feedback to the deep layers of V-2, but these layers do not project to MT (Rockland and Knutson 2000). Moreover, the feedback axons from V-2 to V-1 are slightly horizontally offset from the feedforward neurons that project from V-1 to V-2 (Rockland and Virga 1989).

A remarkable feature of feedback pathways is their anatomical diversity. Whereas V-2 axons target layers 1, 2, 3, and 5 (Rockland and Virga 1989), MT axons target layers 1, 4B, and 6. Moreover, a single MT axon may target only layer 1, only layer 4B, layers 1 and 4B, or layers 1, 4B, and 6 (Rockland and Knutson 2000). This diversity of connection patterns could indicate the existence of parallel feedback pathways as there are parallel feedforward pathways. Consistent with this idea, Henry and
Fig. 3. Response properties and strength of geniculocortical connections. A. On the left, the figure shows the receptive fields from a geniculate cell (top) and a simple cell (bottom) that were monosynaptically connected. Each receptive field is shown as a contour plot at three different time delays between stimulus and response. On-responses are represented in gray, and off-responses in black (the grid can be used as spatial reference to superimpose both receptive fields). The geniculate receptive field is roughly circular and has a center-surround organization; on-center (first frame: 0–25 ms) and off-surround (second frame: 25–50 ms). The simple receptive field has two elongated and parallel subregions, one off- and the other on- (first frame: 0–25 ms). These strong subregions are flanked by weaker subregions that can be seen on the second frame (25–50 ms). The geniculate center is overlapped with a simple-cell subregion of the same sign (on- superimposed with on-) and similar response time-course (both responses start at the 0–25 ms frame and peak at the 25–50 ms frame). On the right, there is a correlogram showing a narrow peak displaced from zero (asterisk) indicating that the geniculate cell was monosynaptically connected to the simple cell. (Reproduced from Alonso and others 2001 with permission from The Journal of Neuroscience). B. Visual responses of a simple cell to a moving bar. On the left, a histogram shows the total number of spikes generated by each bar sweep (each histogram bin is a bar sweep). On the right, a raster illustrates the individual spikes (each spike is represented by a dot, and each bar sweep by a raster line). The simple cell had three subregions that were sequentially stimulated by the sweeping bar and can be seen as three columns of spikes in the raster. The arrows indicate the injections of tiny volumes of GABA in a region of LGN (layer A) that was retinotopically aligned with the simple receptive field. The largest injections completely inactivated the response of the simple cell for several seconds (15 nl represented by the largest black circle at the bottom). The smallest injections (smallest black circle at the top) inactivated only the third subregion of the simple cell. At the bottom, the duration of the blockade is shown as a function of the volume of GABA injected in LGN. [Reproduced from Martinez and Alonso, 2001 with permission from Neuron]. C. A tiny injection of GABA in LGN (layer A) is able to inactivate a single subregion in the receptive field of a simple cell. The dotted circle represents the receptive field of the geniculate multiunit activity recorded at the center of the injection.
Feedback pathways

Layer 1
Layers 2+3
Layer 4
Layer 5
Layer 6
18 19 LS

Cat

Layer 1
Layers 2+3
Layer 4A
Layer 4B
Layer 4C
Layer 5
Layer 6
V-2 MT TEO

Monkey

Fig. 4. Feedback pathways to the primary visual cortex. Top, three different feedback pathways to cat area 17 originate in area 18 (red), area 19 (black), and the lateral suprasylvian area (blue). The cartoon does not illustrate the lateral spread and the cluster organization of the axonal projections in the cat due to lack of enough data from single axon labeling (Henry and others 1990; Shipp and Grant 1991). Bottom, three different feedback pathways to monkey V-1 originate in V-2 (red), MT (black), and the inferotemporal area (blue). The cartoon illustrates the laminar targets and lateral spread of the three pathways (Rockland and Virga 1989; Rockland and others 1994; Rockland and Knutson 2000). The cluster organization is very diverse and is not represented.

others (1990) suggested that cells in the superficial and deep layers of cat area 18 form two parallel pathways that, respectively, target the superficial and deep layers of area 17 (Fig. 4, top).

Topography and Clustering of Synaptic Terminals

Feedback axons cover larger cortical distances than feedforward axons (Figs. 2, 4). On average, axonal arbors from V-2, V-4, and TEO span distances of 1, 5, and 6 mm, respectively, and the axonal arbors from MT/V5 can span distances of up to 8 mm within layer 4B of V-1 (Rockland and Virga 1989; Rockland and others 1994; Rockland and Knutson 2000). There seems to be a "distance rule" in feedback connections—areas that are farther from V-1 cover larger cortical regions than nearby areas (Rockland and Knutson 2000). At least in part, this distance rule could reflect differences in receptive field size (receptive field size is larger in farther areas than nearby areas to V-1).

Although feedback connections can cover large V-1 distances, they are far from being diffuse. Like geniculate axons, they form clusters. The periodicity and the presence of clusters of axonal arbors vary for different cortical layers. For example, MT axons usually form clusters within layer 4B (250 to 750 microns) but rarely within layer 6 (Rockland and Virga 1989). At least for the case of MT, the cluster organization could be related with the patchy distribution of projecting feedforward neurons from V-1 (Boyd and Casagrande 1999).

Response Properties

We know little about the response properties of cells that receive or send feedback inputs and the properties shared between neurons connected by feedback pathways. In fact, we can hardly answer elementary questions about the retinotopic topography of these pathways. For example, we know that many V-1 cells sharing input from a common MT axon are not retinotopically aligned (MT axonal arbors can cover distances of up to 8 mm within V-1). However, we still do not know whether MT neurons are retinotopically aligned with all its V-1 targets—the receptive field of an MT neuron may be large enough to overlap the receptive fields of all the V-1 cells it feeds.

In comparison with feedforward pathways, feedback pathways target a smaller percentage of inhibitory neurons (Johnson and Burkhalter 1996). Feedback pathways are also weaker than feedforward pathways, and their inactivation rarely silences a V-1 cell (Alonso and others 1993) even if a large number of feedback connections are inactivated or removed (Mignard and Malpeli 1991; Hupe and others 1998). In contrast, the inactivation of a small group of feedforward geniculate inputs has a dramatic effect on cortical activity (Malpeli 1983; Martinez and Alonso 2001). Figures 3b and 3c show the visual responses of a simple cell in area 17 during the inactivation of its geniculate inputs. By injecting tiny volumes of GABA in layer A of the LGN, it is possible to inactivate the response of a cortical cell entirely (Fig. 3b) or inactivate restricted portions of its receptive field (Fig. 3b and c). This level of precision is consistent with the idea that each strong subregion in the receptive field of a simple cell is dominated (or driven) by just a few geniculate inputs.

Recently Sherman and Guillery (1998) and Crick and Koch (1998) reemphasized the importance of classifying neural connections as drivers or modulators based on their synaptic strength. Paraphrasing Crick and Koch (1998), the drivers are inputs that, by themselves, can make the relevant neurons fire strongly. And the modulators are inputs that, by themselves, cannot make the relevant neurons fire strongly, but can modify the firing produced by the driving inputs. Under this distinction, the results from inactivation studies suggest that feedforward inputs are the drivers of corticocortical activity and feedback inputs the modulators. An interesting hypothesis is that feedback
pathways serve to modulate the gain of lower cortical areas during selective visual attention (Desimone and Duncan 1995) and improve the discrimination between foreground and background stimuli (Hupe and others 1998).

**Inputs from Vertical Connections**

**General Characteristics and Clustering of Synaptic Terminals**

Both feedforward and feedback afferents feed into the intrinsic circuitry of the primary visual cortex. The primary visual cortex is organized in layers of neurons that are crossed by vertical connections running orthogonal to the cortical surface. In cat area 17, layer 4 projects to layers 2+3, layers 2+3 project to layer 5, and layer 5 projects to layer 6 (in addition, layers 5 and 6 project to the superficial layers and layer 6 projects to layer 4). In the monkey, a very similar circuit can be proposed if layer 4C and layers 2-4B are considered to be analogous to cat layer 4 and layers 2+3, respectively (the connections from layer 5 to layer 6 have not been described in the monkey; for review, see: Gilbert 1983; Callaway 1998).

Layer 4, the main recipient of geniculocortical input in the primary visual cortex, sends its main output to layers 2+3. These connections are totally unidirectional. That is, all excitatory connections run in the direction from layer 4 to layers 2+3 (Alonso and Martinez 1998; Martinez and Alonso 2001; see also Feldmeyer and others 2002). The connections from layer 4 to layers 2+3 are also relatively strong and fast. In vitro studies in the rat somatosensory cortex (Feldmeyer and others 2002) indicate that the axon from a layer 4 cell makes about four to five synaptic contacts with the basal dendrites of a layer 2+3 pyramidal neuron generating EPSPs of 0.7 ± 0.6 mV. For comparison, a cell in layers 2+3 makes about one to five synaptic contacts with the apical trunk or proximal oblique dendrites of a layer 5 cell generating EPSPs of 0.3 ± 0.3 mV (Reyes and Sakmann 1999).

The connections from layer 4 to layers 2+3 are very specific. In the macaque, the two subdivisions of layer 4C target different cortical layers—layer 4C, projects to layer 4B and layer 4C projects to layers 2+3. Furthermore, this specificity is improved at the single cell level within layer 4B—spiny stellate cells receive most of their input from layer 4C, whereas pyramidal cells (whose dendrites widely cross layer boundaries) receive mixed input from layer 4C, and layer 4C, (Yabuta and others 2001). Similarly, in tree shrew, the cortical depth of a layer-4 neuron determines its projection pattern within layers 2+3 (Fitzpatrick 1996). Surprisingly, however, this level of specificity has not yet been demonstrated in the cat. In the cat, layer 4 cells show a diverse pattern of projections some of which are restricted to a small cortical cylinder in layers 2+3 (~300 microns; e.g., Fig. 2 of Hirsch and others 1998a), whereas other span distances of up to 5 mm in the form of multiple very narrow clusters (~100 microns; e.g., Fig. 9 of Martin and Whitteridge 1984).

In addition to their layer 4 inputs, layers 2+3 receive connections from basically every cortical layer. If vertical connections are seen as part of a serial circuit (for cat: layer 4→layers 2+3→layer 5→layer 6), the inputs from layer 4 could be considered as vertical feedforward whereas the inputs from the other layers would be vertical feedback (Callaway 1998; Fig. 5a). In support of this interpretation, feedforward and feedback vertical inputs have been shown to target different types of neurons. For example, within layers 2+3, layer 4 inputs target pyramidal cells and fast spiking cells (the main drivers of excitatory and inhibitory activity within layers 2+3), whereas layer 5 inputs target a population of adapting inhibitory neurons that are mainly modulators (Fig. 5b; Dantzker and Callaway 2000).

The connections from layer 6 to layer 4 can be also considered as vertical feedback in that layer 4 neurons remain strongly active during the inactivation of layer 6 (Bolz and Gilbert 1986; Grieve and Sillito 1991). Feedback connections from layer 6 to layer 4 originate specifically in corticogeniculate neurons (Katz 1987), and there are at least two populations of these neurons in monkeys. One population is dominated by magnocellular input and targets layer 4C, whereas the other population is dominated by parvocellular input and targets predominantly layer 4C, (Briggs and Callaway 2001). In the cat, layer 4 also receives indirect feedback from a different population of layer 6 cells through the claustrum (layer 6→claustrum→layer 4; LeVay and Sherk 1981).

**Response Properties**

While the geniculocortical connections link cells with receptive fields matched in position and response sign (on- or off-), the connections from layer 4 to layers 2+3 link cells with receptive fields matched in position and orientation preference (Alonso and Martinez 1998; Martinez and Alonso 2001). In layers 2+3, receptive field sign is no longer relevant because most neurons are complex cells (generate on- and off-responses in the same region of the receptive field). In contrast, orientation preference becomes important because the projections from layer 4 to the superficial layers are at the very center of the orientation column. The orientation preference of a cortical column is likely to be determined mainly by vertical feedforward inputs, whereas the bandwidth of the orientation tuning could be modulated by horizontal and feedback connections (Alonso and others 1993; White and others 2001). It is important to emphasize that most layer 4 axons cover very restricted regions in layers 2+3 and their convergence should be able to generate narrow orientation bandwidths (e.g., less than 45 degrees for arbors 300 microns wide).

Figure 6 illustrates the receptive field properties of a layer 4 simple cell and a layer 2+3 complex cell that show correlated firing consistent with a monosynaptic connection (Fig. 6c). The simple cell has a receptive field with separate on- and off-subregions and the complex cell an on-off receptive field that could only be mapped with moving bars (both light and dark). Like in
Vertical connections

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<th>Vertical feedback connections</th>
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<td>Layers 2+3</td>
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B

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- △: Excitatory pyramidal neuron
- ○: Inhibitory fast-spiking cell
- □: Inhibitory adapting interneuron

Fig. 5. Vertical connections in the primary visual cortex. A, Vertical connections in the cat visual cortex are classified as feedforward and feedback assuming the existence of a serial circuit in the cortical column: layer 4→layers 2+3→layer 5→layer 6 (for the cat; see text for more detail). B, In the rat visual cortex, feedforward and feedback vertical connections target different types of cells within layers 2+3. Feedforward inputs from middle layers target excitatory pyramidal cells and inhibitory fast-spiking cells, whereas feedback inputs from the deep layers target inhibitory adapting interneurons (Dantzker and Callaway 2000).

This example, most excitatory connections between layer 4 and layers 2+3 link cells with overlapping receptive fields (Fig. 6a) and similar orientation preferences (Fig. 6b). In all cases studied, the connections were found to run in the direction from the layer 4 simple cell to the layers 2+3 complex cell and none in the opposite direction (Alonso and Martinez 1998).

The properties of the feedforward circuit LGN→layer 4→layers 2+3 are very consistent with a Hubel and Wiesel model of receptive field generation (Hubel and Wiesel 1962). According to this model, the convergence of geniculate inputs generates simple receptive fields in layer 4 (Reid and Alonso 1995) and the convergence of layer 4 inputs generates complex receptive fields in layers 2+3 (Alonso and Martinez 1998). Also in support of this model, the inactivation of a small group of geniculate inputs is enough to silence most layer 4 simple cells and most complex cells in the superficial layers (Martinez and Alonso 2001; cf. Malpeli 1983). Finally, several theoretical models have been successful at constructing complex receptive fields from simple cell inputs (e.g., Adelson and Bergen 1985; Ohzawa and others 1990) or simple cell inputs combined with complex cell inputs (Chance and others 1999). Still, some complex cells are known to receive direct geniculate input (Hoffmann and Stone 1971) and could be constructed by other mechanisms (e.g., Mel and others 1998).

Layers 2+3 and layer 4 also receive vertical feedback from the deep cortical layers. Although little is known about the role of these connections in receptive field generation (Bolz and Gilbert 1986; Grieve and Sillito 1991), several lines of evidence indicate that most of the vertical feedback to layer 4 originates from simple cells. Data from intracellularly labeled neurons show that many layer 6 cells projecting to layer 4 have simple receptive fields (Gilbert and Wiesel 1979; Martin and Whitteridge 1984; Hirsch and others 1998b), and combined anatomical and physiological studies demonstrate that most layer 6 cells projecting to layer 4 are corticogeniculate cells (Katz 1987; Usrey and Fitzpatrick 1996), and most corticogeniculate cells are simple cells (Grieve and Sillito 1995). Finally, the layer 6 cells projecting to the claustrum (another source of input to layer 4) have also simple receptive fields (Grieve and Sillito 1995).

Inhibitory Inputs

General Characteristics and Clustering of Synaptic Terminals

Local inhibitory neurons are an essential part of the circuitry within the primary visual cortex. Without inhibition, excitation saturates and the selectivity for a large variety of response properties is lost. Orientation selectivity, direction selectivity, simple-cell subregion antagonism, and end-inhibition are just a few examples of properties that are seriously affected by extracellular blockade of inhibition (e.g., Sillito 1975). Cortical inhibition is not only crucial to balance excitation but also has an important role in cortical plasticity (Hensch and others 1998). However, in spite of its undeniable importance, we know little about the connections made by inhibitory neurons and their role in generating cortical receptive fields.

Inhibitory neurons make up about 20% to 25% of all cortical cells (Gabbert and Somogyi 1986) and show a large variety of morphologies, physiological properties, and molecular structure (Gupta and others 2000). A large proportion of inhibitory neurons belong to a class
identified by Ramon y Cajal (1899) and named by Marin-Padilla (1969) as basket cells. There are several types of basket cells that differ in morphological and physiological properties (Kisvarday 1992; Gupta and others 2000). Small basket cells are involved in local connections within a few hundred microns, whereas large basket cells have axonal fields that can cover up to 2.5 mm of cortical distance (Buzás and others 2001).

In addition to basket cells, pyramidal neurons receive input from at least two other types of inhibitory neurons: chandelier cells and double bouquet cells (Fig. 7a). Chandelier cells are an extraordinary example of specificity in the cerebral cortex—they only connect to axon initial segments (Somogyi 1989) mostly of pyramidal cells (DeFelipe and Farías 1992). Among pyramidal cells, corticocortical cells in layers 2+3 receive the largest number of axoaxonic synapses (22–28) and corticothalamic pyramids the smallest (1–5; DeFelipe and Farías 1992). The other type of inhibitory neuron—the double bouquet cell—was first described by Cajal (1899) and is characterized by axons that form tightly intertwined bundles of vertical collaterals across layers. Double bouquet cells are the major source of a rare type of symmetric synapse on dendritic spines of pyramidal cells (DeFelipe and Farías 1992).

Inhibitory neurons can also be classified based on their physiological properties in at least two categories: fast-spiking and adapting inhibitory neurons (Gibson and others 1999; Dantzker and Callaway 2000). Although the relation between the morphological and physiological classification is still rather loose, most fast-spiking cells are likely to be basket cells. Fast-spiking cells have short-duration spikes and reach high firing rates with little or no adaptation. In contrast, adapting inhibitory neurons have spikes of longer duration and show considerable adaptation in their firing rates. This physiological distinction is important because it relates to specific cortical circuits. Feedforward inputs tend to target fast-spiking cells, whereas feedback and horizontal inputs most frequently target adapting inhibitory neurons (Gibson and others 1999; Dantzker and Callaway 2000). Moreover, electrical synapses tend to connect inhibitory neurons of the same type (Gibson and others 1999; Fig. 7b).

Recent in vitro studies revealed a dense interconnected network of inhibitory neurons that regulate their outputs through both chemical and electrical reciprocal connections (Galarreta and Hestrin 1999; Gibson and others 1999) in addition to self-connections or autapses (Tamas and others 1997). Only one type of inhibitory neuron seems to avoid this promiscuous connectivity—the chandelier cell (Somogyi 1989). Among the reciprocal inhibitory connections, the connections between basket cells generate the strongest and fastest IPSPs (Tamas and others 1998) by making an average of 12 synapses per connection all located on somata and proximal dendrites. Basket cells also make connections with double bouquet cells and excitatory cells, but these connections are weaker. The connections between spiny stellate cells and basket cells are likely to be important for receptive field generation—in the cat visual cortex, 30% of simultaneously recorded spiny stellate cells and basket cells are reciprocally connected (Tarczy-Hornoch and others 1998).

Response Properties

We know little about the response properties of inhibitory neurons. In vivo intracellular recordings from these neurons are sparse. The available sample suggests that, like excitatory cells, inhibitory cells can have simple or complex receptive fields (Gibert and Wiesel 1979; Martin and others 1983; Azouz and others 1997). Also like excitatory cells, most inhibitory cells are orientation selective, although some of them are nonoriented (Martin and others 1983).

Despite these similarities, excitatory and inhibitory neurons are likely to differ in several response properties. An important one is sensitivity. In vivo, extracellularly recorded fast-spiking cells respond to higher stimulation frequencies and lower stimulus intensities than excitatory cells (Swadlow 1989). Similarly, in vitro inhibitory
Inhibitory connections (general scheme)

Basket cell
Double bouquet cell
Chandelier cell

Two physiological types of inhibitory neurons

Feedforward Feedback

Layers 2+3
Layer 4
Layer 5

Fast-spiking cell Adapting interneuron Electrical synapse

Thalamus

Fig. 7. Inhibitory connections. A, Cartoon of the connections made by three different types of inhibitory neurons on pyramidal cells. B, Two physiological types of inhibitory neurons. In the rat, fast-spiking cells and adapting interneurons receive input from different cortical layers (middle layers for fast-spiking cells, deep layers for adapting interneurons; Dantzker and Callaway 2000), and only fast-spiking cells receive input from the thalamus (Gibson and others 1999). Moreover, electrical synapses link inhibitory cells of the same type (Gibson and others 1999).

neurons show greater increments in firing rate for a given increment of current than excitatory neurons (3 to 4 times greater increments; McCormick and others 1985). The sensitivity of inhibitory networks is further increased by a very precise synchrony (± 1 ms) that was described in vivo for fast-spiking cells (Swadlow and others 1998). This precise synchrony is probably generated by highly divergent thalamocortical inputs (Swadlow and others 1998) and amplified by electrical coupling (Galarreta and Hestrin 1999; Gibson and others 1999).

Intracortical inhibition should have an important role in shaping cortical response properties. After all, most excitatory responses are followed by disynaptic inhibition. Previous pharmacological experiments suggested that inhibition played a crucial role in generating orientation selectivity by connecting cells with different orientation preferences (for review, see Ferster and Koch 1987). However, this idea is not supported by recent evidence. First, orientation selectivity is not affected by intracellular blockade of inhibition (Nelson and others 1994). And second, the blockade of most cortical inputs to a simple cell (excitatory and inhibitory) does not affect the orientation selectivity of its synaptic potentials (Ferster and others 1996; Chung and Ferster 1998). It is still possible that orientation selectivity is modulated beyond the classical receptive field by inhibitory inputs and horizontal connections. This interpretation could explain some strong cross-inhibitory effects observed when using full-field stimuli (e.g., Blakemore and Tobin 1972; Sillito and others 1995; Ringach and others 1997). Indeed, although long-range horizontal connections (both excitatory and inhibitory) link cells with similar orientation preferences (e.g., Ts’o and others 1986; Dalva and others 1997), the axonal arbors are not totally restricted to a given orientation column (Kisvarday and others 1997) and locally may be even less specific (Malach and others 1993).

Within layer 4, cortical inhibition is likely to play a major role in contrast adaptation (Carandini and Ferster 1997) and in generating subregion antagonism in simple cells (Ferster 1988; Hirsch and others 1998a). In a simple cell, a light spot presented in an on-subregion generates a strong response that is shut down when the spot also covers an adjacent off-subregion. This effect can be easily explained by a push-pull mechanism—off-subregions receive excitatory input from cells that generate off-responses (push) and inhibitory inputs from cells that generate on-responses (pull). The push-pull model has received strong support from both extracellular and intracellular data (Palmer and Davis 1981; Tolhurst and Dean 1987; Ferster 1988; Hirsch and others 1998a). Recent results from Borg-Graham and others (1998) indicate, however, that on- and off-inhibition could be randomly intermingled within the simple receptive field. A possible explanation for Borg-Graham and others’ results is simply that they recorded from cells that lacked push-pull (most of these cells are outside layer 4; Hirsch and others 1998a). It would be interesting to use Borg-Graham and others’ approach to measure the distribution of inhibition within identified layer 4 cells. A push-pull mechanism is appealing for its simplicity and can be used to explain many properties of layer 4 simple cells like orientation selectivity, subregion antagonism, and certain nonlinearities such as the invariance of orientation tuning (Troyer and others 1998).

Inputs from Horizontal Connections

General Characteristics and Clustering of Synaptic Terminals

Cortical neurons also make short-range local connections within their own cortical layer. These connections are limited to a few hundred microns, they are frequently reciprocal, and they can be quite strong. In the rat
somatosensory cortex, a single layer 4→layer 4 connection within a “barrel” is reciprocal in 30% of the cases and generates EPSPs of 1.55 ± 1.53 mV with 2 to 5 synaptic contacts (Egger and others 1999; Feldmeyer and Sakmann 2000). Similarly, connections within layer 5 cells generate EPSPs of 1.3 ± 1.1 mV amplitude with around 5 synaptic contacts mostly in the basal dendrites (Deuchars and others 1994; Markram and others 1997; Feldmeyer and Sakmann 2000). Connections within layer 4 are highly reliable (Tarczy-Hornoch and others 1998) and generate faster EPSPs than connections within layer 5, probably due to differences in the location of the synaptic contacts and the NMDA/AMPA receptor ratios (Deuchars and others 1994; Markram and others 1997; Feldmeyer and Sakmann 2000).

In addition to the local connections, some neurons make long-range horizontal connections that can span several millimeters of distance within a single layer (Fig. 8a). A narrow lesion through all cortical layers can produce a horizontal degeneration of several millimeters. This degeneration is largest (5–6 mm) when the lesion is restricted to layer 4B and smallest (2–3 mm) when the lesion is restricted to layer 4C (Szentagothai 1973). Similarly, injections of HRP in V-1 generate a patchy projection within layers 2+3 that can span 8 mm² (Rockland and Lund 1982). The patchy organization of long-distance connections has been beautifully demonstrated in intracellularly labeled single cells (Gilbert and Wiesel 1979, 1983; Martin and Whitteridge 1984). Clusters of axonal arbors have an average periodicity of 1 mm and can be found in all cortical layers in more than half of the pyramidal and spiny stellate cells (Gilbert and Wiesel 1983).

Response Properties and Function: Local Horizontal Connections

Local horizontal connections make contact with neighboring neurons within a radius of a few hundred microns. Since most neighboring neurons have similar response properties (Hubel and Wiesel 1962; DeAngelis and others 1999), local connections should link cells with similar properties also. There seems to be an important exception to this rule. Neighboring neurons near pinwheel centers (layers 2+3) have different orientation preferences and can still be linked by local connections (e.g., Malach and others 1993). Therefore, the connectivity of local connections within the superficial layers does not appear to show the specificity for orientation that is characteristic of feedforward vertical connections (Alonso and Martinez 1998; Martinez and Alonso 2001).

Little is known about the role of local horizontal connections in receptive field generation. Within layer 4, local connections have been proposed to serve as a cortical amplifier for the incoming thalamic inputs (Douglas and others 1995; Somers and others 1995; Feldmeyer and Sakmann 2000). Original versions of the “cortical amplifier” suggested that geniculate inputs were weak because they made only 5% to 25% of the total excitatory synapses on cortical cells (for review, see Peters and Payne 1993). However, recent evidence indicates that geniculate inputs are likely to be stronger than intracortical inputs. First, thalamocortical synapses are larger, have more synaptic release sites, are more reliable, and are located more proximally in the dendrites than corticocortical synapses (Stratford and others 1996; Gil and others 1999). Second, geniculate inputs have
higher firing rates and are more precisely synchronized than the cortical excitatory inputs to layer 4 (Alonso and others 1996; Alonso and Martinez 1998). And third, the inactivation of a relatively small group of geniculate inputs is enough to make a “tiny hole” in the receptive field of a layer 4 cell even if most cortical inputs are still active (Martinez and Alonso 2001; Figs. 3b,c).

Even if the geniculate inputs are strong, the idea of a cortical amplifier within layer 4 is still attractive. Layer 4 is the main entrance of sensory information to the cortex, and its gain should be tightly regulated.

Response Properties and Function: Long-Range Horizontal Connections

Long-range horizontal axons also break one of the most common rules of visual cortical wiring: retinotopic alignment. Within layers 2+3, two cells separated by several millimeters can be reciprocally connected even if their receptive fields do not overlap (Fig. 8a). Unlike local connections, long horizontal axons target neurons with similar orientation preferences (e.g., Ts’o and others 1986; Dalva and others 1997).

The functional role of long-range horizontal connections within layers 2+3 has been intensively studied during the past decade. These connections have a major role in cortical plasticity, and following a retinal lesion, they grow to innervate cortical cells that no longer receive visual information from their feedforward inputs (Gilbert and Wiesel 1992; Darian-Smith and Gilbert 1994; Das and Gilbert 1995). Horizontal connections are also weaker than vertical feedforward connections (Hirsch and Gilbert 1991) and are likely to be responsible for interactions beyond the classical receptive field (e.g., Maffei and Fiorentini 1976; Kapadia and others 1995).

Circuitry of the Primary Visual Cortex: Hypothesis

If the properties of feedforward, feedback, and horizontal connections were known in enough detail, we should be able to make precise comparisons of their specificity and synaptic strength. Figure 8b shows a cartoon representing this hypothetical data. The central circle represents a cortical cell, and each arrow its synaptic inputs (the arrow width represents synaptic strength). The x-axis shows differences in response properties between the input and the target, and the y-axis receptive field complexity (e.g., lower for a geniculate cell than for an MT cell). As shown in this hypothetical graph, feedforward inputs are strong, small in number, and share many properties with the cortical cell they feed. In contrast, the inputs from feedback and horizontal connections are weaker, more numerous, and share fewer properties with their target.

It is risky to make any classification of circuits in the primary visual cortex because cortical connections are numerous and are likely to differ in many aspects that are still unknown. However, if we are willing to take the risk, the different pathways to V1 could be classified in two main categories—drivers (strong inputs) and modulators (weak inputs) (Crick and Koch 1998; Sherman and Guillery 1998). In this classification scheme, feedforward connections (both from LGN and from vertical inputs) would be the drivers of cortical activity, whereas horizontal and feedback connections would be the modulators. This organization could provide a basic “feedforward frame” that is flexible enough to be modulated through horizontal and feedback connections by new stimulus arrangements and experience.

References


