Circuits that build visual cortical receptive fields

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Neural sensitivity to basic elements of the visual scene changes dramatically as information is handed from the thalamus to the primary visual cortex in cats. Famously, thalamic neurons are insensitive to stimulus orientation whereas their cortical targets easily resolve small changes in stimulus angle. There are two main types of cells in the visual cortex, simple and complex, defined by the structure of their receptive fields. Simple cells are thought to lay the groundwork for orientation selectivity. This review focuses on approaches that combine anatomy with physiology at the intracellular level, to explore the circuits that build simple receptive fields and that help to maintain neural sensitivity to stimulus features even when luminance contrast changes.

Introduction

Neural receptive fields in the early visual pathway have captured attention for decades because of their potential to explain how sensory input is analyzed. The link between receptive-field structure and stimulus selectively was first made in studies that compared neural responses at the first three stages of the early visual pathway of cats: the retina, thalamus and primary visual cortex [1–3]. For example, retinal ganglion cells and the thalamic relay neurons they contact have circular receptive fields made of two concentric subregions, a center and a surround [1,3,4]. The subregions have opposite preferences for stimulus contrast such that On cells are excited by bright spots shone in the center or by dark annuli in the surround; Off cells respond in a reciprocal manner [1,3,4]. Furthermore, the center and surround have a mutually antagonistic relationship because stimuli of the reverse contrast evoke push–pull responses: within each subregion, bright light excites where dark stimuli inhibit [1,3,4]. Taken together, the geometry of center and surround and the suppressive interactions between them help retinal and thalamic cells to resolve local changes in stimulus contrast [1,3,5].

When Hubel and Wiesel first recorded from the primary visual cortex, they found a population of neurons reminiscent of cells in the thalamus; the receptive fields were divided into On and Off subregions that had an antagonistic effect on one another [2]. However, unlike the subcortical concentric arrangement, the On and Off

subregions were elongated and side by side. This observation was interesting because the new geometric configuration correlated with the emergence of neural sensitivity to stimulus orientation. In the thalamus, a bar of any orientation drove cells vigorously. Cortical cells responded briskly to a stimulus aligned with the long axis of sign-matched subregions, but fired less vigorously, if at all, to stimuli tilted away from the preferred angle. By making small lesions in the cortex to estimate recording sites, Hubel and Wiesel linked the novel class of cells to layers 4 and 6, where thalamic afferents terminate. They then proposed a model to explain how the cortical receptive fields were made. The essence of the idea was that convergent input from On and Off relay cells built the subregions of the cortical fields. Because this scheme was straightforward, cortical cells with adjacent, antagonistic On and Off subregions were called simple. Other neurons, found mainly outside of layer 4, had receptive fields that lacked spatially separate subregions and were called complex cells. The assumption was that simple cells relayed orientation selectivity to neurons at later stages of processing.

The feedforward circuit for the simple receptive field in the cat has received substantial experimental support and refinement. For example, recordings from the axonal arbors of relay cells showed that thalamic receptive fields line up along the axis of orientation of local cortical cells [6]. Cross-correlation analyses demonstrated that monosynaptic connections between a relay cell and a cortical cell occur when receptive fields of each neuron share the same sign and spatial position [7–10]. Lastly, intracellular recordings from cortical cells made when firing was greatly suppressed by cooling [11] or inhibition [12] showed that excitatory (presumably thalamic) input is tuned for orientation.

Yet alternative lines of evidence suggested that a basic feedforward circuit might not explain the simple receptive field. For example, some studies raised the possibilities that the simple and complex fields of Hubel and Wiesel represent two ends of a continuum found in all cortical layers and that there are distributed mechanisms for orientation selectivity [13–17]. These diverse points of view might have developed for several reasons [18]. First, most quantitative studies of receptive-field structure are made using extracellular electrodes. Over time, various authors developed diverse definitions of the simple receptive field, in part based on inferences about

subthreshold patterns of inputs that extracellular recordings cannot resolve. For example, cells with a single subregion, On or Off, were called simple (or S_1) [19] when their responses indicated hidden adjacent inhibitory subfields [19,20]. This practice sometimes expanded to include all cells that had just one subregion, such that many cells are called complex (or C_1) by some [2,18–23] and simple by others (e.g. [16,24]). Furthermore, many investigators classify simple and complex cells by response properties such as linearity rather than receptive-field structure *per se* [25]. Thus, the same name is often used to refer to different classes of cells and it seems likely that semantics have had a strong impact on views of cortical circuitry. In addition, it is difficult to establish recording sites precisely by extracellular means; even small errors can lead to incorrect assignments of layers. Moreover, species differences are sometimes overlooked, even though organization of the primary visual cortex changes with phylogeny [24,26–33]. Finally, a separate line of argument against feedforward models is that they cannot account for various aspects of cortical responses, such as the maintenance of orientation selectivity over a range of stimulus contrasts [34–38].

Combined physiological and anatomical approaches to the study of receptive fields

The combination of physiological with anatomical techniques has long been used to understand the structural basis of function. By the late 1970s, such analyses extended to the level of the microcircuit when it became possible to stain single cells whose responses had been recorded extracellularly [24,39,40]. Furthermore, intracellular techniques have improved and can now reveal patterns of synaptic excitation and inhibition that underlie visually evoked activity [15,17,18,22,41–52]. Figure 1 illustrates how receptive fields change as the recording site shifts from the thalamus to the first stage (layers 4 and upper 6) and then the second stage (layer $2+3$) of cortical processing. The recordings are drawn from our results because no other studies have combined intracellular staining with quantitative receptive-field mapping in the visual thalamus or cortex. The insets on the left of each panel are conventional contour plots in which red codes for On and blue for Off subregions; the stimuli were individually flashed dark and bright squares [53,54]. The larger maps are arrays of trace pairs in which each spatial coordinate is represented by the averaged responses to corresponding bright and dark
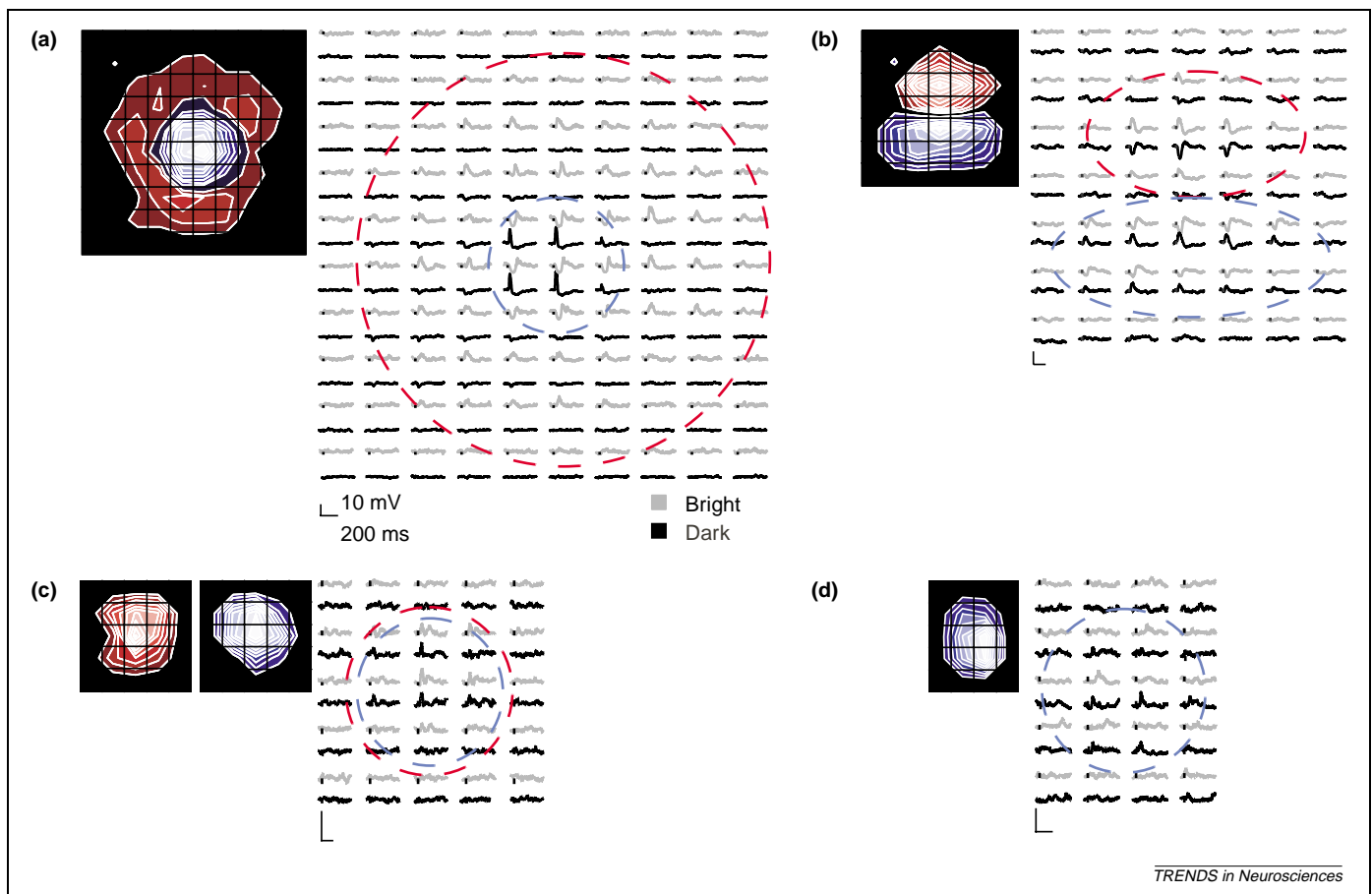

Figure 1. Main types of receptive field in the visual thalamus and cortex. The receptive fields are shown in two ways: as contour plots, in which each contour represents a 10% decrement from the peak response and brightness indicates response strength; and as arrays of trace pairs, in which each position in the stimulus grid is represented by averages of the corresponding responses to dark (black traces) and bright (gray traces) squares. Red represents On subregions and blue represents Off subregions; these are approximated by dashed circles or ovals in the arrays of trace pairs. For the relay cell in the thalamus **(a)** and the simple cell in cortical layer 4 **(b)**, stimuli of the reverse contrast evoked responses of the opposite sign (push–pull) in each subregion. For the complex cell in layer 4, both bright and dark stimuli evoked excitation (push–push) in overlapping regions of visual space **(c)**, whereas dark but not bright squares (push–null) excited the complex cell in layer 6 **(d)**. The stimulus was flashed for 31 ms or 47 ms (in the maps of trace pairs, the vertical lines indicates stimulus onset); square size was 0.85° or 1.7° and grid spacing was 0.85° (i.e. each square in contour plots or arrays represents 85° of visual angle).

stimuli. The receptive field of an Off-center relay cell is typical of recordings made in the lateral geniculate nucleus (Figure 1a). In both the center (broken blue line) and the surround (broken red line), stimuli of the reverse contrast evoked push–pull responses. That is, dark squares flashed in the center evoked an initial depolarization (push) followed by a hyperpolarization that corresponded to withdrawal of the stimulus (cells respond to stimulus onset and termination because both events cause a change in local luminance). Bright squares flashed at the same positions evoked the opposite response – a hyperpolarization (pull) followed by a depolarization. The responses from the surround also reveal a push–pull pattern.

As in the thalamus, most receptive fields in cortical layer 4 were built of On and Off subregions with a push–pull structure; unlike the thalamus, these subregions lay parallel and adjacent to one another [2,18,20,54–60]. In the Off subregion of a simple receptive field (Figure 1b), dark squares evoked excitation where bright squares elicited inhibition, with the reverse situation in the On subregion (when stimuli straddled the borders between subregions, correspondingly mixed responses were seen [48]); the motif of push–pull was repeated along the length of each subregion. Most remaining cells in layer 4 had complex receptive fields built of superimposed On and Off subregions [18,22,49]. Because bright and dark excitation overlapped, these fields had a push–push rather than a push–pull structure (Figure 1c). Cells at later stages of processing, in layers 2+3, 5 and lower 6, were much less responsive to sparse static stimuli (some failed to respond at all) [22,23]. Of the responsive group, there was often a strong, or absolute, preference for stimuli of one polarity [20,22]; the map in Figure 1(d) is from a cell that responded to dark but not bright squares (note that some investigators might use the terms simple or S_1 for such a field).

Description of receptive-field structure

The first descriptions of cortical receptive fields [2] were qualitative; later, attention focused on developing quantitative metrics [13,18,20,54,56,60–62]. From the perspective afforded by intracellular recordings, it becomes clear that two indices can capture the most salient qualitative features of the simple receptive fields. First, the overlap index [63] measures the degree of separation between On and Off subregions (Figure 2a). Second, the push–pull index [18] measures the balance of antagonistic responses to stimuli of the opposite contrast within individual subregions (Figure 2b). Cells that had segregated subregions (shaded bars) also had push–pull responses, as did two cells with only one subregion. By contrast, cells with overlapping On and Off subregions had high values of the push–pull index. A third measure, Pearson's cross-correlation coefficient [13,15,18], combines features the push–pull and overlap indices (Figure 2c). The plot of overlap index versus push–pull index divides into two statistically independent clusters: one of simple cells and the other of complex cells (Figure 2d; only cells that responded to bright and dark stimuli could be included, so many complex cells are not represented). Thus, simple receptive fields are easily defined by segregated On and Off subregions with push–pull structure.

Caveats about the measures above deserve comment [18]. Stimuli that overlap two subregions commonly conflate boundaries by evoking push and pull simultaneously [48]. Furthermore, recordings made too close to the reversal potential for inhibitory postsynaptic potentials cannot reveal inhibition and could lead to artificially flattened distributions for the push–pull or cross-correlation indices. A separate study of receptive fields in the cortex found a flat distribution of values for the correlation coefficient [15]. However, in that study no effort was made to visualize inhibition, nor was the potential impact of stimulus overlap considered. Lastly, the measures we have discussed describe spatial structure near the peak of response but do not apply to the full spatiotemporal receptive field [54,64].

Receptive-field structure, laminar position and morphology

Extracellular studies in which recording sites are marked have often linked the simple receptive fields with zones receiving input from the thalamus [2,20,21,55,56,65]. The improved anatomical resolution provided by combined intracellular labeling and recording goes one step further to show that the simple receptive field, as defined by segregated subregions with push–pull structure, is an exclusive feature of the first stage of visual processing (in cats). Cells with simple receptive fields are located in regions where thalamic afferents terminate – that is, layer 4, the borders of layer 4, or upper layer 6 [18]. Figure 3(a) shows receptive fields plotted as a function of laminar depth of the soma, with the deepest cells in each layer on the left and the most superficial on the right. The plot reveals a trend for cells with relatively short subregions to lie in lower regions of layer 4 and those with more elongated subregions to occupy the superficial half of the layer. Others have reported a similar arrangement, with simple fields in upper layer 4 and its border having narrower and more numerous subregions than those in the deep aspect of the layer [55,65]. The authors of those studies noted that the distribution in receptive-field structure correlated with projection patterns of X and Y relay cells – Y inputs are densest in upper layer 4 [66,67]. Such observations recall the primate cortex, in which lower layer 4 is supplied by parvocellular (X-like) relay cells and the upper tier by magnocellular (Y-like) inputs [29].

In both cats and monkeys, receptive-field structure and response properties vary as a function of layer, although in somewhat different ways [62,68–73]. Many cells in lower layer 4 of the macaque cortex are unoriented [62,68–74] or broadly tuned [75]; orientation tuning develops fully in upper layer 4 and later stages of processing [69,74,75] (but see [76]). Furthermore, in monkeys, simple receptive fields seem to be missing from lower layer 4, which receives parvocellular input; rather they have been associated with regions that receive magnocellular input [74,70]. In tree shrews, which might be phylogenetically related to primates, simple cells appear to be absent altogether. In that species, orientation tuning emerges in the superficial layers [77], apparently created by aligned,
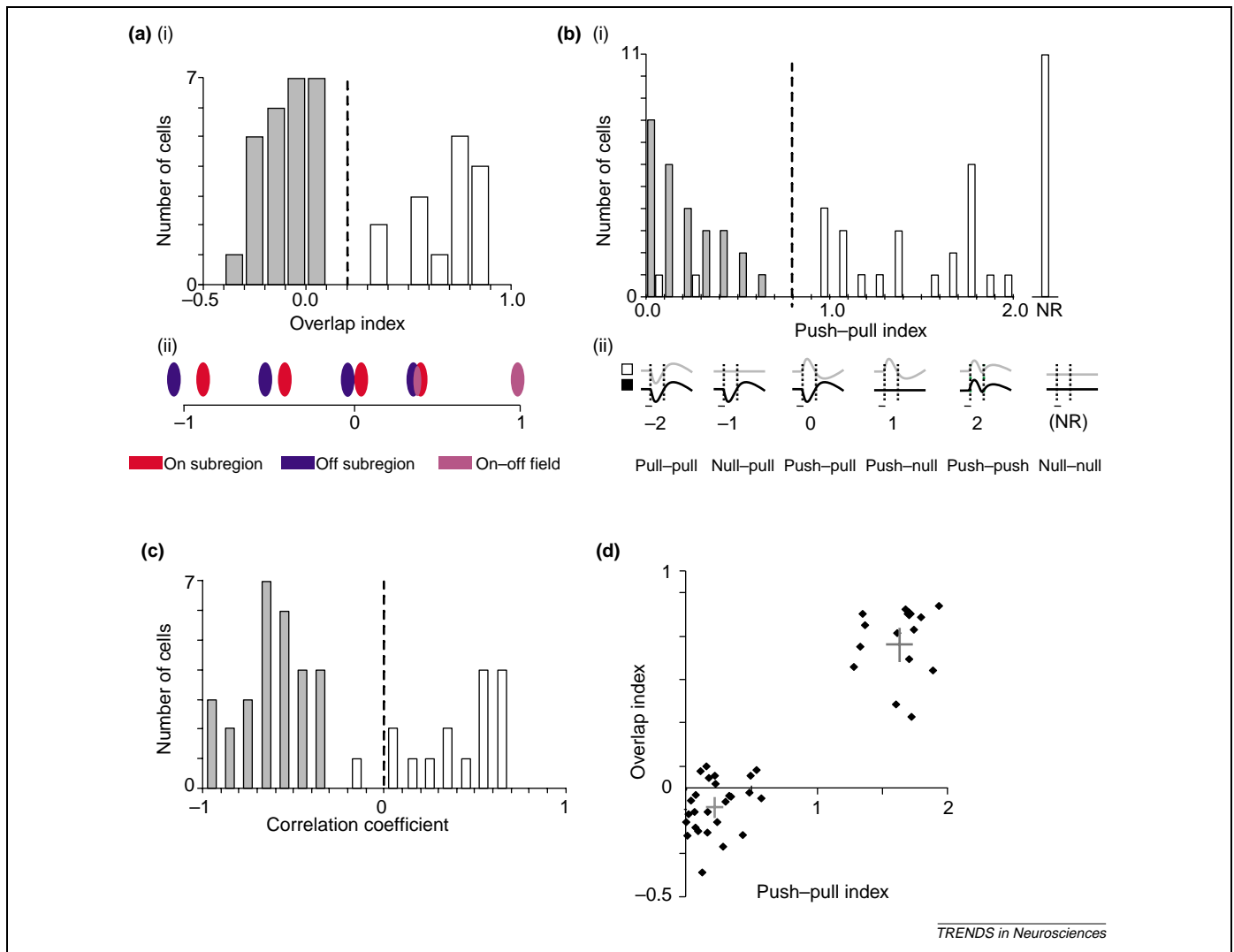
Figure 2. Quantification of receptive-field structure in the visual cortex. **(a)** (i) The distribution for the overlap index formed two modes (broken line); cells with separate On and Off subregions are represented by shaded columns in this and the following histograms. The overlap index is defined as:

$$\text{Overlap index} = \frac{0.5Wp + 0.5Wn - d}{0.5Wp + 0.5Wn + d}$$

where W_p and W_n are the widths of the On and Off subregions and d is the distance between the peak positions of each subregion. The parameters W_p, W_n and d were determined by separately fitting each On and Off excitatory response region with an elliptical Gaussian function [18]. (ii) A graphical explanation of the overlap index. The index has a value of 1 when subregions are cospatial, has a value of 0 for juxtaposed subregions and becomes negative for separated subregions. **(b)** (i) The distribution of the values for the push–pull index was also bimodal, with all cells that had simple scores on the overlap index contained within one mode; NR indicates that there was no response to the flashed stimulus. The push–pull index is defined as:

$$\text{Push–pull index} = |P + N|$$

where P and N represent synaptic responses to bright and dark stimuli, respectively; the absolute values of the index range from 0 for push–pull to 2 for push–push or pull–pull. (ii) A graphical explanation of the push–pull index. **(c)** The distribution of values for Pearson's correlation coefficient was similar to those for the push–pull and the overlap indices. Bimodality was determined using Hartigan's dip test; the probability of rejection for a unimodal distribution was 0.99 for distributions for all three indices. **(d)** A scatter plot of values for subregion overlap versus push–pull forms two clusters, with the left-most defining simple cells; the intersection of the crosses in each cluster corresponds to the mean and the length of each line to the 95% confidence intervals calculated using a bootstrap method. Similar distributions were found for plots of Pearson's correlation coefficient against push–pull or against overlap (not shown).

feedforward input from unoriented cells in layer 4 [78] and intralaminar connections from co-oriented cells whose receptive fields lie along a common spatial axis [79]. It is possible that simple receptive fields in the cat cortex and in the magnocellular zones of monkey cortex are made by similar feedforward mechanisms: the origin of orientation selectivity in the parvocellular stream might be built by composite feedforward and intralaminar circuits similar to those described in the tree shrew [78,79] or by other means that rely heavily on the strength of inhibition [80,81].

Receptive-field structure does not appear to vary with morphological class [18,22–24,28,39,82]. Simple cells can have spiny stellate, pyramidal and interneuronal profiles (Figure 3b). There is, however, precedent for correlation between receptive-field structure and patterns of inter-laminar connectivity [83]. Specifically, simple cells in layer 6 extend robust dendritic and axonal arborizations through layer 4, where simple cells dominate, whereas complex cells in layer 6 target the superficial layers and hence prefer other complex cells [83]. There is also evidence that receptive-field structure correlates with
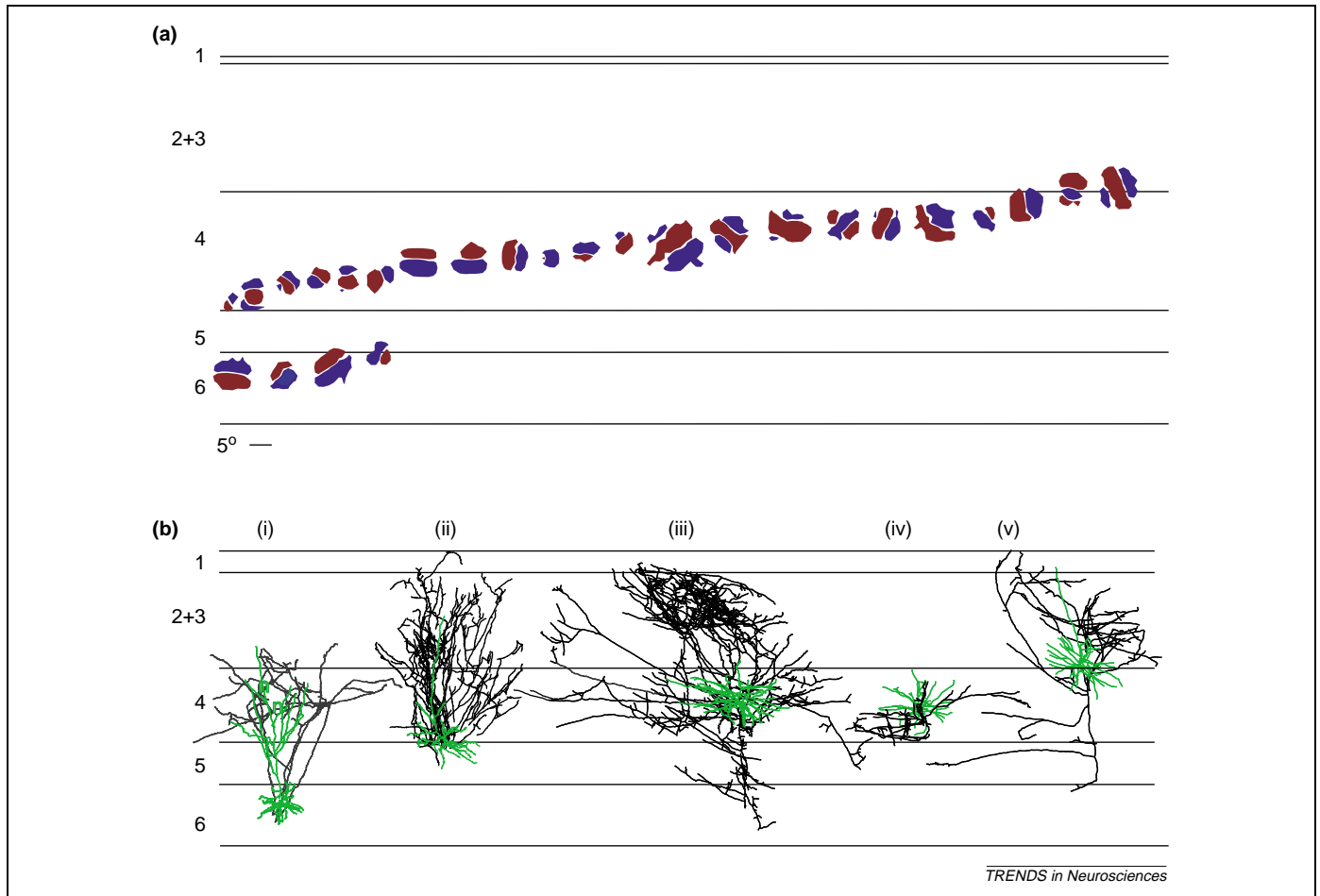
Figure 3. Laminar distribution of simple receptive fields and morphology of simple cells. **(a)** Simple receptive fields were found exclusively in layer 4 and its borders or in upper layer 6. The receptive fields are ordered from left to right according to depth of the soma; red represents On subregions and blue represents Off subregions. There are statistically significant differences in the shapes and number of subregions of receptive fields in the upper versus the lower tiers of layer 4: length:width ratio (average $\pm$ SD) was 1.89 ± 0.57 in lower layer 4 versus 3.19 ± 0.8 in upper layer 4 ($P=0.00029$); number of subregions (average $\pm$ SD) was 2.25 ± 0.45 in lower layer 4 versus 2.7 ± 0.48 in upper layer 4 ($P=0.018$). **(b)** Anatomical reconstructions taken from the simple cell populations: (i) a pyramidal cell in upper layer 6, (ii) a pyramidal cell at the 4–5 border, (iii) a spiny stellate cell in layer 4, (iv) a smooth cell in layer 4 and (v) a pyramidal cell at the 3–4 border. Dendrites are in green and axons are in black.
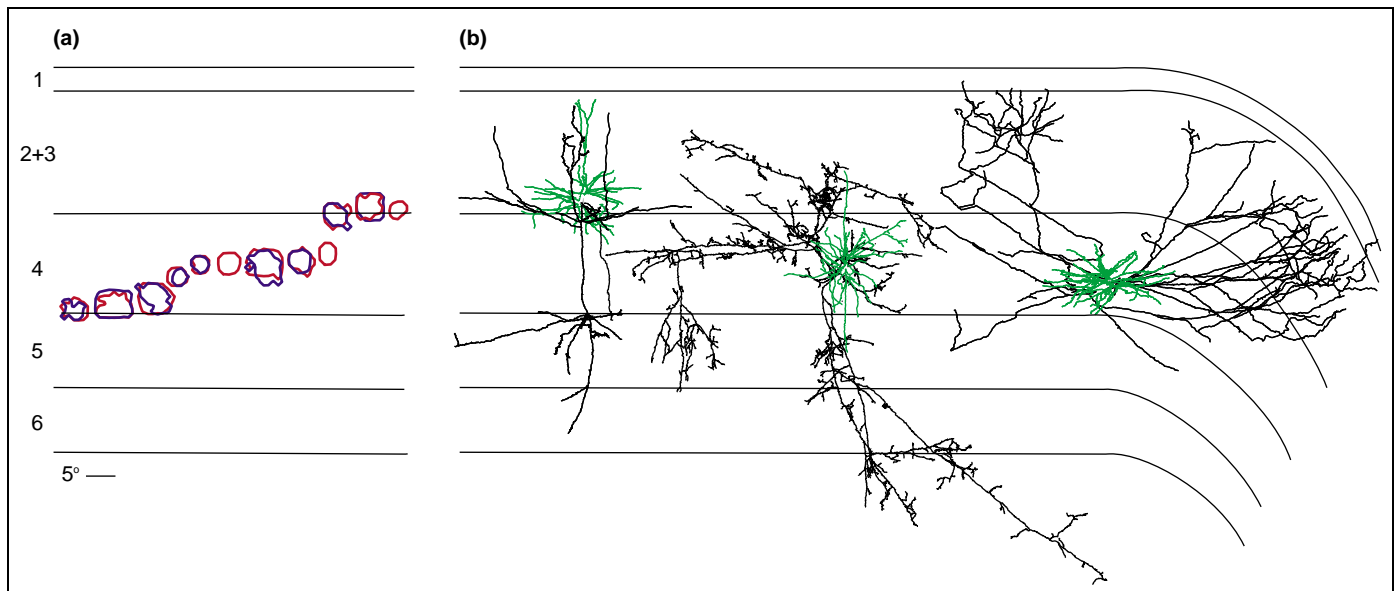

Figure 4. Complex receptive fields and morphology of complex cells in layer 4. **(a)** Receptive fields are plotted as in Figure 3 except that On and Off subregions are shown as outlines because they overlapped; three cells had one subregion only, and of these two in mid-layer 4 had push–pull responses. **(b)** Anatomical reconstructions of some complex cells: (i) a pyramidal cell at the layer 3–4 border, (ii) a large basket cell and (iii) a spiny stellate cell. Dendrites are in green and axons are in black.

subcortical projection pattern. First, most cells antidromically activated from the thalamus have simple receptive fields [84]. Second, simple cells in layer 6 [83] resemble neurons that are retrogradely labeled from the lateral geniculate nucleus but not from other subcortical regions [85].

Most complex receptive fields in layer 4 have cospatial On and Off subregions (push–push) [18,49], although some had just one subregion with push–pull structure (Figure 4a). Similar to simple cells, complex cells are found throughout the layer and are anatomically diverse [24,39,51] (Figure 4b).

Synaptic physiology of responses at thalamocortical versus intracortical levels of processing

Studies *in vitro* show that connections between different types of neuron vary in strength and reliability [86]. It is possible to examine responses *in vivo* for clues about the synaptic physiology of connections at different stages of the microcircuit [22]. For example, the responses at a given point in a simple subregion bear a striking resemblance to those in the center of thalamic fields (Figure 1a,b). The responses recorded from the simple cell and from the relay cell have a prominent push–pull structure and similar time-courses. Furthermore, despite the difference in receptive-field structure, simple and complex cells in layer 4 respond reliably to the flashed spots [22] and the time-courses of their responses follow patterns of thalamic activity [20,22]. Thus, all cells in layer 4 seem capable of capturing and relaying information from the thalamus.

The quality of response in layer 4 is stereotypically different from that at later stages of cortical processing. Early on, it was noted that many complex cells responded far less strongly to stationary images than to stimuli with real or simulated motion [25,61]. Another study reported weak and inconstant responses to flash and that discharges of complex cells were typically transient, unlike those of simple cells [20]. These behaviors correlate with laminar position. Flash-evoked synaptic responses in upper layers 2+3 were variable, intermittent and brief – usually lasting only half the duration of evoked spike trains in layer 4 or the thalamus [22]. Responses recorded at dendritic versus somatic locations were more reliable, but still brief [22]. Larger spots or bars were scarcely more effective [22], even though moving stimuli easily drove every cell [48,22].

Thus, although information about static objects is reliably handed from thalamus to cortex, intracortical circuits transmit only stimuli that meet novel standards, such as having motion. This form of selectivity has been hypothesized to involve facilitatory interactions [61] that might operate at the synaptic and dendritic levels [22,48]. Receptive fields and response properties are summarized in Figure 5.

Inhibitory contributions to the simple receptive field
Source of the pull
The first wiring diagram for the simple receptive field [2], in which the push was shaped by thalamic afferents, has received strong support [2,6–8,11,12,48,78,87], although it
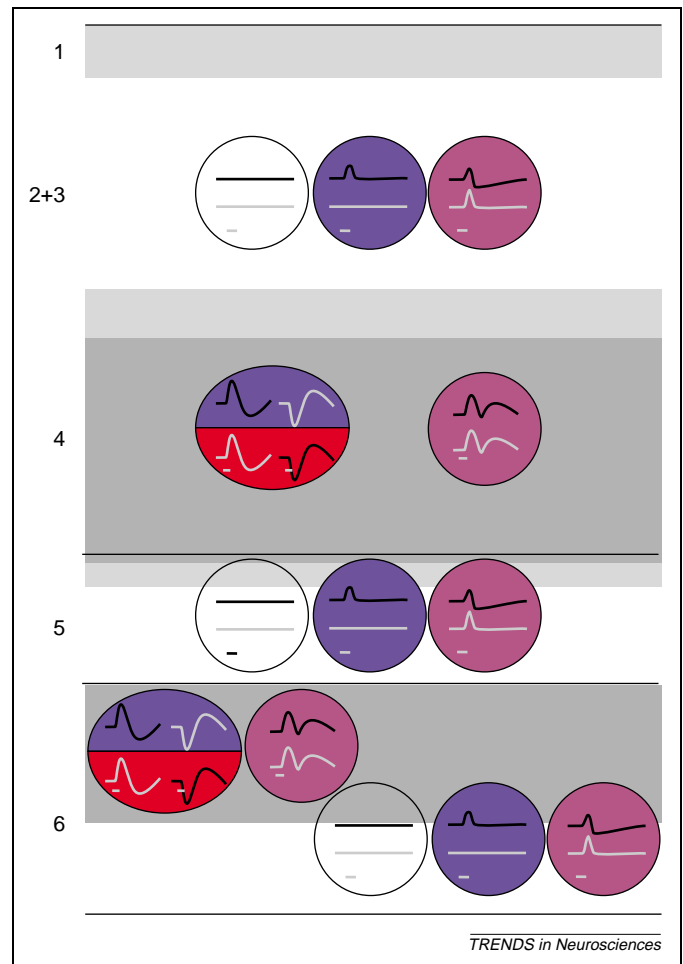
Figure 5. Laminar distribution of common receptive fields in primary visual cortex. Ovals with red and blue On and Off subregions are simple cells, purple disks are complex cells with cospatial On and Off subregions, blue disks are complex cells that responded to stimuli of just one polarity, and open disks are complex cells that responded to moving but not to static stimuli. Dark gray bands indicate regions that receive input from the primary (A) layers of the thalamus and light gray marks regions that receive input from the lower (C) layers. Traces within the receptive fields indicate the sign and time-course of response to bright and dark stimuli. Receptive fields drawn in the middle of layer 6 were found both in the superficial and deep aspects of the lamina.

is now clear that there is also a cortical contribution [12,88] (Figure 6a,i). What about the pull? Active suppression in the cortex is likely to come from intrinsic sources [89,90] because thalamic afferents are glutamatergic and excitatory [91,92]. Iontophoretic studies have shown that cortical inhibition is powerful; blockade of inhibitory transmission strongly reduces stimulus specificity [93–95]. In addition, it is now accepted that the pull results from intracortical inhibition (rather than withdrawal of thalamic drive) because its reversal potential is below rest [48] and because it is accompanied by a large increase in membrane conductance [41,48,96]. Furthermore, quantitative extracellular recordings have provided specific evidence that spatially opponent suppression in the simple receptive field comes from local interneurons [20,97–99]. Moreover, extracellular [20,97–100] and intracellular [43,48] recordings have long indicated that the pull is generated by interneurons with simple receptive fields (Figure 6a,ii). In fact, some inhibitory interneurons
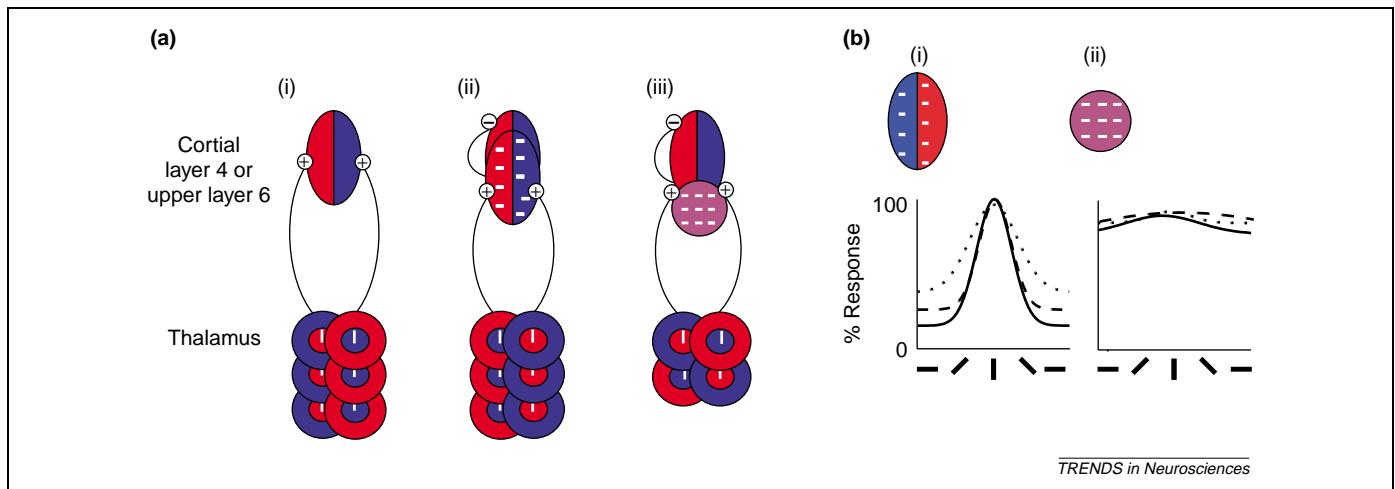
Figure 6. Push–pull circuitry and orientation tuning of interneurons in layer 4. **(a)** Wiring diagrams for inputs to simple cells in layer 4. Red represents On subregions, blue represents Off subregions and purple represents complex cells with cospatial On and Off subregions. Cells are drawn as their receptive fields, interneurons are marked with white dashes, and the signs of the synaptic connections between cells are given by the plus and minus symbols in the stylized axon terminals. (i) The push in simple subregions is built from On-center and Off-center relay cells of the lateral geniculate nucleus of the thalamus whose receptive fields form parallel rows in visual space. (ii) The pull is made by thalamic input routed through smooth simple cells whose receptive fields resemble those of their partners except that overlapped subregions have the opposite polarity. (iii) A second source of inhibition is provided by smooth complex cells that receive input from On-center and Off-center relay cells that have spatially overlapping receptive fields. Note that this scheme applies for the receptive fields of excitatory and inhibitory cells alike. **(b)** Orientation selectivity of interneurons in layer 4. Gaussian fits to averaged orientation tuning curves for excitation (dotted lines), spikes (solid lines) and inhibition (dashed lines) are shown for simple cells (i) and complex cells (ii); the bars under the abscissas indicate different stimulus orientations.

have simple receptive fields built in the same way as those of excitatory cells [18,24,39,49]. Remarkably, simple cells with receptive fields that mirrored each other, but whose overlapped subregions preferred opposite contrasts, have been recorded simultaneously using the same electrode [2,20,100], indicating that there actually are circuits such as that in Figure 6(a,ii). Of course, that diagram simplifies the actual case. The ratio of inhibitory to excitatory cells is ~1:4 [101]; hence, interneurons must supply several nearby cells. This idea is supported by studies showing that interneurons connect with numerous local targets [102–104].

Potential role of inhibition in contrast-invariant orientation tuning
Purely feedforward models [2,37,38,105,106] of orientation selectivity fail to explain how cortical neurons retain their orientation sensitivity over a wide range of stimulus contrasts [34–36,107]. Although cortical responses to stimuli at or near the preferred orientation grow stronger with increasing stimulus strength, responses to orthogonal stimuli remain small. Thus, stimulus contrast has little effect on the bandwidth of cortical orientation tuning curves [34–36]. The situation is different for relay cells; as contrast grows stronger these neurons fire harder in response to stimuli of any orientation [34–36]. Feedforward models hold that a subset of the afferent input to each simple cell is 'untuned': it is activated by stimuli of any orientation, including the orthogonal (imagine that the untuned input comes from relay cells with centers at the pivot point of a rotating stimulus). However, these models do not provide a means to counter the contrast-dependent increase in untuned thalamic firing that should elevate cortical tuning curves and thus broaden bandwidth [38,106] because, at the orthogonal orientation, inhibitory simple cells are minimally active [38,106] (Figure 6b,i).

Some of the inhibitory interneurons in layer 4 [24,39, 50,51] have complex rather than simple receptive fields [49]. These complex cells are insensitive to stimulus angle; they might correspond to unoriented cells reported in extracellular studies of layer 4 [108–110] (Figure 5b). Their receptive fields could easily be built by convergent input from On and Off relay cells with spatially overlapping receptive fields (Figure 6a,iii). These cells also have dense axonal arbors that, in aggregate, spread throughout the layer and have the potential to contact simple and complex cells alike [49]. Complex inhibitory cells in layer 4 might not only contribute to contrast-invariant orientation tuning but also govern excitability in general [37,106]. It is worth noting that untuned inhibitory cells are present in layer 4 of the somatosensory cortex [111,112]. Lastly, untuned complex cells seem exclusive to layer 4 and upper layer 6 because interneurons in layers 2+3, 5 and lower 6 are tuned for stimulus orientation [113].

Receptive-field structure and response linearity
A separate means of classifying simple versus complex cells is based not on receptive-field structure *per se* but on linearity of response to moving sinusoidal gratings [25,60, 114]. The test for linearity grew out of an important approach to visual processing founded on spatial and temporal frequency analyses [60,61,114,115]. Linear responses were once thought to be restricted to cells whose receptive fields had separate On and Off subregions [25]. The absolute fidelity of this relationship has been challenged, however, by work showing that some cells with complex receptive fields have linear responses [70] and by the report that the correlation between subregion overlap and linearity is weak when measured from synaptic inputs even though it is high when measured from spikes [15]. In fact, it is easy to imagine that complex cells that respond more strongly to dark stimuli than to

bright ones would respond to gratings in a roughly linear manner. Indeed, linear responses are found in all cortical layers [116], suggesting that different types of circuit operate in this fashion.

Summary

Determining how the cortex is wired to extract sensory information is a continuing challenge. Early studies of visual cortical function, by Hubel and Wiesel, were made using the then-new technique of extracellular recording, and interpreted in the context of existing knowledge of cortical connectivity. Research has moved forward from this foundation, with results from novel methods of physiology and anatomy bound together in updated theoretical frameworks. Here, we recount current views of circuits that build receptive fields at the initial (thalamocortical) level of cortical processing in cats, with the focus on understanding how these circuits contribute to the ability to resolve stimulus orientation and maintain that selectivity over a wide range of luminance contrasts. We have provided only a rough outline of the real situation; we expect that new approaches will reveal a fuller picture of connectivity among different cell types and a deeper understanding of how these connections give rise to visual function.

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