Revisiting horizontal connectivity rules in V1: from like-to-like towards like-to-all

Frédéric Chavane1 · Laurent Udo Perrinet1 · James Rankin2

Received: 5 June 2021 / Accepted: 3 January 2022 / Published online: 5 February 2022
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2022

Abstract
Horizontal connections in the primary visual cortex of carnivores, ungulates and primates organize on a near-regular lattice. Given the similar length scale for the regularity found in cortical orientation maps, the currently accepted theoretical standpoint is that these maps are underpinned by a like-to-like connectivity rule: horizontal axons connect preferentially to neurons with similar preferred orientation. However, there is reason to doubt the rule’s explanatory power, since a growing number of quantitative studies show that the like-to-like connectivity preference and bias mostly observed at short-range scale, are highly variable on a neuron-to-neuron level and depend on the origin of the presynaptic neuron. Despite the wide availability of published data, the accepted model of visual processing has never been revised. Here, we review three lines of independent evidence supporting a much-needed revision of the like-to-like connectivity rule, ranging from anatomy to population functional measures, computational models and to theoretical approaches. We advocate an alternative, distance-dependent connectivity rule that is consistent with new structural and functional evidence: from like-to-like bias at short horizontal distance to like-to-all at long horizontal distance. This generic rule accounts for the observed high heterogeneity in interactions between the orientation and retinotopic domains, that we argue is necessary to process non-trivial stimuli in a task-dependent manner.

Keywords Primary visual cortex · Horizontal intra-cortical axons · Orientation and retinotopic maps · Structural advanced anatomy · Functional optical imaging · Computational and theoretical neuroscience · Connectivity rules

Introduction
Retinotopy and orientation are two of the main features processed and topographically organized into maps in primary visual cortex (V1) of carnivores, ungulates and primates. Anatomical connections between neurons separated on the cortical sheet, through the so-called intrinsic, intra-cortical or horizontal axons, have a crucial theoretical importance for understanding the computational operations that V1 can perform. Indeed, these axons connect different points in the retinotopic and orientation maps and thereby generate a set of possible topological interactions within a multidimensional representation of space, orientation and time. It is therefore critical to characterize structural horizontal interactions in order to understand their functional relevance. A vast majority of presynaptic contacts in cortex originate from neurons located in the same area as the postsynaptic target (>80% in macaque V1, Markov et al. 2011), thus forming an important intra-cortical network. In the primary visual cortex, the feedforward thalamocortical inputs drive the cortical network, which in turn strongly shapes the evoked response through excitatory and inhibitory recurrent circuits within the column (Douglas et al. 1991), a canonical circuit that constitutes nearly 2/3 of intra-cortical connectivity (Markov et al. 2011). The rest of the intra-cortical network connects neurons in adjacent columns separated laterally over distances up to several millimeters, the horizontal network. Early anatomical observations reported that the horizontal connectivity of carnivores, ungulates and primates is spatially distributed into regular clusters (Fig. 1A; Braitenberg 1962; Fisken et al. 1975; Creutzfeldt et al. 1977; Gilbert and
Wiesel 1979; Rockland et al. 1982) forming a radially projecting pattern that resembles a daisy’s petals (Douglas and Martin 2004). Since orientation maps are also regular with comparable spatial frequency, the currently accepted theoretical standpoint is that these maps are underpinned by a like-to-like connectivity rule: cortical columns are connected by...
horizontal connections only if they share similar orientation preference (Fig. 1A), a hypothesis originally put forward by Mitchison and Crick (1982). Correlative studies, comparing bouton labelling with autoradiography, or with optical imaging maps, qualitatively supported the like-to-like rule (Gilbert and Wiesel 1989). Later combined quantitative anatomy with optical imaging studies confirmed the existence of an orientation preference bias (Fig. 1B, in the range of 1.5–2 times greater than chance, Bosking et al. 1997, Kisvárday 1997; Schmidt et al. 1997; Malach et al. 1993; Rochefort et al. 2009), with high cell-to-cell variability. Probably due to its simplicity and its elegant topological implications, the highlighted iso-orientation biases have led to a general acceptance of the hypothesis of a simplified and unique like-to-like connectivity. One consequence is that theoretical and computational models have implemented it as a strict rule, not as a bias (e.g. Bressloff et al. 2001; Raizada and Grossberg 2003; Rangan et al. 2005; Sarti et al. 2008; Baker and Cowan 2009; Kaschube et al. 2010; Rubin et al. 2015; Carroll and Bressloff 2010). However, we believe such an oversimplified schema may impair the development of our theoretical understanding of the primary visual cortex function.

Actually, there are reasons to doubt the explanatory power of a global and strict like-to-like connectivity rule. First, a growing number of quantitative studies show that there is a wide variety of connectivity biases (like-to-like bias, no bias, like-to-unlike bias) depending on cell type (Fig. 1C, excitatory vs inhibitory neurons, see Kisvárday et al. 1994; Buzás et al. 2001), layer origin (Fig. 1D, no bias in layer 4 or layer 6, see Yousef et al. 1999; Karube and Kisvárday 2010; Karube et al. 2017) and position in the orientation map (Yousef et al. 2001, iso-orientation domain vs pinwheels). Second, the effect is mostly observed at short range where most of the connectivity arises (<1–1.5 mm), but connections can connect neurons over distances of a few millimeters. The rare analyses over larger cortical distances (more difficult because far fewer boutons are present) showed a global tendency for the iso-orientation bias to reduce with distance (Fig. 1E) due to wider selectivity or deviation from the iso-orientation bias, as observed in Buzás et al. (2006, Fig. 8C), Kisvárday et al. (1997, Fig. 9—area 17) and Bosking et al. (1997, Fig. 5); however, see a counter example for area 18 in Kisvárday et al. (1997, Fig. 10—area 18). As a consequence, the effective functional selectivity of horizontal axons beyond the short-range distance is not very clear. Lastly, the functional impact of the structural organization, as described by anatomy, is far from trivial to predict. Indeed, any visual stimulation will activate a neuronal mass encompassing all layers, both excitatory and inhibitory neurons and at least a full hypercolumn composed of pinwheels and iso-orientation domains (see Fig. 1D in Chavane et al. 2011). Furthermore, not only neurons with preferred orientation matching the orientation of the stimulus will be significantly activated, but also a distribution of neurons with say, ±15° around the stimulus orientation. The intracortical horizontal network triggered by this functionally activated neuronal mass will forcibly contact a diversity of orientation tuned neurons (ranging from an iso-orientation, Fig. 1F, to an omni-orientation interaction, Fig. 1G) with an overall net effect beyond short-range distance that is particularly difficult to predict without a computational approach.

In this review, we present a body of recent evidence from anatomy, physiology and computational modelling, leading to the conclusion that horizontal interactions do not forcibly conform with a like-to-like orientation preference. In the last decade, structural (Hunt et al. 2011; Martin et al. 2014, see Kisvárday 2016 for review) and functional (Chavane et al. 2011; Huang et al. 2014) studies have shown that the rule is not valid for long-distance connections. Chavane et al. (2011) proposed revisiting the connectivity rule as a function of horizontal distance: from like-to-like at short distance towards like-to-all and long distances (Fig. 1E; see discussion in Alonso and Kremkow 2014a, b). In their computational modelling study, Rankin and Chavane (2017) showed that this behaviour is in fact to be expected based on the anatomical observations made by Buzás et al. (2006). The functional implications of such evidence is further discussed in the framework of natural scenes analysis (Perrinet and Bednar 2015; Boutin et al. 2021). In light of converging evidence from a range of approaches, this review argues for a timely, in-depth revision of V1 horizontal connectivity rules. Revisiting this textbook mindset is an important prerequisite to better understand the relationship between structure and function in the visual cortex.

**New physiological evidence**

**Neuronal population activity measures**

Here, we review more recent evidence for versatile connectivity rules reported in different species and with different recording techniques. Importantly, one should keep in mind that long-range horizontal axons only have a subthreshold influence on their postsynaptic targets (Bringuier et al. 1999). In order to study the selectivity of the postsynaptic target of these axons, it is therefore important to use methods that are sensitive to subthreshold membrane potential changes. Indeed, methods that only record spiking activity necessitate experimental protocols that co-activate the presynaptic source and postsynaptic target of the horizontal network, for instance to study cross-correlation between neurons (Michalski et al. 1983; Ts’o et al. 1986; Schwarz and Bolz 1991; Das and Gilbert 1999). Under these conditions, it is hard to tease apart the direct effects of the horizontal
axons from secondary activation of recurrent columnar circuits.

Chavane et al. (2011) used complementary recording tools that specifically record the subthreshold activity of a mesoscopic population (voltage-sensitive dye imaging, VSDI), and of individual neurons (intracellular recordings) in areas 17 and 18 of the anaesthetized cat. The first method allowed us to visualize and quantify the orientation selectivity of the laterally spreading activity evoked by a local stimulus (Jancke et al. 2004). The second method enabled a precise measurement of the impact of this subthreshold spread of activity on individual neurons. Using VSDI in the cat areas 17 and 18, the authors showed that a local oriented stimulus evokes a spread of activity along the horizontal dimension, extending up to 3 mm laterally (see also Bringuier et al. 1999; Reynaud et al. 2012; Muller et al. 2014, 2018). It is to be noted that the spread of activity did not show any patchiness, contrary to the anatomical observations. We believe that this is to be expected considering the large variability in the patches that will be activated from different neurons, varying as a function of a neuron’s type, layer and position in the orientation map. As a consequence,
Fig. 2 Probing for the orientation selectivity of the horizontal network with functional imaging. A–C: Adapted from Chavane et al. (2011) with CC-BY permission and D–E: modified from Huang et al. (2014) with CC-BY permission. A Voltage-sensitive dye imaging of the orientation-selective response evoked by local oriented gratings, example from area 17 of an anesthetized cat. (Left) Polar orientation map averaged over the final 145 ms of the response (time stamps indicated above the frame). Colour hue and brightness code, respectively, for the preferred orientation and the strength of the orientation tuning. Contours delineate the outer border of the cortical domain within which significant activation level (thin grey contour) or significant orientation selective response (thick white contour) are observed. (Right) Spatial extent of the activated area (grey) and of its orientation selective component (black) as a function of time. A red line indicates the expected limit of the feedforward imprint, defined and estimated from Albus (2004) as the population of neurons directly or partially activated by the feedforward stream. Dotted red line indicates the retinotopic area of the stimulus representation. Inset: the spatial extent of the activation spread (grey) and the orientation-selective activation (black) are shown in comparison with the expected limit of the feedforward imprint (red). B Population analysis over nine hemispheres [three in area 17 (o) and six in area 18 (+)] of the horizontal distance-dependent decrease of orientation selectivity. (Top) Iso-orientation bias as a function of the spatial eccentricity of the lateral spread. The first point corresponds to the area of the initial cortical activation. Exponential fit is shown in black. (Bottom) Decrease in condition-wise modulation depth with lateral propagation distance. C Visuotopic orientation polar map of an intracellular recording site, colour hue and brightness code, respectively, for the preferred orientation and the strength of the membrane potential’s orientation tuning. The white contours delineate the significant responsive regions when combining both amplitude and orientation selectivity criteria. Middle: averaged subthreshold responses to four different orientations (same colour code) presented for particular locations (circle, triangle and square); scale bars: 50 ms and 1 mV; right: Normalized orientation tuning curves, integrated within a fixed temporal window (shaded area of middle panel). The black circle indicates the spontaneous level for the depolarizing integral measure. D Three orientation maps measured with optical imaging of intrinsic signals (Huang et al. 2014) with the extracellular recording site (white “+”). Optogenetic layout stimulation sites that were centred over orientation domains with the same orientation preference (blue solid hexagons) as the recording site (+), and stimulation sites that were centred over domains with the orthogonal preference (light blue dashed hexagons). Scale bars: 500 μm. E Extracellular responses to optogenetic stimulation of preferred domains (dark blue) and orthogonal domains (light blue) in the three example cases shown in D, and the average responses to stimulation of preferred or orthogonal domains across all cases examined (n = 10) and in sharp contrast to the extended horizontal activation, the orientation selective component of this spread remains confined to the cortical feedforward imprint of the stimulus (Fig. 2A). The feedforward imprint being defined in Chavane et al. (2011) as the population of neurons directly or partially activated by the feedforward stream. This effect was systematically observed in both areas 17 and 18, and quantified using complementary methods to quantify decrease of the orientation selectivity with horizontal distance. Both at the level of orientation preference and orientation selective response, the bias towards like-to-like activation (and therefore functional connectivity) decreases exponentially with horizontal distance with a similar characteristic cortical space constant of about one mm or one hypercolumn (Fig. 2B). Importantly, this signifies, that, for a lateral radius of about 1.5 mm, the iso-orientation bias (Fig. 2B) was in the same range as that observed in the anatomy for similar lateral distance (Bosking et al. 1997, Kisvárday 1997; Schmidt et al. 1997; Malach et al. 1993; Rochefort et al. 2009). However, VSDI is a population measure of the subthreshold activation that pools activity from all neurons (excitatory and inhibitory), all compartments (dendrite, soma and axons) and mostly the upper layer (see Chemla et al. 2017). VSDI offers a unique population view of the functional activation but it is less precise than anatomical studies: it is for instance possible that the lack of overall bias comes from the mix of tuned and untuned subpopulations (see Kisvárday 2016 for further discussion). Chavane et al. (2011) therefore used intracellular recordings to confirm the VSDI observations and further showed that this loss of orientation selectivity actually arises from the diversity of converging synaptic inputs originating from outside the classical RF (Fig. 2C). The conclusion from this work is that the lateral spread of cortical activity gradually loses its orientation iso-preference at a distance of around one hypercolumn and that there exists a range of strategies for different postsynaptic neurons.

A more recent work, Huang et al. (2014) provided complementary results in a different species, V1 of the tree shrew and using a different methodological approach. The authors used optical imaging of intrinsic signals to monitor the impact of intra-cortical optogenetic stimulation under various stimulation configurations. In particular, their results show that the optogenetic stimulation of excitatory neurons within a set of orientation domains in the cortex generated the same response amplitude for either iso- or orthogonal domain stimulation (Fig. 2D, E). The responses actually depended primarily on intra-cortical distance (similar to the results obtained via cross-correlation in Das and Gilbert (1999)). Using their innovative approach, the authors also tested stimulation along an axis in the retinotopic map, either collinear with the preferred orientation or orthogonal to it. The authors found no bias in either direction. Huang et al. (2014) therefore provides independent and complementary evidence that the horizontal network, when probed at the population level with functional measures, does not show a bias for iso-orientation preference in V1. It should be noted, however, that using optogenetic stimulation of excitatory neurons may drive complex dynamical activation of the cortex (Li et al. 2019), mixing excitatory and inhibitory recruitment of the lateral network with different dynamics. Since the authors have used intrinsic optical imaging, they could not access to the dynamics of the lateral activation that would be averaged out in the observed activation maps (see Kisvárday 2016 for further discussion).
Anatomical measures

In a recent anatomical study, Martin et al. (2014) carefully re-evaluated the orientation bias of horizontal boutons from upper layer pyramidal neurons in cat area 17 using single cell intracellular labelling, optical imaging to reveal the orientation map and advanced cluster-by-cluster analysis of synaptic boutons. In their analysis, Martin et al. (2014) compared the distribution of the preferred orientations spanned by the neuron’s dendritic arbors (used to estimate the neuron’s preferred orientation) and the preferred orientation covered by axonal clusters of the neuron (Fig. 3A). In the example of Fig. 3A, B, the preferred orientation of the dendrite (red) matched the one of the local cluster (green) but not of the distal cluster (blue). Over 33 neurons, their results revealed a very large variability in the orientation selectivity of their distal clusters (coloured in Fig. 3C), as estimated by their Similarity Index (1 corresponding to the same orientation preference distribution with respect to the neuron’s preferred orientation, 0 to an orthogonal orientation preference). Their results demonstrated the existence of a very large variance of SI (0.13–0.96) out of all 51 clusters they observed over the 25 neurons. To test whether the clusters positions within the orientation maps occur by chance, the authors made a detailed bootstrap statistical analysis of all 51 clusters, taking into account the bias that is introduced by the orientation map layout, the cluster size and position relative to the soma. Using this analysis, they found that a quarter of their clusters (14/51 clusters recently updated to 17/65, personal communication from Ruesch and Martin) were not positioned randomly in the map. Interestingly, only 9% (6/65) of these clusters (see their suppl Fig. 10l) had a significantly high SI, above the upper bound (hence iso-oriented), and 5% (3/65) below the lower bound (hence cross-oriented). In contrast 12% (8/65) were located in position of the orientation map unlikely to occur by chance whilst being neither iso- nor cross-oriented with the labelled cell. As a conclusion, only a small minority of clusters (9%) are significantly tuned to iso-orientation from non-random position in the orientation map. Furthermore, as shown by Buzás et al. (2006), this bias tends to decrease with lateral distance of the clusters, which is further in accordance with Chavane et al. (2011). Finally, as observed in Huang et al. (2014), Martin et al. (2014) did not find any specific alignment of the cluster distributions in the retinotopic map that could favour collinear vs orthogonal interactions with the cell’s preferred orientation. At a more macroscopic level, diversity was also shown from animal to animal in tree shrew V1, specifically

**Fig. 3** Probing for the orientation selectivity of individual horizontal axons (modified from Martin et al. 2014 with CC-BY permission). A Axon of an intracellular labelled neuron is displayed over the orientation map. Ellipses show clusters of boutons (not shown) for local and more distal positions. Dendritic tree (inset) was colour coded by the orientation value of their corresponding pixels (white dot indicates the soma). Scale bar, 0.5 mm. B Radial plots of the normalized distribution of the number of boutons counted within each local (green line) and distal clusters (blue line), but also the dendrite (red line) over the preferred orientations. The individual vectors forming these hemispheric plots were summed up to generate one sum vector (bold vector). The length of this sum vector is termed as the “tuning” of the dendrite or cluster. C Similarity index (SI) values for individual clusters of 33 neurons sorted by normalized depth of soma. (Top) Neurons (x axis) can have clusters (colour coded by rank) with different SI values (y axis). The histogram on the right summarizes the SI across clusters of all neurons (grey = distal, black = local). Note the large variance within and across neurons.
in the fine orientation/retinotopic arrangement of extracellular anatomical labelling (i.e. a population of neurons). Their detailed analysis of Hunt et al. 2011 showed that there is a diversity of co-circular connectivity rules across animals, some showing a significant bias towards co-circular rules, some towards anti-circular rules and others without biases. Thus, as stated by Martin et al. (2014), the horizontal axons thus cannot be treated as an homogeneous network with a net iso-oriented bias, but rather should be described as strongly heterogeneous, an heterogeneity that may be the core of its function (see also Kisvárday 2016).

**Computational model linking structure to function**

Population measures and anatomical data constrain connectivity in cortical space; however, the link between known anatomical details and the resulting functional expression (in terms of neural activity) is not obvious. Computational models provide a means to explore this relationship directly. Modelling studies of V1 consider a range of connectivity rules, and these frequently allow for the shaping of connection strengths based on the difference of orientation preference between connected sites. Abstracted models of single hypercolumns implement cross-orientation interactions in local circuits that further tune selectivity derived from weakly tuned LGN inputs (Ben-Yishai et al. 1995). Similar mechanisms for orientation selectivity in V1 have been explored in models with recurrent, lateral connections over short distances (between neighbouring hypercolumns in L4) (Somers et al. 1995; Kang et al. 2003; Chariker et al. 2016). Connections that extend over many mm of cortex (i.e. across multiple pinwheels) are considered in visual cortex modelling studies of contextual modulation (Rubin et al. 2015), motion illusions (Rangan et al. 2005), geometric visual patterns (Bressloff et al. 2001; Baker and Cowan 2009; Carroll and Bressloff 2016), travelling waves (Bressloff and Carroll 2015), and in a general setting (Raizada and Grossberg 2003). Whilst models do commonly feature a decay (e.g. exponential or Gaussian) in the strength of orientation-based connections with distance (Goldberg et al. 2004; Blumenfeld et al. 2006), the tuning strength is not distance dependent, is rarely systematically investigated and is not constrained by anatomical data. The function of patchy long-range connections has further been investigated in contexts not specific to orientation encoding (Voges et al. 2010; Voges and Perrinet 2012). In general, long-range connections feature a strong iso-orientation bias motivated by long-held assumptions that do not take into account the more recent functional and anatomical studies that motivate a modification of this rule.

Furthermore, a common modelling choice for local excitation-inhibition connectivity is the so-called Mexican hat with inhibition extending further than excitation (Marr and Hildreth 1980; Grossberg 1983; Somers et al. 1995; Bressloff et al. 2001). This choice is known to generate stable localized patterns of activity (rather than spatial unstable dynamics that spreads across cortex) (Laing and Troy 2003); however, excitatory connections in V1 can extend many mm further than the local inhibitory footprint. In general, models that also feature long-range excitation are used to study unbounded patterns of activity rather than localized responses to inputs (Bressloff et al. 2001; Blumenfeld et al. 2006). Rankin et al. (2014) extended the results of Laing and Troy (2003) to demonstrate that localized inputs can generate stable localized activity patterns (rather than spreading activity) with a connectivity rule (as suggested in Buzás et al. 2001), and similar to Fig. 4A that features long-range excitation, extending much further than the local inhibitory network.

Rankin and Chavane (2017) developed a planar spatial model of orientation selective activation in V1 L2/3 with the aim of bridging between known anatomical constraints on the tuning of long-range connections (Buzás et al. 2006) and the functional expression of laterally propagating activity driven by localized stimuli (Chavane et al. 2011). A neural field architecture with orientation-specific subpopulations provides a mesoscopic description of neural activity, ideal for comparison with the temporal and spatial resolution in VSDI imaging experiments. A novel connectivity function was flexibly parameterized to investigate clustering of connections, their orientation bias and balance between excitation and inhibition. We adopted the non-orientation-specific nature of local excitatory connections (Buzás et al. 2006) and inhibitory connections (Buzás et al. 2001); see also Koch et al. (2016) for a discussion of orientation specificity of excitatory and inhibitory connections. Taking motivation from Buzás et al. (2001), longer-range excitatory connections are proposed here to, although decaying with distance, form in rings at multiples of the hypercolumn separation L (Fig. 4A). This allows for the following important features to be captured: that excitatory connections (1) drop in number at a range of $L/2$, (2) have a peak at a range of $L$ (and multiplies therefore) and (3) can extend several mm across cortex. Two parameters were tuned to agree with the available data from Buzás et al. (2006), the width of peaks in number of excitatory connections (RW; two values shown in Fig. 4A) and their orientation bias (BR; illustrated in Fig. 4B, C).

We found a significant overlap between the anatomically relevant parameter range and patterns of cortical activation consistent with imaging experiments (see Fig. 4D-F, Chavane et al. 2011). Hence, this computational approach allowed us to reconcile the imaging results with the reported level of orientation bias from anatomical studies. Specifically, Chavane et al. (2011) found a sharp decay of orientation selective activation at the stimulus...
retinotopic footprint border, resulting in peripheral activation that was not orientation selective (compare Fig. 2A with 3D-E). Our results demonstrate that this sharp decay is contingent on three factors: the diffuse clustering of long-range connections, the intermediate range (consistent with anatomy) of their orientation bias and sufficient balance between excitation and inhibition. It is worth noting that orientation-biased long-range connections can recruit a local non-orientation-biased network at the target, resulting in non-orientation-specific activation (like
Neural field model to reconcile structure with function in primary visual cortex. Definition of model connectivity with anatomical constraints (A–C) and illustration of model behaviour with operating region in agreement with functional characteristics (D–F). A Radial connectivity profile for inhibition (Gaussian decay) and excitation (locally Gaussian decay, longer-range connections peak in number at distance L and multiples thereof). Ring width (RW) of peaks in excitatory connections illustrated for two values. B Example of local preference map and resulting lateral connectivity for two values of the orientation bias of recurrent connections (BR). C Orientation tuning for each panel in B above (circles) with tuning parameter $k$ from a best-fit von Mises distribution (solid lines). Orientations are evenly represented in the global map but strongly biased at around $-60^\circ$ for the local excitatory component (local map). The orientation bias of lateral connections increases to around $k=1$ for BR > 0.5 (similar values reported in Buzsáki et al. 2006). D Model simulation snapshot at 600 ms showing the orientation-selective component within a thin white contour, confined to the feedforward footprint FFF of the stimulus in red; the much broader non-orientation-specific activity falls within a grey contour extending beyond the plot limits. E Time history of the area within the non-orientation-specific contour and the orientation-selective contour. F Colour map across range of RW and BR values showing the selective area as in D normalized by FFF. Within the red contour the selective activation is constrained to the FFF. White contours show the anatomically constrained range for the connectivity parameters RW and BR where $k=0.7–1.2$. In the green region other constraints on the correct orientation and the radial decay rate of orientation selectivity are also satisfied (modified from Rankin and Chavane 2017 with CC-BY permission).

Fig. 4

Functional advantages of such an organization

The insights we have reviewed at the physiological and modelling levels support a range of novel hypotheses for the organization of long-range lateral connectivity in the primary visual cortex. A functional approach, asking "why should neurons in V1 be connected laterally?" provides a complementary perspective. Indeed, a major argument is that the structure of V1 should fulfil its function and implement principles of perceptual organization, such as the principle of good continuation to bring a contour’s constituent edges together into a unified global percept (Wertheimer 1923). How might these principles connect knowledge across anatomy, physiology, theory and modelling?

Principles of perceptual organization in natural images

A major constraint for neurons in the primary visual cortex is that information is encoded locally and must be integrated globally across the visual field. Perceptual principles organizing the different fragments of an image can be directly extracted by analysing a database of natural images. One such principle is that pairs of edges in natural images are most likely organized along aligned contours, and more generally on a common circle (Sigman et al. 2001); the authors extracted edges from natural images and estimated the orientation of each edge. For each pair of active edges, they showed that the angle of maximum interaction corresponds to a configuration for which they are close to co-circularity. This long-range correlation is a marker of the structure of natural images and may provide strong prior knowledge for the perceptual organization of low-level features.

Such a structural prior can be described as a form of "association field" extending the concept of a neural receptive field to long-range local interactions. The seminal paper by Field et al. (1993) defines the association field as the set of local oriented elements (edges) in the visual field that facilitates the detection of a central oriented target. They showed that the association field obeyed a co-circular rule. In other words, if a common circle can pass through the central target and the peripheral element, they will facilitate each other’s detection and generate suppression otherwise. This association field is invariant to translations or rotations. It extends the prior of collinearity (like-to-like) or co-circularity (Sigman et al. 2001) to a more generic description of
all possible co-occurrences. In particular, by exploring the interactions of edge pairs, they showed that these association fields explain the detection of paths embedded within a field of randomly oriented edges. The association field can then be understood in light of the computer vision problem of curve tracing. Parent and Zucker (1989) described it as a diffusion process over the tangent field of oriented edges, thus suggesting a principled and biologically realistic framework for association fields using long-range interactions.

This principle can be extended to explain psychophysical experiments in humans. Geisler et al. (2001) took a similar approach by reporting the full statistics of natural image edge co-occurrences. This yields a valuable model for the statistics of neighbouring edges. First, the edges are organized into parallel textures favouring parallel edges, and second, there is a bias for co-circular edges (see Fig. 5A). Using a Bayesian approach, the authors derived a clustering scheme for chaining edges into contours that was confirmed by psychophysical experiments. This approach was later extended to the high-level cognitive problem of image categorization (Perrinet and Bednar 2015). The authors showed that using supervised learning, one could derive a scheme using the association field in that image to categorize whether it contains an animal. This simple model achieved similar performance to humans and to a deep hierarchical model (Serre et al. 2007). Surprisingly, the model made similar errors to humans. This illustrates first that association fields can be used to both group edges based on different tasks or to categorize images. This also shows that for the association field reflecting the statistics of edge co-occurrences in natural images, different datasets may lead to different association field structures (see Fig. 5A). As a consequence, it seems relevant at behavioural and ethological levels that mechanisms exist to tease apart the slight differences between the co-occurrence patterns present in different images, for instance, the surprising patterns of a perfect co-circularity, or that of a pair of rare but informative orthogonal edges forming a T-junction. This would then explain part of the variability in the association fields which can be involved in visual integration processes.

How do these principles translate to the cortical space?

As Geisler et al. (2001) states, “the obvious hypothesis for the local grouping is a neural population with the receptive field structure matched to the edge co-occurrence statistics”. Yet, the emergence of receptive field properties is a combination of anatomy and the dynamics of individual neurons. Can we link the statistics of natural images to the structure of processing in the primary visual cortex?

Fig. 5 Function and diversity of association fields. A Following the work of Geisler et al. (2001), one could derive the association field from the statistics of natural images. This involves extracting edges from images (red segments) and computing for each pair the difference of angle $\theta$ and the relative azimuth $\phi$ of one edge compared to the other. This allows one to quantify the association field as a histogram, relative to a reference edge placed in the middle, for the most likely difference of angle—showing a prominent preference for parallel textures (top) or the relative azimuth, showing a prior for co-circular co-occurrences (bottom). The association field may vary for different databases with an excess of co-circularity in images containing animals, illustrating the variety of statistics faced by the visual system (Perrinet and Bednar 2015; modified with permission CC-BY).

B Boutin et al. (2021) described a biologically realistic multi-layer model of the visual cortex. The model is shown natural images and is optimized to represent images in the most efficient way. Edge-like filters emerge (see an example in the inset) and we show here the interaction of this edge with other edges outside the range of its classical receptive field. This pattern shows a large facilitatory (green) or inhibitory (purple) effect relative to a model without feedback. This functional modulation of the association field shows the importance of the activity in the whole network and we have further shown its shape could widely vary within the network and for different types of images, such as images of faces (Boutin et al. 2021; modified with permission CC-BY).
Olshausen and Field (1996) set out to show how the structure of V1 microcolumns can optimize the efficiency of the neural representation for natural images. Hyvärinen and Hoyer (2001) extended this to include a regularization of the representation with cortical topography. Franciosini et al. (2021) recently developed a biologically realistic, two-layered V1 sparse predictive coding model, including pooling mechanisms to impose a neighbourhood prior in cortical space, which includes by construction the possibility of representing as channels in each layer a variety of interaction patterns. Similarly, complex cells and topographic maps emerge, demonstrating the transfer of cortical connectivity in V1 to perceptual grouping principles. More surprisingly, depending on the density of neurons, different structures emerge to optimize cost efficiency: in addition to mammalian-specific features (such as topographical maps), a rodent-specific salt-and-pepper map emerges for models with a lower cell density. Interestingly, by focusing on this multi-channel convolutional architecture, the second layer showed a diversity of connectivities across channels, suggesting that differing anatomical constraints may induce different patterns of long-range lateral interactions.

A multi-layer sparse predictive coding model (Boutin et al. 2021) allows for the influence of an extrastriate cortical area, such as V2 on to V1 to be modelled. The activity in the layers of this model emerge from the recurrent interactions between neurons within and across layers (rather than a feed-forward pass as in convolutional networks). Convergence to an efficient representation of edge filters and interaction maps (resembling association fields) emerges after several processing iterations. However, training on different natural image datasets can produce different interaction maps, in accordance with Perrinet and Bednar (2015). For example, training on images of human faces generated features resembling mouths or eyes, resulting in more sparse and longer-range interactions. This suggests that instead of a simple similarity rule, lateral interactions between neurons reflect the variety of feature dependencies attached to the respective neurons. In addition, similarly to physiological observations (Gilbert and Li 2013), we observed that the interaction becomes sharper with stronger feedback (see Fig. 5B), which provides a synergy between the different pieces of information encoded by the network, as illustrated by improved performance for denoising natural images.

**Function and dynamics of long-range lateral interactions**

Overall, these theoretical models propose, as an alternative to the like-to-like structure, that there should be a wide variety of long-range lateral interaction patterns. It should be noted that most of the models described above deal with static natural images, whereas the visual world is characterized by a wealth of different dynamic scales, which raises the question of the role of neural dynamics in long-range lateral interactions.

If one imagines an edge moving in a direction parallel to its orientation, we can infer that we are following the tangent to a continuous contour. On the contrary, if the orientation of the edge is perpendicular to its direction, it is more likely that we are seeing a moving bar. This simple prototypical example shows that depending on the local intrinsic context, the optimal integration rule may change, as evidenced by intracellular recordings (Gerard-Mercier et al. 2016). If these interactions can be implemented via different contextual cues, such as recurrent or feedback connections, it is also possible that the multidimensional representation of information on the cortical surface is much more than a simple topographical orientation map.

In addition, there is physiological evidence that association maps can be dynamically influenced by the task at hand. In McManus et al. (2011), using a delayed-to-sample matching task, the authors trained monkeys to detect different patterns: a circle, a wiggle, or a line, which were embedded in a grid display of randomly oriented edges similar to that of Field et al. (1993). They found that depending on the pattern being searched, the recorded association field adapted to preferentially exploit collinearities (for lines) or co-circularities (for circles). Such a differential processing raises an implementation problem for the unsupervised schemes described above. This problem could be solved in a supervised learning scheme (Perrinet and Bednar 2015) but raises the question of how this supervised credit is assigned in V1.

A similar problem is inherent in the backpropagation rule in generic deep learning paradigms which can be solved in a predictive coding framework (Boutin et al. 2021).

Lastly, the anatomical connectivity may be patchy for different functions than just connecting like-to-like orientation patches. Indeed, patchy connections likely play an important role in combining information from multiple visual cues beyond orientation, including context (Martin et al. 2017). Indeed, modelling work has shown that patch-based connectivity increases the versatility of the dynamic repertoire of neural states (Voges et al. 2010). That work compared networks of realistic conductance-based neurons with a range of connectivity rules. These rules had different complexities, from a completely random connectivity, to a neighbourhood-based local connectivity, and more interestingly, clustered networks, including a patch-based connectivity rule. This was extended in a further modelling study (Voges and Perrinet 2012) to include a comparison between a pure random patch-based connectivity and partially overlapping patches. As noted in Kisvárday (2016), these patch-based connectivity rules were sufficient to induce a large dynamic repertoire, such as rhythms or travelling waves, and were for instance
characterized by enhanced variety in the shape of the power spectrum of population activity. In particular, such a range of dynamic behaviours is much richer when compared to those obtained with a random or local connectivity rule. Patchy connectivity rules introduce a heterogeneity in the lateral connections, which seems essential for building up an efficient population code (Martin et al. 2014). In particular, this would allow the propagation of combinations of contextual cues which would reflect the richness of visual information in natural scenes.

To conclude this section, the function studied in these theoretical models hints at a solution using a superposition of different long-range connectivity profiles. The diversity of patterns and their adaptability to the task or statistics should overall improve processing efficiency in the primary visual cortex. Yet there remain open questions regarding the richness of these like-to-all patterns. Theories suggest potential strategies for addressing these open questions explicitly in neurophysiology, for example, by synthesizing optimally responsive, model-driven dynamic stimuli (Walker et al. 2019).

**Discussion**

In this review, we have documented convergent evidence from physiology, anatomy and computational models that the orientation selectivity of horizontal network connectivity in the primary visual cortex of carnivores, ungulates and primates is more versatile than initially proposed, which motivates the necessity to revisit the like-to-like connectivity rule (Mitchison and Crick 1982) still dominant today. At the anatomical level, there seems to be a diversity of connection rules between presynaptic source and postsynaptic target. At the individual cell level, anatomical studies have shown that the rule changes as a function of cell type (excitatory vs inhibitory) and layer/map locations (Yousef et al. 2001, 1999; Kisvárday et al. 1994; Buzás et al. 2001; Karube and Kisvárday 2010; Karube et al. 2017). Within one presynaptic origin, a large diversity exists with only moderate bias in the range of 1.5–2 times greater than chance (Bosking et al. 1997; Kisvárday 1997; Schmidt et al. 1997; Malach et al. 1993; Rochefort et al. 2009). More recent work by Martin et al. (2014) on the upper layer pyramidal neurons of the cat V1, with a cluster-by-cluster analysis of horizontal boutons, has shown the existence of a very large diversity from like-to-like, like-to-any, like-to-all and like-to-unlike connectivity rules. Altogether no net significative bias towards one of these rules could be observed in their bootstrap statistical analysis. Taken together, these anatomical results show that there is diversity in the connectivity rules both within and between neuronal types and locations (see Kisvárday 2016 for an extensive review). At a more macroscopic level, it is interesting to note that Hunt et al. (2011) also observed that the co-circularity rule varies from animal to animal.

When probed with functional measures of neuronal activity in response to a local visual stimulus, using techniques sensitive to subthreshold membrane potential fluctuations (Chavane et al. 2011) or an optogenetic activation of specific orientation columns (Huang et al. 2014), the diversity revealed in anatomical studies leads not only to the absence of net bias towards like-to-like interactions along the horizontal network (see Alonso and Kremkow 2014a, b), but also the absence of patchy activation of the horizontal spread of activation. Importantly, VSDI measures demonstrate a clear exponential decay of the like-to-like connectivity bias with horizontal distance, an effect also observed in anatomy (Buzás et al. 2006; Martin et al. 2014). At short-range distances, similar iso-orientation biases, as reported in anatomical studies, were observed. However, after the equivalent of one hypercolumn, no significant bias could be observed (Chavane et al. 2011).

All these papers therefore demonstrate the existence of a connectivity rule that links neurons in the primary visual cortex depending on their preferred orientation, neuronal type, position (layer and orientation map) and intra-cortical distance. This multidimensional connectivity rule is also subject to large diversity not just from neuron to neuron but also from animal to animal. Due to the difficulty in making predictions from this complex pattern, it is necessary to use computational approaches to probe for the expected functional behaviour of such a network. In Rankin and Chavane (2017), we developed a neural field model and demonstrated that the functional results observed in Chavane et al. (2011) are indeed the expected mesoscopic behaviour of such a network when its connectivity is constrained to match the orientation bias of connections from anatomy (Buzás et al. 2006), thus demonstrating that the functional observations are to be expected given our understanding of anatomical characteristics.

In this review, we wish to update the accepted like-to-like connectivity rule widely assumed as the building block for connecting a local neuronal network from one position in the visual field to its postsynaptic targets. The connectivity rule should be revised to a distance-dependent formulation: from like-to-like bias at short horizontal distance to like-to-all at long horizontal distance (Fig. 1E). The space constant of the decrease of the like-to-like bias is about one hypercolumn distance. Functionally we can speculate that this translates to an iso-orientation bias for neurons with overlapping receptive fields and no net bias for neurons with non-overlapping receptive fields.

This may be at odds with the well-documented association field schema and co-circularity rules observed in natural scenes (Sigman et al. 2001; Geisler et al. 2001). However, it is important to differentiate the basic connectivity building.
block, that specifies unidirectional rules from a presynaptic region to a postsynaptic target, from lateral interactions, that are evoked by more complex stimuli that co-activate both presynaptic and postsynaptic regions (e.g. as in crosscorrelation studies). The like-to-all long-distance connectivity rule can be seen as generic and allows for a variety of interactions in the orientation and spatial domain. Importantly, this is possible if we take into account the large local diversity observed at the neuronal level (Chavane et al. 2011, Martin et al. 2014, see also Monier et al. 2003). Our proposition here is that such a rule could account for a wealth of interaction rules depending on the stimulus and/or the task. For instance, this would allow one to account for the interactions necessary to process orientation discontinuities, such as junctions or corners. Neurons in V1 have indeed been reported to be sensitive to orientation discontinuities, independent of the absolute orientation of the stimulus set (Sillito et al. 1995; Jones et al. 2001). This result could not be explained solely by iso-oriented lateral interactions. Such diversity could also contribute to shaping the orientation tuning of neurons away from the primary orientation preference (i.e. horizontal and vertical orientations, Vidyasagar and Eysel 2015). More generally, using natural, stationary scenes and/or contour integration tasks may indeed favour association field interactions. However, depending on the type of natural images, Perrinet and Bednar (2015) have shown that these interactions may already differ significantly (see also Boutin et al. 2021). Moreover, dynamic non-stationary visual stimuli, such as a simple moving object, and tasks that rely on motion integration for instance could lead to different associative rules for motion (Gerard-Mercier et al. 2016). In the case of integrating information along a coherent path, for instance, visual information should be transported in a direction of motion that can be in the cross-orientation dimension (Perrinet and Masson 2012).

Importantly, co-circularity rules that link orientation and position with respect to a central oriented feature are not found in the anatomy (Martin et al. 2014; Hunt et al. 2011), nor were they found by Huang et al. (2014) using optogenetic stimulation pattern in the horizontal network. This further supports a dynamic, context-dependent emergence of specific rules, such as co-circularity for contour integration in natural images, through higher-order network interactions. In that respect, Chavane et al. (2011) observed that increasing spatial summation of the stimulus increases the propagation of iso-orientation activity, even if the basic connectivity profile was shown to be not selective to orientation at long range. This means that from a basic unselective building block, selective interaction can occur (for a proposition of possible mechanisms see suppl FigA5 in Chavane et al. (2011)). This effect could result from the fact that inhibitory neurons tend to make more horizontal connections with cross-orientation neurons (Kisvárday et al. 1994; Buzás et al. 2001). Increasing spatial summation could change the orientation dependence of excitatory/inhibitory balance and lead to the emergence of tuned activity at longer distance. More generally, the emergence of new selectivity depending on the stimulation pattern (or the task) is rendered possible by the existence of local diversity of orientation-selective connections at neuronal level (Monier et al. 2003; Chavane et al. 2011; Martin et al. 2014). Therefore, different stimulation patterns will lead to activation of different recurrent subnetworks and the emergence of a variety of selectivity characteristics. It is indeed now well documented that non-trivial, paradoxical effects can arise from recurrent balanced networks (Tsodyks et al. 1997; Ozeki et al. 2009; Pattadkal et al. 2018). In our model, we indeed observed that manipulating the balance between excitation and inhibition (i.e. reducing inhibition strength) predicts the emergence of spurious orientation selective activation through long-range lateral connections (Rankin and Chavane 2017).

Given the non-trivial effects that can arise with more complex stimuli, a number of avenues remain open to build on theoretical and modelling work. The model developed in Rankin and Chavane (2017) could also be used to investigate selective recruitment and spatial summation in regions between localized oriented stimuli (Chavane et al. 2011; Huang et al. 2014). Indeed, increasing spatial summation increases the slope of selectivity decay at the stimulus boundary, whilst selective propagation reaches further across cortex, a property easily explored in the model by a more diverse class of localized stimuli. More generally, the model could be used to make predictions to decipher the selective functional connectivity rules that link position and orientation in cortical space. Importantly, it could also be extended to differentiate inhibitory cell subclasses as reported in Buzás et al. (2001). As such it could generate functional predictions on, e.g. the role of long-range basket cell connections that preferentially target cross-orientations. Extending the framework further, a feature space including spatial frequency could be used to investigate lateral connections in light of recent work on interactions between orientation and spatial frequency maps (Romagnoni et al. 2015; Ribot et al. 2016).

In this review, we mostly focus on revisiting the connectivity rule of intra-cortical horizontal networks. However, it is important to consider that such connectivity patterns can also be influenced by feedback from higher cortical areas that provides a more diffuse and divergent input to the primary visual cortex (Salin et al. 1989, 1992). Anatomical studies in the cat suggest that area 17 and area 18 cells are preferentially connected when they share similar preferred orientations (Gilbert and Wiesel 1989). In the monkey, feedback from higher areas (V2 and V3) to V1 show the variable level of patchiness (Stettler et al. 2002; Angelucci et al. 2002), unselective to orientation (Stettler...
et al. 2002). In the cat, electrophysiological and inactiva-
tion studies of various downstream areas seem to influence
only response amplitude or tuning width of neurons in area
17 of the cat, but not orientation preference (Martinez-
Conde et al. 1999; Wang et al. 2000, 2007; Huang et al.
2004, 2007; Liang et al. 2007; Shen et al. 2006, 2008;
Galuske et al. 2002). However, it is important to consider
that feedback will interact with the horizontal network as
demonstrated in monkey visual cortex, with either spe-
cific interactions as suggested by Gilbert and Li (2013,
for review), or contributing to centre-surround processing
(Hupé et al. 1998; Roberts et al. 2007; Poort et al. 2012;
Nurminen et al. 2018).

In conclusion, we believe that there are enough argu-
ments today to accept a change to the connectivity rules
for horizontal axons in V1, that is consistent with both
new structural and new functional evidence. It remains to
be established how this complex multidimensional rule
(orientation x distance x neuron type x neuron location) is
expressed under different stimuli and task configurations.
It would be important to understand what is the minimal
stimulus design that can trigger particular tuned interac-
tions for various spatial positions and whether it involves
precisely the same neurons in the large-scale neural net-
work. To test predictions that can arise from theoretical
and computational approaches, new experimental tools to
visualize large massive neural networks at neuronal level
and sensitive to membrane potential fluctuations will be
needed. Recent neuro-technological advances in awake
animals, such as all-optical tools to measure and control
a large set of neurons (Ju et al. 2018; Zhang et al. 2018),
and the development of new genetically encoded voltage
indicators that allow simultaneous two-photon micros-
copy of subthreshold activity recording from many cells
(Villette et al. 2019); this provides the ideal experimental
setting to probe the complex and dynamic network inter-
actions underlying stimulus and task-dependent processing.

Author contributions All the authors contributed equally to the review.

Funding LP and FC are supported by CNRS and AMU and ANR
“HorizontalV1” ANR-17-CE37-0006-02.

Availability of data and material Not applicable.

Code availability Not applicable.

Declarations

Conflict of interest The authors have no relevant financial or non-fi-
ancial interests to disclose.

Research involving humans and/or animals Not applicable.

References

Albus K (2004) A quantitative study of the projection area of the cen-
tral and the parasagittal visual field in area 17 of the cat. Exp
Brain Res 24:159–179
Alonso J-M, Kremkow J (2014a) Faculty Opinions recommendation
of optogenetic assessment of horizontal interactions in primary
visual cortex. Faculty Opinions—post-publication peer review
of the biomedical literature
Alonso J-M, Kremkow J (2014b) Faculty Opinions recommendation
of lateral spread of orientation selectivity in V1 is controlled by
intracortical cooperativity. Faculty Opinions—post-publication
peer review of the biomedical literature
Angelucci A et al (2002) Circuits for local and global signal integration
in primary visual cortex. J Neurosci 22:8633–8646
Baker TI, Cowan JD (2009) Spontaneous pattern formation and pinning
in the primary visual cortex. J Physiol 103:52–68
Ben-Yishai R, Bar-Or RL, Sompolinsky H (1995) Theory of orientation
tuning in visual cortex. Proc Natl Acad Sci 92:3844
Blumenfeld B, Bichitckov D, Tsodyks M (2006) Neural network model
of the primary visual cortex: from functional architecture to lat-
eral connectivity and back. J Comput Neurosci 20:219–241
Bosking WH, Zhang Y, Schofield B, Fitzpatrick D (1997) Orientation
selectivity and the arrangement of horizontal connections in tree
shrew striate cortex. J Neurosci 17:2112–2127
Boutin V, Franciosini A, Chavane F et al (2021) Sparse deep predic-
tive coding captures contour integration capabilities of the early
visual system. PLoS Comput Biol 17:e1008629
Braitenberg V (1962) A note on myeloarchitectonics. J Comp Neurol
118:141–156
Bressloff PC, Carroll SR (2015) Laminar neural field model of later-
ally propagating waves of orientation selectivity. PLoS Comput
Biol 11:e1004545
Bressloff PC, Cowan JD, Golubitsky M et al (2001) Geometric visual
hallucinations, Euclidean symmetry and the functional archi-
tecture of striate cortex. Philos Trans R Soc Lond B Biol Sci
356:299–330
Bringuer V, Chavane F, Glaeser L, Frégnac Y (1999) Horizontal propa-
gation of visual activity in the synaptic integration field of area
17 neurons. Science 283:695–699
Buzás P, Eysel UT, Adorján P, Kisvárday ZF (2001) Axonal topogra-
phy of cortical basket cells in relation to orientation, direction,
and ocular dominance maps. J Comp Neurol 437:259–285
Buzás P, Kovács K, Ferencskő ÁS et al (2006) Model-based analysis
of excitatory lateral connections in the visual cortex. J Comp
Neurol 499:861–881
Carroll SR, Bressloff PC (2016) Phase equation for patterns of orienta-
tion selectivity in a neural field model of visual cortex. SIAM J
Appl Dyn Syst 15:60–83
Chariker L, Shapley R, Young L-S (2016) Orientation selectivity from
very sparse LGN inputs in a comprehensive model of macaque
V1 cortex. J Neurosci 36:12368–12384
Chavane F, Sharon D, Jancke D et al (2011) Lateral spread of orienta-
tion selectivity in V1 is controlled by intracortical cooperativity.
Front Syst Neurosci 5:4
Chemla S, Muller L, Reynaud A, Takerkart S, Destexhe A, Chavane
F (2017) Improving voltage-sensitive dye imaging: with a little
help from computational approaches. Neurophotonics 4:031215.
https://doi.org/10.1117/1.nph.4.3.031215
Creutzfeldt OD, Garey LJ, Kuroda R, Wolf JR (1977) The distribu-
tion of degenerating axons after small lesions in the intact and
isolated visual cortex of the cat. Exp Brain Res 27:419–440
Das A, Gilbert CD (1999) Topography of contextual modulations
mediated by short-range interactions in primary visual cortex.
Nature 399:655–661
Douglas RJ, Martin KAC (2004) Neuronal circuits of the neocortex. Annu Rev Neurosci 27:419–451
Douglas RJ, Martin KA, Whitteridge D (1991) An intracellular analysis of the visual responses of neurones in cat visual cortex. J Physiol 440:659–696
Field DJ, Hayes A, Hess RF (1993) Contour integration by the human visual system: evidence for a local “association field.” Vision Res 33:173–193
Fisken RA, Garey LJ, Powell TP (1975) The intrinsic, association and commissural connections of area 17 on the visual cortex. Philos Trans R Soc Lond B Biol Sci 272:487–536
Franciosini A, Boutin V, Chavane F, Perrinet LU (2021) Pooling in a predictive model of V1 explains functional and structural diversity across species. BioRxiv. https://doi.org/10.1101/2021.04.19.440444
Galuske RAW, Schmidt KE, Goebel R, Lomber SG, Payne BR (2002) The role of feedback in shaping neural representations in cat visual cortex. Proc Natl Acad Sci USA 99:17083–17088
Geisler WS, Perry JS, Super BJ, Gallogly DP (2001) Edge co-occurrence in natural images predicts contour grouping performance. Vis Res 41:711–724
Gerard-Mercier F, Carelli PV, Pananceau M et al (2016) Synaptic correlates of low-level perception in V1. J Neurosci 36:3925–3942
Gilbert CD, Li W (2013) Top-down influences on visual processing. Nat Rev Neurosci 14:350–363
Gilbert CD, Wiesel TN (1979) Morphology and intracortical projections of functionally characterised neurones in the cat visual cortex. Nature 280:120–125
Gilbert CD, Wiesel TN (1989) Columnar specificity of intrinsic horizontal and corticocortical connections in cat visual cortex. J Neurosci 9:2432–2442
Goldberg JA, Rokni U, Sompolinsky H (2004) Patterns of ongoing activity and the functional architecture of the primary visual cortex. Neuron 42:489–500
Grossberg S (1983) The quantized geometry of visual space: the coherent computation of depth, form, and lightness. Behav Brain Sci 6:625–657
Huang L, Chen X, Shou T (2004) Spatial frequency-dependent feedback of visual cortical area 21a modulating functional orientation column maps in areas 17 and 18 of the cat. Brain Res 998:194–201
Huang JY, Wang C, Dreher B (2007) The effects of reversible inactivation of postero-temporal visual cortex on neuronal activities in cat’s area 17. Brain Res 1138:111–128
Huang X, Elyada YM, Bosking WH et al (2014) Optogenetic assessment of horizontal interactions in primary visual cortex. J Neurosci 34:4976–4990
Hunt JJ, Bosking WH, Goodhill GJ (2011) Statistical structure of lateral connections in the primary visual cortex. Neural Syst Circuits 1:3
Hupe JM, James AC, Payne BR, Lomber SG, Girard P, Bullier J (1998) Cortical feedback improves discrimination between figure and background by V1, V2 and V3 neurones. Nature 394:784–787. https://doi.org/10.1038/29537
Hyvärinen A, Hoyer PO (2001) A two-layer sparse coding model learns simple and complex cell receptive fields and topography from natural images. Vis Res 41:2413–2423
Jancke D, Chavane F, Naaman S, Grinvald A (2004) Imaging cortical correlates of illusion in early visual cortex. Nature 428:423–426
Jones HE, Grieve KL, Wang W, Sillitoe AM (2001) Surround suppression in primate V1. J Neurophysiol 86:2011–2028. https://doi.org/10.1152/jn.2001.86.4.2011
Ju N, Jiang R, Macknik SL et al (2018) Long-term all-optical interrogation of cortical neurones in awake-behaving nonhuman primates. PLoS Biol 16:e2005839
Kang K, Shelley M, Sompolinsky H (2003) Mexican hats and pinwheels in visual cortex. Proc Natl Acad Sci 100:2848–2853
Karube F, Sári K, Kisvárday ZF (2017) Axon topography of layer 6 spiny cells to orientation map in the primary visual cortex of the cat (area 18). Brain Struct Funct 222:1401–1426
Karube F, Kisvárday ZF (2010) Topographical organization of layer 4 and 6 spiny neurons over functional maps for visual signals in cat area 8. Neurosci Res 68:e152
Kaschube M, Schnabel M, Lowel S, Coppola DM, White LE, Wolf F (2010) Universality in the evolution of orientation columns in the visual cortex. Science (new york, ny). https://doi.org/10.1126/science.1194869
Kisvárday Z (1997) Orientation-specific relationship between populations of excitatory and inhibitory lateral connections in the visual cortex of the cat. Cereb Cortex 7:605–618
Kisvárday Z (2016) Axons and brain architecture. Sect Microcirc. https://doi.org/10.1016/b978-0-12-801393-9.00007-4
Kisvárday ZF, Kim DS, Eysel UT, Bonhoeffer T (1994) Relationship between lateral inhibitory connections and the topography of the orientation map in cat visual cortex. Eur J Neurosci 6:1619–1632
Kisvárday ZF, Töth E, Rausch M, Eysel UT (1997) Orientation-specific relationship between populations of excitatory and inhibitory lateral connections in the visual cortex of the cat. Cereb Cortex (New York, NY; 1991) 7:605–618
Koch C, Jin J, Alonso JM, Zaidi Q (2016) Functional implications of orientation maps in primary visual cortex. Nat Commun 7:1–13
Laing CR, Troy WC (2003) PDE methods for nonlocal models. SIAM J Appl Dyn Syst 2:487–516
Li N et al (2019) Spatiotemporal constraints on optogenetic inactivation in cortical circuits. eLife 8:226
Liang Z, Shen W, Shou T (2007) Enhancement of oblique effect in the cat’s primary visual cortex via orientation preference shifting induced by excitatory feedback from higher-order cortical area 21a. Neuroscience 145:377–383
Malach R, Amir Y, Harel M, Grinvald A (1993) Relationship between intrinsic connections and functional architecture revealed by optical imaging and in vivo targeted biocytin injections in primary striate cortex. Proc Natl Acad Sci USA 90:10469–10473
Markov NT, Misery P, Falchier A et al (2011) Weight consistency specifies regularities of macaque cortical networks. Cereb Cortex 21:1254–1272
Marr D, Hildreth E (1980) Theory of edge detection. Proc R Soc Lond B Biol Sci 207:187–217
Martin KAC, Roth S, Rausch ES (2014) Superficial layer pyramidal cells communicate heterogeneously between multiple functional domains of cat primary visual cortex. Nat Commun 5:5252
Martin KAC, Roth S, Rausch ES (2017) A biological blueprint for the axons of superficial layer pyramidal cells in cat primary visual cortex. Brain Struct Funct 222:3407–3430
Martinez-Conde S et al (1999) Effects of feedback projections from area 18 layers 2/3 to area 17 layers 2/3 in the cat visual cortex. J Neurophysiol 82:2667–2675
McManus JNJ, Li W, Gilbert CD (2011) Adaptive shape processing in primary visual cortex. Proc Natl Acad Sci USA 108:9739–9746
Michalski A, Gerstein GL, Czarkowska J, Tarnbeck R (1983) Interactions between cat striate cortex neurons. Exp Brain Res 51:97–107
Mitchison G, Crick F (1982) Long axons within the striate cortex: their distribution, orientation, and patterns of connection. Proc Natl Acad Sci USA 79:3661–3665
Monier C, Chavane F, Baudot P et al (2003) Orientation and direction selectivity of synaptic inputs in visual cortical neurons: a diversity of combinations produces spike tuning. Neurosci 37:663–680
Muller L, Reynaud A, Chavane F, Destexhe A (2014) The stimulus-evoked population response in visual cortex of awake monkey is a propagating wave. Nat Commun 5:3675
Muller L, Chavane F, Reynolds J, Sejnowski TJ (2018) Cortical traveling waves: mechanisms and computational principles. Nat Rev Neurosci 19:255–268

Nurminen L, Merlin S, Bijnazadeh M, Federer F, Angelucci A (2018) Top-down feedback controls spatial summation and response amplitude in primate visual cortex. Nat Commun. https://doi.org/10.1038/s41467-018-04500-5

Olshausen BA, Field DJ (1996) Natural image statistics and efficient coding. Network (Bristol, Engl) 7:333–339

Ozeki H, Finn IM, Schaffer ES et al (2009) Inhibitory stabilization of the cortical network underlies visual surround suppression. Neuron 62:578–592

Parent P, Zucker SW (1989) Trace inference, curvature consistency, and curve detection. IEEE Trans Pattern Anal Mach Intell 11:823–839

Pattadkal JJ, Mato G, van Vreeswijk C et al (2018) Emergent orientation selectivity from random networks in mouse visual cortex. Cell Rep 24:2042-2050.e6

Perrinet LU, Bednar JA (2015) Edge co-occurrences can account for rapid categorization of natural versus animal images. Sci Rep 5:11400

Perrinet LU, Masson GS (2012) Motion-based prediction is sufficient to solve the aperture problem. Neural Comput 24:2726–2750. https://doi.org/10.1162/neco_a_00332

Poort J, Raudies F, Wannig A, Lamme VAF, Neumann H, Roelfsema PR (2012) The role of attention in figure-ground segregation in areas V1 and V4 of the visual cortex. Neuron 75:143–156. https://doi.org/10.1016/j.neuron.2012.04.032

Raizada RDS, Grossberg S (2003) Towards a theory of the laminar architecture of cerebral cortex: computational clues from the visual system. Cereb Cortex 13:100–113

Rangan AV, Cai D, McLaughlin DW (2005) Modeling the spatiotemporal cortical activity associated with the line-motion illusion in primary visual cortex. Proc Natl Acad Sci USA 102:18793–18800

Rankin J, Chavane F (2017) Neural field model to reconcile structure with function in primary visual cortex. PLoS Comput Biol 13:e1005821

Rankin J, Avitabile D, Baladron J et al (2014) Continuation of localized coherent structures in nonlocal neural field equations. SIAM J Sci Comput 36:B70–B93

Reynaud A, Masson GS, Chavane F (2012) Dynamics of local input normalization result from balanced short- and long-range intra-cortical interactions in area V1. J Neurosci 32:12558–12569

Ribot J, Romagnoni A, Millerei C et al (2016) Pinwheel-dipole configuration in cat early visual cortex. Neuroimage 128:63–73

Roberts M, Delicato LS, Herrero J, Gieselmann MA, Thiele A (2007) Attention alters spatial integration in macaque V1 in an eccentricity-dependent manner. Nat Neurosci 10:1483–1491

Rockefeller NL et al (2009) Functional selectivity of interhemispheric inhibition in sensory cortex. Neuron 85:402–417

Salin PA, Bullier J, Kennedy H (1989) Convergence and divergence in the afferent projections to cat area 17. J Comp Neurol 283:486–512

Salin PA, Girard P, Kennedy H, Bullier J (1992) Visuotopic organization of corticocortical connections in the visual system of the cat. J Comp Neurol 320:415–434

Sarti A, Citti G, Petittot J (2008) The symplectic structure of the primary visual cortex. Biol Cybern 98:33–48

Schmidt KE, Kim DS, Singer W et al (1997) Functional specificity of long-range intrinsic and interhemispheric connections in the visual cortex of strabismic cats. J Neurosci 17:5480–5492

Schwarz C, Bolz J (1991) Functional specificity of a long-range horizontal connection in cat visual cortex: a cross-correlation study. J Neurosci 11:2995–3007

Serre T, Oliva A, Poggio T (2007) A feedforward architecture accounts for rapid categorization. Proc Natl Acad Sci USA 104:6424–6429

Shen W, Liang Z, Chen X, Shou T (2006) Posteriormedial lateral suprasylvian motion area modulates direction but not orientation preference in area 17 of cats. Neuroscience 142:905–916

Shen W, Liang Z, Shou T (2008) Weakened feedback abolishes neural oblique effect evoked by pseudo-natural visual stimuli in area 17 of the cat. Neurosci Lett 437:65–70

Sigman M, Cacci GA, Gilbert CD, Magno MO (2001) On a common circle: natural scenes and Gestalt rules. Proc Natl Acad Sci USA 98:1935–1940

Sillichto AM, Grieve KL, Jones HE et al (1995) Visual cortical mechanisms detecting focal orientation discontinuities. Nature 378:492–496

Stettler DD, Das A, Bennett J, Gilbert CD (2002) Lateral connectivity and contextual interactions in macaque primary visual cortex. Neuron 36:739–750

Somers DC, Nelson SB, Sur M (1995) An emergent model of visual cortical orientation selectivity in cat visual cortical simple cells. J Neurosci 15:5448–5465

Ts’o DY, Gilbert CD, Wiesel TN, (1986) Relationships between horizontal interactions and functional architecture in cat striate cortex as revealed by cross-correlation analysis. J Neurosci 6:1160–1170

Tosdlyk MS, Skaggs WE, Sejnowski TJ, McNaughton BL (1997) Paradoxical effects of external modulation of inhibitory interneurons. J Neurosci 17:4382–4388

Vidyasagar TR, Eysel UT (2015) Origins of feature selectivities and maps in the mammalian primary visual cortex. Trends Neurosci 38:475–485. https://doi.org/10.1016/j.tins.2015.06.003

Villelle V, Chavarha M, Dimov IK et al (2019) Ultrafast two-photon imaging of a high-gain voltage indicator in awake behaving mice. Cell 179:1590-1608.e23

Voges N, Perrinet L (2012) Complex dynamics in recurrent cortical networks based on spatially realistic connectivities. Front Comput Neurosci. https://doi.org/10.3389/fncom.2012.00041

Voges N, Guijarro C, Aertsen A, Rotter S (2010) Models of cortical networks with long-range patchy projections. J Comput Neurosci 28:137–154

Walker EY, Sinz FH, Cobos E et al (2019) Inception loops discover what excites neurons most using deep predictive models. Nat Neurosci 22:2060–2065

Wang C, Walsczysk WJ, Burke W, Dreher B (2000) Modulatory influence of feedback projections from area 21a on neuronal activities in striate cortex of the cat. Cerebral Cortex (New York, NY: 1991) 10:1217–1232

Wang C, Walsczysk WJ, Burke W, Dreher B (2007) Feedback signals from cat’s area 21a enhance orientation selectivity of area 17 neurons. Exp Brain Res 182:479–490

Wertheimer M (1923) Untersuchungen zur Lehre von der Gestalt. II Psychologische Forschung 4:301–350

Yousef T, Bonhoeffer T, Kim DS et al (1999) Orientation topography of layer 4 lateral networks revealed by optical imaging in cat visual cortex (area 18). Eur J Neurosci 11:4291–4308

Yousef T, Töth E, Rausch M et al (2001) Topography of orientation centre connections in the primary visual cortex of the cat. NeuroReport 12:1693–1699
Zhang Z, Russell LE, Packer AM et al (2018) Closed-loop all-optical interrogation of neural circuits in vivo. Nat Methods 15:1037–1040

Publisher’s Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.