



THE UNIVERSITY *of* EDINBURGH

Edinburgh Research Explorer

The "silent" surround of V1 receptive fields: theory and experiments

Citation for published version:

Series, P, Lorenceau, J & Frégnac, Y 2003, 'The "silent" surround of V1 receptive fields: theory and experiments', *Journal of Physiology - Paris*, vol. 97, no. 4-6, pp. 453-474.
<https://doi.org/10.1016/j.jphysparis.2004.01.023>

Digital Object Identifier (DOI):

[10.1016/j.jphysparis.2004.01.023](https://doi.org/10.1016/j.jphysparis.2004.01.023)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Peer reviewed version

Published In:

Journal of Physiology - Paris

General rights

Copyright for the publications made accessible via the Edinburgh Research Explorer is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

The University of Edinburgh has made every reasonable effort to ensure that Edinburgh Research Explorer content complies with UK legislation. If you believe that the public display of this file breaches copyright please contact openaccess@ed.ac.uk providing details, and we will remove access to the work immediately and investigate your claim.



The “silent” surround of V1 receptive fields: theory and experiments

Peggy Seriès^{*}, Jean Lorenceau, Yves Frégnac^{*}

Unité de Neurosciences Intégratives et Computationnelles, UPR CNRS 2191, 1 Avenue de la Terrasse, 91198 Gif sur Yvette, France

Abstract

The spiking response of a primary visual cortical cell to a stimulus placed within its receptive field can be up- and down-regulated by the simultaneous presentation of objects or scenes placed in the “silent” regions which surround the receptive field. We here review recent progresses that have been made both at the experimental and theoretical levels in the description of these so-called “Center/Surround” modulations and in the understanding of their neural basis. Without denying the role of a modulatory feedback from higher cortical areas, recent results support the view that some of these phenomena result from the dynamic interplay between feedforward projections and horizontal intracortical connectivity in V1. Uncovering the functional role of the contextual periphery of cortical receptive fields has become an area of active investigation. The detailed comparison of electrophysiological and psychophysical data reveals strong correlations between the integrative behavior of V1 cells and some aspects of “low-level” and “mid-level” conscious perception. These suggest that as early as the V1 stage, the visual system is able to make use of contextual cues to recover local visual scene properties or correct their interpretation. Promising ideas have emerged on the importance of such a strategy for the coding of visual scenes, and the processing of static and moving objects.

© 2004 Elsevier Ltd. All rights reserved.

Keywords: Primary visual cortex; Horizontal intracortical connectivity; Feedback projections; Visual receptive field; Contextual influences; Association field; Binding; Cortical dynamics; Apparent motion; Perceptual saliency

1. Introduction

The receptive field of a visual neuron is classically defined as the region of retina, or of visual space, within which the presentation or the extinction of impulse-like stimuli, such as light or dark spots, evokes action potentials (classical receptive field, CRF) [53]. In primary visual cortex (V1), neurons have been shown to have very localized CRFs, and to be selective to the orientation of the object presented in this region. By definition, stimuli falling in the surrounds of the CRF are not sufficient for driving spiking responses. In functional models of visual processing, this region is thus usually ignored.

However, it has long been known that the CRF is an incomplete description of the area of space to which neurons have access. In particular, it was observed that

when multiple objects or natural scenes are shown, stimuli placed outside the CRF can modulate the activity evoked by the stimulus placed within the CRF [37,39]. Surprisingly little importance was attached to these so-called “center/surround” modulations, which tended to be regarded as minor determinants of physiological response properties. The last decade has seen a resurgence of interest for these phenomena, with a pluridisciplinary effort involving physiological, psychophysical and theoretical studies. Important progress has been made and there is now a growing sense that these contextual influences may be of fundamental importance in understanding the operation of visual neurons.

Here, we review a number of experimental and theoretical findings related to center/surround (C/S) modulations in V1. Section 2 provides an overview of the electrophysiological data describing these effects. Section 3 then presents the different theoretical attempts that have been made to describe these phenomena in a unified framework, to identify their underlying circuits or to explore their functional implications in the representation of visual information. C/S modulations are often interpreted as the physiological correlates of a number of psychophysical results showing that the

^{*} Corresponding authors. Present address: Brain and Cognitive Sciences Department, University of Rochester, Meliora Hall, Rochester, NY 14627, USA.

E-mail addresses: pseries@bcs.rochester.edu (P. Seriès), jean.lorenceau@chups.jussieu.fr (J. Lorenceau), fregnac@iaf.cnrs-gif.fr (Y. Frégnac).

perception of an object depends on the spatial context in which it is embedded [47,55]. In Section 4, we describe the analogies that motivate this parallelism and discuss the validity of the models that were designed to bridge physiology and psychophysics. Finally, based on the recent experimental exploration of the dynamics of C/S modulations at the synaptic level using intracellular recordings and optical imaging *in vivo*, we show that their influence may not be limited to the processing of static contours: C/S modulations can be expected to affect—or could even possibly support—the processing of moving signals.

2. Center/surround modulations of the spiking response of V1 cells

2.1. Suppressive interactions

Hubel and Wiesel [62,63], on the basis of single unit extracellular recordings, had observed that some cells of cat areas 18 and 19 were selective to the length of an optimally oriented bar. For these cells, most of which had a complex receptive field, extending the bar in one or both directions beyond a critical length caused a marked fall-off of the spiking response, or even its complete suppression. They named “hypercomplex” the cells showing this property. Later studies revealed that a large number of cells in cat area 17 and monkey V1, whether they were simple or complex, were also sensitive to the length of the stimulus and that a similar effect was observed when the width of the stimulus (or number of cycles in the case of sinusoidal luminance modulation gratings) was varied. These properties—now usually termed “end-stopping” and “side-inhibition”—are supposed to be due to the presence of inhibitory regions outside the CRF, along the preferred orientation axis (“end-zones”) and on its flanks (“side-bands”). They can be viewed as the first type of C/S modulations to be described in V1.

More recent studies have extended these explorations by (i) using a variety of stimuli in the center and the surround of the CRF (a single bar, rectangular or circular grating of increasing size; or two or more simultaneous stimuli in the center of the CRF and at various positions of its surround), (ii) systematically varying the parameters of the stimulation (contrast, orientation, spatial frequency etc.). They have come to the following conclusions: C/S modulations are observed for a majority of V1 cells. In most cases, as in the example shown in Fig. 1A, the presentation of a surround stimulus results in a *suppression* of the spiking responses to the center stimulus. Electrophysiological studies have found that 56% [159] to 86% [128] of cells in cat V1 and more than 90% [71] in monkey V1 show significant suppression when increasing the diameter of a central

grating beyond the CRF, or adding to the central grating a large annular iso-oriented surround. In many cells, the observed suppression is strong: recent studies indicate that 38% of cells are suppressed by more than 40% in cat [159] and 40% of cells by more than 70% in monkey [71]. Similar effects are found when the surround is composed of a texture of oriented bars (monkey: [81,103], cat: [78,79]). The diameter of the region comprising both the CRF and modulatory surround is estimated to be at least 2–5 times larger than the CRF [89,93]. Simple and complex cells exhibit similar C/S modulations, and these phenomena seem to vary little with the laminar position of the recorded cell [10,70,71, 159].

The positions of the surround that are able to induce a marked suppression of a given cell’s activity are often limited to a specific spatial area. The most sensitive surround regions greatly vary from cell to cell, and are often asymmetrically positioned around the CRF [10,38,71,158]. In cat area 17, the most suppressive regions are most often found along the preferred orientation axis, at one of the “end-zones” of the receptive field [38].

Furthermore, the surround is highly sensitive to the characteristics of the test stimulus, with a selectivity that is often similar—but broader—than that of the CRF [30,89]. The modulations are generally maximal when center and surround stimuli have the same orientation [30,81,88,89,128,134,158], and decrease or disappear when the relative orientation of the two stimuli is increased, although this rule is not rigidly followed [76,88,110,128]. Similarly, maximal effects are found for stimuli of similar spatial frequencies [30,89,158] and speeds [89]. Whether this “similarity” rule also applies to motion direction (monkey: [71,88]) is yet unclear, especially in cat [30,89,158]. It has also been noted that these effects are not sensitive to the relative phase of the center and surround stimuli [30,88]. Their amplitude increase almost linearly when the contrast of the surround increases [30,158]. Finally, these effects often decrease but do not disappear for dichoptic presentation of the center and surround. These various features suggest that these phenomena have a dominant cortical origin taking place after binocular integration of visual input [30]. Surround suppression differs in this respect from cross-orientation suppression elicited within the CRF, which is blocked when the test and the mask are seen through different eyes.

2.2. Facilitator interactions

Facilitatory modulations have also been reported in a number of studies. In most cases, they appear for discrete surround stimuli (bars, Gabor patches) presented at the “end-zones” of the CRF. The contrast of the center stimulus relative to the cell’s contrast threshold

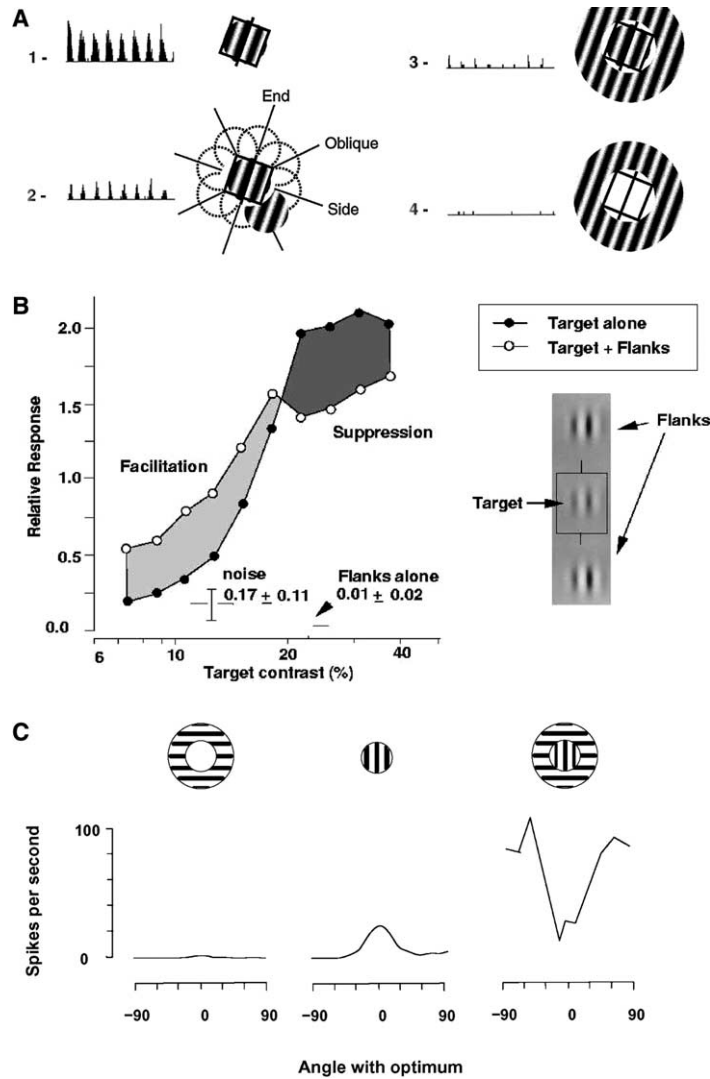


Fig. 1. (A) Example of surround suppression in one cell of cat area 17. (1) Response to an optimal drifting grating placed in the CRF. (2) Influence of the most sensitive modulatory region, here located at an oblique position of the surround, on the response to the central stimulus. (3) Influence of an annular surround. (4) Response to the surround stimulus alone. Reproduced from Walker et al. [158]. (B) Contrast-response functions of a single cell in cat area 17 when only a target is shown (filled circles) and when it is flanked by two other collinear Gabor elements (open circles). The cell response is facilitated at low contrast and suppressed at intermediate and high contrast. Reproduced from Polat et al. [110]. (C) Facilitation for cross-oriented configurations (orientation contrast selectivity). Orientation tuning of one simple cell of macaque monkey VI (layer IVB) in response to a central drifting grating alone (contrast: 36%, outer diameter = 1°) and a surround grating alone, and influence of the surround orientation when the central grating is shown at the cell's preferred orientation. Reproduced from Sillito and Jones [135].

then appears to control the sign of the modulation (cat: [100,110,128,150], monkey: [88]). For many cells (~30% in cat [26]) a single surround stimulus can facilitate the responses to a threshold or low-contrast center stimulus, and suppress the responses to a high-contrast center stimulus. This sign-switching behavior is illustrated in Fig. 1B. Maximal modulations are generally observed when center and surround stimuli are iso-oriented and co-aligned (cat: [26,102,110], awake monkey: [74,76,81]). They decrease when the spatial separation between the center and surround patches increases, but can still be observed for distances of up to 12° of visual angle in some cases [100].

As mentioned above, surround suppression is usually stronger when the surround stimulus is presented at the same orientation as the center stimulus. Thus, compared to iso-oriented surrounds, surrounds that are orthogonal to the center stimulus usually induce a *relative facilitation* of the response. In some cases [72,134], however, it has been found that cross-oriented surrounds could even induce a *net facilitation* of the test response. In this case, as illustrated in Fig. 1C, the response is enhanced by the surround beyond the maximal level evoked by an optimal center alone. This effect could be maintained even for non-preferred orientations of the center stimulus, suggesting that it was sensitive to

the “T”-type configuration of the stimuli, or the “orientation contrast” between the two stimuli, and not to the absolute orientation of the surround or its shift relative to the preferred orientation of the cell. This effect was observed in simple and complex cells that are suppressed by an iso-oriented annular surround, independently of their laminar position. It seems to be preferentially observed at high contrast of the center stimulus, a moderate contrast center often giving rise to suppressive interactions for all orientations of the surround [88,134].

2.3. Beyond the firing rate

In general, physiological studies of C/S modulations have focused on the influence of the surround on the recorded cell’s *mean firing rate*. Interestingly, a few studies have documented modulations of other aspects of the response. First, it has been observed that the orientation preference could shift, or that the orientation tuning shape could change, when surround stimuli are present [17,49]. Moreover, facilitatory interactions at threshold contrast have been found to be accompanied by a decrease in trial-to-trial variability [77]. Finally, there is some evidence showing that the temporal dynamics of the response can be modulated by surround stimulation [10] (see Section 5).

2.4. Diversity and controversies

Taken together, published studies on C/S modulations report a diversity of behaviors which are often difficult to interpret and reconcile. These discrepancies can be explained by a number of factors.

1. They seem to partly derive from differences in the characteristics of the stimuli that have been used (localized vs large annular surround; contrast level of the center stimulus, relative orientation of the center and the surround stimuli etc.). In particular, it seems that localized surrounds are more likely to evoke facilitation than large surrounds, specially when the central stimulus is presented at low contrast.
2. How the size of the CRF is defined differs among studies. Two methods are classically used: the minimum discharge field (MDF) and the spatial summation field (SSF). The MDF estimates the extent of the excitatory influence by selecting the regions in which a small edge or bar of light elicits a spiking response from the neuron. By contrast, the SSF estimates the region of summation by using patches of drifting gratings of increasing diameter. It corresponds to the smallest stimulus diameter at which the evoked response stops increasing. The MDF can be viewed as the “peak of the iceberg” in a neu-

ron’s cortical sensitivity profile [16]. When one moves away from this region, sensitivity to impulse-like stimuli declines to subthreshold activation below the spike initiation level. Because SSF measurements include parts of this large region of subthreshold excitation, the SSF receptive field diameter is usually more than twice that of the MDF [23,159]. As a consequence, a number of facilitatory regions, that appear to be *outside* the CRF using the MDF assessment, seem to lie *within* the CRF when using the SSF measurement, leaving mostly suppressive influences outside the defined center region [23,38,159]. Some authors, however, have demonstrated that facilitatory effects can be elicited from regions beyond the summation field [74,100,134]. Further complications arise from the fact that the size of the summation field is not a rigid entity, but depends on the stimulus contrast [75,123] (see Fig. 1B) and the level of cortical adaptation [23].

3. C/S modulations have been shown to be sensitive to the level of anesthesia, and brain EEG [86,166], and, for the awake animal, to be dependent on attentional factors [67], which might differ between studies.
4. There may exist important interspecies differences. For example, recent data show that surround suppression is stronger in monkey than in cat [71]. Moreover, the facilitatory modulations for orientation or direction contrast that have been reported in monkey [71,134] do not seem to be present in cat [159].
5. Finally, as the above explanations cannot account for the variability from cell to cell that is generally reported under identical experimental conditions (see e.g. [26,88,158]), it has been proposed that the latter, and some of the observed diversity, could be related to the position of the recorded cells in the orientation map [29,129] and the local context of the cortical connectivity in which they are embedded.

2.5. Possible anatomical substrate

Although the incidence of certain types of facilitatory interactions is still controversial, the fact that V1 cells receive information concerning relatively distant regions outside their CRFs is indisputable. Where does this influence come from? Through what type of anatomical projections does it travel?

The spatial extent of these interactions suggests that they cannot be conveyed by divergent thalamo-cortical inputs and thus cannot be simply described within a “feedforward” framework. Indeed, the estimates of the divergence of thalamo-cortical axons limit the spread to less than 2 mm (2° in the cat). The sensitivity of C/S modulations to stimulus orientation and direction, as well as the fact that they persist for dichoptic presentation also support a cortical origin.

Most existing models thus assume that they are mediated by the network of intrinsic *horizontal connections* observed in V1 layers 2/3. These long-range projections originate from pyramidal cells and can link regions over several millimeters (cat: [48,80,95]; tree shrew [13]; monkey: [5,138]). They seem well suited to explain the orientation and position selectivity of C/S modulations, as they tend to connect cells with similar orientation preferences, and more specifically, cells whose receptive fields are topographically aligned along an axis of collinearity for distance beyond 700 μm (in cat: [124]; tree shrew: [13,27]; monkey: [138], but see the study of [6] in macaque monkeys). Furthermore, they contact both excitatory and inhibitory cells, thereby potentially mediating both long-range monosynaptic excitation and long-range disinaptic suppression [98, 151,152].

However, *feedback connections* from extra-striate areas (e.g. V2, V4, TEO, MT) could provide an alternative or additional substrate for these effects. Indeed, feedback connections are known to modulate V1 activities by controlling the response gain of their target neurons [132]. The inactivation of V2 or MT, for example, leads to a decrease of V1 responses [99]. Moreover, since neurons within these “higher” areas have much larger CRFs than V1 neurons, they can convey information from large subregions of the visual field (the projections from V2 to V1 in monkey can convey information from a region 5–6 times larger than that covered by a V1 CRF [6]). Similar to horizontal projections, their distribution is “patchy”. It has been suggested that they also link points of like-orientation preference [6,50] (but see [146] for an opposite result) and, in the macaque, cover anisotropic parts of visual space [6].

The respective role of each type of connections is currently debated. Two types of results support the participation of feedback projections:

- First, when the retino-cortical magnification factor is taken into account, the spatial scale of horizontal projections, contrary to that of feedback projections, seems insufficient to account for the full dimensions of the surround modulatory field, at least in monkey cortex [6,23]. The relative extent of horizontal and feedback projections is however still a matter of dispute [6,146].
- Second, it has been shown in the same species that the inactivation of area MT reduces the suppressive influence of surround motion stimulation in V3, V2 and V1 neurons [66].

On the other hand, several observations minor the importance to be given to the feedback control exerted on V1 by higher-order areas and support the implication of intracortical “horizontal” connectivity:

- Inactivation of V2 does not seem to affect response modulations by static texture surrounds in V1 neurons [64].
- Second, the network of horizontal connections seems to be an order of magnitude denser than the feedback projection [146].
- Finally, these two pathways have been shown to differ in their temporal dynamics. In vivo intracellular recording of visual cortical neurons during subthreshold processing of lateral input have demonstrated that horizontal projections, whose axons are often unmyelinated, are characterized by a slow conduction velocity [16,25] (see also Section 5). On the contrary, feedback connections have been shown to be extremely rapid in their conduction time, and to act within a few ms on the early part of V1 responses [65]. This contradicts the naive assumption that the “top-down” influences of feedback projections should occur with a marked temporal delay. It also provides additional support for the participation of horizontal connections, whose slow conduction velocity well matches the dynamics of the lateral spread of subliminal activity evoked by the activation of the surround [16,51,119].

It seems likely that both types of connections play a role in C/S modulations: horizontal connections would serve the closest interactions, i.e. those lying within the summation field, and underlie contrast-dependent changes in SF size, while feedback projections would mediate modulations from the far surround [6,17,23,27].

3. Theoretical models of center/surround modulations

C/S modulations challenge our understanding of V1 function and circuits. They reveal that V1 CRFs do not function independently of one another but interact in a highly nonlinear way. This implies that the characterization of all individual CRFs is not sufficient to deduce how neurons collectively represent visual information, and thus that current models of sensory processing need to be revised. At the theoretical level, we would like to be able to answer three types of questions:

- What is the informational operation, or input-output transformation performed by single V1 cells when a central stimulus and a contextual surround are simultaneously presented?
- How do these non-linear phenomena emerge from the known properties of V1 cells and circuits?
- What is the computational role of C/S modulations in visual processing?

These issues have been respectively explored using three different levels of models: (i) “phenomenological”

(or “functional”) models which aim at characterizing the response properties within the context of a visual information processing algorithm, (ii) “structural” models which aim at characterizing the biophysical neural mechanisms that are responsible for the physiological data, and (iii) “optimized” model that try to predict the physiological data from an optimized strategy of visual coding.

3.1. Phenomenological models of surround suppression

Focusing on surround suppression, different authors [23,122,123] have tried to describe the properties of the “extended” receptive field (ERF, which represents the topological union of the classical receptive field and its surround) in a unified phenomenological framework.

Sceniak et al. [122,123] have proposed that the ERF could be viewed as a single entity—described by a difference of Gaussian (DoG) model composed of 2 overlapping mechanisms, interacting subtractively. In this model (Fig. 2A), a first Gaussian (L_c), represents the excitatory contribution of the CRF center and can be assumed to correspond to the envelope of a Gabor function representing the CRF’s spatial structure [73], while the second Gaussian (L_s), centered at the same position, describes the suppressive contribution of the surround. The response of a neuron to a circular grating of radius x is then given by a function of the form:

$$R(x) = K_c L_c(x) - K_s L_s(x) \quad (1)$$

where K_c and K_s are the gains of the center and surround mechanisms; $L_{c,s}(x) = \int_{-x/2}^{x/2} e^{-(2y/\sigma_{c,s})^2} dy$ and σ_c and σ_s represent the spatial extent of the center and surround components.

Other authors have questioned the fact that center and surround mechanisms could interact linearly [23]. Indeed, it has been observed that the way a neuron’s contrast response is changed by stimulating the surround can be better described by a vertical scaling of the curve in log-linear coordinates (a change in response gain, corresponding to a *divisive* mechanism) rather than by a simple downward shift and thresholding of the curve, which would correspond to a subtractive mechanism (see Fig. 3).

Cavanaugh et al. [23] have thus proposed an alternative model based not on the difference of two Gaussians, but on their *ratio* (RoG). The response to a circular grating of radius x is then given by a function of the form:

$$R(x) = \frac{K_c L'_c(x)}{1 + K_s L'_s(x)} \quad (2)$$

where

$$L'_{c,s}(x) = \left(\int_{-x/2}^{x/2} e^{-(2y/\sigma_{c,s})^2} dy \right)^2.$$

Interestingly, this proposal can be viewed as an extension of the standard normalization model [3,54] to account for surround phenomena (see also [26,126], and in psychophysical contexts: [105,140,168]). According to the standard normalization model, the activity of each cortical neuron is normalized (i.e. divided) by the responses of a pool of surrounding neurons, chosen approximately uniformly in a local neighborhood (i.e. belonging to the same hypercolumn). This suppression is supposed to be aspecific, or broad in orientation and spatial frequency selectivities. Such a model can account for a number of non-linearities observed in the response to stimuli placed within the CRF [3,54]. The RoG model

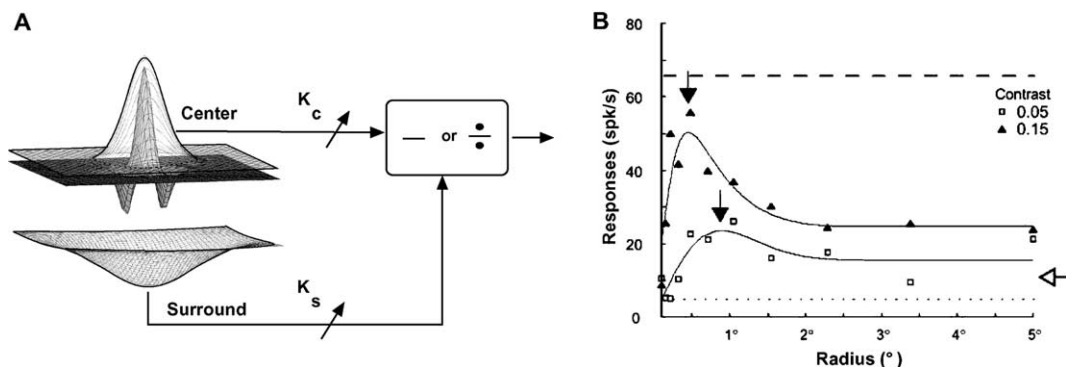


Fig. 2. (A) The Difference of Gaussians (DoG) and Ratio of Gaussians (RoG) models proposed by Sceniak et al. [123] and Cavanaugh et al. [23]. In both models, the envelope of the CRF and the suppressive surround are modeled as two overlapping Gaussians of different spatial extent. Whereas the DoG model assumes that the center and surround mechanisms interact linearly, the RoG model suggests that the influence of the surround is divisive. (B) Example of spatial summation for one neuron in macaque monkey V1 at low (5%) and high contrast (15%). The visual stimulus was a circular patch of sine-wave grating at the cell’s preferred orientation and spatial and temporal frequencies. The black arrows indicate the stimulus radius eliciting the maximum response for each contrast level. The smooth curves were fit to the data using the DoG model. With this model, the expansion of the summation field when contrast decreases can be accounted for by an increase of the space constant σ_c (here σ_c (low)/ σ_c (high) = 2.62—see text for more details). Reproduced from [123].

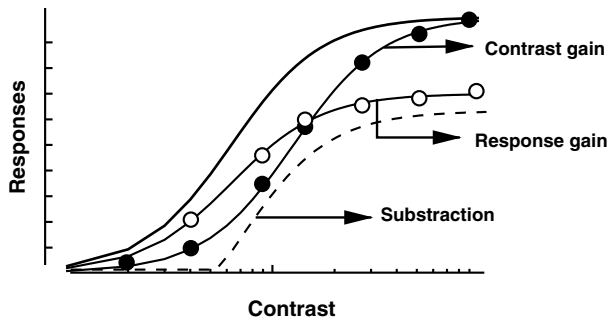


Fig. 3. Possible forms of suppression. The bold curve represents a neuron's response to a stimulus placed in the CRF as a function of its contrast in log-linear coordinates. In theory, there are three ways by which the response to a stimulus placed in the CRF might be suppressed by the concomitant stimulation of the surround. First, surround influence could induce a horizontal displacement in the neuron's contrast response curve (filled dots). This represents a change in *contrast gain*. It does not change the maximal response but effectively scales contrast sensitivity for the neuron. Second, surround stimuli could induce a compression of the curve ordinates (empty dots). This represents a change in *response gain*: it does not alter the range of contrasts to which a neuron responds but simply scales responses by a constant ratio at all contrasts. Changes in both contrast gain and response gain are divisive forms of suppression. A third possibility is a *subtractive influence* from the surround, that reduces responses by the same amount at all contrasts (---). Suppressive effects *within* the CRF (such as the phenomenon of cross-orientation inhibition) are known to be best described by a contrast gain model [22,127], whereas surround suppression was found to be best accounted for by a response gain model [23,127].

extends this description by suggesting that cells responding to surround stimuli can also contribute to the "normalization pool". Note however that, surround suppression being selective to the characteristics of the test stimulus, the cells participating to the surround normalization pool should not be chosen uniformly, but more specifically in the regions where the orientation and spatial frequency preferences are similar to that of the receptive field [126].

The success of the DoG and the RoG models is due to their ability to satisfactorily fit experimental summation curves (Fig. 3). They can also be used to describe the observed expansion of the size of the RF when contrast decreases, provided that either the space-constant σ_c of the central excitatory mechanism [123], or the gains K_c and K_s of both mechanisms [23,26] change dynamically when contrast is varied. These phenomenological models thus offer a synthetic description of the main features of surround modulations, which can be integrated into large-scale analysis of visual processing and can help understand their functional implications (see below). However, since they do not specify the circuits or biophysics by which these functions are implemented, their explanatory and predictive power at the physiological level remains limited. The RoG model, for example, raises a question that is also found in many

other contexts (e.g. [21,24,120]): how can division be implemented by cortical neurons?

3.2. Modeling the underlying circuits

Uncovering the cortical circuits that could be responsible for C/S modulations has been the aim of a second group of theoretical investigations. Stemmler et al. [144] and Somers et al. [143] have tried to understand how surround facilitation at low contrast of the center stimulus and suppression at high contrast [110] can simultaneously emerge in a single network with fixed cortical connections.

Briefly, these "structural" models describe a few V1 hypercolumns composed of a large number of excitatory and inhibitory cells. The circuits within each hypercolumn are responsible for the properties of the CRF and the local excitatory/inhibitory balance. At the single-unit integrative level, both models make the crucial assumption that there is an asymmetry of the functional threshold and response gain between excitatory and inhibitory neurons such that, for weak visual inputs, inhibitory neurons are essentially silent, while, for strong inputs, the activity of inhibitory neurons rapidly increases, provoking the response saturation of excitatory cells. This gain asymmetry could be due to the intrinsic spiking characteristics of excitatory and inhibitory cells ("regular spiking" vs "fast spiking" [97]). Alternately, it could reflect differences in the efficacy or in the kinetics of activity-dependent depression between intracortical excitatory, thalamo-cortical excitatory and inhibitory synapses [143,148], or different levels of spontaneous activities for excitatory and inhibitory cells [144]. Both models then assume that the different hypercolumns interact through long-range horizontal excitatory projections, which preferentially connect cells with similar orientation tuning and make synapses on both excitatory and inhibitory neurons. The influence of the surround can then be described as an orientation-specific modulation of the local excitation/inhibition balance.

The behavior of these models can be captured by simple firing-rate models of a cortical column [34] or hypercolumn [145], composed of an excitatory population and an inhibitory population, both receiving direct inputs in response to a central stimulus, and additional excitatory inputs when the surround is activated (Fig. 4; see also discussion in [39]). They are based on the following simple mechanism:

- When the contrast of the center stimulus is low, the local inhibitory cells are silent. The excitatory inputs induced by the activation of the surround are insufficient to drive them above threshold. However, they do amplify the responses of the excitatory cells (Fig. 4A).

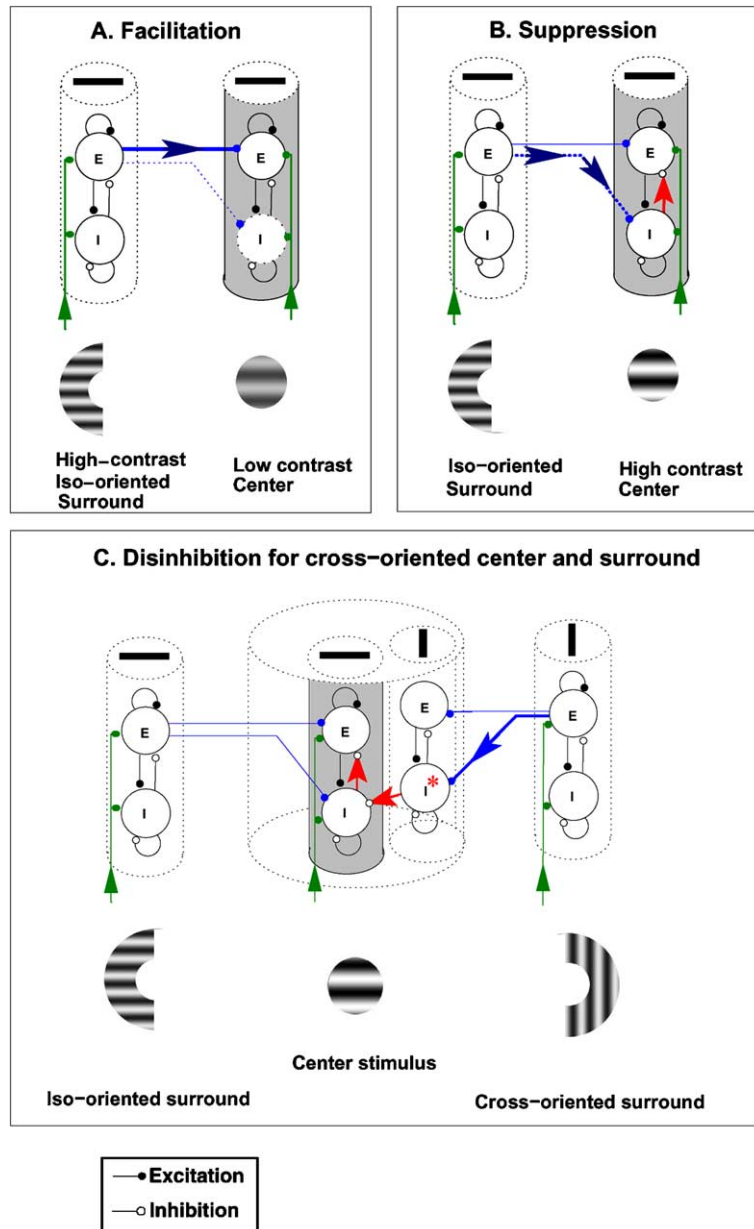


Fig. 4. (A, B) Cartoon of the mechanism underlying the models of Stemmler et al. [144] and Somers et al. [143] to account for facilitation at low contrast, and suppression at high contrast, when center and surround stimuli are iso-oriented. (A) When the center stimulus is shown at low contrast, only excitatory neurons are active, and surround inputs are amplified. (B) When the center stimulus is at high contrast, the response of excitatory neurons saturates, due to the strong activation of local interneurons. Direct surround inputs on the excitatory population have only a limited influence. By contrast, surround inputs strongly enhance the response of the inhibitory population, which results in the suppression of the excitatory response. (C) Cartoon of the mechanism underlying the model of Dragoi and Sur [31] to account for facilitation for cross-oriented center and surround stimuli. Cross-oriented facilitation is due to the disinhibition of local interneurons, via the activation of another pool of inhibitory neurons (*), selective to the same orientation as the surround stimulus.

- When the contrast of the center stimulus is increased, inhibitory cells become active and provoke the saturation of excitatory cells. In that case, the dominant effect of the surround is to enhance the activity of the local inhibitory neurons, provoking a decrease in the response of excitatory cells (Fig. 4B).

These models provide a possible explanation for the observed expansions of the size of V1 receptive fields (SSF) when contrast decreases [75,123]. The spatial extension of a central stimulus beyond the MDF results in a progressive recruitment of horizontal interactions. At low contrast, this leads to a progressive enhancement

of the response (up to a certain level). At high contrast, on the contrary, the spatial extension of the stimulus beyond the MRF results in progressive suppression of the response. Therefore, these models, like the RoG/DoG models, suggest that the contrast dependency of the size of the receptive field is directly related to the contrast sensitivity of C/S interactions. The mechanism they propose is also consistent with recent intracellular data showing that length-tuning is lost at low contrast [4]. Finally, it is worth mentioning that Somers' model predicts that the divisive gain modulation hypothesized in the RoG model can arise in a network model through population effects, even when hyperpolarizing (subtractive) inhibition is used at the level of single cells.

Recently, Dragoi and Sur [31] have developed a different model to account for another “paradoxical” aspect of center/surround modulations that previous models could not explain: the fact that V1 cells can be facilitated beyond optimal levels when the surround stimulus is cross-oriented with respect to the center stimulus, while they are suppressed for iso-oriented surrounds [88,134]. At the local level, their model (Fig. 4C) assumes that inhibitory cells are broadly tuned and that inhibitory cells of different orientation selectivities mutually interact. At the long-range level, and as in the previous models, surround influences are mediated by excitatory horizontal connections, that connect preferentially neurons of similar orientation. Suppression for iso-oriented surround is achieved as before, through the excitation of the local inhibitory neurons that have the same orientation preference as the recorded cell. Cross-oriented facilitation is accounted for by the disinhibition of these local interneurons, via the activation of another pool of inhibitory neurons, selective to the same orientation as the surround stimulus (Fig. 4C, see [39] for a related hypothesis).

These simulation studies provide important new tools to test the overall coherence of our understanding of V1 neurons and circuits. While often based on the previous generation of ring or hypercolumn models of orientation selectivity with which they seek to remain compatible [15,143,145], they extend them, for example by describing neural populations and connectivity in cortical space and distances (vs orientation space and orientation differences) and taking into account the topological singularities of orientation maps.

Ironically, one of the most important predictions of this new generation of models is that the nature and selectivity of long-range interactions (between hypercolumns) should critically depend on the properties of the *local* circuits (within the hypercolumn) and excitatory/inhibitory balance to which the studied neuron is submitted to, which varies with orientation and contrast. Thus, accounting for surround modulations and for the local properties of the CRF is not easily dissociable. Because of this, the development of more detailed

models of C/S modulations is hindered by the lack of consensus concerning the mechanisms responsible for orientation selectivity [35], or for contrast gain control [1,143]. Similarly, we can expect that progress in the understanding of the laminar structure of the cortex, the diversity of GABAergic cells [52], feedback connections, or the cortical representation of retinotopic space will motivate the development of new generations of more realistic network models.

Surprisingly, most existing models ignore the functional diversity expressed at the single cell level, and are implicitly based on an hypothesis of cortical homogeneity of structure and function. They aim at providing a “canonical microcircuit” that could account for all aspects of C/S modulations. However, that such a universal circuit should exist is not obvious both at the experimental and at the theoretical levels. Indeed, recent results show that local circuits exhibit marked heterogeneities, depending for instance on their position in the orientation map [125] or in the different cortical layers [96]. It is tempting to predict that this heterogeneity should be reflected in the expression of C/S modulations. In this context, it is worth noting that the models of Somers et al. [143]/Stemmler et al. [144] and Dragoi and Sur [31] are theoretically not incompatible [129]. However, the model of Dragoi and Sur [31], unlike the others, requires that strong connections exist between (inhibitory) cells of orthogonal, or—at best—oblique orientations. The existence of such cross-oriented inhibitory connections has long been denied [35]. However, they have recently been characterized at the synaptic level, using a variety of electrophysiological techniques to dissect out inhibition from excitation [101]. They are thought to appear preferentially at certain positions in the orientation maps, i.e. in the neighborhood of “pinwheels” where a diversity of orientations is locally represented [29].

One intriguing possibility is thus that the different local circuits which cohabitate in the orientation map give rise to different types of C/S modulations. They would be specialized in the processing of a particular type of comparison between center and surround stimuli, and taken together, would form a “map” of C/S modulations superimposed on the other maps of preferred features [29,129]. Support for this proposition is found in the recent observation that in cat area 17, neurons with similar suppressive or facilitatory surround properties tend to aggregate in spatial clusters [169].

3.3. Role of C/S modulations in the coding of visual inputs

The recent development of functional and structural models of C/S modulations has provided new elements to describe the main features of these phenomena (“*what*” they are) and their potential underlying circuits

(“how” they emerge). A fundamental question remains: “Why” do these phenomena exist? What could their functional role be?

As detailed below, recent theoretical and experimental studies provide a first type of answer, by suggesting that C/S modulations could play a role in the optimization of the coding of visual inputs [116,137,155].

3.4. Theoretical approaches: “optimized” models

On the theoretical front, a long-standing hypothesis, rooted in information theory, states that sensory neurons adapt their integrative properties in response to the statistical properties of the signals to which they are exposed, and that their role is to remove redundancies in the sensory input, resulting in a set of neural responses that are statistically independent [7,8]. This “efficient coding” hypothesis has been tested by “deriving” models of early sensory processing according to some statistical optimization criterion and exploring whether they provide a “good” description of the response properties of a set of neurons (see [136] for a review).

Different models, based on the linear superposition of basis functions and adapted to maximize some statistical criterion such as sparseness and independence, have been shown to be successful in accounting for the structure of V1 CRFs (e.g. [12,104]). However, because they are limited to linear operations, they are found to never lead to completely independent responses [126,137]. Interestingly, Simoncelli and Schwartz [126, 137] recently demonstrated that the remaining dependencies can be eliminated using a variant of the RoG model presented above, i.e. a non-linear form of processing in which the linear response of each basis function is rectified and then normalized (i.e. divided) by a weighted sum of the responses of neighboring neurons. When the weights used in the computation of the normalization signal maximize response independence, the resulting model predicts a variety of suppressive phenomena, including the main properties of surround suppression (e.g. their sensitivity to relative orientation, spatial frequency and separation of the center and surround stimuli).

Following a similar approach, Rao and Ballard [116] have hypothesized that surround effects could reflect the fact that the visual system uses a particularly efficient form of coding termed “predictive coding”. “Predictive coding” postulates that neural networks learn the statistical regularities of the natural world, and then only signal the *deviations* from such regularities: all the predictable, hence redundant, is silenced. To test this idea, they have developed a model of visual processing in which each level of the hierarchy (e.g. V2) attempts to predict the responses at the next lower level (e.g. V1) via feedback connections. The error between this prediction and the actual responses is then sent back via feedfor-

ward connections (e.g. from V1 to V2), and used to correct the estimate of the input signal at this level. This cycle occurs concurrently throughout the hierarchy at different spatial scales. They show that, after being exposed to natural images, the model basis functions develop simple-cell-like receptive fields. Interestingly, a subset of neurons responsible for carrying the residual errors also show end-stopping and other surround effects. Rao and Ballard [116] thus suggest that C/S modulations could be interpreted as the detection of residual errors, signaling the difference between an input signal and its statistical prediction based on an efficient internal model of natural images. In this context, for example, the fact that a neuron stops responding to a bar when it is extended beyond the borders of its CRF (“end-stopping”) could simply reflect the fact that the length of the bar becomes consistent with the statistics of the visual world (in which longer edges are more common than short ones).

3.5. Experimental approaches

The idea that C/S modulations subserve a form of efficient coding is supported on the experimental front as well. Vinje and Gallant [155,156] have investigated how the stimulation of the surround affects cortical representations and information transmission by V1 neurons during simulated natural vision in awake, behaving macaques [155,156]. They show that the stimulation of the surround increases the selectivity of individual V1 neurons, decorrelates their responses (by reducing the overlap in their tuning functions) and increases the sparseness of the population response distribution. This reduction in the effective bandwidth of single neurons does not reduce the amount of information that is represented. Indeed, the information transmission rate (bits per second and bits per spike) of a majority of neurons effectively increases. The authors thus suggest that during natural vision, the classical and non-classical receptive fields function together to form a sparse and efficient representation of the visual world. Conversely, their results imply that under conditions where stimuli are confined to the CRF, V1 neurons operate below their true potential and transmit less information with lower efficiency than they would if both the CRF and the surround were stimulated.

Recent electrophysiological correlates have been obtained at the intracellular level, which suggest that the increase in spike coding efficiency during full field vision of natural images may result from the large-scale enhancement of inhibitory synaptic interactions between center and surround. Studies by the group of McCormick [121] in the anesthetized preparation show that the visual responsiveness of cortical neurons, and consequently the size of their discharge field, adapt over a few tens of seconds as a function of the imposed level

of on-going stimulation of the silent surround of their receptive field. These intrinsic and synaptic adaptation mechanisms account for the contextual dependency of the CRF size. When the surround is left unstimulated, the RF extent (measured with sparse noise input) expands [47]. In contrast, when the periphery is constantly stimulated, the RF extent shrinks in a reversible way. Intracellular data in our lab confirm these observations and furthermore indicate that the stimulus-locked variability of the membrane potential subthreshold is highly dependent on the surround context: the presence of dense noise in the immediate periphery of the RF (where each pixel, at any time, is randomly stimulated with positive or negative contrast), results in an increased inhibitory drive when compared with that produced by sparse noise stimulation (where only one pixel, at a time, is set either ON or OFF). This inhibitory drive constrains the trajectory of the membrane potential and increases the temporal precision in the evoked spike emission (Baudot and Frégnac, unpublished). Thus, the contextual scene provided by dense noise or natural images may optimize visual input coding within the RF by exerting an inhibitory control of the spiking process.

4. Perceptual correlates

Saying that C/S modulations participate in an efficient form of representation is of course a very partial answer to our interrogations: *what* is effectively being represented is unknown. In particular, it is not clear whether surround influences modulate the representation of some structures of the image that are inside the CRF, or allow for the representation of features covering both the CRF and the surround.

Both scenarios are attractive for the kind of problems that early visual processing is confronted with. In the first case, surround influence could help disambiguate local signals and direct their interpretation. In the second case, C/S modulations could be a way to encode the “global” visual structures that extend beyond the CRF, or the geometrical relationships that exist between the object within the CRF and the structures of the surround. There is in fact experimental evidence for both types of processes.

4.1. C/S modulations and psychophysical lateral interactions

What we “see” does not seem to strictly reflect the physical characteristics of the different elements composing the visual scene, but to correspond to the result of complex mechanisms by which their neural representations are “organized”, bound together and interpreted. We do not perceive a collection of isolated visual features but structured ensembles, which are related to

one another and where the perception of the characteristics of a given element (its contrast, orientation, size etc.) depends on the context in which it is presented [161].

First described by the psychologists of the Gestalt School at the beginning of the 20th century, the laws of this “perceptual organization” and the contextual sensitivity of object perception have long been difficult to reconcile with our understanding of visual processing in the brain. Things are now changing, thanks to the quantitative re-exploration of these phenomena with the tools of modern psychophysics.

Psychophysical results demonstrate that the mechanisms involved in perceptual organization are not the province of “superior” visual areas, but should be present as early as in V1. Moreover, they reveal striking similarities between how the presentation of an object can influence the perception of another (as observed in psychophysics), and C/S modulations (as observed in electrophysiology). Three particular types of psychophysical phenomena have been directly compared with the physiological findings described above:

- In experiments where subjects are required to judge the *apparent contrast* of a central grating embedded in an iso-oriented surround grating (Fig. 5A), the central stimulus is judged to be of a lower contrast than in the absence of the surround [19,20,28,32,105,142,167,172]. Similar to the suppressive modulations observed in V1 with identical sets of stimuli, (a) maximal effects occur when the center and the surround are of similar orientations and spatial frequencies [19,28]; (b) surround suppression is insensitive to the relative spatial phase of the C/S stimuli [168], (c) surround suppression increases when the contrast of the surround increases [32,168], (d) surround suppression increases with the size of the surround stimulus over a large region of visual space (at least up to an outer diameter of about 10–12 deg [168]); (e) it is observed for various positions of the surround stimulus, and not only at “end-zones” or “side bands” [19,168]. These effects have been thought to explain why an edge oriented orthogonally to a group of other neighboring elements sharing the same orientation is immediately detected (it “pops out”), in contrast to the case where the target element shares the same orientation as the group of edges in which it is embedded. More generally, the enhancement of local differences and the suppression of homogeneous textures are believed to be key mechanisms for the segmentation of visual contours.
- In experiments where *contrast detection thresholds* are measured in the presence or absence of surround patterns (Fig. 5B), target detection is facilitated by the presence of collinear flanks at the same orientation [74,111,112,141,164]. As found for V1 facilitatory

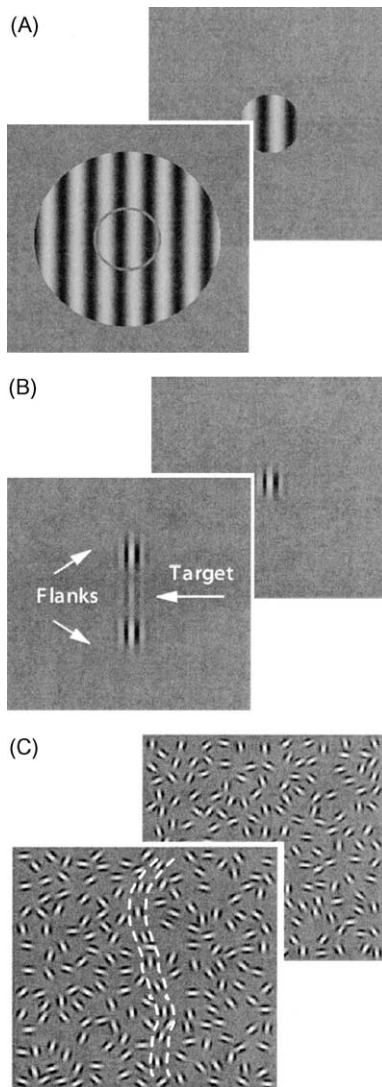


Fig. 5. Three types of psychophysical phenomena that are thought to be related to center/surround modulations in V1. (A) In 2-alternative forced choice experiments where subjects are required to compare the contrast of a central grating when it is presented alone vs. when it is embedded in a surround grating, the apparent contrast of the central grating is found to be reduced by the surround [19,32]. (B) In experiments where subjects are required to judge the presence or absence of a central target presented at sub-threshold or threshold contrast, detection is found to be facilitated by the presence of collinear flankers (contrast thresholds are lower), compared to when the target is presented in isolation [111]. (C) The saliency of a contour (indicated by the white dashed lines) made of a number of oriented elements immersed in a random texture depends on the relative orientation, separation and co-alignment of the contour elements [36].

modulations at “end-zones”, these effects decrease when the relative orientation and distance between the stimuli increase, or when the degree of collinearity decreases [74,111,164,171]. In psychophysics, the effect is found to be maximal for a spatial separation of $2-3\lambda$, where λ , is the wavelength of the stimulus, and to decrease to baseline up to 10λ . For the lowest spatial frequency that has been tested (3.33 c.p.d.),

this maximal distance corresponds to a separation of about 3° of visual angle. This effect is thought to play an important role in line completion, and in the extraction of degraded or incomplete contours.

- The rules governing the *saliency* of a contour immersed in a random texture [11,14,36,56–58,83,108,109], are also reminiscent of the conditions required for C/S facilitation. Indeed, it was found that the degree to which two visual elements are perceived as belonging to the same contour increases with their degree of collinearity and decreases with their distance and relative orientation difference. Field et al. [36] coined the term “association field” to describe the spatial architecture of these grouping interactions. The “association field” is viewed as an extension of the Gestalt description of the laws of “proximity” and “good continuation” [161].

In psychophysics, differences have been observed in the parametric dependency of these three phenomena. It is unlikely, for example, that collinear facilitation at threshold and supra-threshold contour extraction depend on identical mechanisms [164]. However, in general, when the parametric dependency observed in each of the psychophysical paradigm is compared to that obtained in physiology under similar stimulation, strong similarities are found.

More recently, other studies have shown that *orientation discrimination* was also affected by the presence of contextual stimuli [90,94]: presenting surround patterns of similar orientation and spatial frequency markedly impairs observer’s performance. Here again, the conditions required for this interference to appear show striking resemblance with those leading to surround suppression in V1 [90].

These analogies have led to the notion of a possible mapping, or “isomorphism”, between these two classes of phenomena (see e.g. [162]). As discussed below, they have also often been implicitly interpreted as a sign of causality, where C/S modulations in V1 would directly “explain” the contextual sensitivity of object perception.

4.2. Bridging physiology and psychophysics

A number of models have attempted to “bridge” physiology and psychophysics. In general, they (explicitly or implicitly) make the following assumptions:

1. The mean firing rate of a V1 cell responding to a given stimulus is correlated with the “neural representation” of the visibility and/or saliency and/or apparent contrast of that stimulus (see e.g. the “saliency map hypothesis” of [92], and [2,144]).
2. The change in the perception of an object *X* induced by the simultaneous presentation of another object *Y* is due to the modulation of the firing rates of the V1

neurons sensitive to X , when their surround is stimulated by Y .

In this way, suppression of a cell's activity has been viewed as a correlate of suppression in perceived contrast [91,144]. Similarly, collinear facilitation of the neural response has been put forward as an explanation for the increased detectability of a threshold contrast stimulus, when it is flanked by collinear masks [2,92].

Indirectly, thus, these models raise two fundamental questions. The first one is a problem of coding: when V1 responses increase or decrease due to surround influences, what aspect of the visual representation is modulated? The second issue is the implication of V1 activity in perceptual judgment.

4.2.1. Surround modulation and the format of visual representations

These models treat the firing rate as reflecting simultaneously the apparent contrast of the encoded object (e.g. [91,144]), its visibility (e.g. [2]), its saliency [92], and its relationship with other objects (“binding”).

This is problematic, since there is a basic ambiguity in relating a single variable (the mean evoked firing rate) with different dimensions of the stimulus. Is it possible that the visual system does not distinguish between contrast, saliency, visibility and “binding”? Hess et al. [59] have addressed this question by testing one of its implications: that the detectability of a visual contour should be correlated with an increase in the perceived contrast of the contour elements. Using a stimulus similar to that of [36], they found no systematic bias in the estimated contrast of the contour elements compared to the background elements. This suggests that contrast and binding are encoded separately, and cannot both rely on the mean firing of single cells.

One possible solution to this problem is that the temporal properties of V1 responses also carry information: while firing rate modulations could explain the modulations in perceived contrast, the modulations of the dynamics of the response could reflect the modulations in perceptual saliency. Models based on the latter hypothesis usually propose that saliency and binding are encoded in the synchronization of V1 activities (see e.g. [170]). This assumption is supported by the abundant evidence on oscillatory patterns in the γ -frequency range and response synchronization, whose probability and strength have been argued to reflect the Gestalt rules of continuity, proximity and similarity [84,139], a view that is lively debated [40,131].

Alternately, it is possible that different aspects of the stimulus are encoded at different times in V1 responses: The initial burst of V1 responses would mainly reflect feedforward inputs, hence providing information regarding contrast, while the variations in the later sustained components of the response would provide

information regarding spatial context [59]. This latter model is supported by the finding that the latency of V1 cells' responses to a stimulus presented in the CRF can be reliably used to predict the stimulus contrast, contrary to later components of the response [41,42]. It is also fully consistent with the fact that C/S modulations are often expressed with a delay of a few ms to a few tens of ms after response onset [81,85] and may be constrained by the slow propagation of surround information through horizontal connections [16].

4.2.2. The role of V1 in conscious perception

These models assume that V1 activity does not only reflect the content of the visual representation, but also plays a functional role in what will be the perceptual decision (or the subject's performances). This suggestion is consistent with a number of recent experimental findings in electrophysiology and fMRI (see [106,149] for a review). Recently, new evidence has also been obtained using optical imaging techniques in the laboratories of A. Grinvald and A. Roe (private communication). These latter studies show that the optical signal recorded in primary visual and somatosensory cortical areas in the anesthetized subject seems more correlated with the perceived illusion reported psychophysically by the awake subject than with the feedforward mapping of the stimulation imposed at the sensory periphery.

Obviously, however, more criteria than the observed correlations should be fulfilled if we want to establish a causal link between V1 activity and the perceptual event [107]. In particular, it will be invaluable to perform new studies in which V1 responses and behavioral performances are measured simultaneously in the same animal. This will first eliminate confounding species and inter-subject differences, as well as worrisome differences in stimulus and anesthetic conditions. Further, simultaneous acquisition of neural and psychophysical data can be used to assess whether the fluctuations of V1 neural responses *are predictive* of the psychophysical decisions on a trial-to-trial basis [107,147].

5. Dynamics: a role in motion processing?

The psychophysical and physiological studies cited above have all used displays where center and surround stimuli were presented simultaneously. As discussed in the previous section, the observed modulations have commonly been thought to play a role in the analysis of *form* in *static* images (contour integration, segmentation, “pop out”, etc.). However, in theory, simultaneous presentation of center and surround stimuli is not a critical requirement for C/S modulations to occur. If the dynamics of these effects are not too fast, it is conceivable that the presentation of a visual object, processed by a neural population X_1 induces a modulation of the

responses of a population X_2 sensitive to another object, presented at a later point in time, in a neighboring position of the visual field. In that case, these phenomena could also influence the perception of *moving stimuli*.

To investigate this possibility, it is useful to first distinguish between two aspects of the dynamics of C/S modulations that should be critical.

- First, how long (*propagation delay*) does a contextual signal need to travel from one cortical site, say X_1 , to another locus, say X_2 ? Imaging studies in cat [69] and monkey V1 [51] and intracellular recordings in cat area 17 of visually evoked subthreshold synaptic activity [16] have shown that the horizontal propagation of intracortically relayed visual activity is slow (0.05–0.5 m/s). Bringuier and colleagues reported in our laboratory that a focal impulse-like visual stimulation outside the RF elicits a depolarization of the neuron's membrane potential whose onset occurs after a temporal delay that depends linearly on the distance between the focal stimulation and the RF locations, and this delay intrinsic to intracortical propagation can be as long as 50 to 80 ms depending on the size of the subthreshold receptive field. Mapped in visual field coordinates, and taking into account the magnification factor of the feedforward projection from the retina to cortex, this propagation speed corresponds to fast retinal motion, in the order of 250°/s in cat and 60°/s in monkey or man.
- Second, how long does the propagated signal remain “visible” at the postsynaptic site X_2 (*persistence*)? Or, to word it differently, what is the time-course of the laterally evoked modulation of the membrane voltage of the postsynaptic population, when the presynaptic population has been transiently stimulated? There is limited data concerning integration time constants in vivo during visual activation, but the duration of membrane response to a flashed stimulus in the periphery of the RF can be expected to last in cortical cells a few tens of ms ([61] in vitro, [10] in vivo), specially in the case of sparse (low density) stimulation protocols.

5.1. Modulation of response latency and influence on the perception of apparent speed

Using a simplified model of V1 connectivity and realistic assumptions concerning the propagation and persistence of horizontal signals, we have recently investigated the influence of C/S dynamics on the processing of sequences of oriented stimuli [130]. As illustrated in Fig. 6A, our model suggests that the excitatory subthreshold activity evoked by a 1st stimulus and spreading through horizontal axons could influence the processing of a 2nd stimulus presented from a few ms to a few tens of ms later at neighboring positions in visual

field. More precisely, if the horizontal signal evoked by the response to the 1st stimulus arrives just before—or in phase with—the feedforward activation evoked by the 2nd stimulus, the summation of the two signals should result in a modulation of *the latency* of the evoked subthreshold and spiking responses to the 2nd stimulus.

In our model, this effect requires that horizontal and feedforward signals are appropriately “synchronized”. Therefore, it only appears for particular configurations of the visual sequence, that satisfy a specific set of spatial (distance Δx , between the two stimuli, orientation and alignment) and temporal constraints (temporal interval Δt). The spatial constraints are dictated by the spatial architecture of horizontal connections (extent, anisotropy). The temporal constraints are primarily controlled by the speed of propagation along horizontal connections and by the persistence of horizontal signals.

Because long-range horizontal projections tend to connect iso-oriented iso-aligned RFs, our model predicts that these latency modulations should be maximal for sequences made of *collinear* elements (e.g., for a vertical edge or Gabor patch flashed in different locations along a vertical axis), and decrease when the angle between the motion axis and the orientation of the sequence's elements increases. It also predicts that the range of sequence speeds ($\Delta x/\Delta t$), for which response latency modulations are expected is bounded by the speed of horizontal propagation, and corresponds to fast motion on the retina.

These predictions were tested in our laboratory using intracellular recordings in the area 17 of anesthetized cats [10]. Baudot and colleagues flashed oriented Gabor patches across the width or length axis of the receptive field of the recorded cell in sequence, from the center to the far surround of the RF (centrifugal sequence) or from the surround to the center of the RF (centripetal sequence). The test stimulus flashed in the MDF center was always the same and optimally oriented. The contextual stimuli flashed in the MDF periphery had either the same orientation as that of the test stimulus (iso-orientation condition) or were perpendicular to it (cross-orientation condition). The apparent motion speed of the sequence was adjusted in retinal space (150–250°/s) to match that of spike propagation along horizontal axons in cortical space (0.15–0.25 mm/ms). The results show that fast collinear centripetal (from surround to center) sequences of iso-oriented Gabors along the length axis (preferred orientation) often resulted in a significant shortening of the subthreshold and spiking latencies by 5–15 ms, a range of values that is consistent with the model's predictions. In contrast, minor modulation effects, if any, were observed for centrifugal sequences. Furthermore, no modulation effect was observed for cross-oriented stimuli flashed along the length axis or for iso-oriented stimuli flashed across the width

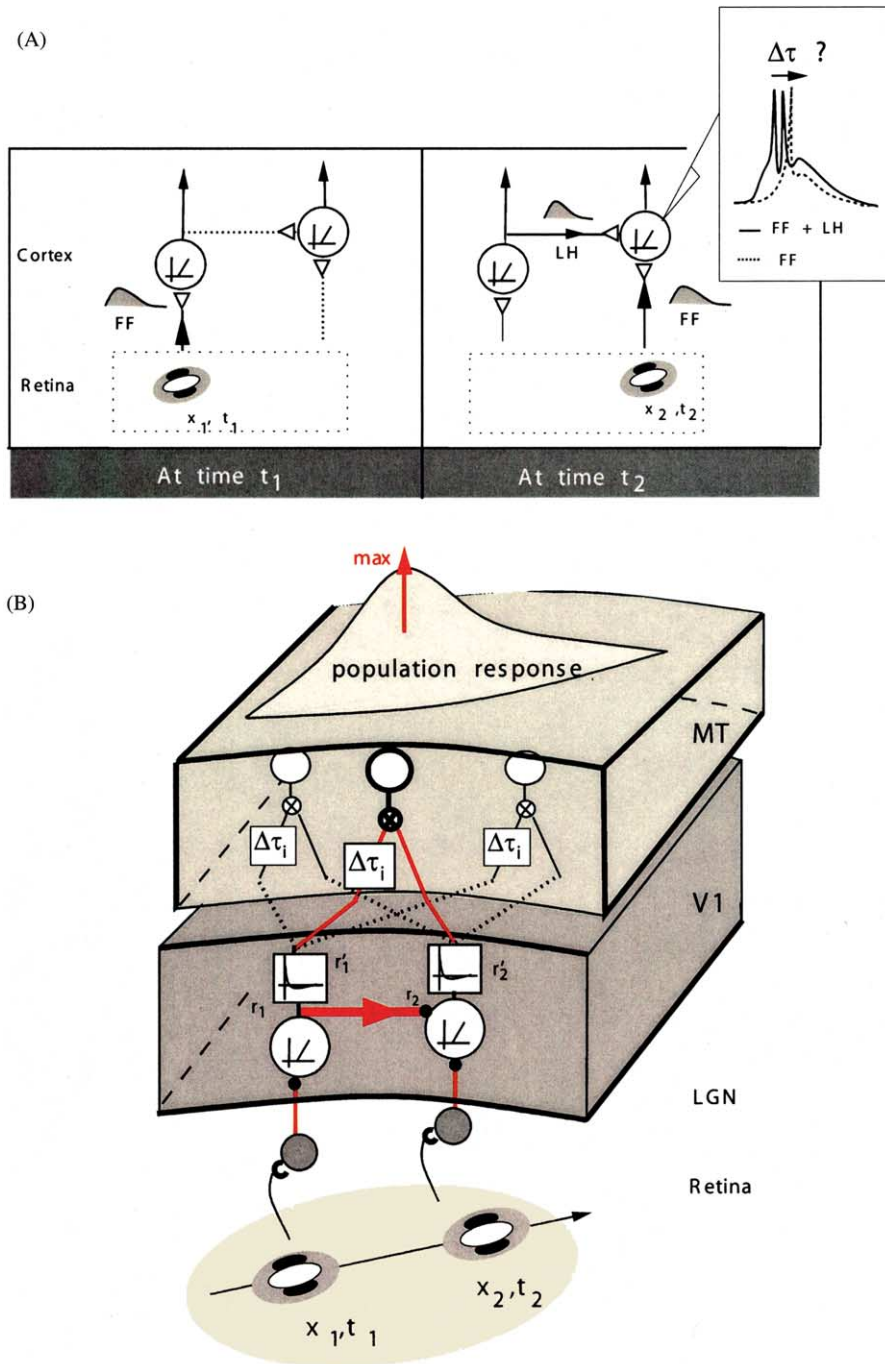


Fig. 6. Cartoon of the V1-MT model that we studied [130]. (A) The V1 stage represents an array of cortical units that have the same preferred orientation and non-overlapping RFs. Units that have collinear RFs interact through long-range horizontal (LH) connections. The response of each unit evokes a wave of sub-threshold horizontal activity that slowly propagates in cortex. For particular spatio-temporal configurations of the visual inputs (sequence speeds), horizontal and feedforward inputs temporally overlap, which results in a modulation of response latency. (B) The MT stage consists in a large population of Reichardt-type detectors. At this stage, the apparent speed of the sequence is given by the read-out of the correlator that is maximally active. The reduction in response latency resulting from the summation of feedforward and long-range horizontal signals in V1 biases the spatio-temporal correlation performed by the MT detectors towards higher speeds [130].

axis, whether the stimulation sequence direction was centripetal or centrifugal.

For human observers submitted to similar spatio-temporal patterns, it was noticeable that the sequences

for which latency modulations were predicted elicited a perception of motion (apparent motion). Relative differences in neural latencies are often believed to influence the processing of visual motion, potentially

explaining a variety of motion illusions [60,163]. Motivated by these findings, we further examined whether the latency modulations that we predicted could have functional consequences, detectable at the perceptual level.

As illustrated in Fig. 6B, our model was extended, so that a retinotopic array of V1 cells converged onto a second “MT-like” processing stage, composed of a large population of direction- and motion-selective Reichardt-type detectors. This stage serves to evaluate sequences’ speed on the basis of the spatio-temporal correlation between V1 responses. The apparent speed of the sequence is given by the read-out of the correlator that is maximally active. This model predicts that the latency modulations in V1 cells produced by the interaction of the horizontal and feedforward waves of visual activity should result in a perceptual bias in the estimation of the speed of the sequences. More particularly, it predicts an overestimation of the speed of fast collinear sequences, compared to sequences of non-aligned elements [130].

Experimentally, we have shown that this prediction was valid. Psychophysical studies in humans indicate that fast [40–96°/s] apparent motion sequences appear faster when the visual elements they contain are aligned with the motion path than when they are flashed at an angle with it [46]. Consistent with the model’s predictions, the effect disappears at low speeds (4°/s) and decreases monotonously with the angle between the motion axis and the orientation of the Gabor patch. Although extremely simple in its principle, our theoretical model was shown to be sufficient to quantitatively fit the psychophysical data, using a range of parameters constrained by physiology. In particular, the range of speed for which the psychophysical effects occur in humans, and the optimal value at which it is strongest (64°/s) can easily be accounted for if long-range horizontal connections are anisotropic, cover a few mm and are characterized by a slow conduction speed (0.1–0.6 m/s [16]). Thus, the physiological findings reported at the single cell level in the cat, extrapolated in monkey, seem to provide a plausible mechanism for the perceptual bias in apparent motion measured psychophysically in humans.

5.2. The substrate of the “Motion streaks”?

In principle, the summation of feedforward and horizontal signals should not only affect response latency, but also the supra-threshold amplitude and dynamics of the response. This could have interesting physiological and perceptual implications. In particular, if the summation of feedforward and horizontal signals results in a *facilitation* of the response, V1 cells should develop a *preferred motion axis aligned with their preferred orientation*. As for latency modulations, this effect

should be absent at very low speeds and increase with speed (up to a critical speed).

Interestingly, such a phenomenon has been reported in physiology [44,68,165]. Jancke [68] has explored how a moving spot was represented in the responses of a population of V1 cells. Responses were analyzed in terms of information related to the position of the stimulus and orientation (that would not have a direct physical counterpart in the stimulus). Using classical decoding techniques, Jancke found that, while the early part of the population response sharply reflects the stimulus position, the later part was dominated by the activity of cells whose preferred orientation is aligned with the motion trajectory. The forming of this orientation signal was dependent on motion speed, and its sharpness increased when speed increased.

Similarly, Geisler et al. [44] measured the responses of cat and monkey V1 neurons to a spot moving perpendicular to, or parallel to the preferred orientation of each neuron’s receptive field. Contrary to the classical view, many cells were found to show some degree of direction selectivity for motion parallel to the preferred orientation axis. Further, when stimulus speed was increased, the ratio of the responses to parallel motion versus perpendicular increased, and above some critical speed, the response to parallel motion exceeded the response to perpendicular motion.

Geisler et al. proposed that direction selectivity along the preferred orientation axis, like the classical perpendicular direction selectivity, could be the result of certain combinations of non direction-selective inputs that are appropriately positioned (or phase-) shifted in space and time [9,117]. More precisely, they suggest that direction selectivity parallel to the preferred orientation could be accounted for by a Reichardt-type detector in which the orientation of the components is simply rotated by 90° (Fig. 7). Further experimental and theoretical work will be needed to clarify the relation between these findings and the dynamics of C/S modulations. However, we note that our model provides a natural substrate for the motion detector depicted in Fig. 7B. Cortical cells situated in distinct hypercolumns form the subunits of the detector. The horizontal connections that run between them can be described as “delayed lines”, with a temporal delay $\Delta\tau$ given by the ratio of the distance between the subunits over the speed of horizontal propagation. Sensitivity to the direction of movement arise if the horizontal connections between the two subunits are not perfectly reciprocal.

At the functional level, selectivity to a motion axis collinear to the orientation axis could play an important role in the perception of fast motion, when classical direction mechanisms become unreliable. It has been suggested to provide a robust orientation signal corresponding to the trajectory of the motion, or—more precisely—to the “motion streak” left in the wake of the

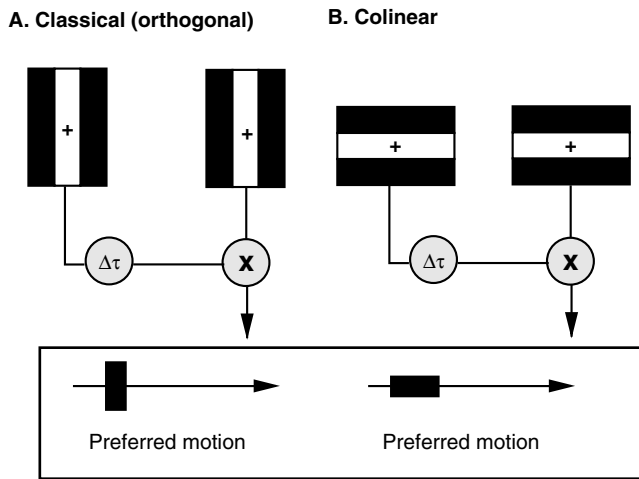


Fig. 7. (A) Traditional model of direction selectivity in V1. Spatial offset (or spatial phase differences) are combined with temporal offsets Δt (or temporal phase differences) to produce direction selectivity for motion perpendicular to the spatial orientation of the receptive field. (B) Direction selectivity of motion collinear to the spatial orientation the CRF can be modeled in a similar fashion by rotating the preferred spatial orientation of the two non direction-selective inputs. Reproduced from [44].

moving object [43]. That such a spatial orientation signal is used by the visual system for the detection and discrimination of fast motion is supported by a number of recent psychophysical studies [18,43,118].

5.3. Possible role of a spatio-temporal “association field”

In the spatial domain, C/S modulations have commonly been thought to participate in feature binding, contour integration and line completion. In the Bayesian approach of visual processing [82,113], lateral interactions are thought to provide contextual *priors* that influence the inference process (see e.g. [33,87]). The idea is that the response to each visual object would lead to the spatial propagation of a set of constraints, that bias the estimation of neighboring patterns, based on the statistics of the visual world [45,133].

In analogy with these propositions, it is tempting to speculate that C/S modulations in the spatio-temporal domain could help solving the problem of motion correspondence, that they could play a role in the temporal grouping of motion signals, and/or in the facilitation or extrapolation of continuous trajectories. In the Bayesian terminology, lateral interactions could provide prior information related not only to the spatial context but also to the past history of the network, biasing the estimation of the object’s motion towards particular (coherent) trajectories.

Interestingly, the fact that an “association field” exists in the spatio-temporal domain is well supported experimentally. Similar to the spatial “association field”

that facilitates the processing of continuous contours, the spatio-temporal “association field” favors the processing of smooth trajectories [115,160]. It is known, for example, that in a situation of uncertainty concerning the direction of a moving stimulus, the visual system favors the processing of trajectories that continue along the same direction as in the past motion (“visual inertia”) [114]. This suggests that the interpretation of local motion is strongly biased by the past sequence of local motions. More recently, Watamaniuk et al. [160] have shown that human observers can easily detect a signal dot moving in apparent motion on a trajectory embedded in a background of random-direction motion noise. High performance levels are possible even though the spatial and temporal characteristics of the signal are identical to that of the noise, making the signal indistinguishable from the noise on the basis of a single pair of frames.

There is also some indication that this spatio-temporal “association field” is sensitive to the orientation of the moving elements. Moving dots arranged in a collinear configuration relative to their trajectory are more easily detected than dots arranged in a perpendicular configuration [153]. Similarly, speed discrimination is facilitated when signals are extended along the direction of motion, compared to when they are extended along an axis perpendicular to the direction of motion [157]. The properties of the dynamical association field cannot easily be explained using a classical model of motion selectivity because they seem to involve spatial and temporal integration across longer distances and temporal windows than would be expected if the integration mechanism were a low level motion detector [154].

The neural substrate of these phenomena is unknown. However, it is often proposed that they should reflect interactions between motion-sensitive units. The idea is that there exists a “trajectory network” in which each motion detector, when stimulated, sends facilitatory signals in the direction of the motion to detectors with which it is connected. If the detector receiving this facilitatory signal is also stimulated within a short time, its signal is enhanced and it sends another facilitatory signal forward, and so on [160]—a mechanism that shows striking resemblance with the one we describe.

6. Conclusion

Historically, the single-cell search for feature-trigger specificity has fostered a view of visual neurons as static and localized windows of the visual world, functioning independently of one another. The observation of C/S modulations shows that this assumption is inaccurate. V1 CRFs, their size and functional selectivities, are found to be dynamically altered by the spatial and temporal context of the visual stimulation. When

multiple objects or natural scenes are shown, they interact non-linearly over extended cortical regions and periods of time.

Through recent progresses in anatomical techniques, intracellular measurements, coupled extracellular and optical imaging techniques as well as computer simulations, the neural bases of C/S modulations are beginning to be deciphered, revealing a subtle interplay between a variety of circuits that are simultaneously activated, and among which horizontal and feedback inputs play a major role.

Understanding the dynamic interplay and functional significance of these phenomena has become an area of intense investigation, which has brought a critical re-evaluation of prior concepts on early visual cortical processing. It is now well recognized that computation intrinsic to V1 could play a critical role in “mid-level” perception processes, such as pop-out, contour integration and segmentation. Theoretically, it has been suggested that visual processing was akin to a Bayesian inference process. In this context, a recent proposition that needs to be further explored is that surround interactions within V1 itself provide contextual priors that help disambiguate local information based on the statistics of natural scenes. This could apply to the domain of moving stimuli as well, and provide a mechanism by which the system is dynamically influencing the interpretation of future events based on past activity.

We still lack a general theory of visual coding that would account for the complexity of these effects, their dynamics, and the interactions they reveal across large populations of cells, and cortical areas. However, through the correlations that exist between the properties of C/S modulations at the physiological and psychophysical level, these phenomena have shown to provide an invaluable way to refine our understanding of the nature of visual representation, as well as the relationship between neural response and conscious perception.

Acknowledgements

This work has received support from Singer Polignac (to P.S.), and EC (TST 2001-34712) to Y.F. We thank Sébastien Georges and József Fiser for valuable comments on a previous version of the Manuscript.

References

- [1] L.F. Abbott, K. Sen, J.A. Varela, S.B. Nelson, Synaptic depression and cortical gain control, *Science* 275 (1997) 220–224.
- [2] Y. Adini, D. Sagi, M. Tsodyks, Excitatory-inhibitory network in the visual cortex: psychophysical evidence, *Proc. Natl. Acad. Sci. USA* 94 (1997) 10426–10431.
- [3] T.D. Albright, G.R. Stoner, Contextual influences on visual processing, *Annu. Rev. Neurosci.* 25 (2002) 339–379.
- [4] J.S. Anderson, I. Lampl, D.C. Gillespie, D. Ferster, Membrane potential and conductance changes underlying length tuning of cells in cat primary visual cortex, *J. Neurosci.* 21 (2001) 2104–2112.
- [5] A. Angelucci, J.B. Levitt, J.S. Lund, Anatomical origins of the classical receptive field and modulatory surround field of single neurons in macaque visual cortical area V1, *Prog. Brain Res.* 136 (2002) 373–388.
- [6] A. Angelucci, J.B. Levitt, E.J.S. Walton, J.-M. Hupé, J. Bullier, J. Lund, Circuits for local and global signal integration in primary visual cortex, *J. Neurosci.* 22 (2002) 8633–8646.
- [7] F. Attneave, Some informational aspects of visual perception, *Psych. Rev.* 61 (1954) 183–193.
- [8] H.B. Barlow, Possible principles underlying the transformation of sensory messages, in: *Sensory Communication*, MIT Press, Cambridge, MA, 1961.
- [9] H.B. Barlow, W.R. Levick, The mechanism of directionally selective units in rabbit’s retina, *J. Physiol.* 178 (1965) 477–504.
- [10] P. Baudot, F. Chavane, M. Pananceau, V. Edet, B. Gutkin, J. Lorenceau, K. Grant, Y. Frégnac, Cellular correlates of apparent motion in the association field of cat area 17 neurons, *Society for Neuroscience abstracts*, 2000, p. 162.2.
- [11] W.H. Beaudot, K.T. Mullen, Processing time of contour integration: the role of colour, contrast, and curvature, *Perception* 30 (2001) 833–853.
- [12] A.J. Bell, T.J. Sejnowski, The “independent components” of natural scenes are edge filters, *Vision Res.* 37 (1997) 3327–3338.
- [13] W.H. Bosking, Y. Zhang, B. Schofield, D. Fitzpatrick, Orientation selectivity and the arrangement of horizontal connections in tree shrew striate cortex, *J. Neurosci.* 17 (1997) 2112–2127.
- [14] J. Braun, On the detection of salient contours, *Spat. Vis.* 12 (1999) 211–225.
- [15] P.C. Bressloff, J.D. Cowan, An amplitude equation approach to contextual effects in visual cortex, *Neural Comput.* 14 (2002) 493–525.
- [16] V. Bringuier, F. Chavane, L. Glaeser, Y. Frégnac, Horizontal propagation of visual activity in the synaptic integration field of area 17 neurons, *Science* 283 (1999) 695–699.
- [17] H.A. Brown, J.D. Allison, J.M. Samonds, A.B. Bonds, Nonlocal origin of response suppression from stimulation outside the classic receptive field in area 17 of the cat, *Vis. Neurosci.* 20 (2003) 85–96.
- [18] D.C. Burr, J. Ross, Direct evidence that “speedlines” influence motion mechanisms, *J. Neurosci.* 22 (2002) 8661–8664.
- [19] M.W. Cannon, S.C. Fullenkamp, Spatial interactions in apparent contrast: Inhibitory effects among grating patterns, different spatial frequencies, spatial positions and orientations, *Vision Res.* 31 (1991) 1985–1998.
- [20] M.W. Cannon, S.C. Fullenkamp, A model for inhibitory lateral interaction effects in perceived contrast, *Vision Res.* 36 (1996) 1115–1125.
- [21] M. Carandini, D.J. Heeger, Summation and division in primate visual cortex, *Science* 264 (1994) 1333–1336.
- [22] M. Carandini, D.J. Heeger, J.A. Movshon, Linearity and normalization in simple cells of the macaque primary visual cortex, *Vis. Neurosci.* 17 (1997) 8621–8644.
- [23] J.R. Cavanaugh, W. Bair, J.A. Movshon, Nature and interaction of signals from the receptive field center and surround in macaque V1 neurons, *J. Neurophysiol.* 88 (2002) 2530–2546.
- [24] F.S. Chance, L.F. Abbott, A.D. Reyes, Gain modulation from background synaptic input, *Neuron* 35 (2002) 773–782.
- [25] F. Chavane, V. Bringuier, P. Baudot, C. Monier, L. Borg-Graham, J. Lorenceau, Y. Frégnac, The visual association field: a gestalt myth or a psycho-physiological reality? *J. Physiol. (Paris)* 94 (2000) 333–342.

- [26] C.C. Chen, T. Kasamatsu, U. Polat, A.M. Norcia, Contrast response characteristics of long-range lateral interactions in cat striate cortex, *Neuroreport* 12 (2001) 655–661.
- [27] H.J. Chisum, F. Mooser, D. Fitzpatrick, Emergent properties of layer 2/3 neurons reflect the collinear arrangement of horizontal connections in tree shrew visual cortex, *J. Neurosci.* 23 (2003) 2947–2960.
- [28] C. Chubb, G. Sperling, J. Solomon, Texture interactions determine perceived contrast, *Proc. Natl. Acad. Sci. USA* 86 (1989) 9631–9635.
- [29] A. Das, C.D. Gilbert, Topography of contextual modulations mediated by short-range interactions in primary visual cortex, *Nature* 399 (1999) 655–661.
- [30] G.C. DeAngelis, R.D. Freeman, I. Ohzawa, Length and width tuning of neurons in the cat's primary visual cortex, *J. Neurophysiol.* 71 (1994) 347–374.
- [31] V. Dragoi, M. Sur, Dynamic properties of recurrent inhibition in primary visual cortex: Contrast and orientation dependence of contextual effects, *J. Neurophysiol.* 83 (2000) 1019–1030.
- [32] Y. Ejima, S. Takahashi, Apparent contrast of a sinusoidal grating in the simultaneous presence of peripheral gratings, *Vision Res.* 25 (1985) 1223–1232.
- [33] J.H. Elder, R.M. Goldberg, Ecological statistics of Gestalt laws for the perceptual organization of contours, *J. Vision* 2 (2002) 324–353.
- [34] U. Ernst, K. Pawelzik, F. Wolf, T. Geisel, Theory of non-classical receptive field phenomena in the visual cortex, *Neurocomputing* 26–27 (1999) 367–374.
- [35] D. Ferster, K.D. Miller, Neural mechanisms of orientation selectivity in the visual cortex, *Annu. Rev. Neurosci.* 23 (2000) 441–471.
- [36] D.J. Field, A. Hayes, R.F. Hess, Contour integration by the human visual system: evidence for a local "association field", *Vision Res.* 33 (1993) 173–193.
- [37] D. Fitzpatrick, Seeing beyond the receptive field in primary visual cortex, *Curr. Opin. Neurobiol.* 10 (2000) 438–443.
- [38] R.D. Freeman, I. Ohzawa, G. Walker, Beyond the classical receptive field in the visual cortex, *Prog. Brain Res.* 134 (2001) 157–170.
- [39] Y. Frégnac, V. Bringuier, Spatio-temporal dynamics of synaptic integration in cat visual cortical receptive fields, in: A. Aertsen, V. Braitenberg (Eds.), *Brain Theory—Biological and Computational Principles*, Elsevier, 1996, pp. 143–199.
- [40] Y. Frégnac, V. Bringuier, A. Baranyi, Oscillatory neuronal activity in visual cortex: A critical re-evaluation, in: G. Buzsáki (Ed.), *Temporal Coding in the Brain*, Springer-Verlag, Berlin, Heidelberg, 1994, pp. 82–102.
- [41] T.J. Gawne, The simultaneous coding of orientation and contrast in the responses of V1 complex neurons, *Exp. Brain Res.* 133 (2000) 293–302.
- [42] T.J. Gawne, T.W. Kjaer, B.J. Richmond, Latency: another potential code for feature binding in striate cortex, *J. Neurophysiol.* 76 (1996) 1356–1360.
- [43] W.S. Geisler, Motion streaks provide a spatial code for motion direction, *Nature* 400 (1999) 65–69.
- [44] W.S. Geisler, D.G. Albrecht, A.M. Crane, L. Stern, Motion direction signals in the primary visual cortex of cat and monkey, *Vis. Neurosci.* 18 (2001) 501–516.
- [45] W.S. Geisler, J.S. Perry, B.J. Super, D.P. Gallogly, Edge co-occurrence in natural images predicts contour grouping performance, *Vision Res.* 41 (2001) 711–724.
- [46] S. Georges, P. Seriès, Y. Frégnac, J. Lorenceau, Orientation dependent modulation of apparent speed: psychophysical evidence, *Vision Res.* 42 (2002) 2757–2772.
- [47] C.D. Gilbert, A. Das, M. Ito, M. Kapadia, G. Westheimer, Spatial integration and cortical dynamics, *Proc. Natl. Acad. Sci. USA* 93 (1996) 615–622.
- [48] C.D. Gilbert, T.N. Wiesel, Clustered intrinsic connections in cat visual cortex, *J. Neurosci.* 3 (1983) 1116–1133.
- [49] C.D. Gilbert, T.N. Wiesel, The influence of contextual stimuli on the orientation selectivity of cells in primary visual cortex of the cat, *Vision Res.* 30 (1990) 1689–1701.
- [50] C.D. Gilbert, T.N. Wiesel, Columnar specificity of intrinsic horizontal and corticocortical connections in visual cortex, *J. Neurosci.* 9 (1989) 2432–2442.
- [51] A. Grinvald, E.E. Lieke, R.D. Frostig, R. Hildesheim, Cortical point-spread function and long-range lateral interactions revealed by real-time optical imaging of macaque monkey primary visual cortex, *J. Neurosci.* 14 (1994) 2545–2568.
- [52] A. Gupta, Y. Wang, H. Markram, Organizing principle for a diversity of GABAergic interneurons and synapses in the neocortex, *Science* 287 (2000) 273–278.
- [53] H.K. Hartline, The response of single optic nerve fibers of the vertebrate eye to illumination of the retina, *Am. J. Physiol.* 121 (1938) 400–415.
- [54] D.J. Heeger, Half-squaring in responses of cat striate cortex, *Vis. Neurosci.* 9 (1992) 427–443.
- [55] R. Hess, D. Field, Integration of contours: new insights, *Trends Cogn. Sci.* 3 (1999) 480–486.
- [56] R.F. Hess, S.C. Dakin, Absence of contour linking in peripheral vision, *Nature* 390 (1997) 602–604.
- [57] R.F. Hess, S.C. Dakin, Contour integration in the peripheral field, *Vision Res.* 39 (1999) 947–959.
- [58] R.F. Hess, K.H.A. Beaudot, K.T. Mullen, Dynamics of contour integration, *Vision Res.* 41 (2001) 1023–1037.
- [59] R.F. Hess, S.C. Dakin, D. Field, The role of "contrast enhancement in the detection and appearance of visual contours", *Vision Res.* 38 (1998) 783–787.
- [60] O. Hikosaka, S. Miyauchi, S. Shimojo, Focal visual attention produces illusory temporal order and motion sensation, *Vision Res.* 33 (1993) 1219–1240.
- [61] J.A. Hirsh, C.D. Gilbert, Synaptic physiology of horizontal connections in the cat's visual cortex, *J. Neurosci.* 11 (1991) 1800–1809.
- [62] D. Hubel, T. Wiesel, Receptive fields and functional architecture of monkey striate cortex, *J. Physiol. (London)* 195 (1958) 215–243.
- [63] D.H. Hubel, T.N. Wiesel, Receptive fields and functional architecture in two non-striate visual areas (18 and 19) of the cat, *J. Neurophysiol.* 28 (1965) 229–289.
- [64] J.M. Hupé, A.C. James, P. Girard, J. Bullier, Response modulations by static texture surround in area V1 of the macaque monkey do not depend on feedback connections from V2, *J. Neurophysiol.* 85 (2001) 146–163.
- [65] J.M. Hupé, A.C. James, P. Girard, S.G. Lomber, B.R. Payne, J. Bullier, Feedback connections act on the early part of the responses in monkey visual cortex, *J. Neurophysiol.* 85 (2001) 134–145.
- [66] J.M. Hupé, A.C. James, B.R. Payne, S.G. Lomber, P. Girard, J. Bullier, Cortical feedback improves discrimination between figure and background by V1, V2 and V3 neurons, *Nature* 394 (1998) 784–787.
- [67] M. Ito, C.D. Gilbert, Attention modulates contextual influences in the primary visual cortex of alert monkeys, *Neuron* 22 (1999) 593–604.
- [68] D. Jancke, Orientation formed by a spot's trajectory: a two-dimensional population approach in primary visual cortex, *J. Neurosci.* 20 (2000) RC86.
- [69] D. Jancke, F. Chavane, A. Arieli, A. Grinvald, Motion modulates speed and shape of cortical spread in cat visual cortex: population dynamics revealed by real-time optical imaging, *Society for Neuroscience abstracts*, 2001, p. 349.12.

- [70] H.E. Jones, I.M. Andolina, N.M. Oakely, P.C. Murphy, A.M. Sillito, Spatial summation in lateral geniculate nucleus and visual cortex, *Exp. Brain Res.* 135 (2000) 279–284.
- [71] H.E. Jones, K.L. Grieve, W. Wang, A.M. Sillito, Surround suppression in primate V1, *J. Neurophysiol.* 86 (2001) 2011–2028.
- [72] H.E. Jones, W. Wang, A.M. Sillito, Spatial organization and magnitude of orientation contrast interactions in primate V1, *J. Neurophysiol.* 88 (2002) 2796–2808.
- [73] J. Jones, L.A. Palmer, An evaluation of the two-dimensional Gabor filter model of simple receptive fields in cat striate cortex, *J. Neurophysiol.* 58 (1987) 1233–1258.
- [74] M.K. Kapadia, M. Ito, C.D. Gilbert, G. Westheimer, Improvement in visual sensitivity by changes in local context: parallel studies in human observers and in V1 of alert monkeys, *Neuron* 15 (1995) 843–856.
- [75] M.K. Kapadia, G. Westheimer, C.D. Gilbert, Dynamics of spatial summation in primary visual cortex of alert monkeys, *Proc. Natl. Acad. Sci. USA* 96 (1999) 12073–12078.
- [76] M.K. Kapadia, G. Westheimer, C.D. Gilbert, Spatial distribution of contextual interactions in primary visual cortex and in visual perception, *J. Neurophysiol.* 84 (2000) 2048–2062.
- [77] T. Kasamatsu, U. Polat, M.W. Pettet, A.M. Norcia, Colinear facilitation promotes reliability of single-cell responses in cat striate cortex, *Exp. Brain Res.* 138 (2001) 163–172.
- [78] S. Kastner, H.C. Nothdurft, I.N. Pigarev, Neuronal correlates of pop-out in cat striate cortex, *Vision Res.* 37 (1997) 371–376.
- [79] S. Kastner, H.C. Nothdurft, I.N. Pigarev, Neuronal responses to orientation and motion contrast in cat striate cortex, *Vis. Neurosci.* 16 (1999) 587–600.
- [80] Z.F. Kisvárdy, E. Toth, M. Rausch, U.T. Eysel, Orientation-specific relationship between populations of excitatory and inhibitory lateral connections in the visual cortex of the cat, *Cereb. Cortex* 7 (1997) 605–618.
- [81] J.J. Knierim, D.C. Van Essen, Neuronal responses to static texture patterns in area V1 of the alert macaque monkey, *J. Neurophysiol.* 67 (1992) 961–970.
- [82] D. Knill, W. Richards, Perception as Bayesian Inference, Cambridge University Press, 1996.
- [83] I. Kovacs, B. Julesz, A closed curve is much more than an incomplete one: effect of closure in figure-ground segmentation, *Proc. Natl. Acad. Sci. USA* 90 (1993) 7495–7497.
- [84] A.K. Kreiter, W. Singer, Stimulus-dependent synchronization of neuronal responses in the visual cortex of the awake macaque monkey, *J. Neurosci.* 16 (1996) 2381–2396.
- [85] V.A. Lamme, The neurophysiology of figure-ground segregation in primary visual cortex, *J. Neurosci.* 15 (1995) 1605–1615.
- [86] V.A. Lamme, K. Zipser, H. Spekreijse, Figure-ground activity in primary visual cortex is suppressed by anesthesia, *Proc. Natl. Acad. Sci. USA* 95 (1998) 3263–3268.
- [87] T.S. Lee, Top-down influence in early visual processing: a bayesian perspective, *Physiol. Behav.* 77 (2002) 645–650.
- [88] J.B. Levitt, J.S. Lund, Contrast dependence of contextual effects in primate visual cortex, *Nature* 387 (1997) 73–76.
- [89] C. Li, W. Li, Extensive integration field beyond the classical receptive field of cat's striate cortical neurons—classification and tuning properties, *Vision Res.* 387 (1994) 73–86.
- [90] W. Li, P. Thier, C. Werhahn, Contextual influence on orientation discrimination of humans and responses of neurons in v1 of alert monkey, *J. Neurophysiol.* 83 (2000) 941–954.
- [91] Z. Li, A neural model of contour integration in the primary visual cortex, *Neural Comput.* 10 (1998) 903–940.
- [92] Z. Li, A saliency map in primary visual cortex, *Trends Cogn. Sci.* 6 (2002) 9–16.
- [93] L. Maffei, A. Fiorentini, The unresponsive regions of visual cortical receptive fields, *Vision Res.* 16 (1976) 1131–1139.
- [94] I. Mareschal, M.P. Sceniak, R.M. Shapley, Contextual influences on orientation discrimination: binding local and global cues, *Vision Res.* 41 (2001) 1915–1930.
- [95] K.A.C. Martin, D. Whitteridge, Form, function and intracortical projections of spiny neurones in the striate visual cortex of the cat, *J. Physiol. (London)* 353 (1984) 463–504.
- [96] L.M. Martinez, J.M. Alonso, R.C. Reid, J.A. Hirsch, Laminal processing of stimulus orientation in cat visual cortex, *J. Physiol.* 540 (2002) 321–333.
- [97] D.A. McCormick, B.W. Connors, J.W. Lighthall, D.A. Prince, Comparative electrophysiology of pyramidal and sparsely spiny stellate neurons of the neocortex, *J. Neurophysiol.* 54 (1985) 782–806.
- [98] B.A. McGuire, C.D. Gilbert, P.K. Rivlin, T.N. Wiesel, Targets of horizontal connections in macaque primary visual cortex, *J. Comp. Neurol.* 305 (1991) 370–392.
- [99] M. Mignard, J.G. Malpeli, Paths of information flow through visual cortex, *Science* 251 (1991) 1249–1251.
- [100] K. Mizobe, U. Polat, M.W. Pettet, T. Kasamatsu, Facilitation and suppression of single striate-cell activity by spatially discrete pattern stimuli presented beyond the receptive field, *Vis. Neurosci.* 18 (2001) 377–391.
- [101] C. Monier, F. Chavane, P. Beaudot, L. Graham, Y. Frégnac, Orientation and direction selectivity of excitatory and inhibitory inputs in visual cortical neurons: a diversity of combinations produces spike tuning, *Neuron* 37 (2002) 663–680.
- [102] J.I. Nelson, B.J. Frost, Intracortical facilitation among co-oriented, co-axially aligned simple cells in cat striate cortex, *Exp. Brain Res.* 61 (1985) 54–61.
- [103] H. Nothdurft, J.L. Gallant, D. Van Essen, Response modulation by texture surround primate area in V1: Correlates of “pop out” under anesthesia, *Vis. Neurosci.* 16 (1999) 15–34.
- [104] B.A. Olshausen, D.J. Field, Emergence of simple-cell receptive field properties by learning a sparse code for natural images, *Nature* 381 (1996) 607–609.
- [105] L.A. Olzak, P.I. Laurinen, Multiple gain control processes in contrast-contrast phenomena, *Vision Res.* 39 (1999) 3983–3987.
- [106] M.A. Paradiso, Perceptual and neuronal correspondence in primary visual cortex, *Curr. Opin. Neurobiol.* 12 (2002) 155–161.
- [107] A.J. Parker, W.T. Newsome, Sense and the single neuron: probing the physiology of perception, *Annu. Rev. Neurosci.* 21 (1998) 227–277.
- [108] M.W. Pettet, Shape and contour detection, *Vision Res.* 39 (1999) 551–557.
- [109] M.W. Pettet, S.P. McKee, N.M. Grzywacz, Constraints on long-range interactions, *Vision Res.* 38 (1998) 865–879.
- [110] U. Polat, K. Mizobe, M.W. Pettet, T. Kasamatsu, A.M. Norcia, Collinear stimuli regulate visual responses depending on cell's contrast threshold, *Nature* 391 (1998) 580–584.
- [111] U. Polat, D. Sagi, Lateral interactions between spatial channels: suppression and facilitation revealed by lateral masking experiments, *Vision Res.* 33 (1993) 993–999.
- [112] U. Polat, D. Sagi, The architecture of perceptual spatial interactions, *Vision Res.* 34 (1994) 73–78.
- [113] A. Pouget, P. Dayan, R.S. Zemel, Inference and computation with population codes, *Ann. Rev. Neurosci.* 26 (2003) 381–410.
- [114] V.S. Ramachandran, S.M. Anstis, Extrapolation of motion path in human visual perception, *Vision Res.* 23 (1983) 83–85.
- [115] V.S. Ramachandran, S.M. Anstis, Perceptual organization in moving patterns, *Nature* 304 (1983) 529–531.
- [116] R.P. Rao, D.H. Ballard, Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects, *Nat. Neurosci.* 2 (1999) 79–787.
- [117] W.E. Reichardt, Autocorrelation, a principle for evaluation of sensory information by the central nervous system, in: W.A. Rosenblith (Ed.), Principles of Sensory Communications, John Wiley, New York, 1961, pp. 303–317.

- [118] J. Ross, D.R. Badcock, A. Hayes, Coherent global motion in the absence of coherent velocity signals, *Curr. Biol.* 10 (2000) 679–682.
- [119] A.F. Rossi, R. Desimone, L.G. Ungerleider, Contextual modulation in primary visual cortex of macaques, *J. Neurosci.* 21 (2001) 1698–1709.
- [120] E. Salinas, L.F. Abbott, A model of multiplicative neural responses in parietal cortex, *Proc. Natl. Acad. Sci. USA* 93 (1996) 11956–11961.
- [121] M.V. Sanchez-Vives, L.G. Nowak, D.A. McCormick, Membrane mechanisms underlying contrast adaptation in cat area 17 in vivo, *J. Neurosci.* 20 (2000) 4267–4285.
- [122] M.P. Sceniak, M.J. Hawken, R. Shapley, Visual spatial characteristics of V1 macaque neurons, *J. Neurophysiol.* 85 (2001) 1873–1887.
- [123] M.P. Sceniak, D.L. Ringach, M.J. Hawken, R. Shapley, Contrast's effect on spatial summation by macaque V1 neurons, *Nat. Neurosci.* 2 (1999) 733–739.
- [124] K.E. Schmidt, R. Goebel, S. Löwel, W. Singer, The perceptual grouping criterion of colinearity is reflected by anisotropies of connections in the primary visual cortex, *Eur. J. Neurosci.* 9 (1997) 1083–1089.
- [125] J. Schummers, J. Marino, M. Sur, Synaptic integration by V1 neurons depends on location within the orientation map, *Neuron* 36 (2002) 969–978.
- [126] O. Schwartz, E.P. Simoncelli, Natural signal statistics and sensory gain control, *Nat. Neurosci.* 4 (2001) 819–825.
- [127] F. Sengpiel, R.J. Baddeley, T.C.B. Freeman, R. Harrad, C. Blakemore, Different mechanisms underlie three inhibitory phenomena in cat area 17, *Vision Res.* 38 (1998) 2067–2080.
- [128] F. Sengpiel, A. Sen, C. Blakemore, Characteristics of surround inhibition in cat area 17, *Exp. Brain Res.* 116 (1997) 216–238.
- [129] P. Seriès, Etude théorique des modulations centre/pourtour des propriétés des champs récepteurs du cortex visuel primaire: circuits, dynamiques, et corrélats perceptifs, PhD thesis, 2002, Université de Paris VI.
- [130] P. Seriès, S. Georges, J. Lorenceau, Y. Frégnac, Orientation dependent modulation of apparent speed: a model based on the dynamics of feed-forward and horizontal connectivity in V1 cortex, *Vision Res.* 42 (2002) 2781–2797.
- [131] M.N. Shadlen, J.A. Movshon, Synchrony unbound: a critical evaluation of the temporal binding hypothesis, *Neuron* 24 (1999) 67–77.
- [132] Z. Shao, A. Burkhalter, Different balance of excitation and inhibition in forward and feedback circuits in rat visual cortex, *J. Neurosci.* 16 (1996) 7353–7365.
- [133] M. Sigman, G.A. Cecchi, C.D. Gilbert, M.O. Magnasco, On a common circle: natural scenes and Gestalt rules, *Proc. Natl. Acad. Sci. USA* 98 (2001) 1935–1940.
- [134] A.M. Sillito, K.L. Grieve, H.E. Jones, J. Cudeiro, J. Davis, Visual cortical mechanisms detecting focal orientation discontinuities, *Nature* 378 (1995) 492–496.
- [135] A.M. Sillito, H.E. Jones, Context-dependent interactions and visual processing in V1, *J. Physiol. Paris* 90 (1996) 205–209.
- [136] E.P. Simoncelli, B.A. Olshausen, Natural image statistics and neural representation, *Ann. Rev. Neurosci.* 24 (2001) 1193–1216.
- [137] E.P. Simoncelli, O. Schwartz, Modeling surround suppression in V1 neurons with a statistically-derived normalization model, *Adv Neural Information Processing Systems (NIPS*1998)* 11 (1999).
- [138] L.C. Sincish, G.G. Blasdel, Oriented axon projections in primary visual cortex of the monkey, *J. Neurosci.* 21 (2001) 4416–4426.
- [139] W. Singer, C.M. Gray, Visual feature integration and the temporal correlation hypothesis, *Annu. Rev. Neurosci.* 18 (1995) 555–586.
- [140] R.J. Snowden, S.T. Hammett, The effects of surround contrast on contrast thresholds, perceived contrast and contrast discrimination, *Vision Res.* 38 (1998) 1935–1945.
- [141] J.A. Solomon, M.J. Morgan, Facilitation from collinear flanks is cancelled by non-collinear flanks, *Vision Res.* 40 (2000) 279–286.
- [142] J.A. Solomon, G. Sperling, C. Chubb, The lateral inhibition of perceived contrast is indifferent to on-center/off-center segregation, but specific to orientation, *Vision Res.* 33 (1993) 2671–2683.
- [143] D.C. Somers, E. Todorov, A.G. Siapas, L.J. Toth, D. Kim, M. Sur, A local circuit approach to understanding integration of long-range inputs in primary visual cortex, *Cereb. Cortex* 8 (1998) 204–217.
- [144] M. Stemmler, M. Usher, E. Niebur, Lateral interactions in primary visual cortex: a model bridging physiology and psychophysics, *Science* 269 (1995) 1877–1880.
- [145] M. Stetter, H. Bartsh, K. Obermayer, A mean field model for orientation tuning, contrast saturation and contextual effects in the primary visual cortex, *Biol. Cybern.* 82 (2000) 291–304.
- [146] D.D. Stettler, A. Das, J. Bennett, C.D. Gilbert, Lateral connectivity and contextual interactions in macaque primary visual cortex, *Neuron* 36 (2002) 739–750.
- [147] H. Super, H. Spekreijse, V.A. Lamme, Two distinct modes of sensory processing observed in monkey primary visual cortex (V1), *Nat. Neurosci.* 4 (2001) 304–310.
- [148] A.M. Thomson, J. Deuchars, Synaptic interactions in neocortical local circuits: dual intracellular recordings in vitro, *Cereb. Cortex* 7 (1997) 510–522.
- [149] F. Tong, Primary visual cortex and visual awareness, *Nat. Rev. Neurosci.* 4 (2003) 219–229.
- [150] L.J. Toth, S.C. Rao, D.S. Kim, D. Somers, M. Sur, Subthreshold facilitation and suppression in primary visual cortex revealed by intrinsic signal imaging, *Proc. Natl. Acad. Sci. USA* 93 (1996) 9869–9874.
- [151] T.R. Tucker, L. Katz, Recruitment of local inhibitory networks by horizontal connections in layer 2/3 of ferret visual cortex, *J. Neurophysiol.* 89 (2003) 501–512.
- [152] T.R. Tucker, L. Katz, Spatiotemporal patterns of excitation and inhibition evoked by the horizontal network in layer 2/3 of ferret visual cortex, *J. Neurophysiol.* 89 (2003) 488–500.
- [153] P. Verghese, S.P. McKee, N.M. Grzywacz, Stimulus configuration determines the detectability of motion signals in noise, *J. Opt. Soc. Am. A: Opt. Image Sci. Vis.* 17 (2000) 1525–1534.
- [154] P. Verghese, S.N.J. Watamaniuk, S.P. McKee, N.M. Grzywacz, Local motion detectors cannot account for the detectability of an extended trajectory in noise, *Vision Res.* 39 (1999) 19–30.
- [155] W.E. Vinje, J.L. Gallant, Sparse coding and decorrelation in primary visual cortex during natural vision, *Science* 287 (2000) 1273–1276.
- [156] W.E. Vinje, J.L. Gallant, Natural stimulation of the nonclassical receptive field increases information transmission efficiency in V1, *J. Neurosci.* 22 (2002) 2904–2915.
- [157] D. Vreven, P. Verghese, Integration of speed signals in the direction of motion, *Perception and Psychophysics* 64 (2002) 996–1007.
- [158] G.A. Walker, I. Ohzawa, R.D. Freeman, Asymmetric suppression outside the classical receptive field of the visual cortex, *J. Neurosci.* 19 (1999) 10536–10553.
- [159] G.A. Walker, I. Ohzawa, R.D. Freeman, Suppression outside the classical receptive field, *Vis. Neurosci.* 17 (2000) 369–379.
- [160] S.N. Watamaniuk, S.P. McKee, N.M. Grzywacz, Detecting a trajectory embedded in random-direction motion noise, *Vision Res.* 35 (1995) 65–77.
- [161] M. Wertheimer, Untersuchungen zur Lehre von der Gestalt, *Psychologische Forschung* 4 (1923) 301–350.
- [162] G. Westheimer, Gestalt theory reconfigured: Max Wertheimer's anticipation of recent developments in visual neuroscience, *Perception* 28 (1999) 5–15.

- [163] D. Whitney, I. Murakami, P. Cavanagh, Illusory spatial offset of a flash relative to a moving stimulus is caused by differential latencies for moving and flashed stimuli, *Vision Res.* 40 (2000) 137–149.
- [164] C.B. Williams, R.F. Hess, Relationship between facilitation at threshold and suprathreshold contour integration, *J. Opt. Soc. Am.* 15 (1998) 2046–2051.
- [165] F. Wörgötter, U.T. Eysel, Axis of preferred motion is a function of bar length in visual cortical receptive fields, *Exp. Brain Res.* 76 (1989) 307–314.
- [166] F. Wörgötter, K. Suder, Y. Zao, N. Kersher, U.T. Eysel, K. Funke, State-dependent receptive-field restructuring in the visual cortex, *Nature* 396 (1998) 165–168.
- [167] J. Xing, D.J. Heeger, Center-surround interactions in foveal and peripheral vision, *Vision Res.* 40 (2000) 3065–3072.
- [168] J. Xing, D.J. Heeger, Measurement and modeling of center-surround suppression and enhancement, *Vision Res.* 41 (2001) 571–583.
- [169] H. Yao, C.Y. Li, Clustered organization of neurons with similar extra-receptive field properties in the primary visual cortex, *Neuron* 35 (2002) 547–553.
- [170] S.C. Yen, L.H. Finkel, Extraction of perceptually salient contours by striate cortical networks, *Vision Res.* 38 (1998) 719–741.
- [171] C. Yu, S.A. Klein, D.M. Levi, Facilitation of contrast detection by cross-oriented surround stimuli and its psychophysical mechanisms, *J. Vision* 2 (2002) 243–255.
- [172] C. Yu, D.M. Levi, Surround modulation in human vision unmasked by masking experiments, *Nat. Neurosci.* 3 (2000) 724–728.