On the operating point of cortical computation

Robert Martin, Marcel Stimberg, Klaus Wimmer and Klaus Obermayer
Bernstein Center for Computational Neuroscience Berlin and School of Electrical Engineering and Computer Science, Technische Universität Berlin, FR 2-1, Franklinstr. 28/29, D-10587 Berlin, Germany
E-mail: oby@cs.tu-berlin.de

Abstract. In this paper, we consider a class of network models of Hodgkin-Huxley type neurons arranged according to a biologically plausible two-dimensional topographic orientation preference map, as found in primary visual cortex (V1). We systematically vary the strength of the recurrent excitation and inhibition relative to the strength of the afferent input in order to characterize different operating regimes of the network. We then compare the map-location dependence of the tuning in the networks with different parametrizations with the neuronal tuning measured in cat V1 in vivo. By considering the tuning of neuronal dynamic and state variables, conductances and membrane potential respectively, our quantitative analysis is able to constrain the operating regime of V1: The data provide strong evidence for a network, in which the afferent input is dominated by strong, balanced contributions of recurrent excitation and inhibition, operating in vivo. Interestingly, this recurrent regime is close to a regime of “instability”, characterized by strong, self-sustained activity. The firing rate of neurons in the best-fitting model network is therefore particularly sensitive to small modulations of model parameters, possibly one of the functional benefits of this particular operating regime.

1. Introduction
The major tasks of primary visual cortex (V1) is computing a representation of simple features present in the visual field. Most prominently, its neurons show sensitivity to orientations presented in their receptive fields, and are organized in a topographic map by, amongst others, their orientation preference. Consequently, preferred orientation varies smoothly, with the exception of occasional singularities, the so-called pinwheels. Early models of orientation processing in V1 [1], which combined the center-surround receptive fields of lateral geniculate nucleus to give rise to orientation selectivity, have been shown to be over-simplistic [2, 3]. Yet, even today a debate remains regarding the contribution of afferent and of recurrent excitatory and inhibitory influences, respectively, to the orientation selectivity of V1 [4, 5]. Information processing in cortex changes dramatically with this “cortical operating regime”, i.e. depending on the relative strengths of the afferent and recurrent inputs [6, 7].

For instance, a theoretical study [7] demonstrated that in a Mexican-hat like operating regime, networks can express sharp orientation tuning that is largely independent of map position. Mexican-hat like connectivity patterns arising from broader inhibition have been routinely used in theoretical studies of the visual system [8]. However, recent experimental studies [9] seem to indicate that excitatory and inhibitory short-range connections spread over an approximately similar range, thereby not supporting a Mexican-hat like connectivity pattern. Yet, provided
Inhibition is fast (or conversely, excitation is slow, as in NMDA synapses with a large time constant), Mexican-hat like interaction patterns do occur for similar or even shorter-range inhibition [7]. The study by Kang et al. [7] relied on a mean-field network and allowed analytical treatment under certain simplifying assumptions. Here, we study a similar network but with spiking units, incorporating conductance-based synapses and spike-frequency adaption, thus allowing for a richer, non-linear behavior of the system.

2. The models

In our study we consider two different kinds of network models that both model a patch of approximately $1.56 \times 1.56 \text{mm}^2$ of V1: (1) a firing rate model using a mean-field approximation, similar to the network in [7], and (2) a spiking network consisting of Hodgkin-Huxley type units. Both models share a common network structure where all cells have a spatial position on a two-dimensional grid. The neurons’ preferred orientations are determined by their position in an artificial orientation map and realized by the tuned afferent input (Fig. 1). Pinwheel distance and the spread of recurrent connections of the map is calibrated to match experimental data [9]. Recurrent connections within the map follow a spatially isotropic two-dimensional Gaussian profile with similar spatial extent for excitatory and inhibitory connections, consistent with in vivo data [9]. This leads to characteristic differences in the recurrent input a cell receives, depending on its map position: Cells close to a singularity of the orientation map (pinwheel centers) receive input from cells with very heterogeneous preferred orientations, whereas cells in the linear zones of the iso-orientation domains receive input from cells with very similar preferred orientations. In order to avoid boundary effects, we used periodic boundary conditions.

The activity of the firing-rate units in the mean field models is given by:

\[
\begin{align*}
\tau_{E_i} \frac{dm_{E_i}(\vec{r}, t)}{dt} & = -m_{E_i}(\vec{r}, t) + \left[ I_{\text{Aff}}(\vec{r}) + S_{\text{EE}} \alpha_1 I_{\text{rec}}^{E_1}(\vec{r}, t) + S_{\text{EI}} (1 - \alpha_1) I_{\text{rec}}^{E_2}(\vec{r}, t) - S_{\text{EI}} I_{\text{rec}}^{I}(\vec{r}, t) \right]^+, \\
\tau_{I} \frac{dm_{I}(\vec{r}, t)}{dt} & = -m_{I}(\vec{r}, t) + \left[ I_{\text{Aff}}(\vec{r}) + S_{\text{IE}} \alpha_1 I_{\text{rec}}^{E_1}(\vec{r}, t) + S_{\text{II}} (1 - \alpha_1) I_{\text{rec}}^{E_2}(\vec{r}, t) - S_{\text{II}} I_{\text{rec}}^{I}(\vec{r}, t) \right]^+,
\end{align*}
\]

where $i \in \{1, 2\}$ is an index for the two excitatory populations, $\vec{r}$ is a vector describing a unit’s position in its layer, $\tau_{E_1} = 5 \text{ms}$ and $\tau_{E_2} = 50 \text{ms}$ denote the excitatory synaptic time constants, $\tau_I = 5 \text{ms}$ denotes the inhibitory time constant and $[\ldots]^+$ is the rectification function. The parameters $S_i$ denote the weight of the connections between the pre-synaptic excitatory and inhibitory populations and the postsynaptic excitatory (S_{EE} and S_{EI}) and inhibitory populations (S_{IE} and S_{II}). The recurrent input from the excitatory populations is additionally weighted by $\alpha_1 = 0.4$ and $1 - \alpha_1 = 0.6$, respectively, for the two populations of excitatory neurons, i.e. the total excitatory recurrent input is a mixture from the fast (40%) and the slow population (60%). The recurrent input from a population $j \in \{E_1, E_2, I\}$ is given by

\[ I_{\text{rec}}^j(\vec{r}, t) = \int d\vec{r}’ \varphi(\vec{r}, \vec{r}’) m_j, \]  

where the function $\varphi$,

\[ \varphi(\vec{r}, \vec{r}') = \frac{1}{\sqrt{2\pi} \sigma} \exp \left( -\frac{(\vec{r} - \vec{r}')^2}{2\sigma^2} \right), \]  

defines the connectivity profile.
Figure 1. Network architecture. The cartoon sketches the architecture of both network model classes: A layer of excitatory (blue triangles) and inhibitory neurons (green circles) receives afferent as well as lateral input. In the Hodgkin-Huxley networks, the number of inhibitory cells is one third of the number of excitatory cells. Cells are placed on a grid (inhibitory neurons in random grid positions) of $50 \times 50$ (Hodgkin-Huxley networks), respectively $64 \times 64$ (firing rate networks) positions, modeling a patch of cortex $1.56 \times 1.56 \text{mm}^2$ in size (see scale bar). Examples for lateral connections are indicated for an inhibitory neuron in an iso-orientation domain (lines connecting to the neuron in the center) and an excitatory cell close to a pinwheel center (lines connecting to the neuron at the right). The preferred orientation of each neuron depends on its position in the artificial orientation map with four pinwheels (top; see connecting lines for the two example cells). A circular Gaussian tuning curve with standard deviation $27.5^\circ$ (bottom) determines the afferent input rate for each neuron, depending on the presented orientation and the orientation preference of the cell.

The activity of the Hodgkin-Huxley units in the spiking network is given by:

$$C_m \frac{dV_m}{dt} = -g_L (V_m - E_L) - \sum_{\text{int}} I_{\text{int}} - I_{\text{syn}} - I_{\text{bg}},$$

where $I_{\text{syn}}$, $I_{\text{int}}$ and $I_{\text{bg}}$ denote the voltage-dependent synaptic, intrinsic and background currents, $g_L$ and $E_L$ denote the leak conductance and its reversal potential, $C_m$ denotes the membrane capacitance, and $t$ denotes time. We included three voltage dependent intrinsic currents: a fast Na$^+$ current and a delayed-rectifier K$^+$ current for the generation of action potentials, and a slow non-inactivating K$^+$ current responsible for spike frequency adaptation. For parameters and the functional forms of the activating and inactivating variables, see [10]. The peak conductance of the non-inactivating K$^+$-current is multiplied by the factor 0.1 for inhibitory neurons in
order to reduce their spike-frequency adaptation compared to the excitatory neurons. The synaptic background current \( I_{bg} \) is determined, independently for each cell, from an excitatory and an inhibitory background conductance, which follow an Ornstein-Uhlenbeck-like stochastic process [11]. The synaptic current for neurons of the population \( j \in \{E,I\} \) is composed of the input received from \( N_{Aff} = 20 \) afferent excitatory, \( N_E = 100 \) recurrent excitatory and \( N_I = 50 \) recurrent inhibitory neurons. The currents are given by

\[
I_{syn}^j(t) = \left[ \frac{\tilde{g}_j^{Aff}}{N_{Aff}} g^{Aff}(t) + \frac{\tilde{g}_j^E}{N^E} (\alpha g_{E1}(t) + (1-\alpha) g_{E2}(t)) \right] (V_m - E_e) \nonumber \\
- \frac{\tilde{g}_j^I}{N^I} g_I(t)(V_m - E_i), \quad (6)
\]

where \( g(t) \) are the time-dependent conductances, \( E_e \) and \( E_i \) are the synaptic reversal potentials, \( \alpha = 0.7 \) determines the number of fast (70\%) versus slow (30\%) receptors of recurrent excitatory synapses, and \( \tilde{g} \) are scale factors (peak conductances; for values see [12]).

3. Operating regimes

Following [7] we define the operating regime of a meanfield network by properties of its “cortical feedback kernel” \( D(k) \). For fixed connectivity \( \varphi \), \( D(k) \) depends on the strength of the recurrent connections only:

\[
D(k) = S_{EE}\tilde{\varphi}(k) - S_{EI}S_{IE}\tilde{\varphi}^2(k) - S_{II}\tilde{\varphi}(k) + S_{II}S_{EE}\tilde{\varphi}^2(k).
\]

The different operating regimes (“phases”) shown in Fig. 2A are characterized by certain properties of \( D(k) \): Unstable if \( D(k) > 1 \) for any \( k \); Feedforward (FF) if \( |D(k)| < 0.5 \) for all \( k \); Excitatory dominated (EXC) if \( D(k) > 0 \) for all \( k \) and \( D_{max} = D(0) \); Recurrent (REC) if \( D_{max} > 0.5 \) and \( 1 - D(0) > 2(1 - D_{max}) \); Inhibitory dominated (INH) if \( D(k) < 0 \) for some \( k \) and \( D_{max} < 0.5 \).

Although this analytical classification is not possible in a Hodgkin-Huxley model, we can define similar operating regimes numerically (Fig. 2B). We base this definition on the excitatory and inhibitory currents a cell receives when stimuli with varying orientations are presented, normalizing all currents with respect to the afferent input current at the preferred orientation. This leads to the same operating regimes (Fig. 2C): FF, if the sum of the absolute recurrent excitatory and inhibitory current is less than 0.3; EXC, if the excitatory current is larger than the inhibitory current for all presented orientations; REC, if the excitatory current is larger than the inhibitory currents for some orientations and lower for others; INH, if the excitatory current is lower than the inhibitory current for all presented orientations. We refer to the network as “unstable” if the model neurons show strong responses (average firing rate exceeds 100 Hz) and remain at high firing rates if the afferent input is turned off, i.e. the network shows self-sustained activity. In this regime, the model neurons lose their orientation tuning.

4. Characterizing the operating regimes

Naturally, networks in different operating regimes differ in their behavior. Firstly and quite predictably, as recurrent excitation increases (i.e. moving upward in the phase plot), peak firing rates increase. Moreover, the rate of change in the firing rate increases, too, as parameters approach the unstable region (movement towards the top left in the phase plot).
Figure 2. Operating regimes and their characteristics. (A) Operating regimes of a mean-field network model as a function of the synaptic weights of recurrent excitation ($S_{EE}$) and inhibition ($S_{EI} \times S_{IE}$). Black lines denote analytically obtained borders of the operating regimes [7]: FF – feed-forward, EXC – recurrent excitatory dominated, INH – recurrent inhibitory dominated, REC – strong recurrent excitation and inhibition (cf. phases II and III in [7]) and MP – marginal phase. The borders to the unstable region (thick red line) and to the MP (thin red line) were also determined numerically, defining the network to operate in the MP when for an almost untuned input (mean $A = 1$, modulation $B = 0.001$) the maximum and the minimum activity in the network differ by more than 5%. (B) Operating regimes of a Hodgkin-Huxley network model as a function of the peak conductance of synaptic excitatory connections to excitatory ($g_{EE}$) and inhibitory ($g_{IE}$) neurons. Conductances are given as multiples of the afferent peak conductance of excitatory neurons ($g_{Aff,E}$). The figure summarizes simulation results for $38 \times 28$ different values of $g_{EE}$ and $g_{IE}$. (C) Feedback kernels for selected operating regimes in the Hodgkin-Huxley model. Gray lines depict the recurrent excitatory and inhibitory currents, respectively, relative to the cells’ preferred orientation, averaged across cells for the example models marked in B, normalized to the afferent current received at their preferred orientation. Blue lines depict the corresponding total cortical feedback kernels. (D) Time-course of responses in the Hodgkin-Huxley model, determined using a reverse correlation paradigm, at the cells’ preferred orientation averaged over all pinwheel (map OSI < 0.3; red lines) and iso-orientation domain (0.6 < map OSI < 0.9; blue lines) cells, normalized to a peak of one for the example models marked in B. Shaded areas show the difference between the averaged responses of pinwheel and orientation domain cells.
Secondly, the operating regime influences not only activity, but also temporal dynamics of a cell’s response, as illustrated in Fig. 2D. The employed reverse correlation paradigm (for details see [13]) moreover illustrates characteristic differences between cells at different map positions (Fig. 2D): In the FF and the REC regime, both cells close to pinwheel centers and cells in orientation domains show very similar temporal responses. In the EXC regime on the other hand, the response of both populations is markedly prolonged, but the effect is even more pronounced in iso-orientation domain cells. Although less clear, the opposite relationship is present in the INH regime, where cells close to pinwheel centers show a more prolonged response. Further differences in the variability found in pinwheel- and iso-orientation domain cells are discussed elsewhere [12].

Figure 3. Location dependence of orientation tuning in the network models. The figure shows the slope values of the OSI-OSI regression lines (in gray values) as a function of the peak conductance of synaptic excitatory connections to excitatory \( g_{EE} \) and inhibitory \( g_{IE} \) neurons, separately (A) for the spike rate \( f \), (B) for the membrane potential \( V_m \), (C) for the total synaptic excitatory conductance \( g_e \) and (D) for the total synaptic inhibitory conductance \( g_i \). Conduances are given as multiples of the afferent peak conductance of excitatory neurons \( g_{Aff}^E \). Thin lines denote the borders of the different operating regimes (cf. Figure 2). The arrows at the colorbars indicate the values of the respective experimental measurements in [9].

Thirdly and most importantly for the analysis presented below, the operating regime also has a profound effect on the tuning of the neurons’ firing rate \( f \), membrane potential \( V_m \) and their excitatory and inhibitory input conductances \( g_e \) and \( g_i \). Again, these properties change in a way that is strongly related to the localization of a neuron, either in the region close to a pinwheel center or in an iso-orientation domain. For the further analysis, we describe the strength of tuning of a any property for a particular cell using the orientation selectivity index (OSI). The dependence of the OSI on a cell’s position in the orientation map between pinwheel and iso-orientation domain for any of these properties is described using a linear fit with a certain slope.
(see Appendix for further details). Plotting the slopes, Fig. 3 illustrates how strongly the tuning of \( f, V_m, g_e \) and \( g_i \) varies between these two regions, with positive values indicating a sharper tuning of the variable in iso-orientation domains and negative values vice versa. The rising values show that for all four quantities, the strength of their linear dependence on map position tends to increase as the regime gets closer to the unstable region (top left). In other words, as the regime becomes increasingly recurrently/excitatory dominated, the recurrent contribution leads to more pronounced tuning in the iso-orientation domain than in pinwheel regions. Note the exception in the excitatory regimes close to instability: consistent with the observation of the previous section, here the map-dependence of the tuning almost vanishes (slope approaching zero).

The map-dependence of orientation tuning in different regimes points to one handle on the underconstrained problem of finding the actual biological operating regime, as is illustrated below.

5. Searching biologically plausible operating regimes

Recent experimental and theoretical studies have investigated how the orientation tuning of a cell’s spike output depends on its position in the orientation preference map [7, 14, 15], but none of these has thus far been able to conclude the debate about the cortical operating regime. The wide range of models operating in different regimes that are discussed in the literature are an indication that models of V1 orientation selectivity are underconstrained. We show now that studying the specific location dependence of the tuning of internal neuronal properties can provide further constraints to find the appropriate cortical operating regime.

![Figure 4](image)

**Figure 4.** Tuning curves for experimental data from [9]. Mean responses across cells are shown for the firing rate (\( f \)), the membrane potential (\( V_m \)), the total excitatory (\( g_e \)) and total inhibitory conductance (\( g_i \)), separately for cells in iso-orientation domains (0.6 < map OSI < 0.9, thick lines) and cells close to pinwheel centers (map OSI < 0.3, thin lines). For each cell, responses were individually aligned to its preferred orientation and normalized to its maximum response. To allow comparison of the magnitude of \( g_i \) and \( g_e \) responses, both types of conductances were normalized to the maximum \( g_i \) response.

The data originates from intracellular recordings of cat V1 [9], combined with optical imaging. This allowed to measure *in vivo* the output (firing rate \( f \)) of neurons, their input (excitatory and inhibitory conductances \( g_e \) and \( g_i \)) and further a state variable (membrane potential \( V_m \)) of a neuron as a function of its position in the orientation map. Note that the latter three properties have hitherto not been available and could thus far not constrain the operating regime. Fig. 4 shows population averages of the experimentally observed tuning curves of each of these properties for neurons around pinwheel centers and for neurons within iso-orientation domains.

Note that the tuning of \( V_m \) as well as the tuning of \( g_e \) and \( g_i \) vary strongly with map location. Specifically, these properties are more sharply tuned for neurons within an iso-orientation domain, where the neighboring neurons have very similar orientation preferences, as compared to neurons close to a pinwheel center, where the neighboring neurons show a broad range of orientation...
preferences. The tuning of the firing rate $f$ is on the other hand largely invariant with map location.

6. Finding the biologically plausible operating regime

We analyzed the dependence of the orientation tuning properties on the operating regimes and compared them to the experimental data. For every combination of $g_{EE}$ and $g_{IE}$, we simulated the responses of neurons in the network model to oriented stimuli in order to measure the orientation tuning of $f$, $V_m$, $g_e$ and $g_i$. The OSI of each of the four quantities can then be plotted against the map OSI (varying from 0 close to pinwheel centers to 1 in an iso-orientation domain; see Appendix for details) to reveal the dependence of the tuning on map location. The slope of the linear regression of this OSI-OSI dependence was used to characterize the different operating points of the network. This slope captures the specific map-location dependence of the tuning width for each of the four measured quantities $f$, $V_m$, $g_e$ and $g_i$.

Fig. 3 shows the slopes for the tuning of $f$, $V_m$, $g_e$ and $g_i$ as a function of $g_{EE}$ and $g_{IE}$ of the respective Hodgkin-Huxley network models (gray scale). Model networks with strong recurrent excitation (large values of $g_{EE}$), as in the REC regime, predict steeper slopes than networks with less recurrent excitation. As the experimentally found values (arrows at the color bar) indicate rather steep values for the slopes, $V_m$, $g_e$ and $g_i$ constrain the network parameters to a highly recurrent regime. However, yet closer to the line of instability the map-dependence of the tuning almost vanishes, with flat slopes in the strongly excitatory regimes, where tuning is lost regardless of map location. Also, the strongly inhibitory dominated regimes (large values of $g_{IE}$) at the bottom right corner of Fig. 3 are of interest. Here, the slope of the location dependence becomes negative for the tuning of firing rate $f$ and membrane potential $V_m$. Such a sharpening of the tuning close to pinwheel centers in an inhibition dominated regime has been observed in other theoretical studies operating in an inhibition dominated regime [14]. Note that the slope of the tuning of the firing rate (Fig. 3A) is flat – and thus consistent with the experimental data – for most parts of the parameter space.

We can now quantitatively compare the slopes of the OSI-OSI relationship found in vivo, as indicated by the arrows in the colorbars of Fig. 3, to the model data. For each of the four measured quantities and for each point in the phase plane we determine the likelihood that a network operating at this point has generated the OSI-OSI relationship found in vivo. Fig. 5A shows the product of the four normalized likelihood functions. This “joint likelihood” peaks in a strongly recurrent regime, and we can thus conclude that the experimental data constrains the network to operate in an operating regime with both, strong recurrent excitation and inhibition, approximately balanced with one another, but dominating the afferent input. The normalized likelihood for the firing rate $f$ (Fig. 5B) alone, on the other hand, has high values for most points in the phase space, illustrating the difficulty in determining the correct operating regime by just considering this one property.

7. Discussion

Although much is known about the anatomy of lateral connections in cat V1, the strengths of synapses formed by short-range connections are largely unknown. In this study, we numerically explore the operating regimes of a spiking neural network with different strengths of their recurrent connections. We then use intracellular physiological measurements to constrain the strengths of these connections, and find that neither feed-forward dominated nor recurrent excitatory- or inhibitory-dominated networks are consistent with the tuning properties observed in vivo. We therefore conclude that the cortical network in cat V1 operates in a regime with a dominant recurrent influence that is balanced between inhibition and excitation.

The analysis presented here focuses on the steady state the network reaches when presented with one non-changing orientation. Interestingly, a comparable operating regime has been
Figure 5. Likelihood of regimes. (A) Product of the individual likelihoods for $V_m$, $f$, $g_e$, and $g_i$ for the slopes of the regression lines in the OSI-OSI plots. (B) Likelihood for the slopes of the OSI-OSI relationship of the firing rate response $V_m$.

Both plots are shown as a function of the peak conductance of synaptic excitatory connections to excitatory ($\overline{g}_{EE}$) and inhibitory ($\overline{g}_{IE}$) neurons. Gray values denote the likelihood (scale bars at the right); conductances are given as multiples of the afferent peak conductance of excitatory neurons ($\overline{g}_{Aff}^E$). The area above the thin red line corresponds to parameter values for which the model neurons exhibit untuned responses (all firing rate OSIs are below 0.3). The area above the thick red line corresponds to parameter values for which the model network becomes “unstable”, i.e. model cells fire with an average firing rate above 100 Hz, independent of the stimulus orientation. The likelihood was not evaluated for the unstable regime. The figure summarizes simulation results for $38 \times 28$ different values of $\overline{g}_{EE}$ and $\overline{g}_{IE}$.

indicated in an analysis of the dynamic properties of orientation tuning in cat V1 [13].

The finding that tuning properties of cat V1 are best explained by a network operating in a recurrent regime is robust against variation of other parameters not considered here, e.g. the relative range of the recurrent inhibition and the peak conductances $\overline{g}_{II}$ and $\overline{g}_{EI}$ (data not shown). Nevertheless, the network architecture is based on a range of basic assumptions, notably that all neurons in the network receive tuned input of equal sharpness. Explicit inclusion of location dependence of the input tuning might well lead to tuning properties compatible with the experimental data in different operating regimes. However, there is no evidence supporting such a location dependence of the afferent input, and therefore assuming location-independent input seemed the most prudent basis for this analysis.

In the recurrent regime, neurons responded to their preferred stimulus with a 1.8-fold increased firing rate compared to the feed-forward regime. Previous modeling studies have already attributed such an amplification to the cortical network [8,16], and so has experimental work [17].

Our analysis demonstrates that the cortical operating point seems to be close to instability. Such a network is very sensitive to changes in its governing parameters, e.g. small changes in connection strengths lead to large changes in the overall firing rate. In the “best fitting” operating regime, a 10% change in firing rate, which is of similar magnitude as observed firing rate changes under attention in macaque V1 [18], is easily achieved by increasing $\overline{g}_{EE}$ by just 2%. It therefore seems plausible that one benefit of being in such a regime is the possibility of significantly changing the “operating point” of the network through only small adjustments of the underlying parameters. Candidates for such an adjustment could be contextual modulations, adaptation or attentional effects, which may all be explainable as temporal shifts of the operating
point, for example to make the cortical response particularly sensitive to small changes in afferent or feedback signals. Experimental data, for example detailing spatial and temporal contextual interactions [19], may allow to further investigate the functional implications of the cortical operating regime. For example, Dragoi et al. [20] found pronounced adaptation-induced short-term plasticity close to pinwheel centers, which was explained by a network model operating in a strongly recurrent, balanced regime [21]. Center-surround interactions [22], too, are compatible with such a regime [23].

The peculiar location of the cortical operating point close to the line of instability is reminiscent of the theory of “computing at the edge of chaos” [24], which has attracted some attention in the past decade. Theoretical studies demonstrated abstract networks to accomplish more challenging computations near the border between ordered to chaotic dynamics [25]. Moreover, such networks are responsive to inputs over a wider dynamic range [26]. These theoretical considerations are complemented by in vivo data showing recurrent excitation and inhibition in balance [27], which there, too, has been interpreted as a facilitator for easy transition between different cortical states. Thus, our findings here add to the evidence that the recurrent network contributes to maintaining an operating point which allows easy switching between different cortical states.

Appendix A. Simulation
Appendix A.1. The Hodgkin-Huxley network model
The network contained 50 × 50 = 2500 excitatory cells arranged on a grid and 833 inhibitory neurons (25%) placed at random grid locations. Recurrent excitatory conductances were modeled as arising to 70% from fast (AMPA-like) and to 30% from slow (NMDA-like) receptors. Presynaptic spike were transferred to the postsynaptic neuron with a delay, drawn from a Gaussian distribution. We used exponential models for the synaptic conductances originating from GABA_A-like inhibitory and AMPA-like excitatory synapses [28]. Slow NMDA-like excitatory synapses were modeled by the difference of two exponentials. The Poisson input spike trains exclusively trigger fast, AMPA-like excitatory synapses. Further details and model parameters can be found in [12].

The network usually settled into a steady state within a few hundred milliseconds. Thus, to measure orientation tuning curves of \( f, V_m, g_e \) and \( g_i \), the response of the network to inputs with different orientations was computed for 1.5 s with 0.25 ms resolution. We then calculated the average \( f, V_m, g_e \) and \( g_i \) for every cell in an interval between 0.5 s and 1.5 s.

Appendix A.2. The firing-rate network model
The firing-rate network is similar to the network in [7] with two exceptions: (1) We include self-inhibition (\( S_{II} \neq 0 \)) in our model, and (2) we use the same spatial connectivity function \( \varphi \) for excitatory and inhibitory connections, consistent with experimental observations [9]. Further details and model parameters can be found in [12].

Appendix B. Orientation selectivity index (OSI) and OSI-OSI slopes
We analyze orientation tuning for an arbitrary property \( R(\phi_i) \) in response to a stimulus of orientation \( \phi_i \) using the orientation selectivity index [29], which is given by

\[
\text{OSI} = \frac{\sqrt{\sum_{i=1}^{N} R(\phi_i) \cos(2\phi_i)} + (\sum_{i=1}^{N} R(\phi_i) \sin(2\phi_i))^2}{\sum_{i=1}^{N} R(\phi_i)}. \tag{B.1}
\]

For all measurements, eight stimulus orientations \( \phi_i \in \{-67.5, -45, -22.5, 0, 22.5, 45, 67.5, 90\} \) were presented. The OSI is then a measure of tuning sharpness ranging from 0 (unselective) to 1 (perfectly selective). In addition, the OSI was used to characterize the sharpness of the recurrent
input a cell receives based on the orientation preference map. To calculate this map OSI, we estimated the local orientation preference distribution by binning the orientation preference of all pixels within a radius of 250 µm around a cell into bins of 10° size; the number of cells in each bin replaces $R(\phi_i)$. The map OSI ranges from almost 0 for cells close to pinwheel centers to almost 1 in the linear zones of the iso-orientation domains. The dependence of each tuning property on the local map OSI was then described by a linear regression line using the least squares method.

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References
[1] Hubel D H and Wiesel T N 1962 J. Physiol. 160 106
[2] Sompolinsky H and Shapley R 1997 Curr. Opin. Neurobiol. 7 514
[3] Ferster D and Miller K D 2000 Annu. Rev. Neurosci. 23 441
[4] Martin K A C 2002 Curr. Opin. Neurobiol. 12 418
[5] Teich A F and Qian N 2006 J. Neurophysiol. 96 404
[6] Ben-Yishai R, Bar-Or R L and Sompolinsky H 1995 Proc. Natl. Acad. Sci. USA 92 3844
[7] Kang K, Shelley M and Sompolinsky H 2003 Proc. Natl. Acad. Sci. USA 100 2848
[8] Somers D, Nelson S and Sur M 1995 J. Neurosci. 15 5448
[9] Mariño J, Schummers J, Lyon D C, Schwabe L, Beck O, Wiesing P, Obermayer K and Sur M 2005 Nat. Neurosci. 8 194
[10] Destexhe A and Paré D 1999 J. Neurophysiol. 81 1531
[11] Destexhe A, Rudolph M, Fellous J and Sejnowski T 2001 Neuroscience 107 13
[12] Stemberg M, Wimmer K, Martin R, Schwabe L, Mariño J, Schummers J, Lyon D C, Sur M and Obermayer K 2009 Cerneb. Cortex 19 2166
[13] Schummers J, Cronin B, Wimmer K, Stemberg M, Martin R, Obermayer K, Koerding K and Sur M 2007 Frontiers in Neuroscience 1 145
[14] McLaughlin D, Shapley R, Shelley M and Wieland D J 2000 Proc. Natl. Acad. Sci. USA 97 8087
[15] Nauhaus I, Benucci A, Carandini M and Ringach D L 2008 Neuron 57 673
[16] Douglas R J, Koch C, Mahowald M, Martin K A and Suarez H H 1995 Science 269 981
[17] Sharon D and Grinvald A 2002 Science 295 512
[18] McAdams C J and Maunsell J H 1999 J. Neurosci. 19 431
[19] Schwartz O, Hsu A and Dayan P 2007 Nat. Rev. Neurosci. 8 522
[20] Dragoi V, Rivestella C and Sur M 2001 Nature 411 80
[21] Wimmer K and Obermayer K 2009 Synaptic plasticity changes orientation tuning and provides a mechanistic explanation for the tilt aftereffect in network models of V1 2009 Neuroscience Meeting Planner (Society for Neuroscience) online
[22] Schwabe L, Obermayer K, Angelucci A and Bressloff P C 2006 J. Neurosci. 26 9117
[23] Stemberg M and Obermayer K 2009 The local recurrent network influences surround modulation in models of V1 2009 Neuroscience Meeting Planner (Society for Neuroscience) online
[24] Langton C G 1990 Physica D: Nonlinear Phenomena 42 12
[25] Bertschinger N and Natschläger T 2004 Neural Comput. 16 1413
[26] Kinouchi O and Copelli M 2006 Nature Physics 2 348
[27] Haider B, Duque A, Hasenstaub A R and McCormick D A 2006 J. Neurosci. 26 4535
[28] Destexhe A, Mainen Z F and Sejnowski T J 1998 Kinetic models of synaptic transmission Methods in neural modeling ed Koch C and Segev I (Cambridge, MA: MIT Press) pp 1–25 2nd ed
[29] Swindale N V 1998 Biol. Cybern. 78 45