



A continuum-field model of visual cortex stimulus-driven behaviour: emergent oscillations and coherence fields

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Abstract

The problem of the genesis of oscillatory phenomena in a continuous distribution of excitatory and inhibitory neurons is addressed by introducing a neural field model of the reaction-diffusion type. The presence of the diffusive term, combined with the non-linear point interactions, allows the system to exhibit cooperative activation properties in *both* space and time. A detailed analysis of the resulting oscillatory behaviour of the model evidences its capability of generating stimulus-induced spatio-temporal coherence fields, similar to the ones experimentally observed in the mammalian visual cortex. The perceptual role of the related association fields, as flexible media to establish feature association in the visual space, is discussed.

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1. Introduction

Over the past few years, a large amount of data have been accumulated which demonstrate that coherent perceptual states are associated with collective activities of large ensembles of neurons in cortical areas [2,30,36,46,51,62]. Specifically, it has been observed that visual stimulations drive synchronous oscillatory behaviours

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over a range of spatial scales, from single unit responses to visually evoked potentials [94,78,88]. These stimulus-dependent neuronal oscillations occur mainly in the γ -frequency band (20–70 Hz), and can synchronize across separate cortical locations with a precision in the ms range and with near-zero phase-lag, depending on the configuration of the visual stimulus [19,22,32,38–40,53]. From this perspective, phase relationships of neuronal oscillations may be used to define cortical assemblies, i.e., clusters of spatially distributed neuronal groups that represent segments of a visual scene. On the basis of this body of evidence, synchronous oscillatory cortical responses have been indicated as the physiological substrate for a mechanism of feature binding [19,21,23,33,76,85,90].

Several models have been proposed to study the emergence of synchronous oscillations in networks of reciprocally coupled neural oscillators [1,5,14,20,41,52,54,55,75,81,91,94]. (for a review, see [25,83]). In all these models, synchronization/desynchronization behaviours are achieved by couplings among oscillating units considered as interacting discretely with one another.

In this paper, our aim is to investigate the joint spatio-temporal properties of the sensory-evoked activity in cortical networks. Toward this end, coupling weights among oscillators are modelled as a diffusion process: any cell activates, through a spreading-out process, nearby cells in proportion to its own level of activation. The neural field model associated with this choice of the coupling weights allows us to investigate spatial distributions of coherence and synchrony as *continuum* properties of large fields of interconnected cells. Desynchronization behaviour in our model is introduced by an appropriate long-range inhibitory coupling. In this way, we can analyse the role of horizontal interactions in the establishment of ordered oscillatory behaviours and in the control of the spatio-temporal distribution of coherence. We show that the resulting system exhibits a stimulus-dependent assembly formation of oscillatory responses, similar to those found in the physiological experiments on slow-wave field potentials [14,18].

2. Cortical model

Visual cortex is a densely packed volume of neurons in which intracortical connections greatly exceed afferent projections [9]. This implies that the collective behaviour of neural assemblies depends on complex synaptic and dendritic processes of large cortical networks; therefore, to determine the degree of relevant detail is a hard problem. Given the huge number of cells involved in such networks, macroscopic approaches are frequently adopted to offer simpler insights into the basic physical mechanisms of cortical behaviour, thus avoiding anatomical details as well as physiological complexity.

Following the continuum approach pioneered in the works by Wilson and Cowan [96], Freeman [28], Amari [3] and Amari [4], we considered a one-dimensional (1-D) neural field model of striate visual cortex characterized by two interacting excitatory and inhibitory populations, organized as layered continua. The neural field dynamics is governed by the following pair of coupled, delayed non-linear

diffusion equations:

$$\begin{aligned}\tau_0 \frac{\partial}{\partial t} e(x, t) &= -\alpha_e e(x, t) + D \frac{\partial^2}{\partial x^2} e(x, t) - b[e(x-d, t) + e(x+d, t)] \\ &\quad - w_{ie} F[i(x, t - \tau_{ie})] + s(x, t), \\ \tau_0 \frac{\partial}{\partial t} i(x, t) &= -\alpha_i i(x, t) + w_{ei} F[e(x, t - \tau_{ei})],\end{aligned}\quad (1)$$

where $e(x, t)$ and $i(x, t)$ are, respectively, the excitatory and inhibitory population activities in space (x) and time (t), and $s(x, t)$ is the driving input. The two populations excite and inhibit each other through non-linear point interactions with time-delays τ_{ei} , τ_{ie} . Such delays are due to delays in transmission of information among different parts of the system, e.g., through synaptic transmission and finite conduction velocities of dendrites and axons. In order to keep minimal conditions for generating faithful (cortical-like) spatio-temporal behaviours, both intrinsic properties and the connection architecture were reduced to the simplest cases. *Punctual parameters* characterize the basic oscillatory element: τ_0 is the membrane time constant, α_e (α_i) is the damping constant, w_{ei} (w_{ie}) is the coupling weight between populations, and

$$F(u) = \frac{1}{\exp[\sigma(\theta - u)] + 1}$$

is a static sigmoidal function with slope σ and threshold θ , limiting the excitatory and inhibitory interaction mechanisms. The spatial flow of the activity across the neural field concerns the excitatory population, has a linear behaviour, and is controlled by the *field parameters* D and b , related to diffusion coupling and lateral inhibitory interaction, respectively. The diffusive term has to be related to the bioelectrical phenomena occurring in the extracellular space, taken to be electrically equivalent to an extended homogeneous conductive medium¹ [63,67,68], characterized in Eq. (1) by the diffusive parameter D , representing the square of the diffusion length. The extracellular current flow can be adequately described by a Poisson's partial differential equation relating transmembrane currents to field potentials (e.g., excitatory activity $e(x, t)$). The inhibitory term accounts for the presence of specific interactions (mediated by synaptic processes) among nearby neurons, at a distance $\pm d$. It is worth noting that the effects of this lateral inhibition are also influenced by the diffusion processes occurring in the extracellular conductive medium (a more exhaustive treatment of this issue is presented in the Discussion). As well as non-linear point interactions are fundamental in priming cooperative processes, the spreading of activation over the cortical layers plays a key role in the long-distance transfer of information across the neural field and in influencing the spatio-temporal behaviour of the resulting cell assemblies. A summary of

¹ The extracellular current flow can be adequately described by a Poisson's partial differential equation relating transmembrane currents to field potentials:

$$\nabla \cdot D(\nabla \Phi) = \kappa \nabla \cdot D(\nabla \Phi) = -\kappa I_m = -s,$$

where Φ is the field potential (essentially dominated by the excitatory contributions [67], e.g., $e(x, t)$), I_m is the volume source current density, D can be considered as a conductivity tensor, and κ is an appropriate dimensional [$m^3 \Omega$] normalizing parameter.

Table 1

Typical values of the anatomical and physiological parameters used in the numerical solutions of Eq. (1).

Symbol	Definition	Typical value	Range	Units
Population variables				
$e(x, t)$	Excitatory activity	—	± 4	$10^2 \mu\text{V}$
$i(x, t)$	Inhibitory activity	—	$0 - 4$	$10^2 \mu\text{V}$
$s(x, t)$	External stimulus input	—	$0 - 4$	$10^2 \mu\text{V}$
Punctual parameters				
σ	Slope of the sigmoidal function	6	6	$10^{-2} \mu\text{V}^{-1}$
θ	Threshold of the sigmoidal function	1	1	$10^2 \mu\text{V}$
α_e, α_i	Damping constant	1	1	—
τ_0	Membrane time constant	5	5	ms
τ_{ie}, τ_{ei}	Coupling delays	5	$0.5 - 5.0$	ms
w_{ie}, w_{ei}	Coupling weights between populations	4.4	$1 - 10$	$10^2 \mu\text{V}$
Field parameters				
b	Lateral inhibition strength	0.045	$0 - 0.7$	—
D	Diffusion parameter	$0.06\lambda_0^2$	$(10^{-3} - 0.5)\lambda_0^2$	—
d	Lateral inhibition distance	$0.5\lambda_0$	$0.5\lambda_0$	—
λ_0	Spatial scale	540	540	μm

the punctual and field parameters used in the model, together with their typical values used in the simulations, is presented in Table 1.

To characterize the behaviour of the system, we analyse its response to two types of stimuli: transient and sustained. Eq. (1) are solved numerically by a modified finite difference method proposed by Dilao and Sainhas [16] for numerical integration of diffusion and reaction-diffusion equations; boundary conditions are periodic in all simulations reported. It is worth noting that, if we set $D=0$ and $b=0$, Eq. (1) reminds one of the equations describing the behaviour of the König and Schillen [52] basic oscillatory element, sharing the property of stimulus-dependent transition between a stable fixed point (i.e., a non-oscillatory state) and a limit cycle oscillation. The presence of a diffusion coupling, although, gives the system a joint spatio-temporal character, which is the main novelty of our model. Indeed, the diffusion component allows a weighted averaging of the input signal $s(x, t)$ over a region of a certain extent (cf. the receptive field), while the non-linear reaction components provide a flexible medium on which to base cooperative computation.

Transient response: Fig. 1 (top) shows the spatio-temporal responses of the cortical field to an impulsive activation in space and time (a point stimulation lasting $0.5\tau_0 \simeq 2.5$ ms), for different values of the diffusion parameter D and of the lateral inhibition strength b . The neural field reacts with a central excitation surrounded by inhibitory regions whose amplitude can be controlled by the inhibition strength b . The inhibitory action is also influenced by diffusion processes attenuating the effect of b as the diffusion parameter D increases. The time course of the transient response may have a biphasic or triphasic character, still depending on the joint action of D and b . The effects of

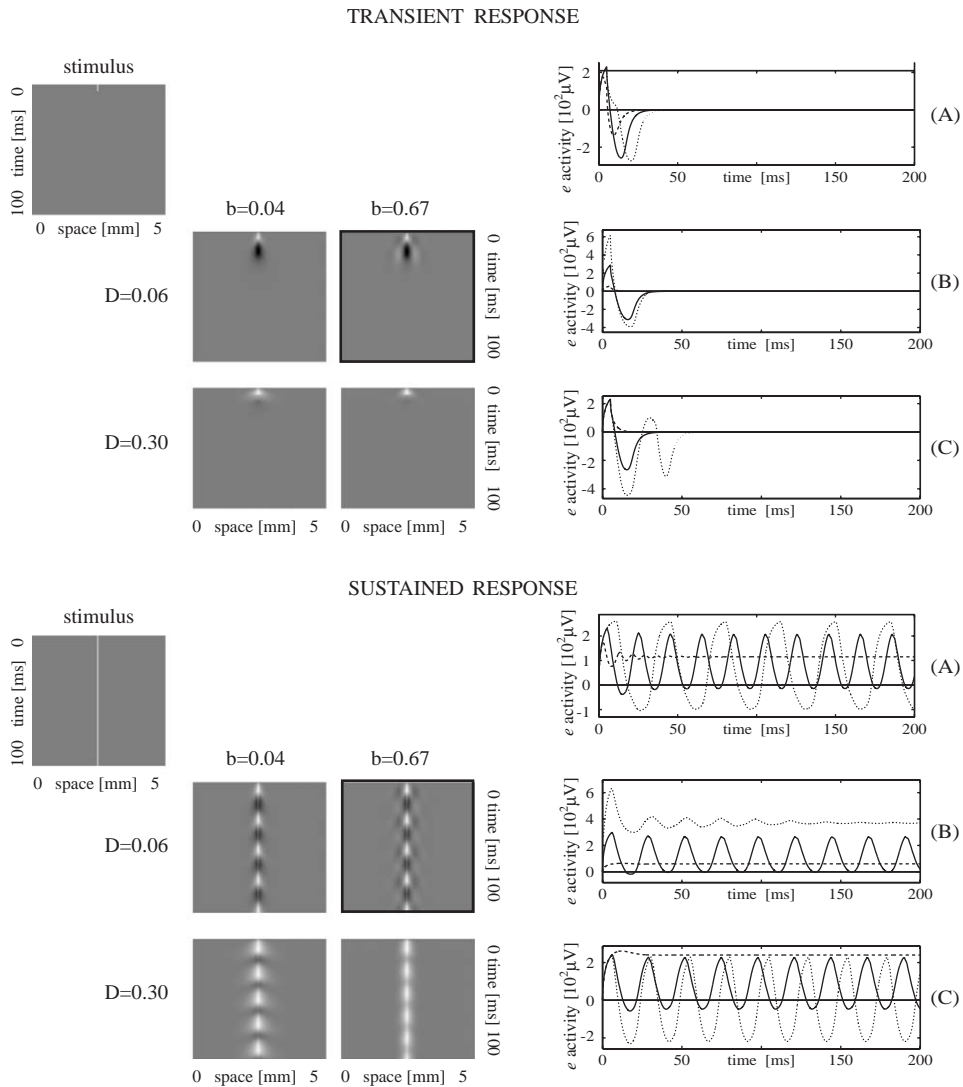


Fig. 1. System responses to a spatio-temporal impulse stimulus (*top*) and to a continuous time step activation of a point in space (*bottom*). Bright and dark greys represent excitatory and inhibitory activities, respectively. Our standard set of parameters is $\tau_0 = 5$ ms, $\alpha \equiv \alpha_e = \alpha_i = 1$, $w \equiv w_{ei} = w_{ie} = 6.6$, $\tau \equiv \tau_{ei} = \tau_{ie} = 2.5$ ms, $s(\cdot, t) = \text{const} = A = 12$, $\sigma = 6.0$, $\theta = 1.0$, $d = 0.5\lambda_0$, with exceptions where noted. (A–C): Effects of the variations of the intrinsic parameters on the temporal responses, with respect to the central spatial position of the spatio-temporal maps pointed out by the black frames. (A) Effect of varying the delay time τ . Dashed, $\tau = 0.5$ ms; solid, $\tau = 2$ ms; dotted, $\tau = 5$ ms. (B) Effect of varying the input level A . Dashed, $A = 3$; solid, $A = 15$; dotted, $A = 32$. (C) Effect of varying the coupling strength w . Dashed, $w = 1.1$; solid, $w = 6.6$; dotted, $w = 9.9$.

varying the point parameters τ and w , and the input level $s(x, t)$ on the temporal response are shown in the plots (A, B, C), for fixed values of $D=0.06\lambda_0^2$ and $b=0.67$. The coupling strength w strongly influences the time course of the transient response (C), whereas the time delay τ affects the duration of the complete response pattern, but not its time course (A). Variations of the input level slightly affects the shape of the transient response (B).

Sustained response: The spatio-temporal responses obtained by stimulating a point in space with a step input in time are shown in Fig. 1 (*bottom*). A sustained input stimulation yields, for a proper parameter set, stable oscillatory behaviours. The dependences of the oscillatory behaviour of our system on the input amplitude $s(x, t)$, on the time delay τ and on the coupling weights w between the populations are similar to the ones obtained by König and Schillen's model (cf. the plots in A, B, C with their Fig. 2 in [52]). In particular, depending on the level of input activity, the system transfers between a non-oscillatory and an oscillatory state: with a too low input, as well as with an excess of activation, the system relaxes to a stable fixed point determined by the other point parameters.

The pattern of excitatory activity for transient stimulations points out a spatio-temporal distribution that, for a linear system, could be representative of a receptive field.² In the case of a non-linear system, this distribution means that each location in the cortical layer weights the “sensorial” input in space and time, even though non-linearly. Considering the spatial integration properties, as mediated by the diffusion processes, it is interesting to investigate the cooperative response to multiple activation sites in relation to the formation of coherently oscillating assemblies (see Section 3). Toward this end, we introduce, for multiple sites in space, volleys of afferent inputs, characterized by short periods (bursts) of continuous activity at uniformly distributed sparse sites of activation in space. Formally, for each spatial location in a given region $x_1 \leq x \leq x_2$, the input signal $s(x, t)$ is a stochastic process taking the value A or 0 with probabilities p and $(1 - p)$, respectively, over each interval $nT \leq t < (n + 1)T$, with $T = k\tau_0$ (typically $k = 2$):

$$\begin{aligned} &\forall x \in [x_1, x_2], \\ &\forall n \in [0, +\infty), \quad \Pr\{s(x, t) = A, \quad nT \leq t < (n + 1)T\} = p, \\ &\quad \quad \quad \Pr\{s(x, t) = 0, \quad nT \leq t < (n + 1)T\} = 1 - p. \end{aligned} \quad (2)$$

If we increase the activation probability p , the temporal frequency of the volley increases, as well as the spatial density of the activation sites.

²The time course of the excitation is considerably shorter, as compared with the temporal properties of visual receptive fields of local intracortical potentials measured by Lohmann et al. [60]. Such differences are due to the fact that our large scale model of cortical activity describes collective properties from the beginning. In real physiological conditions, collective behaviours can be evidenced when a large number of cells are excited by a spatially extended visual stimulation and, therefore, impulse stimulations cannot activate collective responses.

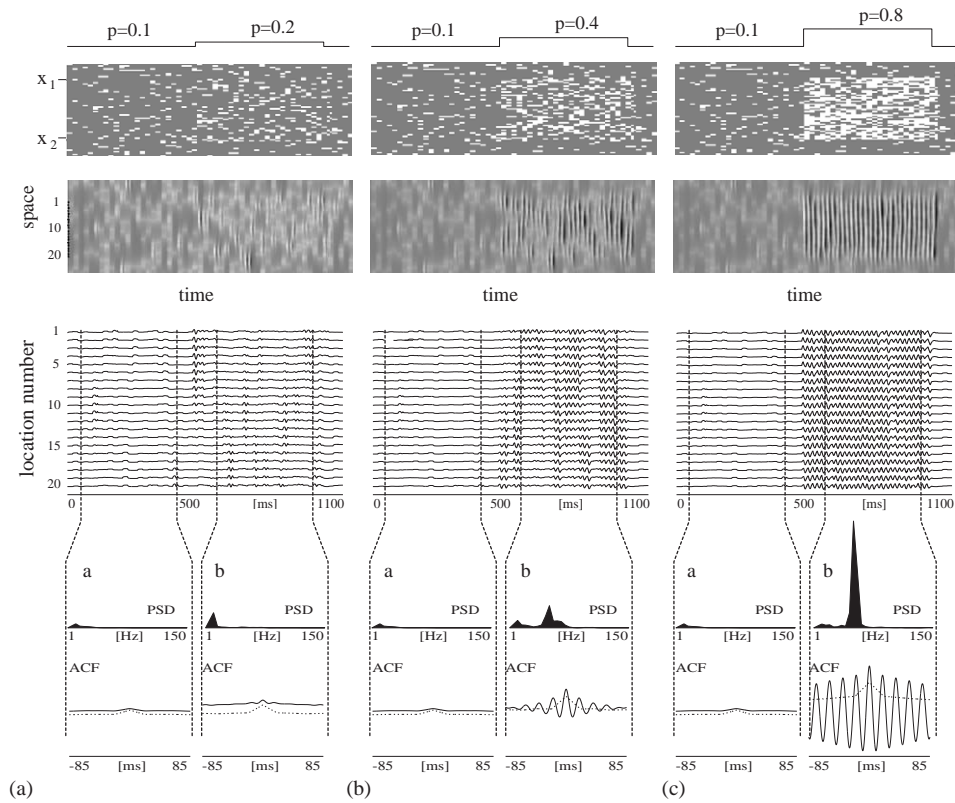


Fig. 2. Stimulus-dependent responses obtained by stochastic input activation (see text). Upper panels: greyscale spatio-temporal maps of the input configuration and of the corresponding cortical responses. Bright and dark greys represent excitatory and inhibitory activities, respectively. After 500 ms, the onset of a specific stimulus that lasts 500 ms more increases the activation probability in the spatial domain $[x_1, x_2]$. Under conditions of sufficient activation probability p , coherent spatio-temporal oscillations emerge in a large spatial region. Lower panels: LFP signal courses for the 20 nearby spatial locations pointed out in the leftmost spatio-temporal map response. The lowermost figures represent the corresponding average power spectra (PSDs) and the normalized autocorrelation functions (ACFs) for the 20 single response epochs delimited by dotted lines. (a) 400 ms epochs before specific stimulation ($p=0.1$) and (b) 400 ms epochs during specific stimulation ($p > 0.1$). Note the sharp peak in the PSD and the Gabor-like shape of the ACF obtained during specific stimulation. The dashed lines in the ACF graphs correspond to the average autocorrelations of the input signals.

3. Results

The spatio-temporal dynamics of a 1-D neural field driven by finite stochastic point sources is studied by numerical simulations. The system parameters used in the following were chosen to produce desirable slow-wave forms resembling LFPs recorded extracellularly in the visual cortices of the cat and the monkey. Our standard set of

parameters is: $\alpha_e = \alpha_i = 1.0$, $\tau_0 = 5$ ms, $w_{ie} = w_{ei} = 4.4$, $\tau_{ie} = \tau_{ei} = 1.5$ ms, $D = 0.06\lambda_0^2$, $b = 0.045$, $d = 0.5\lambda_0$, $A = 4$, $\sigma = 6.0$, $\theta = 1.0$.

3.1. Emergence of oscillatory assemblies

Numerical simulations proved that a rapid successive activation of multiple cortical sites produces a cooperative reaction of the diffusion layer. Such reaction results, for a sufficiently high activation probability p , in the formation of coherent oscillatory states. Specifically, when the increment of the activation probability p occurs over contiguous cortical sites, a stimulus-specific response is observed as a localized oscillatory assembly, if the size of such a group of neurons is larger than the extent of the diffusion process.

To point out the stimulus-dependent property of these assemblies, we stimulated the excitatory cortical layer by both specific and non-specific inputs. Non-specific activation (evoking a spontaneous activity) is provided by a stochastic input $s(x, t)$, as defined in Eq. (2), with low activation probability ($p = 0.1$), initialized from different seed values at each cortical location x . The onset of a specific stimulus is associated with an increment of the activation probability in the spatial domain $[x_1, x_2]$. The assembly formation resulting for this stimulus configuration is illustrated in Fig. 2, for increasing values of the activation probability p . Specific stimulation augments the activity of topologically continuous cortical locations and, under conditions of sufficient excitatory drive, local oscillatory assemblies emerge. The resulting oscillations observed in the excitatory signal $e(x, t)$ closely resemble the time courses of real LFPs recorded in visual cortex [18,78]. The cortical layer exhibits oscillatory activity only at locations to which a sufficient stimulus is applied, and the stimulus response, therefore, need not be segregated from background oscillations. This agrees with experimental evidence of the non-oscillatory character of spontaneous neuronal activity [39]. Moreover, it is worth noting that, after stimulus onset, coherent oscillations emerge rapidly, (approximately in one cycle or less), as well as the transition back to a more stochastic (non-oscillatory) state, after stimulus offset [18]. The cooperative phenomena generating the oscillatory activity remain spatially localized in relation with the spatial extent of the activation sites. For intermediate values of p , there form momentarily existing assemblies (islands) of activity, whereas, for higher values of activation, coherent spatio-temporal oscillations occur over the entire spatial extent of the input activation. The properties of the spatio-temporal distribution of coherent oscillatory activity will be discussed in the next section. The amplitude level of the activation associated with each burst, jointly with its lasting period T , plays a key role in priming oscillations. Indeed, an excessive increase in the activation level, for a fixed p , leads the system back to a stationary, non-oscillatory state (not shown, but cf. Fig. 1B).

To quantitatively characterize the temporal behaviour of the modelled LFP signals, we computed the average power spectral densities (PSDs) and the average autocorrelation functions (ACFs) or autocorrelograms of the LFP signals, calculated over 400 ms and averaged over 20 response epochs of nearby cortical locations (see Fig. 2). The power spectra and the autocorrelograms, as well as the LFP signals, closely approximate experimental findings. The emergence of oscillatory activity is clearly

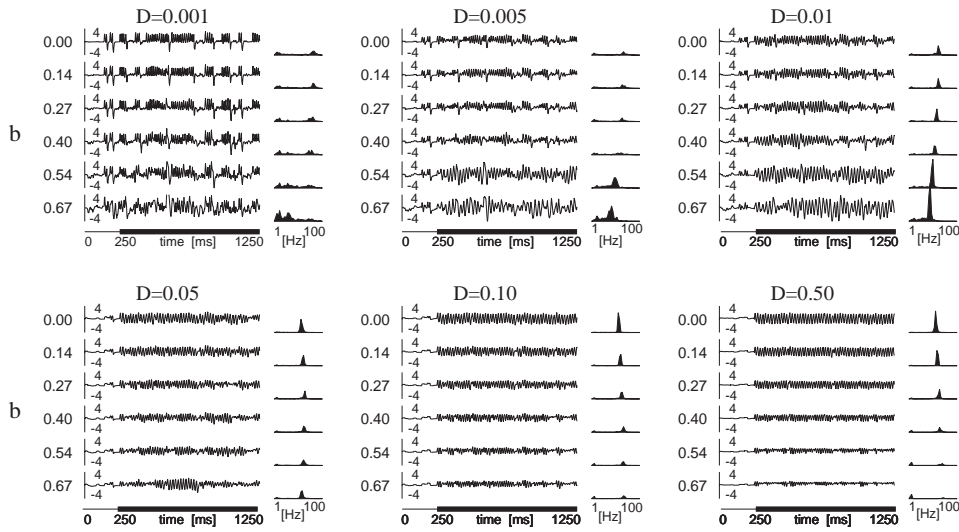


Fig. 3. LFP tracks and the corresponding power spectra obtained at a single spatial location for different combinations of the field parameters D and b . The thick line on the temporal axis indicates the length of the input stimulation starting at 250 ms, with activation probability $p = 0.8$.

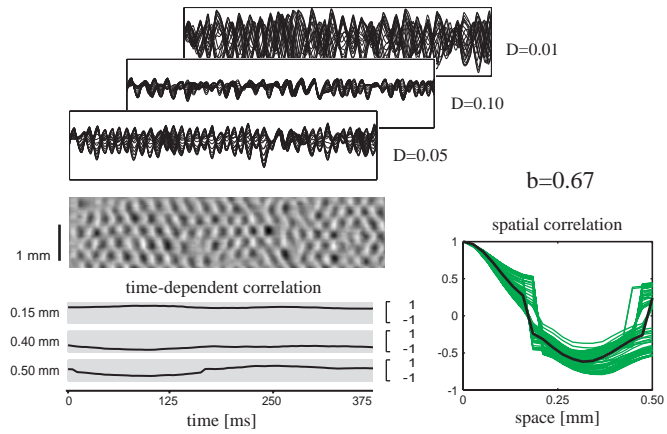
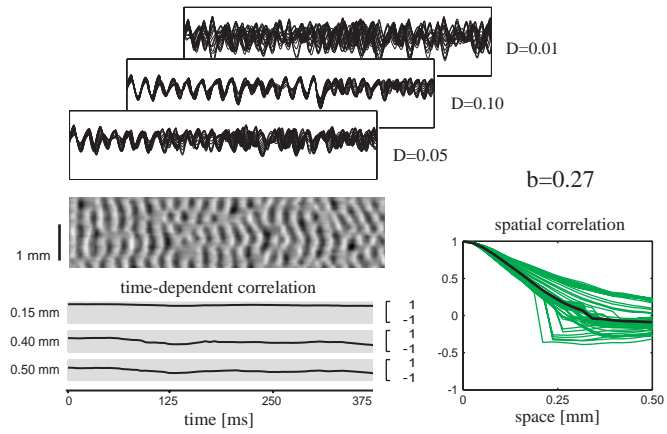
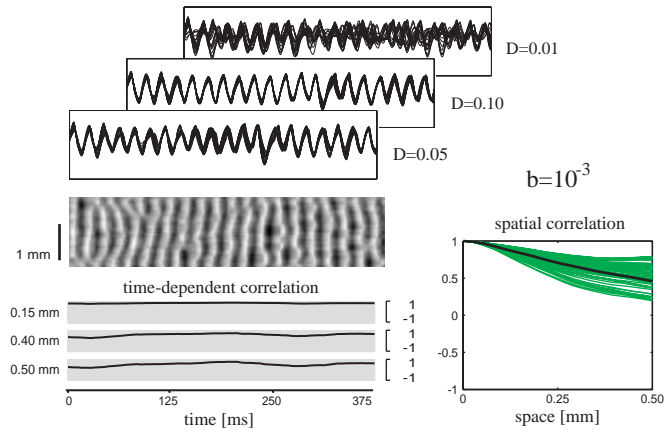
stimulus-dependent: in condition of specific stimulation, the sharp peak in the spectral power density reveals a “generative” oscillatory activity at about 40 Hz, in contrast to the broad-band frequency spectra associated with amplitude fluctuations of the LFPs in the range 1–10 Hz, in the absence of a specific stimulation. Similarly, the ACFs exhibit a Gabor-like shape indicating a rhythmic activity (cf. [18,22]). The dashed lines in the graphs correspond to the average autocorrelograms of the input signal. Note that such autocorrelograms are aperiodic, thus indicating that the input is not driving the oscillatory behaviour by itself. This agrees with the experimental evidence that neuronal oscillations result from intracortical mechanisms and are not driven by oscillatory (i.e., thalamic) input [22,39].

To analyse the effects of the field parameters on the formation of the rhythmic oscillatory activity, we systematically varied both the diffusion parameter D that governs the spread of activity in the neural field and the strength of lateral inhibition b , while keeping fixed the distance from which lateral inhibition occurs ($d = 0.5\lambda_0$). Fig. 3 shows that a certain amount of diffusion is necessary to obtain an oscillatory activation, and that such behaviour can be strongly influenced by lateral inhibitory processes. In particular, according to the amount of diffusion, the effects of lateral inhibition can be opposite: a low level of inhibition is not sufficient to drive oscillations for small values of D , whereas, for higher values of D , an increase in inhibition can prevent rhythmic activity. Although oscillatory behaviours were obtained for a wide range of variations of the parameters, the steadiest behaviours (in the whole range of the considered values of b) were observed for $0.01\lambda_0^2 \leq D \leq 0.10\lambda_0^2$. Therefore, in the subsequent analysis we shall restrict the variations of D to this range.

3.2. Spatio-temporal distribution of coherence

The presence of a diffusive medium operates so that the oscillatory activities elicited, through specific stimulations, at different locations of the cortical layer, turn out to be intrinsically coupled by diffusion, thus yielding large-scale areas of coherent activity. In this section, we analyse the spatio-temporal patterns of the stimulus-induced oscillations by comparing the modelled LFP signals as a function of time and distance, to discuss the role of diffusion and lateral inhibition in the synchronization and desynchronization processes of the oscillatory activity and to point out the spatio-temporal properties of the resulting *coherence fields*. Fig. 4 shows three panels representing different system responses to the same stimulation; such responses were obtained by varying the strength of lateral inhibition b at a fixed value of diffusion $D=0.05\lambda_0^2$. The spatio-temporal maps, shown in the middle of each panel, offer compact representations of the spatio-temporal dynamics of the LFPs, pointing out a certain degree of variability of coherence in both space and time. Specifically, synchronous events appear as vertical straight bands, whereas oblique bands stand for propagating waves or phase-shifts. The corresponding LFP traces are displayed in the insets, together with the responses obtained for lower ($D = 0.01\lambda_0^2$) and higher ($D = 0.10\lambda_0^2$) values of diffusion. The spatial extent of the coherence fields depends on the intensity of lateral inhibition and on the degree of diffusion of the neural field. In particular, an increase in lateral inhibition disrupts spatio-temporal coherence, thus providing an intrinsic mechanism for desynchronizing cortical activity. Low values of diffusion facilitate the formation of high incoherence states, whereas high values of diffusion oppose desynchronization, thus providing an intrinsic synchronization mechanism.

To quantitatively characterize the spatio-temporal distribution of coherence, we computed the normalized temporal cross-correlations of LFP signals at different cortical distances. A measure of spatial coherence is obtained by representing the peaks of the cross-correlations as a function of distance. This quantity provides a closely related measure of spatial correlation (see Fig. 4). In general, the average spatial coherence decreases with cortical distance as a consequence of the increasing phase jitter with distance [15,18,31]. Spatial correlations display marked differences as the amount of lateral inhibition increases. For low values of b , LFPs display a remarkable spatio-temporal coherence, as indicated by the high values of spatial correlations for large distances, in contrast to the steeper decline of spatial correlations for intermediate values of inhibition, up to even an anti-correlation for higher values of inhibition. It is worth noting that, for high levels of inhibition, the coherence field shows abrupt transitions, resulting in small regions (patches) characterized by coherence states (cf. [45]), which are mutually correlated or anti-correlated in an alternate way (cf. the chequered pattern in the lowermost spatio-temporal map in Fig. 4, for $b = 0.67$). The patches have a typical length scale that is of the order of the range of the diffusion length (D). The time-dependence of coherence was investigated in greater detail by analyzing the evolution of local correlations as a function of time. More specifically, the maximum peak of the cross-correlations between two cortical sites at fixed distances were evaluated by using successive time windows (cf. [15]). The maximal correlations as a function of time are displayed in the bottom-left figures of each panel in Fig. 4. These re-



sults indicate that the coherence of cooperative output oscillations present a certain degree of variability (even within short time windows), which becomes more evident for relatively high values of inhibition and large distances (see also Fig. 5D).

3.3. Association fields

The coherence fields of the oscillatory assemblies, like the ones analysed in the previous section, when projected in the visual space, have been termed *association fields* [20] or *context fields* [70], in relation to their possible role in feature association. More specifically, an association field represents the area in the visual space where appropriate local stimulus features can initiate synchronizations in the oscillatory activities of the corresponding assembly. The spatial extent of the association fields is related to the spatial extent of average coherence, and depends on the divergent intra-cortical connectivity, which, in our model, is mediated by diffusion (see Section 3.2). The mechanism underlying feature association requires that neighbouring portions of the same visual object should cause the synchronized oscillatory activities of the neurons that represent those portions. We tested this functionality by measuring, over large distances on the cortical layer, the synchronization properties of the oscillatory activity resulting from spatially extensive (1-D) stimulations. The neural field was configured with $D = 0.05\lambda_0^2$ and low lateral inhibition ($b = 10^{-3}$), and the test stimuli $s(x, t)$ were either disconnected double bar segments or a long single bar segment, homogeneously characterized by $p = 0.9$ in a background with $p = 0.1$. The system showed temporal coherent relations similar to the physiological data [22] and the responses obtained by other models [52] (see Fig. 5). We computed cross-correlations within and between stimulus segments by varying their gap distance; the resulting cross-correlograms are shown in Figs. 5B and C. As demonstrated in Section 3.2, within every single bar segment oscillatory activity is tightly coupled and cross-correlations show zero phase-lag, whereas cross-correlations between segments diminish more as the gap distance increases. In the case of a large gap distance, exceeding the spatial extent of the association fields, synchronization is restricted to the area of each bar segment. Between the two segments, the oscillatory activities related to each other are highly incoherent, resulting in a minimum average cross-correlation. As the gap distance between the two segments

Fig. 4. Spatio-temporal distributions of coherence for different values of lateral inhibition. Each panel represents the spatio-temporal behaviour of the LFPs, together with their correlation properties in space and time. To point out temporal variations of coherence, spatial correlations have been evaluated in consecutive time windows of fixed durations, for a total prolonged system stimulation of 2 s. For the sake of clarity, only 375 ms durations of the signal responses are shown. In this case, the time was sliced into consecutive time windows of 100 ms, and cross-correlations were computed within each window. The resulting spatial correlations are represented as grey lines, whereas the thick black lines represent the average curves. For low values of inhibition, oscillations are locally coherent in space and time, whereas, for high values of inhibition, fast desynchronizations occur, thus resulting in a steep decay of the spatial correlations. The time-dependent correlations of the LFP signals are pointed out in the lowermost left figures of each panel. For representation reasons, we adopted a time scale that is consistent with the one used for the LFP signal representation, though a larger time scale should be used to better appreciate its variability.

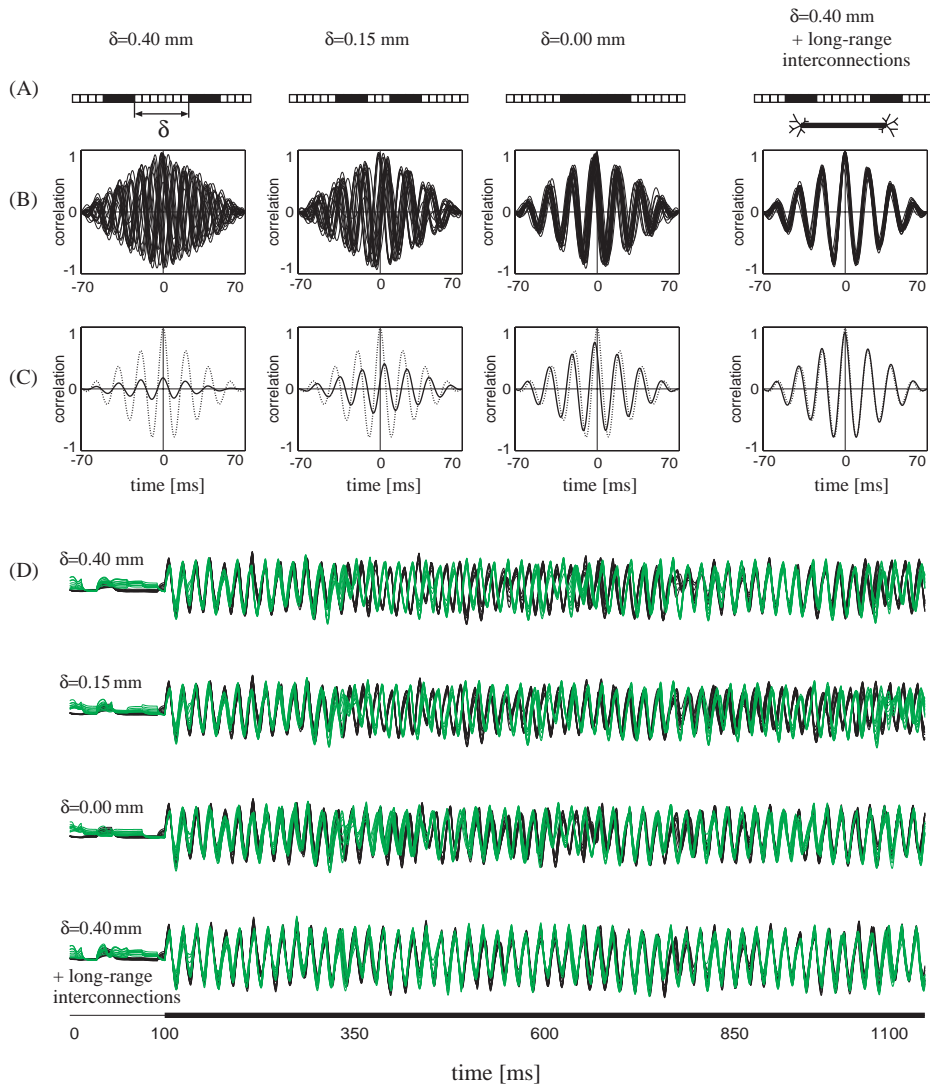


Fig. 5. Effects of stimulus extension and continuity on synchronous (coherent) oscillations. (A) External input stimulation to the cortical field model: two stimulus segments separated by $\delta = 0.40$ and 0.15 mm, and a continuous extended stimulation. (B) Normalized cross-correlations between stimulus segments of 21 epochs of 70 ms each. (C) Mean normalized cross-correlations within (dashed lines) and between (solid lines) stimulus segments. High cross-correlations between stimulus segments correspond to continuity of stimulus properties, in agreement with experimental observations [39,22]. (D) Local field potential oscillations of the simulated cortical field. Segment responses are superimposed to point out synchronization properties. Black traces represent oscillatory responses to the left stimulus segment, whereas grey traces represent oscillatory responses to the right stimulus segment. The lowermost figure shows the responses to the two widely separated stimuli ($\delta = 0.40$ mm), when additional long-range interconnections are superimposed, thus pointing out their role in establishing synchronization among neurons belonging to different columns.

decreases, a coupling occurs up to a complete binding (i.e., synchronization) across the entire stimulated area, when the two bar segments form only one continuous long bar. To avoid accidental long-range synchronizations, we took care of using spatially uncorrelated triggering stimulations. Alternatively, random noise can be applied to introduce additional fluctuations in oscillatory activities and to break accidental periodic phase-locking [52,81].

To further investigate the potentialities of our cortical field model as a powerful medium for feature association, we simulated the responses to two bar segments separated by a large distance when additional long-range excitatory interconnections are superimposed. Such interactions act on the excitatory layer, like those of lateral inhibition, but at a longer distance and with a lower strength. As shown in the right column of Fig. 5, the presence of long-range interconnections results in strong coupling (i.e., association) even between stimuli that are widely apart in the visual space, thus evidencing the possibility of establishing synchronization among distant cortical regions through direct long-range interconnections that couple neurons with non-overlapping receptive fields. In the future, this could have important implications, if we assume a two-dimensional (2-D) architecture in which neurons selective to different parameters are grouped into columns, and a long-range interconnection web that links columns with similar properties, by analogy to cortical feature maps of the primary visual cortex (see Discussion).

4. Discussion

In this paper, we have aimed to model the joint spatio-temporal oscillatory dynamics observed in the visual cortices [18,74,78,88], through the behaviour of a field oscillatory system. Toward this end, we have introduced a second-order delayed partial differential equation characterized by a non-linear point interaction similar to König and Schillen's basic oscillatory element [52] and by a recurrent linear coupling, modelled by an excitatory diffusion term and lateral inhibition. The balance between the excitatory and inhibitory influences can be controlled by acting jointly on the two field parameters b and D (cf. Eq. (1)). Lateral inhibitory processes are, indeed, primed by values of b in its upper range, and their effects are spread over the neural field by diffusive processes, controlled by D . The resulting system behaves as a network of diffusion-coupled oscillators.

The major novelty of our model is the inclusion of the continuous space dimensionality, which allows the system to exhibit cooperative activation properties in both time and space by reacting to spatio-temporal input patterns with ordered oscillatory states in space and time. Specifically, we observed: (1) emergent local oscillatory assemblies, (2) intrinsic synchronization/desynchronization properties and (3) ordered spatial distributions of coherence states that act as a flexible medium to establish feature association. A detailed analysis of the coherent rhythmic oscillations obtained through simulations evidenced how the model is capable of reproducing, with verisimilitude, the macroscopic behaviour observed in real cortical networks.

4.1. Continuous neurodynamics and reaction-diffusion systems

Large-scale cortical dynamics occurs through successive activations of neuronal assemblies that define a new state or a new set of states for the cortical network. Such states are often called *macrostates* [28] and represent widespread coarse-grained expressions for local cooperative activities. Several models have been proposed in the literature to account for the macroscopic behaviour of cortical networks, of both the lumped and unlumped types [7,29,73,95,97–99]. Considering the huge number of cells found in layered cortical areas, neuronal activation is usually defined over spatially continuous domains (neural fields), like continuous distributions of neurons and synapses where each point in space corresponds to a neural population [65]. Formally, the dynamics of each layer is described by integro-differential ordinary equations:

$$\tau \frac{d}{dt} e(x, t) = -e(x, t) + bF \left(\int k(x - x') e(x', t) dx' \right) + s(x, t), \quad (3)$$

where the integral kernel $k(x - x')$ is a smooth function that replaces the synaptic interconnection matrix, and the position variable x replaces the indices of discrete models. In this way, metric relations apply, and it becomes possible to model the geometrical properties, such as spatial nearness and topology, that characterize the rich anatomical structure of cortical areas (e.g., maps, columns, dendritic and axonal arborizations, cell density, etc.) [49,50,66].

If one introduces a diffusive coupling into a neurodynamical architecture, additional local interactions take place, modelled by partial derivatives, rather than by integral kernels [100]:

$$\tau \frac{\partial}{\partial t} e(x, t) = -e(x, t) + D \frac{\partial^2}{\partial x^2} e(x, t) + bF \left(\int k'(x - x') e(x', t) dx' \right) + s(x, t). \quad (4)$$

Local interconnections represented by the term $D(\partial^2/\partial x^2)e(x, t)$ provide a gradual spread of the variations of $e(x, t)$ along x , and simulate the continuity constraint of the neural field. In this way, one can sharply reduce the extent of synaptic interconnections required to obtain smooth activation fields. Indeed, by comparing in the Fourier domain the stationary solutions of the linearized versions of Eqs. (3) and (4), we have (upper-case letters denote Fourier transforms and ω is the spatial frequency):

$$E(\omega) = \frac{1}{1 - bK(\omega)} S(\omega) \quad (5)$$

and

$$E(\omega) = \frac{H_0(\omega)}{1 - bK_{eq}(\omega)} S(\omega), \quad (6)$$

where $H_0(\omega) = 1/(1 + D\omega^2)$ plays the role of an averaging (i.e., smoothing) feedforward kernel (cf. a receptive field), and $K_{eq}(\omega) = K'(\omega)/(1 + D\omega^2)$ is an equivalent feedback interaction kernel. The same effective intracortical coupling, in comparison with the case where no diffusion is incorporated, can be obtained by choosing $K'(\omega) = (1 + D\omega^2)K(\omega)$.

The factor $(1 + D\omega^2)$ acts as a bandwidth extender; therefore, the corresponding kernel $k'(x)$, back in the space domain, will turn out to be shrunk with respect to $k(x)$. Accordingly, the point long-range recurrent interactions introduced into Eq. (1) yield an extended equivalent spatial coupling whose size depends on D .

Reaction-diffusion systems [24,42,57,84,87], like the one adopted in this paper, generalize the approach to providing a phenomenological explanation for the mechanisms responsible for cortical processing in terms of interacting neuronal populations. Indeed, it has been well-known for a long time that, on a macroscopic scale (i.e., phenomenologically), cortical activation states can be modelled by considering the dynamics of two non-linearly coupled populations of excitatory and inhibitory neurons [96], spatially organized into stereotyped modules (cf. the canonical cortical microcircuit [17]). From this perspective, reaction-diffusion systems, regarded as “an assembly of a large number of identical local systems which are coupled (i.e., diffusion coupled) to each other [58],” represent a suitable paradigm to model the processes occurring across cortical networks. The diffusive coupling is representative of the cooperative actions that take place among single cortical modules. More specifically, reaction-diffusion systems are natural candidates for modelling cortical phenomenological processes associated with sensory information processing, as their diffusion components allow a weighted averaging of the input signal over a region of a certain extent (i.e., the receptive field), thus realizing a reduction in the complexity of the signal, while the non-linear reaction components provide a flexible medium through which all kinds of excitatory and inhibitory behaviours can be modelled. A reaction-diffusion system inherits its kinetic properties from the associate kinetic system [27] (obtained by eliminating all spatial interactions), which, in our case, coincides with König and Schillen oscillator [52]. Hence, the oscillatory states of the König and Schillen’s model represent the space-independent solutions of our system. The presence of diffusion propagates such local oscillations to the surrounding region, thus introducing the cooperative behaviour in space.

4.2. Comparison with other models

The conceptual framework on which this paper is based, with its theoretical and modeling development, has been present in the literature for a long time, through several studies aimed at exploring the origin of oscillations in various parts of the brain and devoted to analyzing their computational role from an information-processing perspective. In general, we can distinguish between two (complementary) categories: (i) spatially discrete neural network models and (ii) spatially continuous population models.

In the first category, different choices for the basic unit of the network can be made, corresponding to different levels of abstraction of the neuronal dynamics: such choices range from spiking models [34,35,45,64], excitatory-inhibitory population models [41,52,75,86,91], to phase models [5,37,43,56,72,82]; for a review, see [83]. In all these examples, the spatial character of the model, based on nodes interacting discretely with one another, is discussed considering the influence of different types of couplings and choices of parameters on the synchronous oscillatory behaviour of the network. As

these approaches lack biological empirical details, they fail to reproduce with accuracy the macroscopically observed cortical activity, and provide no clear indication as to the model scale one is considering.

In the second category, i.e., the spatially continuous population models, the idea prevails that the cortical tissue has to be treated as a spatial continuum. Variables and parameters of the model are introduced according to the scale one adopts to describe the empirical phenomena addressed: [96], which could be considered as a “cut across” model between the two categories, [28,59,61,69,89,98,101]. Such continuum-field descriptions of the activity on the cortical tissue are complementary to the more traditional neural network models, as they describe more accurately the behaviour of large-scale cortical “observables” by means of mean-field variables and parameters, even though at the cost of higher model complexity (i.e., a large set of integro-differential or partial derivative equations and a huge number of parameters). Our model combines the structural simplicity of discrete models with a field description to take into account that neurons are immersed in a conductive medium (vascular, glial and extracellular environment), which constitutes approximately 20–30% of the cortical mass [48] and is likely to significantly affect the dynamical properties of the incorporated neurons.

The model’s essentiality allows us to point out the basic architectural principles underlying the observed variety of behaviours. Although it is true that the discretized model described by Eq. (1) corresponds to a network of oscillators coupled with the nearest neighbours (cf. Wang’s scalar diffusive coupling in [10]) the diffusive parameter D , representing the square of the diffusion length, better describes the character and the spatial extent of the coupling. Specific considerations should be made on the similarities and differences between our model and the work by Wang and colleagues. In particular, in [10], they presented a 2-D model of visual cortex that includes local excitation and global inhibition for synchronization and desynchronization processes, respectively. The local character of the diffusive coupling used in our model to control the synchronization of the oscillatory activity ensures the preservation of the geometrical relationships among oscillators, important for perception grouping, and prevents the network from incurring indiscriminate synchronization. As in Wang, our simulations demonstrate that the network (system) is capable of producing phase-locking of stimulus-driven oscillations, without resorting to a global phase coordinator [47], all-to-all connections [82], or fixed delay relations among oscillators [52] (see also [44]). Instead of exploiting a global inhibition (cf. [45,93]), to desynchronize the entire network we resort to a lateral inhibitory coupling at a distance $\pm d$. This long-range recurrent inhibition does not generate a global desynchronization, since it does not prevent an accidental phase alignment of distant parts of the system. To statistically reduce this undesirable effect and to facilitate the desynchronization process, an additional input noise term can be introduced into the model (cf. [52,86]). Simulations using such a noise input (data not shown) validated this statement.

A further difference between our model and Wang’s concerns the ability of our model to account for a spatial cooperative behaviour in sparking system oscillations. Usually, local excitatory (e.g., diffusive) couplings between discrete oscillators are introduced to provide synchronization processes among units that already oscillate in response to proper sustained external inputs. In this paper, we have pointed out that the origin

of spatially extensive oscillatory assemblies is due to the *spatial* cooperative reaction of the diffusive layer to rapid successive activations at multiple cortical sites within a contiguous spatial region. The stochastic nature of the input signals used to stimulate the excitable medium mimics the variability of synaptic events in response to volleys of excitatory afferent activity (see, for instance, [77,80]).

The model presented in this paper has been developed to reproduce, to a certain degree of realism, several experimental results on γ -oscillations observed in visual cortex, rather than address a specific kind of application (e.g., image segmentation and perceptual grouping [11,12], auditory scene analysis and speech recognition [79,92], etc.). From this perspective, the segmentation capabilities shown in Fig. 5 refer to an example of simple feature association reproducible on a 1-D layer. This result suggests that a proper evolution of the proposed model could be profitably exploited to develop perceptual grouping mechanisms based on several and more complex features. Specifically, applications in visual motion segmentation and auditory scene analysis could well suit the joint spatio-temporal synchronization/desynchronization properties of our networks.

4.3. Towards coupled oscillatory maps

The advantages associated with the spatial properties of our field model can be better understood if one considers, in perspective, its 2-D extension. In this case, we should assume a 2-D distribution of excitatory-inhibitory oscillators, so we could receive, for each spatial position, an external input through overlapping receptive fields, whose orientations vary continuously in space according to an orientation map (e.g., [6]). In this way, the field parameters D , d and b , as well as the long-range excitatory connections, can be used to control correlated/anti-correlated states with periods comparable to the hypercolumn width, thus becoming the means for synchronizing columns with similar orientations and for desynchronizing those with orthogonal orientations. More generally, in the 2-D case, it would be possible to obtain distributions of coherence that are oriented in preferred directions. The resulting anisotropies of the association fields in the visual space could be analysed in relation to the degree of coaxiality of the receptive fields of the orientation selective cells, pointing out their possible perceptual role, e.g., in feature binding at elongated object contours [8,13,26,31,50,71].

Due to the high computational load of the 2-D simulations, we deferred a detailed analysis of the 2-D properties of these coupled oscillatory maps to a future work. However, preliminary results have evidenced that the spatio-temporal characteristics of the resulting model local field potentials can be used to solve segmentation problems, yielding a global perception of edges separating one region from another and determining regions on the basis of texture continuity.

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