SUPPLEMENTARY TEXT

Details of the neurocomputational model

Microstructure

Each area consists of two neuronal layers, each of 625 (25x25) cells, one containing excitatory cells and one containing inhibitory ones (in what follows, referred to as e- and i-cells, respectively). To avoid any potential edge effects, layers have a toroidal structure: the top edge is adjacent to the bottom one, and the left edge is adjacent to the right one. In line with Wilson-Cowan models (Wilson & Cowan, 1973), a single pair of e- and i-cell models the average activity of a local population of pyramidal neurons and underlying inhibitory interneurons within one cortical column (grey matter under approximately 0.25 square mm of the cortical surface). Cells are modelled as graded-response neurons (see below).

Each e-cell is restricted to send projections to the 19x19 e-cell neighbourhood within the same area, to topographically corresponding 19x19 e-cell patches in connected areas, and to a 5x5 i-cell patch in the inhibitory layer of the same area (Fig. 1E). The probability of a synapse to be created between an e-cell and another cell falls off with their distance (Braitenberg & Schüz, 1998) according to a Gaussian function clipped to 0 outside the relevant neighbourhood. This produces a sparse, patchy and topographic connectivity, as typically found in the mammalian cortex (Amir et al., 1993; Kaas, 1997).

Membrane dynamics

The state of an (excitatory or inhibitory) cell e at time t is uniquely defined by its membrane potential $V(e,t)$, determined by the following equation:

$$\tau \frac{dV(e,t)}{dt} = -V(e,t) + k_1(V_{in}(e,t) + k_2\eta(e,t)) \qquad (1)$$

where $V_{in}(e,t)$ is the sum of all postsynaptic inputs acting upon cell e (see Eq. (2)), $\eta(e,t)$ is a white noise process with uniform distribution over [–0.5, 0.5], τ is the cell's membrane time constant (note that e- and i-cells have different τ, see Table 1), and k_1 and k_2 are scaling constants. Note that the activity of each e-cell is intrinsically noisy, simulating the spontaneous baseline firing of real neurons (i-cells have k_2=0). The total input to a cell e is defined as:

$$V_{in}(e,t) = (\sum E/IPSPs) - k_G\omega_G(e,t) \qquad (2)$$

where $\Sigma E/IPSPs$ is the sum of all excitatory and inhibitory postsynaptic potentials – I/EPSPs; inhibitory synapses are given a negative sign – acting upon neural cluster (cell) e at time t, $\omega_G(e,t)$ is the global (or area-specific) inhibition (see Eq. (3)) and k_G is a scaling constant. Note that each e-cell gets exactly one IPSP from its twin i-cell (see Fig. 1E).

The global inhibition mechanism is an area-specific inhibitory loop that prevents overall network activity from falling into non-physiological states (Braitenberg & Schüz, 1998). (Note that k_G=0 for i-cells: for simplicity, global inhibition acts only on e-cells). For each model area A, the global inhibition $\omega_G(e,t)$ is defined by:

$$\tau_G \frac{d\omega_G(e,t)}{dt} = -\omega_G(e,t) + \sum_{e \in A} O(e,t) \qquad (3)$$

where $\sum_{e \in A} O(e,t)$ is the sum of all e-cell outputs within area A (see Eq. (4)) and τ_G is the global inhibitory response time constant.

All cells produce a graded response representing the average firing rate of the neural cluster; in particular, the output (transformation function) of an e-cell e at time t is defined as:

$$O(e,t) = \begin{cases} 0 & if\ V(e,t) \leq \varphi(e,t) \\ V(e,t) - \varphi(e,t) & if\ 0 < (V(e,t) - \varphi(e,t)) \leq 1 \\ 1 & otherwise \end{cases} \quad (4)$$

Eq. (4) above is a piecewise-linear sigmoid function of the e-cell's membrane potential $V(e,t)$, clipped into the range [0, 1] and with slope 1 between the lower and upper thresholds $\varphi(e,t)$ and $\varphi(e,t)$+1. The output $O(i,t)$ of an i-cell i is 0 if $V(i,t) < 0$, and $V(i,t)$ otherwise (i.e., unlike e-cells, i-cells do not saturate, reflecting that real interneurons show little firing rate adaptation).

The threshold $\varphi(e,t)$ of an e-cell is not constant but depends on the cell's recent activity, so that the more active the cell, the higher the threshold (see Eq. (5)). This implements a simple form of homeostatic adaptation, or neuronal fatigue (Matthews, 2001):

$$\varphi(e,t) = \alpha\ \omega(e,t) \qquad (5)$$

where $\omega(e,t)$ is the estimated time-average of cell e's recent output (see Eq. (6)) and α is a scaling constant (adaptation strength). The estimated time-average $\omega(e,t)$ of a cell's output is computed by integrating the following differential equation (Eq. (6)) with time constant τ_A, assuming $\omega(e,t)$=0 at time t=0:

$$\tau_A \frac{d\omega(e,t)}{dt} = -\omega(e,t) + O(e,t) \qquad (6)$$

Table S1 *Model parameters*

$\tau_e = 2.5$	e-cells membrane potential time constant (Eq. (1))
$\tau_i = 5$	i-cells membrane potential time constant (Eq. (1))
$k_1 = 0.01$	scaling constant (Eq. (1))
$k_2 = 150\sqrt{(24/\Delta t)}$	noise amplitude (Eq. (1))
$\Delta t = 0.1$	simulation step size (ms)
$\eta \sim U[-0.5, 0.5]$	noise distribution (Eq. (1))
$\tau_G = 60$	global inhibition time constant (Eq. (3))
$k_G = 95$	global inhibition strength (Eq. (2))
$\alpha = 100$	adaptation strength (Eq. (5))
$\tau_A = 50$	e-cells estimated time-averaged activity time constant (Eq. (6))

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